

# Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply

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**ABSTRACT:** Larval supply and early postsettlement mortality are crucial to the maintenance of most marine populations. Larval supply may be especially important in regulating populations of blue crabs *Callinectes sapidus* because many larvae could be lost during long migrations between estuaries and offshore waters. We examined the relative contributions of differential transport and habitat preferences of megalopae (postlarvae) to 5 potential nursery habitats in Mobile Bay and Mississippi Sound, Alabama, USA. Settlement in each habitat was determined daily during summer and fall for 2 yr and was related to sea surface temperature, wind stress, tides, current velocity and the lunar and tidal amplitude cycles. In 1990, most megalopae settled when winds blew megalopae onshore and tidal amplitudes were minimal. In 1991, onshore winds were light and infrequent, and megalopae settled even more densely during minimum amplitude tides. Semidaily collections of megalopae at dusk and dawn revealed that most megalopae recruit to estuaries during nocturnal flood tides, which only occur during summer and fall in this diurnal tidal regime. Thus, onshore winds facilitated transport of megalopae into estuaries episodically, but megalopae recruited regularly and abundantly during nocturnal minimum amplitude flood tides even when onshore winds were light or absent. Most megalopae were collected in the lower bay although some megalopae settled at the head of the estuary 50 km away from the baymouth. Megalopae required about 2 d to travel this distance as they became increasingly competent to settle from the plankton. Physiological tolerances may explain why most larvae settled in high salinity waters, but differences in current regimes may best explain differences in settlement among sites in the lower bay. Several types of substrate were transplanted from nursery habitats to a sandy area at the baymouth to determine whether megalopae prefer to settle in seagrass beds, marshes or unvegetated substrate once they arrive at a site. Megalopae strongly preferred to settle on vegetation, but it remains unclear whether or not they discriminate among plant types. Thus, passive delivery and habitat preferences of megalopae both may determine the initial distributions of juvenile blue crabs.

**KEY WORDS:** Larval settlement · Larval transport · Habitat preferences · Nursery areas · Estuaries

## INTRODUCTION

Most marine animals develop as larvae in the plankton before returning to adult habitats. Larval mortality is generally assumed to be great due to high fecundities

of adults, minute sizes of larvae and highly variable recruitment (Thorson 1950, Rumrill 1990). However, it has been argued that larval mortality may be overestimated because larvae appear to be better adapted to a planktonic existence than was previously thought (see Morgan 1995 for review). For example, it is widely believed that survival primarily depends on the passive return of weakly swimming larvae to appropriate settlement sites. However, it is becoming increasingly apparent that larvae of many species regulate the direction and distance that they travel by migrating between prevailing stratified currents (Boehlert & Mundy 1988, Epifanio 1988, McConaughy 1988) and that they actively select suitable settlement sites (e.g. Johnson 1989, Young 1989, Mokady et al. 1991).

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Mortality of sessile and sedentary animals may be estimated much more reliably once larvae settle. Nevertheless, the uncertainty of larval mortality rates has generated considerable debate concerning the relative contributions of presettlement and postsettlement mortality in regulating population abundances in marine communities. The importance of both sources of mortality was recognized early in the century, postsettlement mortality was emphasized in the 1960s and a more balanced view returned in the mid 1980s (Underwood & Fairweather 1989, Young 1990). It now appears that larval supply may be more important in regulating populations when settlement is low, and postsettlement mortality may be more important when larvae settle densely (Connell 1985, Forrester 1990, Jones 1990, Sutherland 1990, Menge 1991).

The purpose of this study was to determine whether or not this emerging paradigm applies to the population dynamics of blue crabs *Callinectes sapidus* in the Gulf of Mexico, USA. Ovigerous *C. sapidus* migrate to the mouths of estuaries and nearshore coastal waters where they release larvae (Provenzano et al. 1983, McClintock et al. 1993) that are transported as much as 100 km offshore (Smyth 1980, Truesdale & Andryszak 1983, Epifanio et al. 1989) in near-surface waters (A. E. Matthews & S. G. Morgan unpubl.). Approximately 31 to 49 d and 6 or 7 larval stages later they metamorphose into megalopae (Costlow & Bookhout 1959) and mostly return onshore in wind driven surface waters (Johnson 1985, McConaughy 1988, Olmi 1995, Matthews & Morgan unpubl.) or tidally forced internal waves (Shanks 1988). Once inshore, wind forcing (Johnson 1985) or subtidal transport (Goodrich et al. 1989, Little & Epifanio 1991) may carry megalopae into the estuary. Megalopae then are transported by nocturnal flood tides to shallow water habitats (Epifanio et al. 1984, De Vries et al. 1994, Olmi 1994). The megalopa stage lasts approximately 6 to 20 d (Costlow & Bookhout 1959), so that megalopae may not be competent to settle upon reaching suitable habitats (Lipcius et al. 1990, Metcalf & Lipcius 1992, Wolcott & De Vries 1994). Most megalopae settle in the lower estuary, but they can reach the heads of smaller estuaries (King 1971, Williams 1971, Perry 1975, Mense & Wenner 1989).

Juveniles of many estuarine species develop in vegetated areas (Thayer & Stuart 1974, Turner 1977, Nixon 1980, Boesch & Turner 1984), and as many as 95% of *Callinectes sapidus* less than 25 mm may occur there (Zimmerman & Minello 1984, Orth & van Montfrans 1987, Williams et al. 1990). However, different types of vegetated habitats may not be of equal value to the survival of blue crabs. Young juveniles appear to be much more abundant in seagrass beds than in adjacent marshes along both the Gulf and Atlantic coasts of

the USA (Orth & van Montfrans 1987, Thomas et al. 1990). Juvenile crabs use marshes more on the Gulf coast, where prevailing onshore winds and low tidal amplitudes combine to inundate marshes from summer through early fall (Mense & Wenner 1989, Thomas et al. 1990).

Different abundances of juvenile *Callinectes sapidus* in seagrass beds and marshes may be explained by differential transport of megalopae (Olmi et al. 1990), habitat preferences of megalopae (Orth & van Montfrans 1987, Luckenbach & Orth 1992), emigration and immigration of juveniles (Orth & van Montfrans 1987, Mense & Wenner 1989, Olmi et al. 1990) or postsettlement mortality (Wilson et al. 1987). We examined postlarval supply and postsettlement mortality at 5 sites along the coast of Alabama to determine which of these 2 factors most likely controls population abundances of blue crabs. In so doing, the relative contributions of various wetland habitats in maintaining blue crab populations were evaluated. Here we report the availability of postlarvae among habitats and compare our results with those of similar studies that have been conducted in estuaries on the Atlantic coast. The relative contributions of postlarval supply and postsettlement mortality in regulating population abundances of blue crabs are discussed in a companion paper (Heck et al. unpubl.).

This study was designed to provide insight into the mechanisms regulating the supply of megalopae to various habitats in Mobile Bay and Mississippi Sound. Settlement at the entrance to Mobile Bay was surveyed daily for 5 to 6 mo during 2 consecutive years and was correlated with environmental variables to determine whether winds, tides, moonlight or daylight influences the timing of recruitment to the bay. Settlement at 4 vegetated sites throughout the bay also was studied to determine whether physiological stress or current flow likely affects settlement. Megalopae penetrate over 90 km in large estuaries (van Montfrans et al. 1995) and should settle abundantly at the head of Mobile Bay, which is only 50 km from the baymouth. However, physiological tolerances (see Costlow & Bookhout 1959) may limit settlement to the lower estuary. If currents deliver more megalopae to some sites than others (e.g. Connell 1985, Gaines et al. 1985, Eckman 1987), then settlement should be greatest where flow velocities are high. If megalopae are passively deposited (e.g. Butman 1989, Armonies & Hellwig-Armonies 1992) in quiet vegetated backwaters, then settlement should be greatest where flow velocities are low. Finally, seagrasses and marsh grasses were transplanted to a sandy site at the entrance to Mobile Bay to determine whether or not megalopae discriminate among habitats. If so, megalopae should settle more abundantly on vegetated than unvegetated habitats

and they should be most abundant on seagrasses, where juveniles most commonly occur (Orth & van Montfrans 1987, Thomas et al. 1990). Alternatively, thigmotactic megalopae may be most abundant on marsh grasses because they provide the most surface area for settlement.

The lesser blue crab *Callinectes similis* occurs in coastal waters and the mouths of estuaries in the Gulf of Mexico, and therefore it co-occurs with *C. sapidus* in lower estuaries (Williams 1984). Postlarvae of both species recruited to lower Mobile Bay, and the timing, magnitude and distribution of settlement by *C. similis* also are reported.

