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SOFT-SEDIMENT RECRUITMENT DYNAMICS OF EARLY BLUE CRAB STAGES IN MISSISSIPPI SOUND

Chet F. Rakocinski, Harriet M. Perry, Michael A. Abney and Kirsten M. Larsen

ABSTRACT

In order to understand the recruitment dynamics of early blue crabs, it is necessary to sample quantitatively across early stages and habitats at appropriate spatio-temporal scales. Few studies of early blue crab recruitment have considered the potential role of soft-sediment habitat or directly related megalopal supply to local densities of early stages. During a 7-wk peak recruitment period, fluctuations in early stages of blue crabs from settlement collectors were significantly cross-correlated between two sites separated by 7.5 km, showing connectivity on this large spatial scale. Moreover, numbers of megalopae from settlement collectors were directly correlated with densities of early juveniles from nearby soft-sediment, showing that settlement collectors may reflect local recruitment intensity. Significant habitat variables included depth and salinity (i.e., water mass) for small post-settlement juveniles (<6 mm CW), and substrate type for large juveniles (≥6 mm CW). Early juveniles from soft-sediment habitat were spatially aggregated at relatively low densities; although initial rates of loss may not be as high there as in structured habitats. Thus, soft-sediment habitat may subsidize the supply of early juvenile stages to structured habitats.

The extent to which recruitment variability is controlled by postlarval supply or post-settlement mortality defines an important blue crab recruitment question (Perry et al., 1995; Morgan et al., 1996). Blue crabs exemplify the classic estuarine-dependent life cycle, in which recruitment variability is potentially controlled by the interaction of stochastic (oceanographic and meteorological) influences on larval supply and deterministic post-settlement processes (Rabalais et al., 1995). In order to understand the recruitment dynamics of early blue crabs, it is necessary to sample quantitatively across early stages and habitats at multiple spatio-temporal scales. Recent landscape approaches to resource management have increased our awareness of scale-dependent interpretations of population dynamics (Wiens, 1997). To fully account for recruitment variability of estuarine-dependent organisms with complex life cycles, we also need to recognize the functional significance of ontogenetic shifts in habitat-use (Pile et al., 1996; Pardieck et al., 1999). In this regard, it is also important that we consider habitat-specific variability in rates of growth, mortality, and movement.

Because high densities of early stages of blue crabs commonly occur in vegetated and other structured habitats (Houston et al., 1990; Pile et al., 1996), most studies of early blue crab recruitment have focused on the use and value of seagrass habitat. However, Mense and Wenner (1989) found higher densities of early juvenile blue crabs from unstructured sandy-mud substrate than from emergent grass and shell hash substrates. Early juvenile blue crabs may burrow in soft-sediments or seek refuge among the interstices of large particles in unvegetated sediments. Habitat-specific patterns in the occurrence of early juvenile crabs are probably mediated by intraspecific and interspecific predation. For example, cannibalism apparently causes juvenile blue crabs to move into shallow water (Hines and Ruiz, 1995; Moksnes et al., 1997), possibly making it safer for very early instars in deeper water. Subsequent movements of early crabs from unvegetated sediments may thus provide a subsidiary source of early crabs to structured habitats (Orth and van Montfrons, 1987).

In Mississippi Sound, structured habitats such as seagrass and emergent grasses are rapidly declining, while extensive areas of subtidal soft-sediment habitat remain high. For example, the estimated area of submerged aquatic vegetation (SAV) in Mississippi Sound has declined by ~85%, from 5,200 to 800 hectares over the last 30+ years (Moncreiff et al., 1998). Similar historical declines in Chesapeake Bay SAV have induced faunal shifts to the use of non-vegetated shallow water habitats to avoid predation (Ruiz et al., 1993). Large regional blue crab metapopulations are responsible for the widespread dispersal of their zoeal stages (Epifanio, 1995). Thus, whether a given estuarine system may serve as a population source or sink (sensu Pulliam, 1988) may depend on the composite recruitment potential of its nursery habitats. Although relatively low densities of early crab stages imply that the recruitment value of soft-sediment habitat is low, the expansive nature of this habitat may amplify its nursery function.

During a 7-wk period in the summer of 1997, early post-settlement blue crabs were sampled quantitatively from soft-sediment habitat at two sites where standard settlement collectors were also being maintained (Rabalais et al., 1995). Soft-sediments comprise the predominant type of subtidal habitat in Mississippi Sound, including within the vicinity of the settlement collectors. Five objectives were addressed using both settlement collector and suction-plot data: (1) to examine the spatial distribution of early post-settlement crabs from soft-sediment habitat; (2) to consider loss (i.e., mortality and emigration) rates of early post-settlement crabs from soft-sediment habitat; (3) to assess habitat-specific variation in densities of early post-settlement crabs; (4) to compare postlarval supply and post-settlement densities between two sites separated by 7.5 km; and (5) to determine whether abundances of megalopae from settlement collectors correlated with densities of post-settlement crabs from surrounding soft-sediment habitat.

STUDY AREA

This study was conducted at two shoreline sites separated by 7.5 km and located within central Mississippi Sound, at Pointe aux Chenes Road (PaC) (30°22′05″N, 88°46′37″W), and at Belle Fontaine Beach (BF) (30°20′30″N, 88°42′45″W) (Fig. 1). Mississippi Sound is a large, shallow, microtidal embayment off the north central Gulf of Mexico that is separated from the open Gulf by a series of narrow barrier islands. Tides are wind dominated. In the late summer, onshore winds typically increase during the afternoon, subjecting both sites to water mass movements from barrier island passes. Seagrass habitat is largely restricted to protected shorelines of the barrier islands; and much of the natural marsh-edge habitat is modified in this system. Thus, most of the habitat available for crab settlement is soft-sediment. Both sites were situated near large piers where settlement collectors were being maintained. Moderately altered shorelines at these sites comprised low energy beaches of silt or mud-covered sand and unvegetated sand sediments. The nearshore depth profile was considerably steeper at PaC than at BF.

