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SETTLEMENT OF *CALLINECTES SAPIDUS* MEGALOPAE ON ARTIFICIAL COLLECTORS IN FOUR GULF OF MEXICO ESTUARIES

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ABSTRACT

Standardized artificial collectors were used to document trends in settlement of blue crab (*Callinectes sapidus*) megalopae in four Gulf of Mexico estuaries. Blue crab megalopal settlement was generally episodic within an estuary and asynchronous among coastwide sites. Daily settlement of megalopae at a given site and rankings of total numbers among sites varied greatly from year-to-year. Although spawning is protracted and megalopae are available in offshore waters throughout most of the year, most megalopae were collected during August–October. Limited settlement of megalopae in late spring and early summer occurred in the two estuaries (Galveston Bay in 1992 and Terrebonne Bay in 1991) for which sampling was conducted during this period. Within several estuaries, there were no clear environmental variables that corresponded most closely to peak events of megalopal settlement. Combinations of equatorial tides and onshore winds (when present) were the most apparent environmental variables correlated with high daily settlement at Mobile Bay mouth. The majority of high settlement events for Mississippi Sound were associated with tropic tides coupled with onshore winds. The relative importance of environmental variables affecting settlement varied from year-to-year in several of the estuaries. Limited coherence between gulf sites was not supported by plausible mechanisms for transport, with the exception of a 2- to 3-d lag from the mouth of Mobile Bay to a mid-estuary site. Inter-regional comparisons of monthly settlement means during peak settlement months were robust and consistent with regional climatic controls (temperature and salinity) and long-term water level patterns (lunar periodicity and meteorology). Large numbers of blue crab megalopae recruited to gulf estuaries. Numbers of settling blue crab megalopae declined with distance from the Gulf of Mexico, but still recruited in fairly large numbers well into the two estuaries where such data were available.

The blue crab, *Callinectes sapidus,* is a dominant benthic invertebrate of shallow coastal and estuarine habitats of the U.S. Atlantic and Gulf of Mexico coasts and supports a valuable commercial fishery (nearly 200 million pounds in the Gulf of Mexico in 1987; Steele and Perry, 1990). The population levels of *C. sapidus* are, in part, influenced by recruitment dynamics that culminate from interacting abiotic and biological processes that reduce large numbers of eggs and larvae to smaller numbers of postlarvae and juveniles in the appropriate nursery habitats. Physical factors affecting blue crab recruitment include temperature, salinity, circulation patterns, local meteorology and tidal periodicity and vary over seasonal, interannual and long-term climatic scales (Fritz et al., 1990). Biotic interactions, such as food resources and predation, also affect early life stage survival and vary similarly over short- and long-time periods. The blue crab was chosen as the candidate organism for studies of recruitment dynamics of a single species that ranges over a broad distributional spectrum for development of models applicable to other species with similar life history characteristics (Blue Crab Recruitment Group concept proposal, 1992).

A national, cooperative research program to address timing and location of settlement of blue crab postlarvae began in 1989 with the participation of investigators from Delaware, Virginia and South Carolina. The 1989 collaborative effort revealed episodic, synchronous settlement across 1,000 km of coastline (van Montfrans et al., 1995) which indicated settlement may be related to large-scale climatic and hydrodynamic conditions. While the peaks were synchronous, the relative proportion of megalopae differed among sites, possibly varying as a function of the locations of the collector sites and latitudinal differences. Sampling sites from other Atlantic coast states and several from the Gulf of Mexico were added in 1990. The intersite coherence observed in 1989 for the three Atlantic coast estuaries was not repeated in 1990 and 1991; although, coherence was sometimes observed for two of the three sites (van Montfrans et al., 1995).

The tool selected to study the recruitment dynamics of blue crab megalopae was a standard artificial substrate (air-conditioning filter) in a cylindrical design deployed according to a standard protocol (Metcalf et al., 1995). The utility of these "megalopa collectors" was verified by several studies which documented (1) the relationship between planktonic abundance of megalopae and the number of megalopae collected on the filters (Lipcius et al., 1990), (2) timing of settlement of the megalopae just prior to metamorphosis to the first crab stage (Lipcius et al., 1990), (3) episodic events associated with wind events, lunar periodicity, and tidal range (Goodrich et al., 1989; van Montfrans et al., 1990; Boylan and Wenner, 1993), and (4) large-scale differences in abundances (Olmi et al., 1990).