## MATERIALS AND METHODS

**Study sites.** In the northern Gulf of Mexico, blue crab megalopae invade shallow estuarine embayments through inlets in barrier islands. The entrance to Mobile Bay is approximately 5 km wide and 4 m deep except for a 12 m deep dredged ship channel (Fig. 1). The mean depth of Mobile Bay is 3 m and the length is 50 km. The Alabama and Tombigbee rivers discharge  $1850 \text{ m}^3 \text{ s}^{-1}$  of water into Mobile Bay making it the fourth largest river system in the USA (Morisawa 1968). Low discharge (usually less than  $500 \text{ m}^3 \text{ s}^{-1}$ ) generally occurs during summer and fall (Schroeder & Lysinger 1979) when most blue crab megalopae recruit to Mobile Bay. Approximately 85% of water in Mobile Bay is exchanged with the Gulf of Mexico through

Main Pass and the remainder is exchanged with Mississippi Sound (Schroeder 1978). Mississippi Sound is 130 km long, 15 km wide and about 3 m deep at mean low water. The mouth of Mobile Bay is stratified, the rest of the bay is partially mixed and the sound is predominantly well mixed (Eleuterius 1978, Lysinger 1982, Schroeder & Wiseman 1986, Schell et al. unpubl.). Small amplitude (mean amplitude of 43 cm) diurnal tides are dominated by the declinational cycle of the moon and maximum amplitude tropic tides do not always coincide with new and full moons. Tropic tides peak during the afternoon in summer when tidal currents at the baymouth attain  $1 \text{ m s}^{-1}$ . Minimum amplitude equatorial tides occur when the moon crosses the equator 2 wk later and semidiurnal tides occur for 1 or 2 d.

Approximately 3000 acres (1215 ha) of submerged aquatic vegetation and 5000 acres (2025 ha) of marshes along the coast of Alabama (Stout & Lelong 1981) provide abundant habitat for juvenile blue crabs. We selected 4 different habitats in Mobile Bay and Mississippi Sound that might serve as nursery areas for blue crabs, and 1 additional site at the mouth of Mobile Bay to estimate the number of megalopae entering the bay (Fig. 1). The baymouth site was located in sand at the western entrance to Mobile Bay at the eastern end of Dauphin Island. Average salinity here was 24.3 ppt in 1990 and 16.2 ppt in 1991. The airport site was situated in smooth cordgrass *Spartina alterniflora* marsh on the Mississippi Sound side of Dauphin Island. This site was sampled only during 1990 when the average salinity

was 24.0 ppt. The Point aux Pins site was located in an embayment of Mississippi Sound where both seagrass beds and marshes were prevalent. As at the baymouth, mean salinity was higher in 1990 (26.6 ppt) than in 1991 (20.3 ppt). Widgeon grass *Ruppia maritima* and shoal grass *Halodule wrightii* dominated seagrass beds, and marshes mostly were comprised of black needlerush *Juncus roemerianus* and lesser amounts of *S. alterniflora*. The Fowl River site was located just seaward of a *S. alterniflora* marsh midway along the western shore of Mobile Bay. The mean salinity was 24.0 ppt during 1990 and 6.5 ppt in 1991. The delta site was situated in northern Mobile Bay at Meaher State Park and was sampled only during 1990 when salinity averaged 4.8 ppt. Submerged vegetation consisted of tape grass *Vallisneria americana* and smaller amounts of *Myriophyllum* and *Potamogeton*, and marshes were dominated by bullrush *Scirpus robustus*.

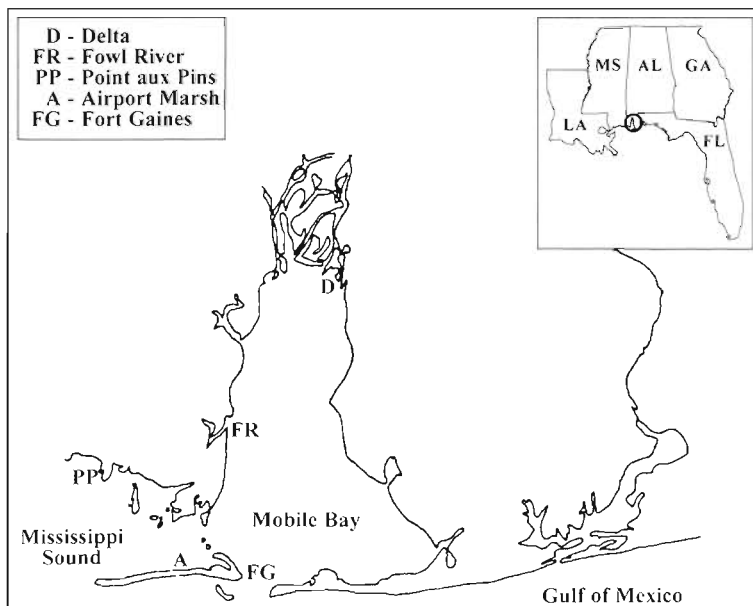


Fig. 1 Mobile Bay and eastern Mississippi Sound, Alabama, USA, showing location of the 5 study sites. The baymouth site is Fort Gaines

**Temporal and spatial patterns of settlement.** The timing and magnitude of settlement at these 5 sites were determined daily for approximately 5 or 6 mo during 1990 and 1991. Settlement is defined here as the number of megalopae that were present on collectors and does not imply that megalopae were ready to metamorphose to juveniles. Megalopae are thigmotactic and aggregate on collectors regardless of their competency to metamorphose. Sampling was conducted from June or July through November when most blue crabs reproduce in the Gulf of Mexico (Williams 1984). Settlers were sampled using passive collectors that were made of 38 cm long PVC pipe (20 cm diam.) and replaceable sleeves of 'hog's hair' air conditioning filter (see Metcalf et al. 1995 for details). Three passive collectors were anchored immediately seaward of seagrass beds and marshes (where present) and were floated near the water's surface in less than 1.5 m of water. Sleeves were replaced daily and returned to the laboratory where they were soaked and rinsed repeatedly in fresh water.

To determine whether most larvae settled during the daytime or at night, collectors were sampled at dusk and dawn at the baymouth. Sampling was conducted during 3 consecutive days during a peak settlement event and during 2 consecutive days when few megalopae settled.

A Folsom plankton splitter was used to subsample megalopae when they were especially abundant. *Callinectes sapidus* megalopae were distinguished from *C. similis* megalopae using the criteria established by Stuck & Perry (1982).

Meteorological and hydrodynamic data were obtained from a NOAA (National Oceanic and Atmospheric Administration) seaman station that was located next to collectors at the baymouth. Salinity was measured daily at the other 4 sites. Current flow was measured concurrently at the baymouth, Point aux Pins and Fowl River during 7 flood tides in 1991. Marsh-McBirney flow meters (model 511) were mounted 0.5 m away from poles that raised them 1 m above the substrate. The meters were oriented in the direction of current flow. Current flow was measured hourly from midnight to dawn (06:00 h) during 1 night of peak settlement (3 August). During 6 other nights, current flow was measured twice 1 h apart. Sampling lasted 20 min at 1 Hz. Current speed was calculated by taking the square root of the sum of squared current speeds in the x and y directions.

**Densities and molt stages of megalopae in the plankton.** Plankton tows were taken concurrently at the baymouth, Point aux Pins and Fowl River sites during 3 nights (3 August, 12 August, 15 October) in 1991 to determine densities and molt stages of megalopae. Three 10 min tows were taken hourly throughout the

night. A flow meter was positioned in the mouth (30 cm) of each net (335  $\mu$ m mesh). Each night, 20 megalopae from each site were molt staged following the methods described by Lipcius et al. (1990). Hence, a total of 180 megalopae were staged.

**Habitat selection.** The ability of settling megalopae to discriminate among habitats was determined twice during 1991. Settlement on different types of substrates was measured during 1 night of peak settlement (3 August) and 1 night of light settlement (12 September). Vegetated plots were dug from *Ruppia maritima* beds and *Juncus roemerianus* marshes at Point aux Pins and *Spartina alterniflora* marshes on Dauphin Island. Plots of unvegetated substrate also were dug from marshes on Dauphin Island. Plots were placed in 25 cm diam. plastic bowls, submerged in aerated water and picked clean of the few megalopae present. Four (12 September) or five (3 August) bowls of each treatment were transplanted into sand in less than 1 m of water at the baymouth site. Bowls were positioned randomly 2 m apart and were leveled with the surface of the substrate. *J. roemerianus* averaged 69 shoots at a mean dry weight of 69.0 mg per plot, *S. alterniflora* averaged 38 shoots at 115.6 mg per plot and *R. maritima* consisted of low-lying filaments at 5.5 mg per plot. Plots were removed after 24 h and were repeatedly bathed in fresh water. Megalopae were collected on a sieve and counted.