METHODS

FIELD AND LABORATORY METHODS.—During a 7-wk period between 7 August and 23 September 1997, megalopae and early juvenile crabs were sampled using two standard quantitative methods, settlement collectors (Rabalais et al., 1995) and suction-sampling (Orth and van Montfrons, 1987). At each site, two standard settlement collectors constructed of PVC pipe and air conditioning filter (Metcalf et al., 1995; Perry et al., 1995) were deployed vertically approximately 15 cm below the water surface on opposite sides of stationary piers. Between 0800 and 1000, collectors were retrieved daily at BF and on weekdays at PaC. Water temperature (°C) and salinity (‰) were measured with a Fluke® (Model 51) digital thermometer and a Reichert® temperature-compensated refractometer, respectively. At the laboratory, collectors were washed over plankton netting (#333 mesh) and the samples sorted for *Callinectes* spp. Megalopae and early juvenile *Callinectes sapidus* and *Callinectes similis* were identified, staged, and enumerated. Abundances per collector per day were averaged.

Once per week at each site, early juvenile stages of blue crabs were sampled from soft-sediment habitat in the vicinity of the settlement collectors. A venturi suction head attached to a 5 hp gas 2″
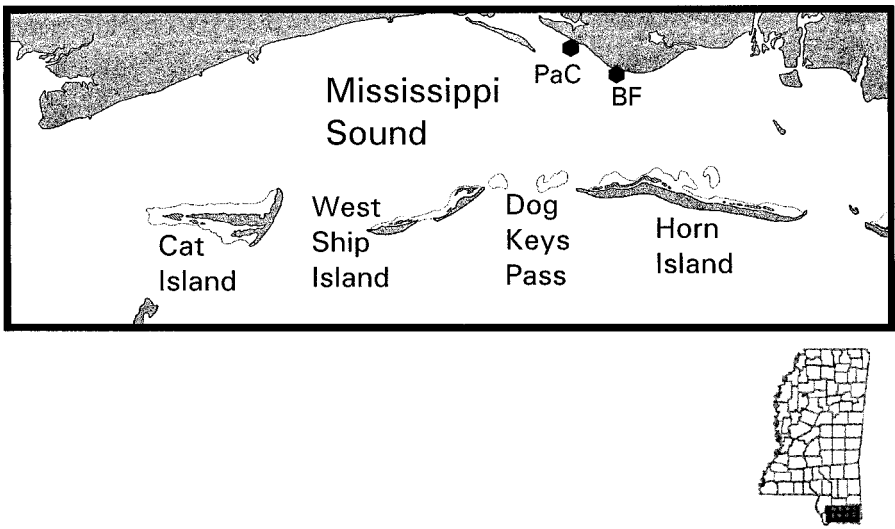
Figure 1. Map of the study area showing sampling sites and potential (dotted outlines) vs actual extent (cross-hatched area) of seagrass habitat around nearby barrier islands. PaC = Pointe aux Chenes road site; BF = Belle Fontaine Beach site. Map adapted from Moncreiff et al. 1998.

centrifugal water pump was used to vacuum the sediment within a 1.77 m² circular drop-net with 1 mm mesh sides (cf. Orth and van Montfrons, 1987). The area of bottom enclosed by the drop net was slowly suctioned twice through a 1 mm mesh bag, and then the bottom and water-column quickly suctioned a third time. All retained materials, including early crabs and considerable coarse sediment, were fixed in 10% formalin and labeled. In the laboratory, crabs were sorted from samples, identified to species, staged, enumerated, and their carapace widths (CW) measured using a WILD® stereo-microscope.

Four transects were each separated by 50 m and located perpendicular to the shoreline. Suction samples were taken at three fixed transect depths, shallow (30 cm), mid-depth (60 cm), and deep (90 cm), yielding twelve samples per collection. For each sample, several environmental variables were also measured or scored, including depth, distance from shore, and sediment characteristics. Sediment was characterized in terms of major dominant and subdominant components, and the depth of the upper silt layer was noted when present. Several physical variables were measured at the mid-depth station of each transect using a YSI® model 85 meter, including salinity (ppt), dissolved oxygen (mg/l), and water temperature (°C), and latitude and longitude were recorded using a SONY® model IPS-360 GPS unit. Tidal and meteorological conditions were also noted for each transect at the time of sampling.

DATA ANALYSES.—To examine spatial coherence across the 7.5 km scale and possible linkage in the occurrence of megalopae and early juveniles, bivariate cross-correlations were run between daily series of log-transformed (i.e., $\ln[x + 1]$) abundances from settlement collectors using SYSTAT 5.05 (Wilkinson et al., 1992). Data was complete for 61 continuous days at BF and concurrently for 43 days (i.e., excluding weekends) at PaC. Missing values in the PaC series were interpolated by local quadratic smoothing. Cross-correlations were calculated between series at 15 lag intervals, ranging from -7 to $+7$ days. Autoregressive modeling was not used to condition the series, since relatively short series (n < 100) do not suffer from spurious cross-correlation due to autocorrelation (Chatfield, 1989). To aid in the interpretation of multiple cross-correlations involving the same data, we used the sequential Bonferroni procedure to adjust rejection levels, thereby appropriately balancing the chances of making TYPE II errors (Peres-Neto, 1999). Finally, daily salinities also were compared and examined for the same period as settlement collectors in order to detect any trends in the series.

In order to examine the spatial distribution of early juvenile crabs from soft-sediment habitat, the frequency distribution of crabs was plotted for 144 1.77 m² suction samples. Crabs of both species were combined for analyses of spatial distribution and habitat variation, because lesser blue crabs (*Callinectes similis*) made up a small portion (9%) of the catch and their occurrence overlapped with that of blue crabs (*Callinectes sapidus*). Also, because one collection at PaC on 16 September 1997 was taken when profuse bryozoan mats were present, crabs from this collection were excluded from analyses of soft-sediment spatial distribution and habitat variation. The spatial frequency-distribution

of blue crabs on soft-sediment was fit with the negative binomial distribution (Krebs, 1989) to determine the degree of aggregation on soft-sediment (Elliott, 1979). To normalize the spatial data, a Box-Cox transformation was performed by using a maximum likelihood function to estimate the coefficient, λ (Krebs, 1989). Both untransformed and transformed frequency data were submitted to the Kolmogorov-Smirnov one-sample test (K-S one-sample test), to test for the fit to a normal distribution (Siegel, 1956).