Early life history of the blue crab is much better known on the Atlantic coast than the Gulf coast (Smyth, 1980; Provenzano et al., 1983; Epifanio et al., 1984; Epifanio, 1988a, 1988b; Lipcius et al., 1990; Olmi et al., 1990; van Montfrans et al., 1990, 1995; Olmi, 1994). While details of larval transport and recruitment remain largely unknown for the Gulf of Mexico, some similarities exist in the life cycles of Atlantic and Gulf blue crabs. Adult blue crabs reside throughout Gulf of Mexico estuaries, and the mature females migrate to the estuary mouth for spawning. Egg-bearing females occur in gulf coastal waters year-round (West, 1980; Perry and McIlwain, 1986; Steele and Perry, 1990), with peaks in spawning in March–April and June–August, depending on the estuary. In the less saline coastal waters of Louisiana, gravid females have been observed releasing larvae well offshore (25 to 30 km) (N. N. Rabalais, pers. observ.). Blue crab zoeae are exported from the estuaries to adjacent shelf waters where they molt through seven to eight zoeal stages to a postlarval stage (=megalopa). Early larval stages and megalopae occur near estuaries and intermediate zoeal stages are concentrated offshore (Truesdale and Andryszak, 1983; Steele and Perry, 1990), as along the Atlantic coast. Portunid megalopae have been collected during every month at a major Louisiana tidal pass (Caminada Pass of Barataria Bay in 1972, F. M. Truesdale and K. C. Stuck, unpubl. data) with peaks in June and August and in Mississippi Sound year round (Perry, 1975). The processes that allow larvae to return to nearshore and estuarine waters likely include large-scale circulation patterns, local meteorology and hydrology, and behavior cued to lunar or tidal periodicity.

The purpose of this synthesis was to (1) compare blue crab megalopal settlement across a variety of Gulf of Mexico estuaries, (2) determine whether there was coherence in settlement among sites, (3) determine timing of settlement relative to various environmental factors, and (4) compare the magnitude of gulf coast megalopal settlement with that occurring in U.S. Atlantic coast estuaries.

Study Area

Data were obtained from the northern and northwestern Gulf of Mexico at Galveston Bay, Texas (1991–1992), Terrebonne Bay, Louisiana (1990–1991), Mobile Bay, Alabama (two of five sites, 1990–

Table 1. Comparative statistics and information for Gulf of Mexico megalopa settlement study sites

Site, year and frequency	Galveston Bay, TX 1991 altern. days	Galveston Bay, TX 1992 altern. days	Terrebonne Bay, LA 1990 5 d/week	Terrebonne Bay, LA 1991 5 d/week	Mississippi Sound, MS 1991 daily	Mississippi Sound, MS 1992 daily	Mobile Bay, AL 1990 daily	Mobile Bay, AL 1991 daily	Fowl River, AL 1991 daily
Collection period	7/10–12/19/91	2/1–12/17/92	5/21/90–1/15/91	4/1–11/27/91	5/3–11/30/91	5/1 11/20/92	7/30 12/1/90	5/16–11/24/91	6/22–10/31/91
Months with settlement	Jul–Dec	Feb–Dec	May–Dec	Apr–Nov	May–Nov	May–Oct	Jul–Nov	May–Nov	Jun–Oct
Months with peak* settlement events	Sep–Dec	Aug–Nov	Sep–Oct	May–Jun, Aug–Oct	Jun–Oct	Jun, Aug–Oct	Aug–Nov	Jun–Sep	Jul–Oct
Mean settlement†	23.7 ± 6.4	28.8 ± 10.5	8.3 ± 0.7	0.6 ± 0.05	172.3 ± 45.0	21.5 ± 4.0	37.8 ± 8.3	170.3 ± 45.0	41.8 ± 7.7
Total settlement‡	6,615	16,542	5,063	432	146,080	14,860	16,399	89,235	15,438
in N days	80	157	152	170	212	192	121	155	127
Mean salinity ± SE	26.1 ± 0.5	22.1 ± 0.6	9.4 ± 0.4	7.6 ± 0.4	15.5 ± 0.6	23.2 ± 0.3	24.4 ± 0.2	15.7 ± 0.6	nd
range	15–35	4–35	0–24	0–21	0–30	8–32	20–28	2–28	
Mean °C ± SE	24.0 ± 0.7	24.0 ± 0.5	25.5 ± 0.5	25.6 ± 0.4	25.0 ± 0.4	26.0 ± 0.2	23.9 ± 0.5	26.0 ± 0.4	27.7 ± 3.1
range	13.5–32	10–35	10–32.5	10–32	9–32	17–31	14–33	11–32	19–32
Distance from gulf	5 km		22 km		13 km		0 km		21 km
Relationships		new moon, salinity	salinity	new moon	tropic tides w/ onshore winds, salinity	tropic tides w/ onshore winds, salinity, temperature	equatorial tides, peak onshore winds, temperature	equatorial tides	2–3 d lag from bay mouth