**Statistical analysis.** Cross-correlation analysis was used to determine whether settlement was related to temperature, onshore-offshore (north-south) wind stress, alongshore (east-west) wind stress or peak wind speed. The Rayleigh test ( $r$ ) was used to determine whether settlement was related to lunar or tidal amplitude cycles (Batschelet 1981). The mean angle (day of peak settlement) and angular deviation ( $s$ , days from peak settlement) were calculated when settlement was nonuniform.

Daily settlement at the baymouth and at each of the other 4 sites was cross-correlated to determine whether or not the timing of settlement was similar among sites. Lags between sites provided an estimate of the time required for larvae to be transported upstream. The Kruskal-Wallis test was used to determine whether or not the number of megalopae in the plankton and settling on collectors differed among sites. This test also was used to determine whether or not current flow at the baymouth, Point aux Pins and Fowl river was similar.

The  $t$ -test was used to determine whether or not megalopae primarily settled during the daytime or nighttime. ANOVA followed by the Tukey-Kramer HSD means comparison test was used to determine whether or not megalopae settled more on one type of substrate than another. For both tests, data were log-

transformed before analysis, and settlement during peak and offpeak recruitment events were analyzed separately to reduce variance.

## RESULTS

### Temporal settlement patterns

Blue crab megalopae recruited to Mobile Bay from offshore waters during every month of the investigation. *Callinectes sapidus* and *C. similis* megalopae settled from July through November in 1990 (Fig. 2) and from June through November in 1991 (Fig. 3). Peak settlement by both species of crabs occurred from mid-

July to mid-August in 1990 and from mid-September to mid-October in 1991. Seawater temperature began to decline in mid-September during both years (Figs. 4 & 5), but settlement and ambient temperatures were correlated fairly well only in 1991 (Figs. 6 & 7). Settlement of *C. sapidus* and *C. similis* was much higher in 1991 than 1990 (Figs. 2 & 3). Settlement by both species was correlated highly in both years ( $r^2 = 0.90$ ); therefore statistical results are presented only for *C. sapidus*.

Onshore winds and tides delivered *Callinectes sapidus* and *C. similis* megalopae to Mobile Bay and Mississippi Sound. In 1990, megalopae settled on substrates in Mobile Bay 5 d after peak onshore (north-south) winds (Figs. 4 & 6), especially near minimum amplitude equatorial tides (Figs. 2 & 8). In 1991,

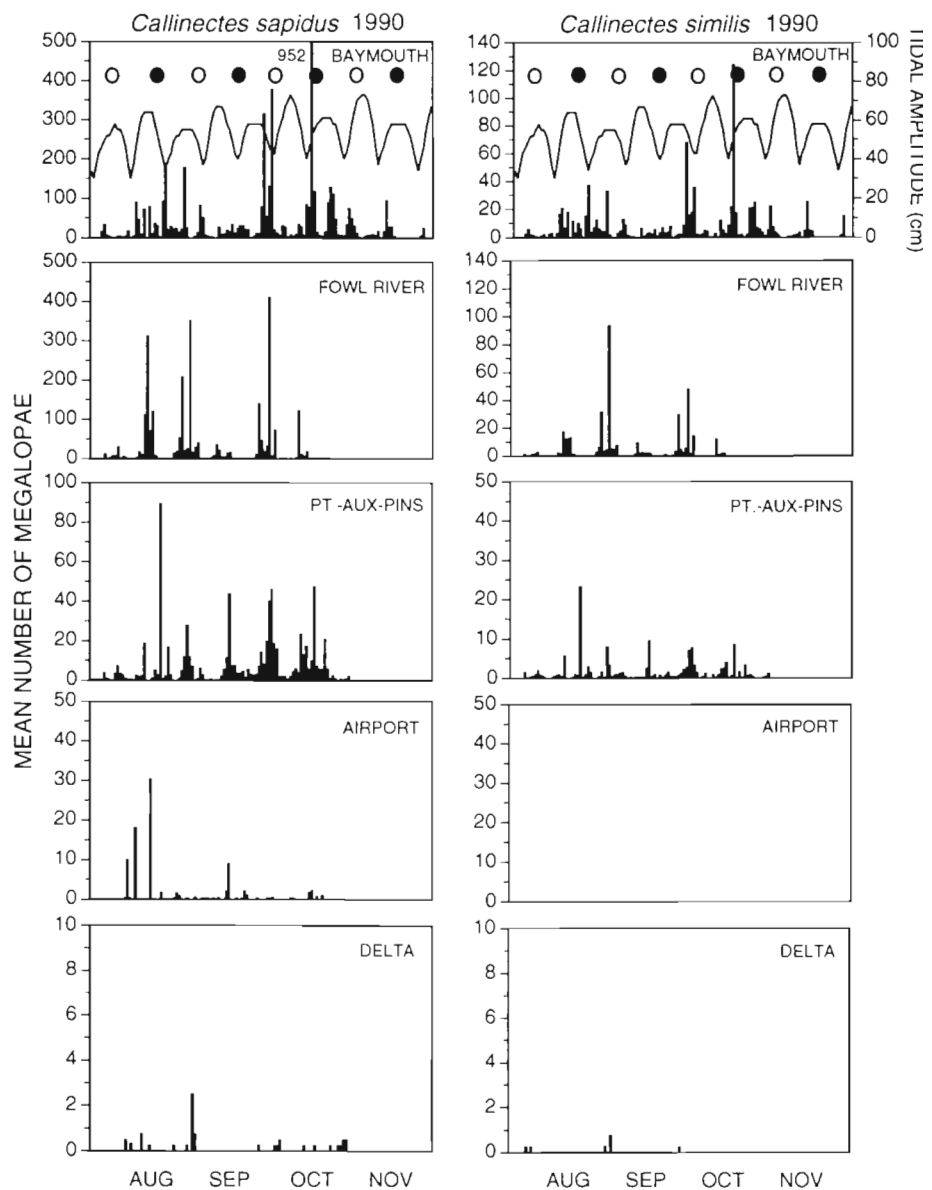


Fig. 2. Daily settlement by *Callinectes sapidus* and *C. similis* megalopae relative to lunar and tidal amplitude cycles at 5 sites in Mobile Bay and Mississippi Sound from July through November 1990. (O) Full moons, (●) new moons. The predicted height of daily high tide is also shown