Size distributions (CW) of *Callinectes sapidus* were compared among dates within sites in order to assess weekly changes in abundances and size distributions as a reflection of supply, growth, and loss (=mortality and emigration). The composite size distribution of *Callinectes sapidus,* including crabs from both sites across all dates from unstructured soft-sediment habitat, was also examined and compared with the size distribution of *Callinectes sapidus* from the PaC collection of 16 September 1997 (i.e., structured bryozoan habitat) using a Kolmogorov-Smirnov two-sample test (K-S two-sample test) (Siegel, 1956).

Habitat-specific variability in transformed densities of small (<6 mm CW) and large (≥6 mm CW) juvenile blue crabs from suction samples was examined using General Linear Model (GLM) ANOVA in SYSTAT (Wilkinson, 1992). We defined small crabs as those that had settled within the previous week of life, which effectively distinguished early instars that could potentially exhibit stage-specific dynamics. Thus, separate GLM models were done for small and large juveniles. Factors included in the full models for both size classes included site, depth, salinity (i.e., two levels), and substrate (i.e., six categories), and all two-way interactions among these factors. Low salinity was defined as <20 ppt and high salinity was ≥20 ppt. This threshold corresponds with level of salinity that signals prevailing onshore currents within the study area. We designated six sediment categories, including sand, low silt, medium silt, high silt, sand/mud and detritus/clay. Based on significance levels of factors in the full models, final ANOVA models were reduced to fewer factors. Bonferroni adjusted post-hoc comparisons were made with least squares means of factors with more than two levels. A Repeated Measures ANOVA design was unwarranted since the analysis was not focused on showing differences in densities over time; moreover, because abundances of small juvenile crabs from suction samples were not correlated between consecutive sampling dates ($r = 0.36$; $P > 0.20$).

To compare abundances between sites over time, total numbers of juvenile crabs per 21.2 m² of total suction sample area and mean transformed numbers of juvenile crabs per sample (i.e., 1.77 m² ± 95% CI) were examined across the sample dates. To determine whether variability in abundances of megalopae from settlement collectors reflected fluctuations in densities of post-settlement crabs in surrounding soft-sediments, log-log regressions were performed between these two variables. Total abundances of small crabs (i.e., <6 mm CW) from suction sample collections were regressed against average numbers of megalopae from settlement collectors for several cumulative daily periods. Since positive relationships were hypothesized, one-tailed significance levels were used for these regressions. Normality and constant variance assumptions were checked through Kolmorgov-Smirnov one-sample tests and Spearman rank correlations between residuals and observed values of the dependent variable (SIGMASTAT, 1992).

RESULTS

Abundances of both megalopae and early juveniles from settlement-collectors fluctuated erratically. However, abundances of megalopae and early juvenile crabs were significantly cross-correlated between the two sites over the 61 d period (sequential Bonferroni $P < 0.01$), showing spatial coherence in crab recruitment on the 7.5 km spatial scale (Fig. 2; Table 1). The strongest cross-correlation between the two sites occurred at a lag of 0 days for megalopae, whereas the strongest correlation for early juvenile crabs occurred at a lag of 1 day, implying that early juvenile crabs peaked one day earlier at the PaC site. Furthermore, cross-correlation indicated that early juveniles peaked two days later than megalopae at the PaC site (sequential Bonferroni $P < 0.0125$). Salinity did not follow a consistent trend across the 61 d period of study at the two sites (Fig. 3). For example, the two periods of highest salinity occurred near the beginning and the end of the study period. Salinity fluctuations also agreed closely between sites, implying that similar hydrological conditions influenced both sites.

A total of 1,399 early crabs were recovered from 156 suction samples comprising the 13 collections, including 91% *C. sapidus* (n = 1,269) and 9% *C. similis* (n = 130). Most crabs were small, ranging between 2 and 28 mm CW.
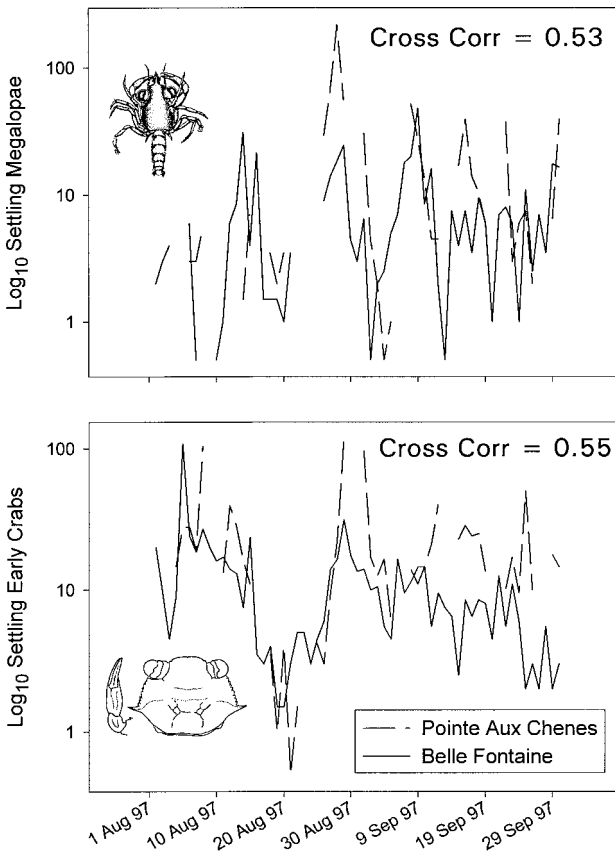
Figure 2. Time series of log abundances of megalopae and early juvenile crabs recovered from artificial settlement collectors over the 61 d period of study at the two study sites. Plotted values represent averages for two settlement collectors.

Typically, crab densities were fairly low from soft-sediment habitats, ranging between 0 and 15.3 m². However, on 16 September 1997 the presence of profuse bryozoan mats at the PaC site essentially converted the study area into a structured habitat, and resulted in an order-of-magnitude higher density of early crabs reaching up to 180 m². Indeed, the number of early crabs collected on this one date

Table 1. Best cross-correlations between abundances of megalopae and early juvenile crabs recovered from settlement collectors at the two sites. Upper values = correlation coefficient; Lower values = lag. Lag = number of days behind (−) or ahead (+) in the correlation. * = $P < 0.05$; ** = $P < 0.01$. Pac = Pointe aux Chenes; BF = Belle Fontaine.