* Peak is >2 × mean.
† No/collector/d ± SE, N = 4 surface collectors, except N = 3 for Fowl River.
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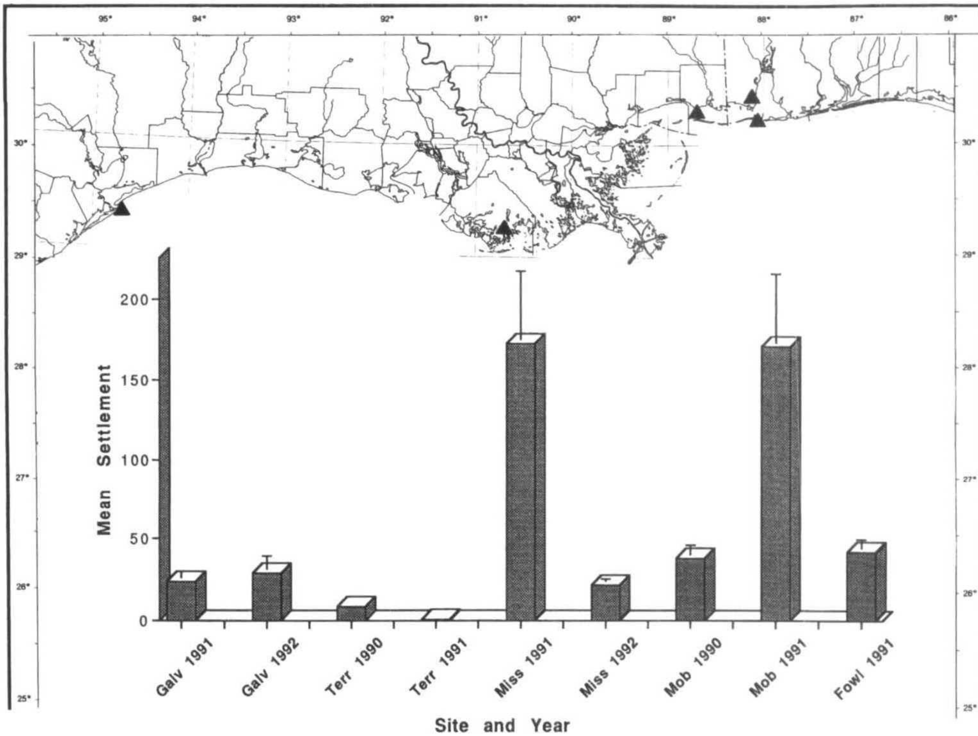

Figure 1. Mean settlement (number of megalopae·collector^{-1}·d^{-1}) of *Callinectes sapidus* megalopae for collection period for each study area by year. Collection frequency and period given in Table 1. General location of study areas on map at top parallel histograms below (Galv = Galveston Bay TX, Terr = Terrebonne Bay LA, Miss = Mississippi Sound MS, Mob = Mobile Bay mouth AL, Fowl = Fowl River AL estuarine site within Mobile Bay).

1991), and Mississippi Sound, (1991–1992) (Table 1, general locations in Fig. 1). Sites varied in distance from the Gulf of Mexico (0 to 22 km) (Table 1).

Galveston Bay, is the second largest estuary on the Texas coast and includes several large embayments (Trinity Bay, Galveston Bay, East Bay and West Bay), as well as several secondary bays around its periphery. Its ocean boundary is outlined by a series of barrier islands, including Bolivar Peninsula and Galveston Island, and most tidal exchange with the Gulf of Mexico occurs through Bolivar Roads. Megalopal collectors were deployed from a pier at the U.S. Coast Guard station on the eastern end of Galveston Island (29:20.00′N, 94:46.25′W) within 5 km of Bolivar Roads and the open Gulf of Mexico (Fig. 2). Extreme fluctuations in salinity (Fig. 3) result from the tidal exchange between the Gulf of Mexico and a low- to medium-salinity Galveston Bay.

Terrebonne Bay is located halfway between the Mississippi and Atchafalaya rivers. Extensive marshes border the northern landward margin and intermingle gradually with the extensive estuarine system of Terrebonne and Timbalier Bays and Lake Pelto. These are connected to the Gulf of Mexico through a series of broad passes. Megalopal collectors were suspended from a pier in shallow Price's Bayou next to the LUMCON Marine Center in Cocodrie (29:15.24′N, 90:39.66′W) which is well within a *Spartina alterniflora* marsh (Fig. 4). The collector site was located 22 km from Cat Island Pass, a major barrier island pass. Salinities, the lowest of all study sites, were low in spring and summer, and increased in fall and winter (Fig. 3).