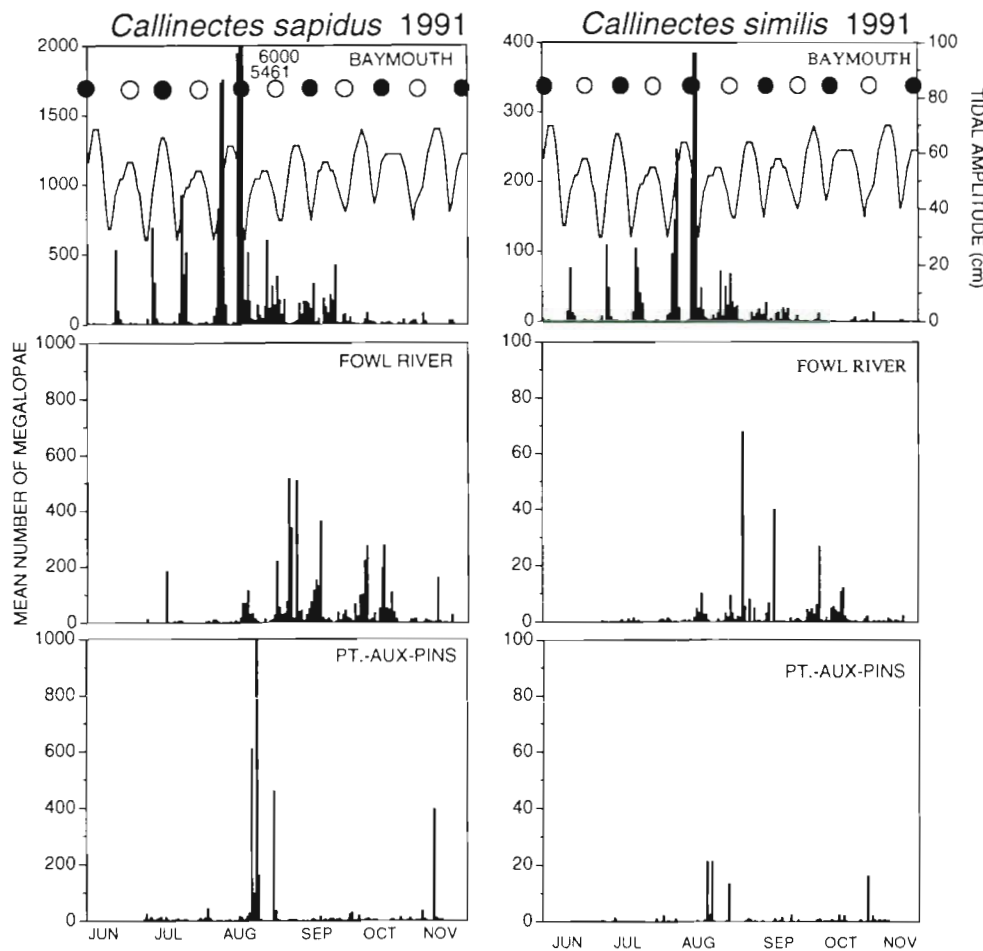


Fig. 3. Daily settlement by *Callinectes sapidus* and *C. similis* megalopae relative to lunar and tidal amplitude cycles at 3 sites in Mobile Bay and Mississippi Sound from June through November 1991. (O) Full moons, (●) new moons. The predicted height of daily high tide is also shown

onshore winds were light (Fig. 5) and settlement was weakly and negatively correlated with onshore wind stress (Fig. 7). Instead, blue crab megalopae recruited biweekly during minimum equatorial tides (Figs. 3 & 8). Seven biweekly pulses of megalopae entered Mobile Bay from mid-June to mid-September 1991. Approximately 6000 *C. sapidus* and 4000 *C. similis* megalopae settled per collector during the largest peak, which is equivalent to about 2500 *C. sapidus* and 1700 *C. similis* megalopae  $m^{-2}$ .

Settlement was better synchronized with the tidal amplitude cycle than the lunar cycle, especially during 1991 when winds were light (Figs. 2 & 3). Peak settlement during both years occurred during equatorial tides (1990:  $r = 0.36$ ,  $s = \pm 3.2$  d; 1991:  $r = 0.45$ ,  $s = \pm 2.8$  d), but it occurred 1 d after new and full moons in 1990 ( $r = 0.29$ ,  $s = \pm 3.8$  d) and 2 d before quarter moons in 1991 ( $r = 0.20$ ,  $s = \pm 4.3$  d). Settlement was not correlated with alongshore (east-west) wind stress (Figs. 4 to 7) during either year.

Blue crabs settled on substrates in Mobile Bay during the daytime and nighttime (Fig. 9). More *Callinectes sapidus* megalopae, *C. sapidus* first stage crabs and

*C. similis* megalopae were collected at night during a peak settlement event from 2 to 4 August 1991, although results were not significantly different (*C. sapidus* megalopae:  $F = 2.84$ ,  $df = 1$ ,  $p = 0.11$ ; *C. sapidus* first stage crabs:  $F = 2.10$ ,  $df = 1$ ,  $p = 0.16$ ; *C. similis* megalopae:  $F = 0.001$ ,  $df = 1$ ,  $p = 0.97$ ). Megalopae of both species and first instar crabs of *C. sapidus* were collected in similar numbers during the daytime and nighttime on 2 days (15 and 17 October 1991) of light settlement (*C. sapidus* megalopae:  $F = 1.21$ ,  $df = 1$ ,  $p = 0.31$ ; *C. sapidus* first stage crabs:  $F = 1.25$ ,  $df = 1$ ,  $p = 0.31$ ; *C. similis* megalopae:  $F = 0.53$ ,  $df = 1$ ,  $p = 0.49$ ). However, significantly more *C. sapidus* megalopae ( $F = 11.35$ ,  $df = 1$ ,  $p = 0.02$ ) and first stage crabs ( $F = 92.91$ ,  $df = 1$ ,  $p < 0.0001$ ) settled at night on 3 August when high tides occurred in darkness at 05:00 h.

#### Spatial settlement patterns

During both years, *Callinectes sapidus* (1990:  $H = 268.18$ ,  $df = 4$ ,  $p < 0.001$ ; 1991:  $H = 66.06$ ,  $df = 2$ ,  $p < 0.001$ ) and *C. similis* (1990:  $H = 178.37$ ,  $df = 4$ ,  $p < 0.001$ ;

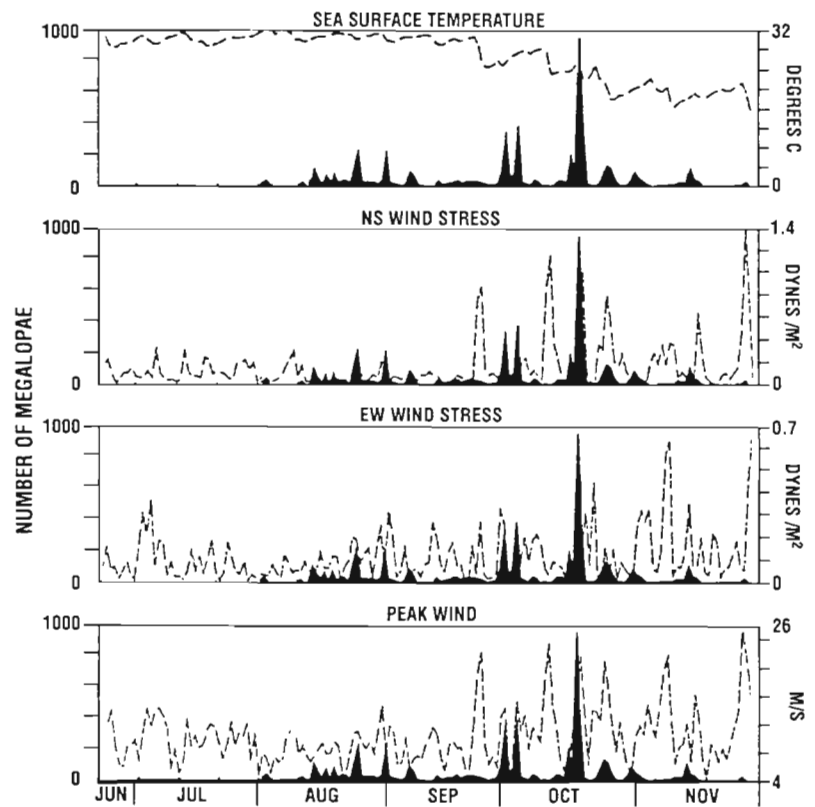


Fig. 4. *Callinectes sapidus*. Daily settlement by megalopae (filled black areas) relative to sea surface temperature, north-south wind stress, east-west wind stress and peak wind velocity (dashed lines) at the mouth of Mobile Bay from July through November 1990. Environmental variables are shown for late June and July because data were analyzed for lags in settlement as long as 40 d relative to water temperature, wind stress and wind velocity

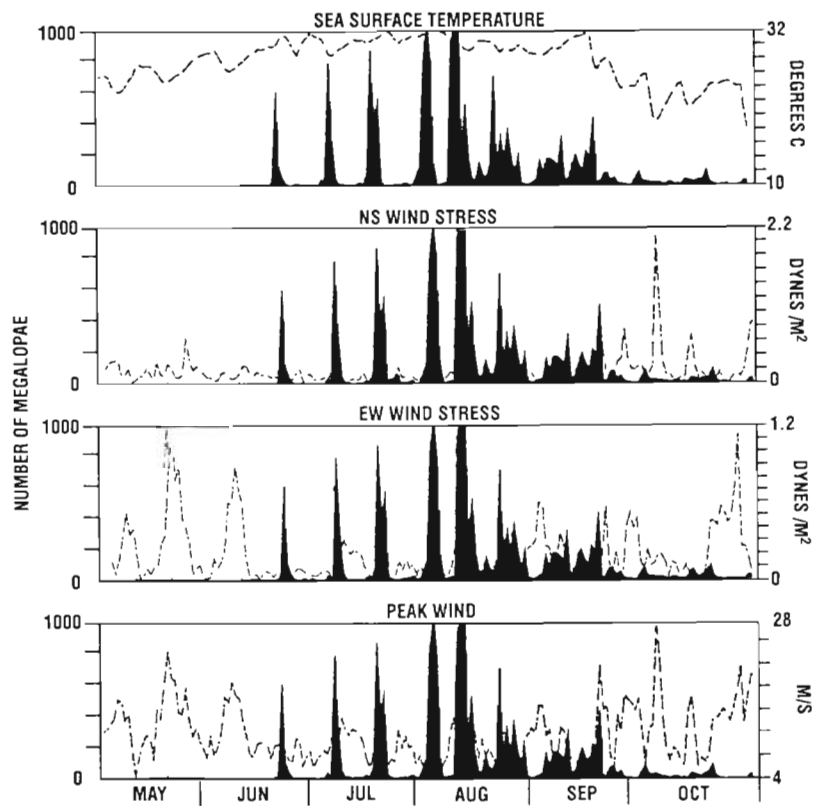


Fig. 5. *Callinectes sapidus*. Daily settlement by megalopae (filled black areas) relative to sea surface temperature, north-south wind stress, east-west wind stress and peak wind velocity (dashed lines) at the mouth of Mobile Bay from mid-June to November 1991. Environmental variables are shown for May because data were analyzed for lags in settlement as long as 40 d relative to water temperature, wind stress and wind velocity