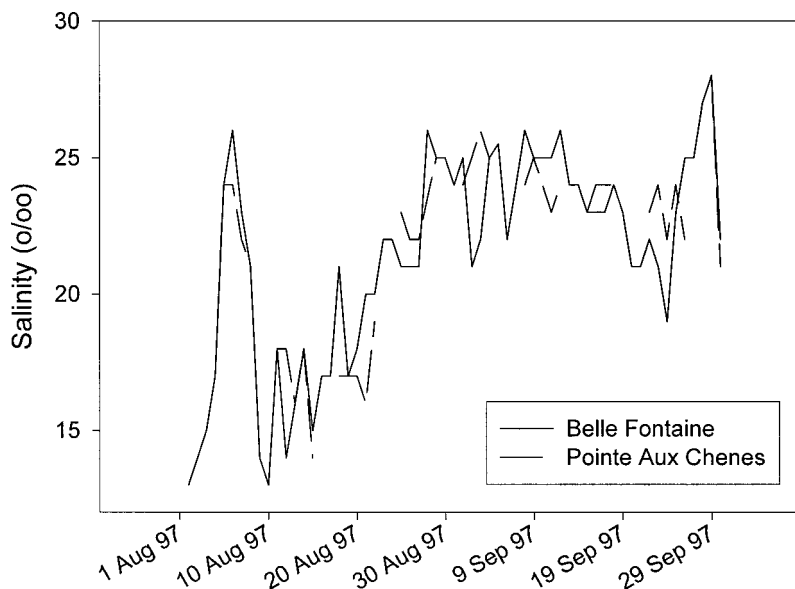|	Log BF megalopae	Log PaC juveniles	Log BF juveniles
Log PaC megalopae	0.53**	0.36*	−0.35*
	0	+2	−7
Log BF megalopae		0.22	−0.33*
		+2	+4
Log PaC juveniles			0.55**
			−1

Figure 3.   Salinity variation at the two sites across the 61 d period of study.

(n = 704) equaled the total catch from soft-sediment at both sites during the entire study period (n = 695).

Early crabs were moderately aggregated on subtidal soft-sediment (i.e., excluding the 16 September 1997 bryozoan collection), as shown by a frequency distribution of the number of crabs per sample (i.e., 1.77 m^2) conforming to the negative binomial distribution (χ^2 = 7.15, df = 5, P > 0.1, k = 0.487). The aggregated distribution pattern was effectively normalized through the Box-Cox transformation, based on a significant λ of -0.146 (i.e., 0 excluded from 95% CI). Whereas the untransformed spatial distribution failed the K-S one-sample test of normality (K-S Distance = 0.27, 12 categories, P = 0.01), the transformed distribution successfully passed the K-S one-sample test (K-S Distance = 0.23, 12 categories, P = 0.08), permitting further parametric analyses.

Notwithstanding offset sampling dates between sites and less frequent sampling than was available for settlement collectors, fluctuations in total abundances of early crabs from suction samples generally agreed between the two sites in direction, while varying inconsistently in magnitude (Fig. 4A). However, except for notable differences (i.e., 95% confidence intervals, CI) in crab abundances between the 16 September PaC bryozoan collection and the two BF collections from adjacent dates, mean abundances of crabs were not different between sites for any other pair of adjacent dates (Fig. 4B).

Size distributions of early *C. sapidus* from suction-samples for the various collection dates showed erratic changes in abundances of crabs and shifts in size distributions throughout the study period (Figs. 5 and 6). Episodic pulses of new recruits might appear or disappear in any given week. Shifts in modes of size distributions implied that it generally took ~1 week for early crabs to grow from 3 mm to 6 mm CW.

The composite size-distribution of *C. sapidus* from all soft-sediment collections (i.e., except for the 16 September PaC bryozoan collection) showed that most crabs were <15 mm CW (Fig. 7A). The mode of the composite size-distribution
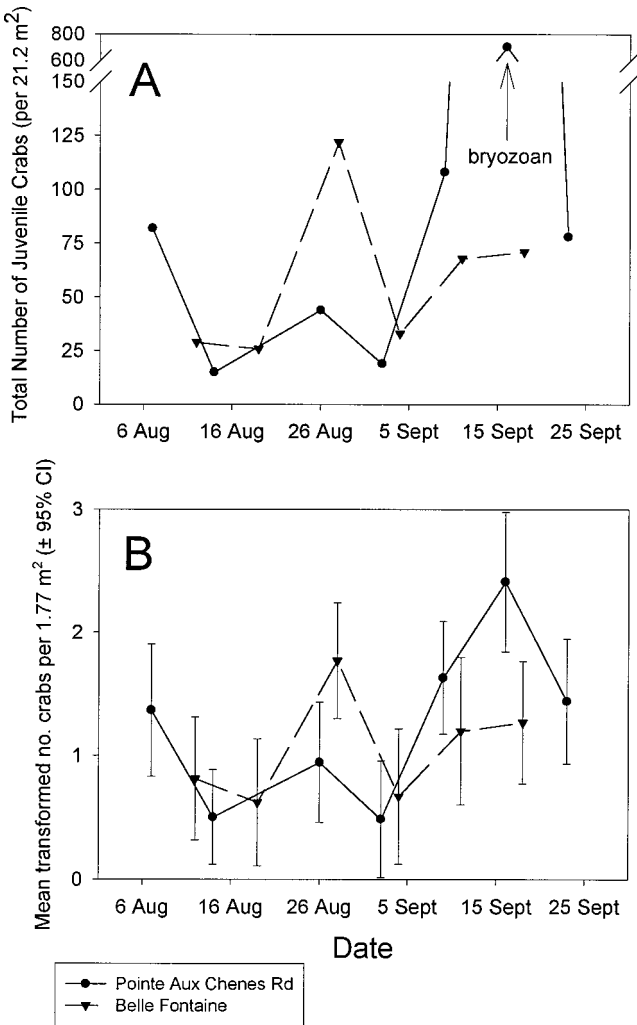
Figure 4.   A. Variation in the total number of early juvenile crabs obtained by suction sampling. B. Mean ± 95% confidence intervals of Box-cox transformed abundances of juvenile crabs corresponding with variation in total abundances shown in Figure 4A.

was 3 mm, a size that represented first crabs. An overall exponential loss rate was also evident from the decline in frequencies of crabs across successive size intervals of the composite size distribution. Based on the assumption that it took 1 week for first crabs to grow from 3 mm to 6 mm CW, an overall daily rate of loss (i.e., $[\log N_{t1} - \log N_{t2}]/[t2 - t1]$) of first crabs from soft-sediment habitat during the period of study of 15% was estimated from the composite size-distri-bution. Early *C. sapidus* from the 16 September PaC bryozoan collection were distributed toward larger sizes than the composite size-distribution from soft-sed-iment (Fig. 7B). A two-sample K-S test confirmed that the two size distributions were significantly different (K-S Distance = 0.34; $P = 0.001$).