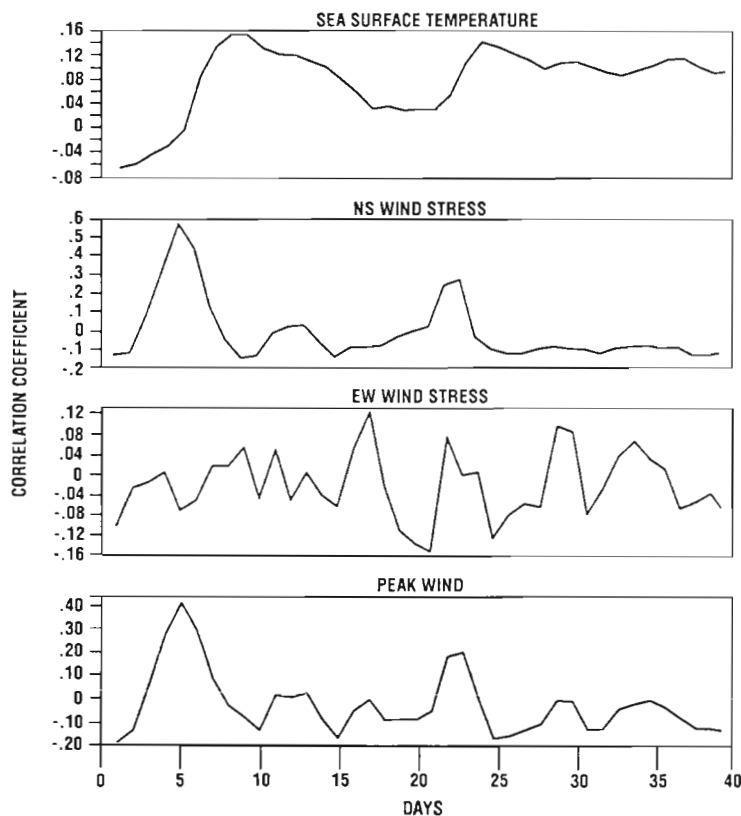


Fig. 6. *Callinectes sapidus*. Cross-correlations of daily settlement by megalopae at the mouth of Mobile Bay in 1990 with sea surface temperature, north-south wind stress, east-west wind stress and peak wind velocity. Data were analyzed for lags in settlement as long as 40 d

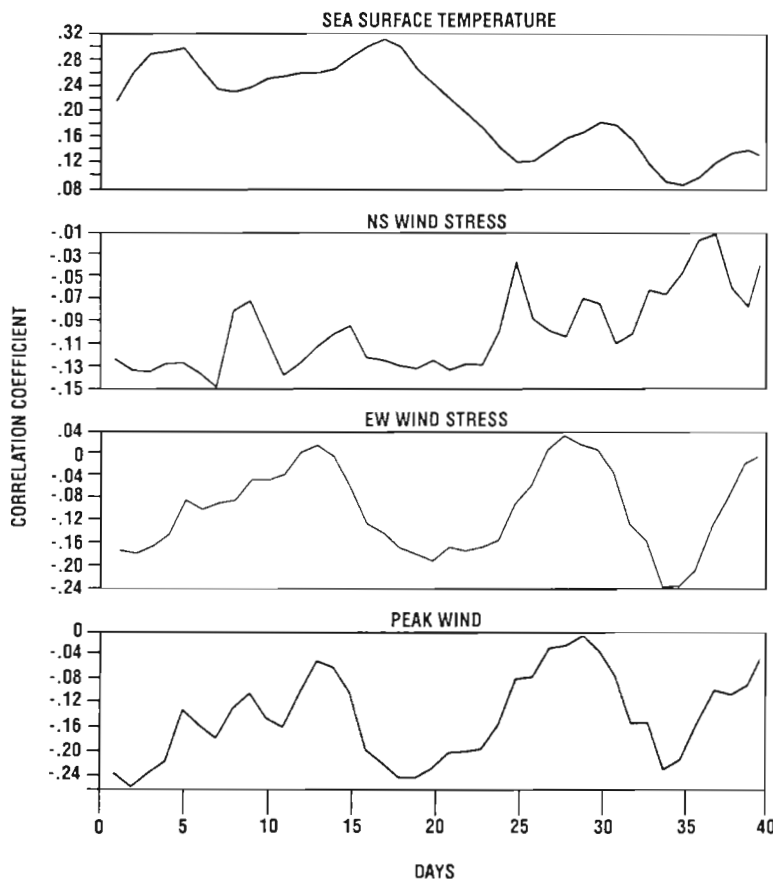


Fig. 7. *Callinectes sapidus*. Cross-correlations of daily settlement by megalopae at the mouth of Mobile Bay in 1991 with sea surface temperature, north-south wind stress, east-west wind stress and peak wind velocity. Data were analyzed for lags in settlement as long as 40 d



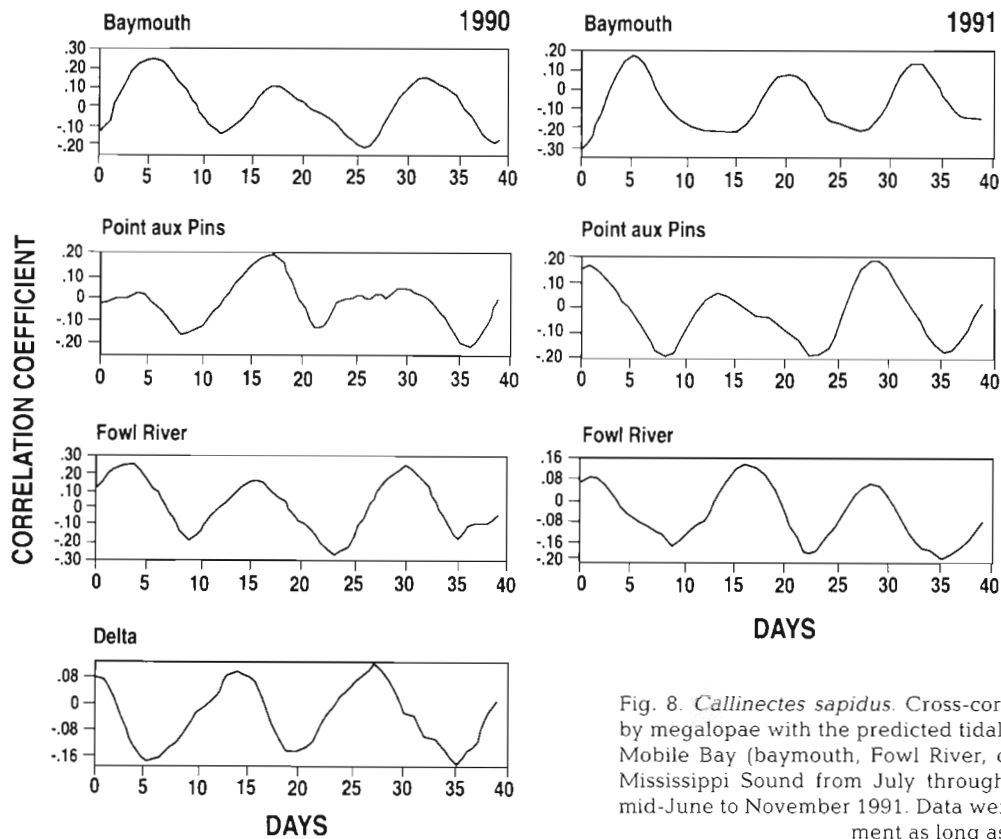


Fig. 8. *Callinectes sapidus*. Cross-correlations of daily settlement by megalopae with the predicted tidal amplitude cycle at 3 sites in Mobile Bay (baymouth, Fowl River, delta) and Point aux Pins in Mississippi Sound from July through November 1990 and from mid-June to November 1991. Data were analyzed for lags in settlement as long as 40 d

1991:  $H = 113.34$ ,  $df = 2$ ,  $p < 0.001$ ) megalopae settled most abundantly at the mouth of Mobile Bay, declined toward the middle of the estuary (Fowl River) and were infrequent at the head of the estuary (delta) (Table 1, Fig. 2). This trend was particularly pronounced in 1991, when even fewer *C. sapidus* and *C. similis* megalopae settled at Fowl River than at the baymouth. Fewer megalopae of both species settled at Point aux Pins than at the baymouth during both years. Settlement by both species also tended to be greater at Fowl River than Point aux Pins. Settlement by the airport nearly was as sparse as at the head of the estuary in 1990.

Abundances of planktonic megalopae and settlers were similar among sites during 1991. *Callinectes sapidus* ( $H = 15.87$ ,  $df = 2$ ,  $p < 0.001$ ) and *C. similis* ( $H = 13.93$ ,  $df = 2$ ,  $p < 0.001$ ) megalopae were most abundant in the plankton at the baymouth and progressively declined upstream (Fig. 10). Most first instar crabs were collected from the plankton at Point aux Pins ( $H = 5.26$ ,  $df = 2$ ,  $p = 0.07$ ), few were taken at Fowl River and none was collected from the baymouth (Fig. 10).

More megalopae may have been delivered to the baymouth where currents were stronger than at other sites (Table 2). Maximum and mean current speeds at the baymouth usually were 2 to 10 times higher than at

Point aux Pins or Fowl River. Flow at the latter 2 sites was similar. Measurements were not taken at the delta or airport but flow appeared to be even slower at these sites.

Megalopae of all developmental stages entered the baymouth, but later molt stages became increasingly abundant upstream (Fig. 11). Late molt stages of blue crab megalopae were more prevalent at Point aux Pins and were even more abundant at Fowl River than at the baymouth, presumably because it took them longer to reach these sites. This is suggested by the lagged correlations between settlement at the baymouth and more shoreward sites (Fig. 8). *Callinectes sapidus* megalopae settled at about the same time to 3 d later at Point aux Pins (1990:  $r^2 = 0.42$ ; 1991:  $r^2 = 0.47$ ), 2 to 3 d later at Fowl River (1990:  $r^2 = 0.25$ ; 1991:  $r^2 = 0.07$ ), and 3 d later at the delta ( $r^2 = 0.10$ ). Settlement at all 5 sites occurred at 15 d intervals during both years, which suggests that tidal currents transported megalopae into Mobile Bay and Mississippi Sound biweekly and carried them to the head of the estuary 3 d later.

Megalopae in early stages of development were more common in August than they were in October at the baymouth (Fig. 11). Stage C and D1 megalopae were common at the baymouth in August but were

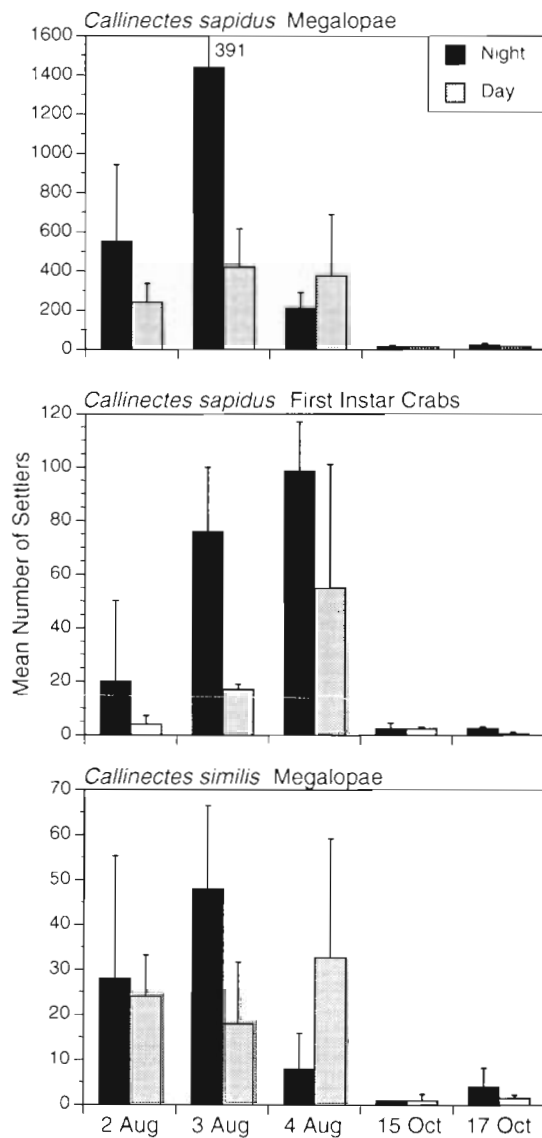


Fig. 9. Settlement by *Callinectes sapidus* megalopae and first instar crabs and *C. similis* megalopae during the nighttime and daytime at the mouth of Mobile Bay on 5 days during 1990

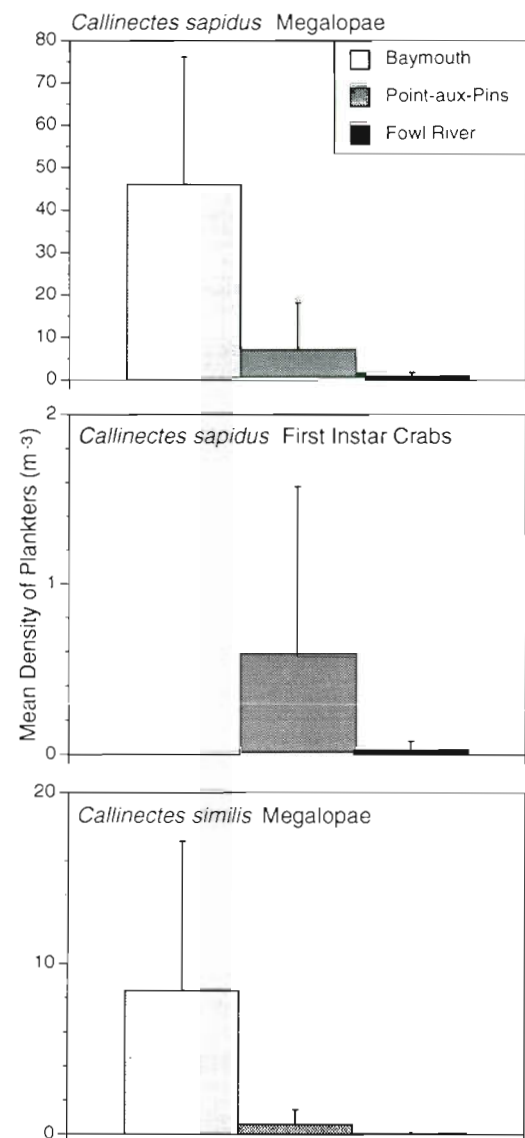


Fig. 10. Mean density ( $\text{m}^{-3}$ ) of *Callinectes sapidus* megalopae and first instar crabs and *C. similis* megalopae collected from the plankton at the baymouth and Fowl River in Mobile Bay and Point aux Pins in Mississippi Sound during 1991

Table 1. Percentage of *Callinectes sapidus* and *C. similis* megalopae settling at 5 sites in Mobile Bay and Mississippi Sound from June through November 1990 and at 3 of these sites from July through November 1991

Species	Year	Site				
		Baymouth	Point aux Pins	Airport	Fowl River	Delta
<i>C. sapidus</i>	1990	56.8	9.2	1.1	32.7	0.1
	1991	69.8	18.8	–	11.4	–
<i>C. similis</i>	1990	63.0	10.1	0	26.8	0.1
	1991	87.0	3.4	–	9.7	–

absent in October, and stage D5 megalopae were rare in August but were common in October.