Significant habitat-specific variability in abundances of early crabs from soft-sediments was identified through separate GLM ANOVAs for small and large
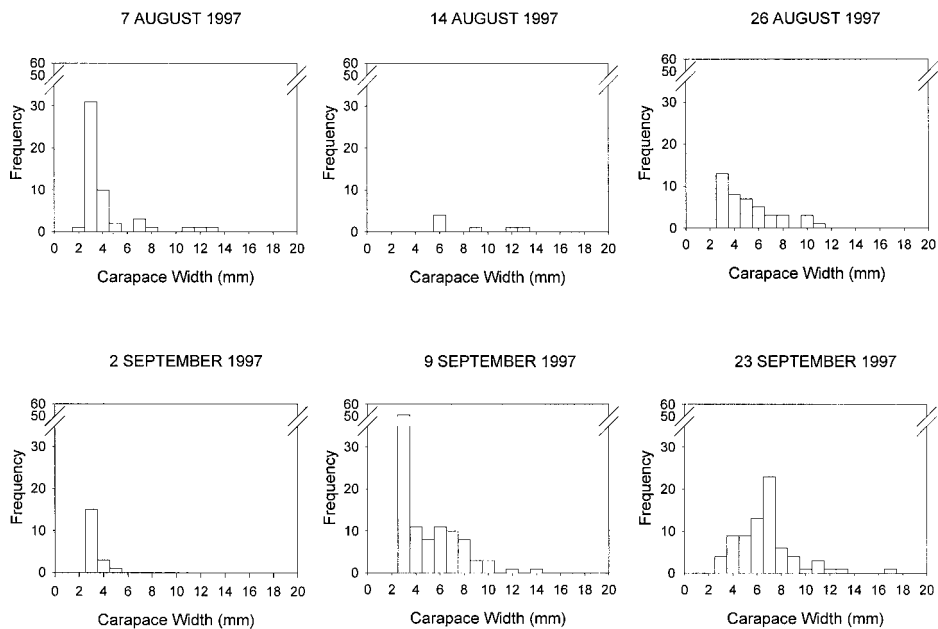
Figure 5.   Size distributions of early juvenile blue crabs obtained from soft-sediment habitat by suction sampling at the Pointe aux Chenes Road site on various dates.
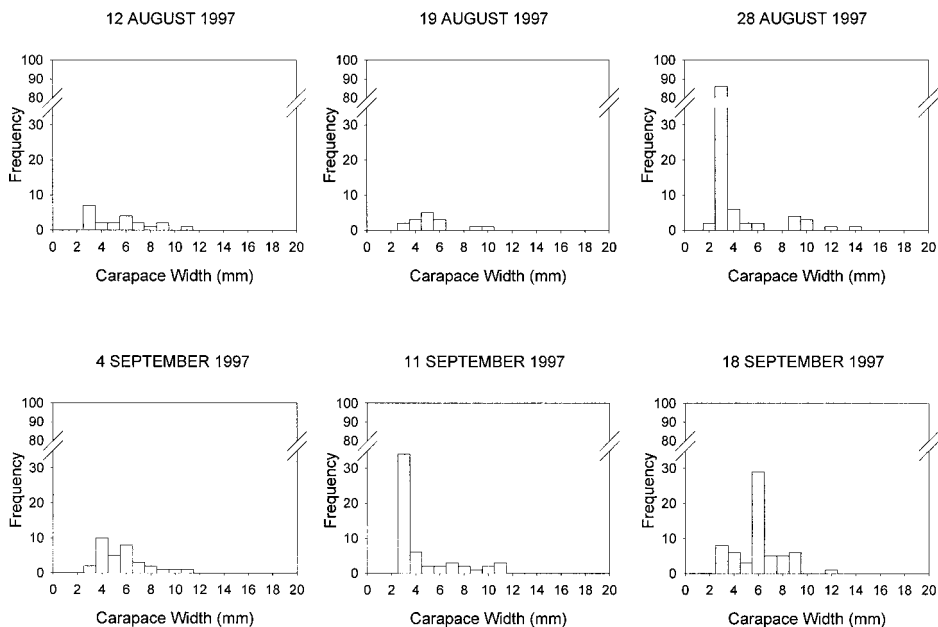

Figure 6.   Size distributions of early juvenile blue crabs obtained from soft-sediment habitat by suction sampling at the Belle Fontaine Beach site on various dates.
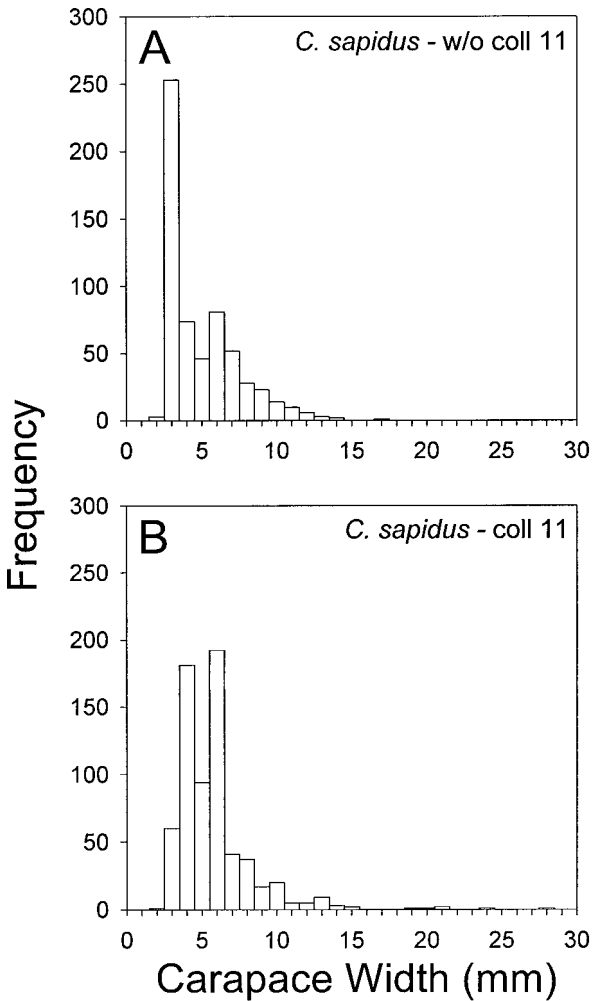
Figure 7. A. Composite size distribution of early blue crabs obtained from soft-sediment habitat by suction sampling at both sites and over various dates depicted in Figures 5 and 6. B. Size distribution of early blue crabs obtained at the Pointe aux Chenes Road site on 16 September 1997, when bryozoan mats converted the area into structured habitat.

crabs (Table 2). All two-way interaction effects between independent factors were non-significant ($P > 0.05$) for both small and large crabs. Thirty-two percent of the variance in transformed abundances of small crabs from 144 suction samples (i.e., excluding the 16 September PaC bryozoan collection) was accounted for by the reduced ANOVA model, which included significant depth and salinity terms ($P < 0.001$). Bonferroni adjusted post-hoc comparisons showed that small crabs were significantly more abundant in deep samples (i.e., 90 cm) than at medium or shallow depths (Fig. 8). Consequently, abundances of small crabs also were higher in substrates characteristic of deep samples, such as low silt and sand/mud. Small crabs were also more abundant at high salinity levels (i.e., ≥20 ppt), reflecting a probable connection with onshore water mass movements. The reduced ANOVA model for large crabs discerned little habitat-specific variability. It explained just 13.6% of the variability in transformed abundances of large crabs,

Table 2. GLM ANOVA results for reduced models describing variability in transformed abundances of small and large juvenile crabs. (TRNS SML = transformed abundances of small (<6 mm CW) crabs; TRNS LRG = transformed abundances of large (≥6 mm CW) crabs.)

Source	Sums of squares	df	Mean-square	F-ratio	P
Dependent variable: TRNS SML	n: 144	Multiple R: 0.569		Squared multiple R: 0.323	
Depth	23.420	1	23.420	48.779	0.001
Salinity	8.936	1	8.936	18.611	0.001
Error	67.698	141	0.480		
Dependent variable: TRNS LRG	n: 144	Multiple R: 0.369		Squared multiple R: 0.136	
Substrate	7.052	5	1.410	4.349	0.001
Error	44.751	138	0.324		

and substrate type was the only significant factor included in the model (Table 2; $P < 0.001$). Bonferroni adjusted post-hoc comparisons showed that large crabs were most abundant from sand/mud, detritus/clay, and high silt substrates, and least abundant from medium silt, whereas they were moderately abundant from sand and low silt substrates. These substrate associations for large crabs did not correspond with any differences in depth.

Abundances of small crabs from suction samples were significantly related to abundances of megalopae from settlement collectors, indicating that amplitudes of settling megalopae provided some measure of local recruitment (Fig. 9). The strongest relationship resulted from a regression between abundances of small
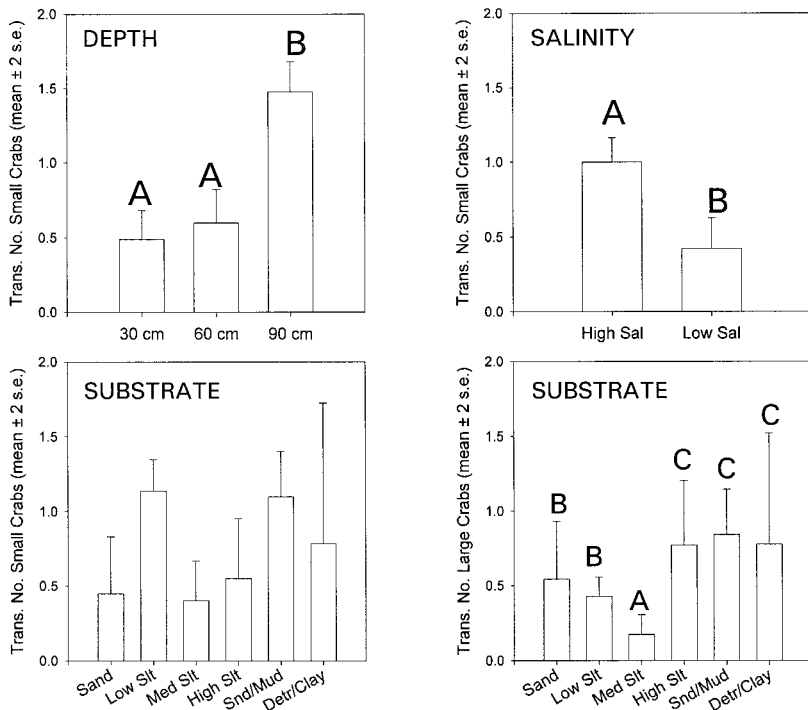