Regardless of whether settlement was heavy in August ( $F = 53.66$ ,  $df = 17$ ,  $p < 0.001$ ) or light in September ( $F = 8.73$ ,  $df = 15$ ,  $p < 0.01$ ), megalopae preferred to settle on vegetated plots. More than 4 times as many *Callinectes sapidus* megalopae settled on *Spartina alterniflora* than on *Ruppia maritima* or *Juncus roemerianus* in August (Fig. 12), although this trend was

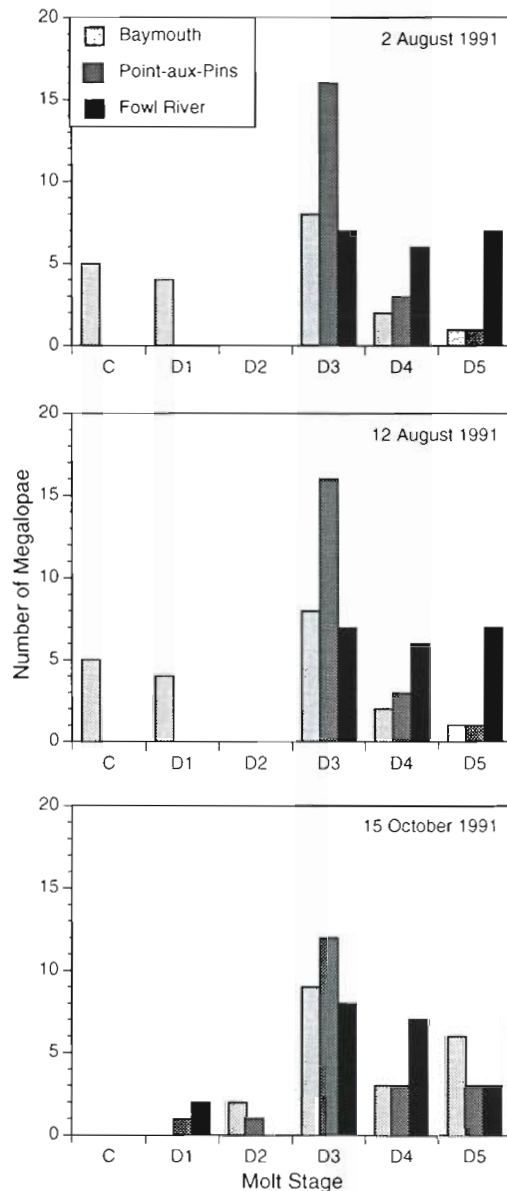


Fig. 11. Molt stage of 20 *Callinectes sapidus* megalopae collected from the plankton at the baymouth and Fowl River in Mobile Bay and Point aux Pins in Mississippi Sound during 3 nights in 1991. The youngest megalopae are in stage C of the molt cycle and the oldest ones occur in stage D5.

not significant. More first instar crabs *C. sapidus* ( $H = 1.94$ ,  $df = 2$ ,  $p = 0.38$ ) and *C. similis* megalopae ( $H = 1.98$ ,  $df = 2$ ,  $p = 0.37$ ) also settled on *S. alterniflora* than the other plants, but these differences also were not significant. The comparatively broad blades of *S. alterniflora* extended throughout the water column and provided more surface area than shorter round *J. roemerianus* shoots or the sparse low-lying filaments of *R. maritima*. This also is reflected in the different dry weights of the plants that were used in these experiments.

A different nonsignificant trend was found 41 d later when settlement on vegetated plots was light. Six times more megalopae of *Callinectes sapidus* occurred on *Ruppia maritima* than on *Spartina alterniflora*, and the first few instar crabs of this species occurred only on *R. maritima* (Fig. 12). Only a few *C. similis* megalopae settled in September, and these occurred only on *Juncus roemerianus*.

## DISCUSSION

### Settlement in Mobile Bay versus Atlantic estuaries

Although settlement by *Callinectes sapidus* megalopae has been studied along the Atlantic coast of the USA, this is one of the first investigations that has been conducted on the Gulf coast. Several striking differences are apparent. Peak settlement was 1 or 2 orders of magnitude greater in Mobile Bay than in estuaries along the Atlantic coast (Olmi et al. 1990, van Montfrans et al. 1990, 1995, Rabalais et al. 1995), except during an unusual year in Charleston Harbor, South Carolina (Boylan & Wenner 1993). Settlement usually may be greater in the Gulf due to higher abundances of adults occurring in this warmer climate. The Gulf of Mexico is near the center of the species' range, which usually extends from Massachusetts to northern Argentina (Williams 1984).

Table 2. Current flow at 3 sites in Mobile Bay and Mississippi Sound during 7 nocturnal flood tides in 1991.

Date	Site	Current speed (cm s <sup>-1</sup> )	
		Max.	Mean
3 Aug	Baymouth	7.2	3.0
	Point aux Pins	2.9	1.3
	Fowl River	4.6	1.6
29 Sep	Baymouth	22.4	10.7
	Point aux Pins	4.5	2.0
	Fowl River	2.8	1.2
4 Oct	Baymouth	4.5	2.1
	Point aux Pins	2.8	1.6
	Fowl River	2.8	1.1
5 Oct	Baymouth	26.1	18.4
	Point aux Pins	6.3	2.7
	Fowl River	4.5	3.3
11 Oct	Baymouth	10.0	4.3
	Point aux Pins	4.5	4.3
	Fowl River	4.5	1.9
12 Oct	Baymouth	12.6	6.3
	Point aux Pins	4.5	1.9
	Fowl River	10.4	5.7
20 Oct	Baymouth	8.9	4.6
	Point aux Pins	4.5	1.6
	Fowl River	6.3	1.9

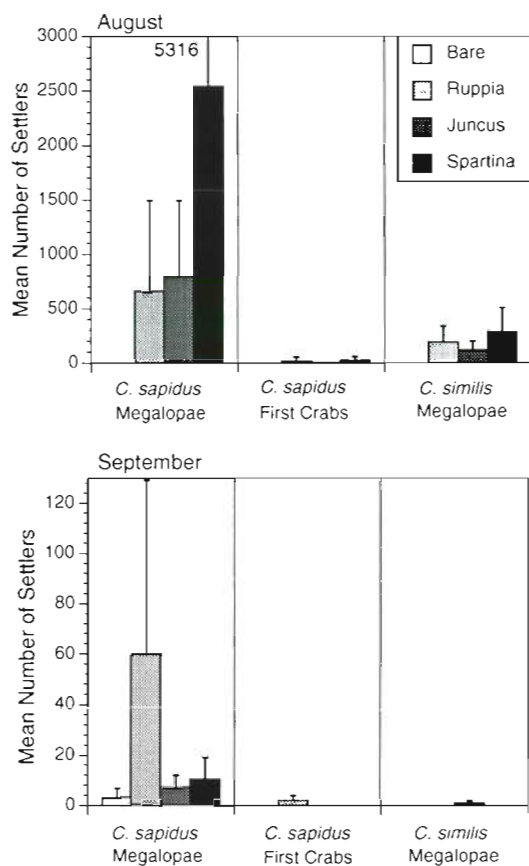


Fig. 12. Settlement by *Callinectes sapidus* megalopae and first instar crabs and *C. similis* megalopae on 4 types of substrates that were transplanted to sandy habitats at the mouth of Mobile Bay during 1991. Settlement was heavy on 3 August and was light on 12 September

Moderate temperatures in the Gulf also may have favored protracted reproduction by *Callinectes sapidus*. Blue crab megalopae recruited to Mobile Bay and Mississippi Sound throughout the summer and fall when this study was conducted. Megalopae probably settle nearly year-round because ovigerous females of *C. sapidus* and *C. similis* have been collected in Mobile Bay and the Gulf of Mexico throughout most of the year (Williams 1984, Hsueh et al. 1993). In colder climates along the Atlantic coast of the USA, *C. sapidus* megalopae generally settle only from summer through autumn (Williams 1984, Boylan & Wenner 1993, van Montfrans et al. 1995).

Along both coasts, onshore winds and tides often facilitate recruitment of blue crab megalopae to estuarine nursery habitats (Rabalais et al. 1995, van Montfrans et al. 1995). Winds have a particularly strong influence on water exchange between the Gulf of Mexico and estuaries where tidal amplitudes are low (Smith 1977, Swenson & Chuang 1983, Schroeder &

Wiseman 1986, Stumpf et al. 1993). In 1991, peak settlement was correlated with onshore winds, which prevail during summer and early autumn (Ward 1980, Schroeder & Wiseman 1986). These winds may transport megalopae shoreward in the neuston until they reach the front of the plume flowing from Mobile Bay. Megalopae then would be subducted with surface currents beneath the buoyant plume and advected into the bay (Gelfenbaum & Stumpf 1993). Peaks in settlement could occur if megalopae aggregate near estuarine fronts until winds begin blowing onshore.

Although onshore winds probably facilitated transport of blue crab megalopae into Mobile Bay, tides may be more important because megalopae recruited effectively even when onshore winds were light. Indeed, settlement was much greater during 1991 when onshore winds were less common and lighter. During both years, blue crab megalopae consistently recruited to Mobile Bay near minimum amplitude equatorial tides. The biweekly periodicity in recruitment was more closely associated with the tidal amplitude cycle than the lunar cycle, which suggests that tides rather than the moon regulate recruitment to estuaries. This distinction is possible along the Gulf coast, where the declination of the moon rather than planetary alignment governs the tidal amplitude cycle.