Figure 8.   Bar graphs of post-hoc comparisons among GLM ANOVA factors, showing habitat-specific variability in abundances of small and large juvenile crabs.
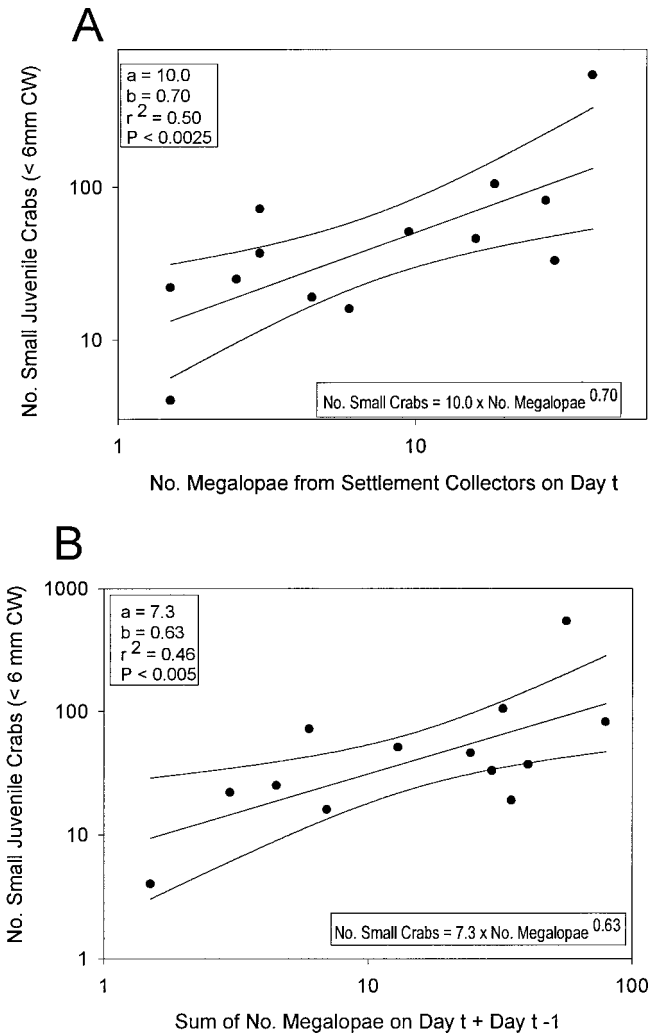
Figure 9.   A. Regression between the abundance of small crabs from suction sample collections vs the abundance of megalopae from settlement collectors on the day (t) of suction sampling. B. Regression between the abundance of small crabs from suction sample collections versus the cumulative abundance of megalopae from settlement collectors for days t and t − 1.

crabs and megalopae on the same date ($r^2 = 0.50$; $P < 0.0025$). The strength of the relationship only decreased slightly when the cumulative number of megalopae from day t and day t − 1 were used as the dependent variable ($r^2 = 0.46$; $P < 0.005$); however, the strength of the relationship diminished rapidly as the average number of megalopae was successively accumulated over previous dates.

DISCUSSION

The combined use of both settlement collectors and suction sampling enabled us to examine the possible connection between postlarval supply and post-settlement, as well as various scale-related processes pertaining to early crab recruitment. Standard settlement collectors have been used extensively to sample me-

galopal settlement, and have been validated as a quantitative indicator of plank-
tonic megalopae (Rabalais et al., 1995). Likewise, plot-sampling methods have
been used widely to measure habitat use by early blue crab stages (Williams et
al., 1990; Pile et al., 1996). These two sampling methods have also been used
together to examine whether relatively high abundances of megalopae and early
juveniles occur in SAV habitat when pulses of megalopae appear in the plankton
(Olmi et al., 1990; Lipcius et al., 1990; Heck et al., in press). Olmi et al. (1990)
did not find a direct relationship between abundances of megalopae in the plank-
ton and megalopae from settlement collectors, probably due to a low sample size,
although Lipcius et al. (1990) found that the abundances of megalopae on both
settlement collectors and in the benthos correlated with the abundance of megal-
opae in the plankton. Furthermore, progressive serial changes in megalopal molt
stages occur in samples from plankton, settlement collectors, and SAV habitats,
demonstrating gradual competency for making the transition to a benthic existence
(Lipcius et al., 1990). Thus, the abundance of megalopae in the plankton may not
reflect the local supply of postlarvae, and data from settlement collectors should
more accurately reflect the local supply of competent megalopae.

Although it is held that settlement collectors provide a good index of early crab
recruitment (Metcalf et al., 1995), abundances of megalopae from settlement col-
lectors have seldom been related to densities of early juveniles in surrounding
habitats. In this study, we found a significant correlation between megalopal abun-
dances on settlement collectors and abundances of small juvenile crabs from soft-
sediments, demonstrating that settlement collectors may indeed provide a measure
of local recruitment intensity. However, the strongest correlation occurred at a lag
of zero days, suggesting that perhaps the correlation reflected either very little
time between settlement and metamorphosis or, alternatively, simultaneous move-
ments of megalopae and early instar juveniles within the same water masses.
Although we have not observed juvenile *C. sapidus* in the plankton with megalo-
pae, early juvenile stages of blue crabs have been reported to occur together with
megalopae in the plankton during recruitment pulses (Mense and Wenner, 1989).
Pardieck et al. (1999) proposed that the occurrence of both postlarvae and small
juveniles was most strongly related to physical forces, such as currents and winds,
whereas larger juveniles are more affected by biotic factors. Indeed, in our study,
abundances of small juvenile crabs from suction samples were positively related
to high salinity levels, presumably reflecting the transport of recruitment pulses
to the two sites by water mass movements associated with onshore winds and
tides. In our study area, Perry et al. (1995) also found significant correlations
between megalopal influx and circulation as influenced by salinity, onshore winds,
and spring tides. In the northern Gulf of Mexico, onshore winds and nocturnal
tides have been shown to facilitate transport of megalopae into estuaries (Perry
et al., 1995; Morgan et al., 1996). The observed lag in peak occurrences of early
juveniles on settlement collectors between sites implied that first crabs appeared
1 day earlier at the PaC site than at the BF site, possibly reflecting a temporal
difference in movements of post-settlement crabs, or in the competency of arriving
early stages. In contrast, the high correlation between early juveniles and megalo-
pae on settlement collectors at a lag of +2 d at the PaC site might reflect either
the time needed for metamorphosis by megalopae, or the delayed arrival of early
juveniles. Time-lag differences in correlations involving early juveniles from set-
tlement collectors and suction samples may be due to the different scales of
sampling involved. Settlement collector data were taken more frequently (~daily)
than suction samples (~weekly), and thus settlement collector data could be cor-
related on a finer temporal scale.

When considering sources of variation in blue crab recruitment, it is important to appraise multiple spatio-temporal scales on which early recruitment occurs (Olmi et al., 1990; Metcalf and Lipcius, 1992). Significant between-site-correlations in abundances of megalopae and early juveniles from settlement collectors implied that an inter-site distance of at least 7.5 km represented an applicable spatial scale for considering early recruitment dynamics of blue crabs, and that spatial distributions in postlarval supply were patchy at the >1 km scale. Olmi et al. (1990) also found that postlarval blue crabs were patchy at the km scale. Patch sizes of early stages of other coastal species, including *Cancer magister* (Booth et al., 1985) and larval *Anchoa mitchilli* (Houde and Lovdal, 1985), are also known to occur at the km scale. In this study, the observed spatial correlation in recruitment probably reflects context-specific hydrological and geomorphological affinities between the two sites. Both sites are situated on the opposing shore of Mississippi Sound from Dog Keys Pass, and at the receiving end of onshore water mass movements. This effect was also reflected by significantly higher abundances of small juveniles from suction samples during periods of high salinity. Yet, fairly large unexplained amounts of variability in suction sample abundances partly reflected episodic variation in the supply of post-settlement blue crabs. Indeed, a recent predictive model of early Dungeness crab recruitment incorporates both stochastic terms to accommodate environmental effects and deterministic terms to accommodate density-dependent effects (Higgins et al., 1997).