Most blue crab megalopae also recruited during nocturnal minimum amplitude flood tides in Charleston Harbor, South Carolina (Boylan & Wenner 1993). Recruitment may be favored during minimum amplitude tides at both locales due to strong stratification (Linden & Simpson 1988, Nunes Vaz et al. 1989, Sharples & Simpson 1993). At that time, surface waters flow offshore and deeper residual currents flow onshore, which would facilitate onshore movement of megalopae that were subducted beneath the estuarine plume. Exchange between coastal and estuarine waters is reduced when the water column is mixed during maximum amplitude tides. Therefore, recruitment may be greatest in Mobile Bay and Charleston Harbor during minimum amplitude tides when prevailing light to moderate onshore winds would subduct neustonic megalopae beneath the estuarine plume and residual currents would advect them onshore.

Peak settlement by blue crabs in Chesapeake Bay occurs during maximum amplitude flood tides when mixing is greatest (Olm et al. 1990, van Montfrans et al. 1990, Olm 1995). This shift in timing suggests that multiple or perhaps other tidally related processes may facilitate recruitment of megalopae to estuaries. One possibility is that internal waves transport megalopae onshore, because spatial variation in the timing of peak settlement relative to the tidal amplitude cycle has been observed for other animals (Pineda 1991).

Plankton and settlement studies on both coasts suggest that most blue crab megalopae move landward during nocturnal flood tides (Epifanio et al. 1984, Olmi et al. 1990, De Vries et al. 1994, Olmi 1994, J. M. Schell & S. G. Morgan unpubl.). However, settlement during the daytime was more common along the Gulf than the Atlantic coast. Megalopae may have timed swimming more precisely on the Atlantic coast, where the 2 flood tides per day usually occur either exclusively during the nighttime or daytime. In this case, swimming simply may not be initiated during daytime flood tides. Along the coast of Alabama, the 1 flood tide per day is twice as long and often occurs during darkness and daylight. Therefore, swimming begun during darkness may continue after dawn as tides continue to flood.

### Postlarval supply and habitat preferences

*Callinectes sapidus* megalopae were much more abundant than *C. similis* in Mobile Bay and Mississippi Sound perhaps because more larvae were released or because megalopae preferred to settle in estuarine habitats. *C. sapidus* females collectively may have released more larvae because they are about an order of magnitude more fecund ( $2.1$  to  $3.2 \times 10^6$  vs  $2.4$  to  $5.5 \times 10^5$  eggs per brood) than smaller *C. similis* females (Hsueh et al. 1993). Whether or not ovigerous *C. sapidus* females also were more abundant than egg-bearing *C. similis* females in the northern Gulf of Mexico is unknown.

Alternatively, interspecific differences in abundance of megalopae may be explained by habitat preferences. *Callinectes similis* does not osmoregulate as well as *C. sapidus* and probably prefers deeper high salinity waters (Engel 1977, Hsueh 1992). This is evident in the distributions of megalopae, juveniles and adults of *C. similis*. Not only were megalopae of *C. similis* less common than *C. sapidus* in Mobile Bay, but more of them occurred at the baymouth than at more landward sites during both years. This matches the distributions of the youngest juveniles of *C. similis* that occur in open unvegetated habitats near the mouth of Mobile Bay and adjacent coastal waters where the salinity usually is greater than 25 ppt (Hsueh et al. 1993). Most juveniles that settle in the bay probably migrate to deeper coastal waters, because adults largely occupy coastal waters and ovigerous females occur there exclusively (Hsueh et al. 1993).

In contrast, *Callinectes sapidus* appears to depend on wetlands as nursery grounds, because environmental cues from marshes accelerate metamorphosis (Wolcott & De Vries 1994) and the smallest juveniles occur near marshes rather than in deeper open waters of the bay (Hsueh et al. 1993, Heck et al. unpubl.). Our study

suggests that settling megalopae primarily maintain this distribution by discriminating among habitats within Mobile Bay.

On a broad scale, most *Callinectes sapidus* megalopae settled on collectors at the baymouth, fewer settled in the middle of the bay and very few megalopae settled at the head of the bay. Most megalopae may have settled in the lower estuary simply because they first encountered suitable habitat there. However, this is unlikely to be the sole explanation of this trend because megalopae penetrate much farther than 50 km into larger estuaries. For instance, megalopae settled abundantly at Tangier Island, which is 90 km from the mouth of Chesapeake Bay (van Montfrans et al. 1995). We suggest that the gradual decline in settlement upstream primarily resulted because *C. sapidus* megalopae survive better and grow faster at high salinities (Kalber 1970, Costlow 1976) and prefer to settle in the lower bay. Although it took only 2 to 3 d to travel from the mouth of Mobile Bay to the head of the estuary, few megalopae settled there, presumably because they survive poorly at 5 ppt (Costlow 1976). Megalopae also survive poorly at 10 ppt, which may explain the proportionally lower settlement at Fowl River than at the baymouth during the second year of the study when salinity averaged 6.5 ppt. In contrast, settlement probably is much greater at Tangier Island because the mean salinity is about 3 times higher, 14.7 to 18.8 ppt (van Montfrans et al. 1995), than at the head of Mobile Bay. Thus, fewer megalopae may have settled in tape grass beds and bullrush marshes at the delta and smooth cordgrass marshes at Fowl River due to salinity preferences of megalopae.

The ability of megalopae to discriminate among habitats in the lower bay is less certain. Differential transport rather than habitat selection primarily appears to determine the abundance of settlers among high salinity habitats. Currents consistently delivered more megalopae to some sites than others. Currents were stronger at the baymouth site and consistently delivered many more megalopae to this site than to the quiet backwaters near the airport and Point aux Pins. Thigmotactic megalopae had little difficulty settling on collectors at the baymouth despite the stronger currents. Thus, delivery by currents rather than passive deposition in quiet backwaters more likely determines where megalopae settle in the lower bay.

Although physiological tolerances and current flow both apparently affect the broad-scale distributions of juveniles, megalopae may discriminate between habitats once they arrive at a site. Blue crab megalopae are strong swimmers that can orient into the flow and swim upstream at low to moderate flow velocities (Luckenbach & Orth 1992). This apparently enabled mega-



lopae to select vegetated rather than unvegetated plots.

Evidence that megalopae discriminated among plants was inconclusive, but the strong nonsignificant trends warrant further investigation. During September, over 6 times more *Callinectes sapidus* megalopae settled on *Ruppia maritima* than any other plant despite its small surface area. Therefore, behavior rather than postsettlement mortality may explain the higher densities of young juveniles in seagrass beds than marshes (Orth & van Montfrans 1987, Thomas et al. 1990). This is further suggested by the similar mortality rates of young juveniles that were measured in these habitats (Heck et al. unpubl.). However, the same trend was not obtained in August when over 4 times more megalopae settled on *Spartina alterniflora*. The differences in settlement patterns on the 2 dates could have resulted if fewer megalopae were ready to metamorphose in August. If so, numerous early stage megalopae may have clung to *S. alterniflora* blades in passing due to the greater surface area provided by these plants, whereas the few late stage megalopae primarily may have sought seagrass in preparation for metamorphosis. Although megalopae were not staged in September, far fewer of them were ready to metamorphose in August than October, providing support for this explanation (Fig. 11). Relatively few megalopae settled on *Juncus roemerianus* at either time perhaps because these plants provided neither large surface areas for settlement nor appropriate settlement cues.

In conclusion, both postlarval supply and habitat selection appeared to determine the initial abundances of blue crabs in Mobile Bay and Mississippi Sound. Blue crab megalopae settled in very high densities in the lower estuary during nocturnal equatorial flood tides and onshore winds. Physiological tolerances probably ensured that most blue crab megalopae settled in the lower bay. Currents delivered more megalopae to some areas than others in the lower bay, and *Callinectes sapidus* megalopae preferred to settle in vegetated than unvegetated habitats. However, it remains uncertain whether megalopae select seagrass beds rather than marshes once they arrive at a site. Predation on recent settlers quickly damped differences in juvenile abundances among sites regardless of initial settlement densities (Heck et al. unpubl.). Thus, differential transport and habitat preferences of megalopae both determined the initial densities of settlers, but there was little evidence of density-dependent postsettlement mortality in this population. Early postsettlement mortality by predators rather than postlarval supply may limit population sizes of blue crabs in the northern Gulf of Mexico.

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