Due to the apparent lack of refuge, unvegetated sediment is typically regarded as a habitat of relatively high risk for early juvenile blue crabs (Moksnes et al., 1997; Orth and van Montfrans, 1987; Pile et al., 1996; Wilson et al., 1990). By using tethering techniques, others have measured relatively higher rates of mortality on juvenile crabs in unvegetated substrates than in SAV. However, most comparisons of mortality involving unvegetated substrates consider unvegetated sand, which clearly lacks refugia. Several studies have shown that decreasing vulnerability with increasing size leads to ontogenetic habitat shifts from SAV to unvegetated habitat by later stages of juvenile crabs (Orth and van Montfrons, 1987; Pile et al., 1996; Pardieck et al., 1999). Differences in functional responses due to intraspecific predation between SAV and unvegetated habitats also show that predation efficiency decreases in structured habitat (Moksnes et al., 1997), suggesting that small juveniles may be at relatively less risk in structured habitats despite overall higher densities of juvenile crabs. However, we observed a much higher abundance ratio of large to small juvenile crabs in bryozoan mats than in soft-sediments, implying greater potential for intraspecific predation pressure in this structured habitat. Moreover, changes in modal densities suggested relatively low daily rates of loss (~15% mortality and emmigration) of early juvenile crabs from soft sediment. By contrast, Wilson et al. (1990) used tethering to estimate mortality rates of 9% for sea lettuce, 20% for eelgrass, and 40% for unvegetated habitat in coastal New Jersey. Hines and Ruiz (1995) measured higher mortality rates ranging between 40–90% for tethered large juvenile blue crabs (i.e., 30–70 mm CW) on unvegetated substrate in Chesapeake Bay. On the Gulf coast, mortality estimates of tethered early crabs in SAV habitat also range very high (~85%) (P. Spitzer et al., this volume). Clearly, more research is needed to measure and compare mortality and movements of early stages of blue crabs in various habitats, seasons, and geographic locations.

In our study, small juveniles were relatively more abundant in deep (90 cm) samples than in shallow habitat, reflecting either lower mortality, lower emigration, higher settling, or higher immigration into to deep habitats. Shallow water is generally considered better refuge habitat than deep water for small estuarine

organisms (Ruiz et al., 1993). For example, mortality of tethered juvenile crabs was significantly lower in shallow (15 cm) than in deep (70 cm) unvegetated habitats in Chesapeake Bay (Hines and Ruiz, 1995), although comparatively large juvenile crabs (30–70 mm CW) were considered in this study. Conversely, water depth did not significantly influence the distribution of early blue crabs within SAV habitat in Chesapeake Bay (Pardieck et al., 1999). In our study, deep habitats were typically characterized by soft-sediments consisting of a thin (1–2 cm) layer of silt over muddy sand, which may provide better refuge for small juvenile crabs than unvegetated sand. Furthermore, relatively low densities coupled with the aggregated spatial distribution of juvenile crabs in soft-sediments may afford additional virtual refuge. Cannibalism is considered to be the strongest mortality pressure limiting crab recruitment (Hines and Ruiz, 1995); and this risk may cascade between consecutive stages, and cause multiple ontogenetic habitat shifts resulting in the simultaneous occupation of nursery habitats by widely separated early stages. Habitat-specific size distributions of blue crab often do reflect apparent habitat partitioning in response to intraspecific predation (Williams et al., 1990).

Whether estuaries comprised of predominantly soft-sediment habitat serve as sources or sinks of recruitment hinges on the role of soft-sediment in mediating early recruitment through habitat-specific effects on growth and survival. Considering the expansive nature of soft-sediment habitat in many estuarine systems, and the major recent decline in structured habitats such as SAV and emergent fringing marsh vegetation, soft-sediment habitat may contribute substantially to early crab recruitment in some regions. Although densities of juvenile blue crabs can be an order of magnitude lower in soft-sediment than in structured habitats, the more expansive coverage of soft-sediment may offset this disparity in density. If the survival rate of small juveniles is higher in soft-sediment than in structured habitat, post-settlement movements of early juvenile crabs from soft-sediments to structured habitats might be subsidizing early blue crab recruitment. Survival rates are also closely linked with growth rates, which should also vary in a habitat-specific manner. Thus, soft-sediment habitat may function as a staging area for early stages of blue crab.

In order to assess Essential Fisheries Habitat, a complete habitat-specific accounting of recruitment processes must be made for any target species. Even habitats that appear unimportant or that are inconspicuous must be considered. Habitats that may contribute to early blue crab recruitment in estuarine systems either historically lacking SAV or with declining SAV include ephemeral habitats like *Ulva* (Wilson et al., 1990), and bryozoan mats (this study), as well as fringing shoreline emergent vegetation and/or shell hash substrate (Mense and Wenner, 1989). Of course, the relative importance of various habitats for blue crab recruitment may also vary seasonally or geographically (Orth and van Montfrans, 1987).

Metapopulation perspectives of marine recruitment recognize that harvestable stocks may originate disproportionately from different regions (Stoner et al., 1996), for example, from different estuaries. The recruitment potential of habitats comprising a given estuary and the degree to which that estuary contributes to stock recruitment hinges on how the habitat components function when integrated across the landscape (Wiens, 1997). For organisms with complex life-cycles, new recruits do not necessarily originate from all areas at levels commensurate with larval supply. Decoupling of supply and recruitment is well-known, although the reasons for decoupling are incompletely understood. Population self-regulation through intraspecific predation is one important factor (Moksnes et al., 1997).

Another key to understanding such decoupling may also be the mediating influence of habitat function. The critical processes of supply, emigration, growth, and survival need to be measured across all stages and types of habitats on the landscape scale to better learn how recruitment variability is manifested.

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