In Mississippi, collectors were suspended from a pier in the Belle Fountaine Beach area (30:20.95′N, 88:44.40′W) on the north shore of Mississippi Sound between Biloxi Bay and the Pascagoula River (Fig. 5). Mississippi Sound is an elongate water body oriented east-west and is separated from the open Gulf of Mexico by a series of barrier islands. The eastern margin of the sound is formed by narrow peninsulas and shallow shell reefs connecting Dauphin Island to the Alabama mainland and separating the sound from Mobile Bay. The western end of the sound is bordered by Lake Borgne, Louisiana. Connections through passes and over shoal areas along the barrier island chain permit the

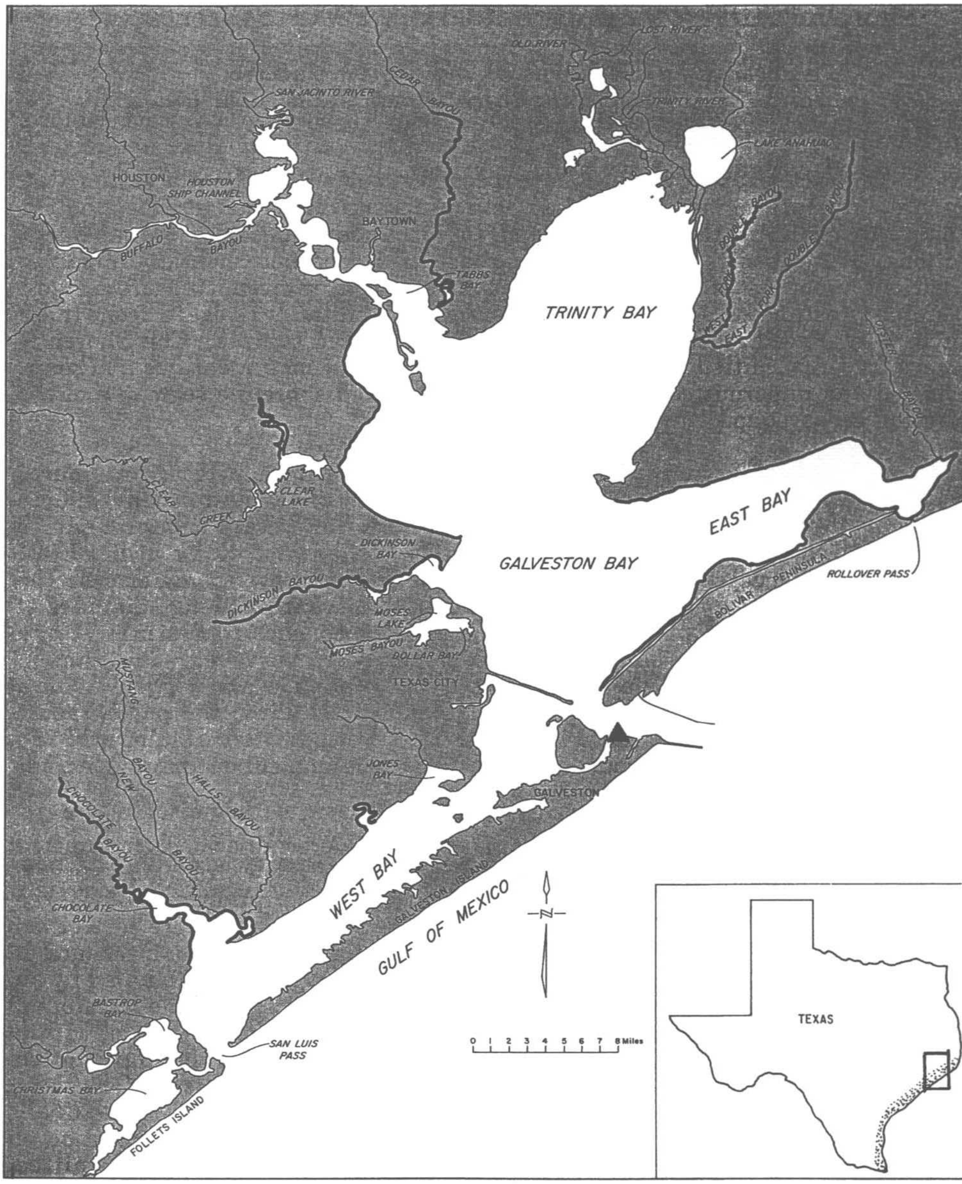

Figure 2. Location of Galveston Bay site near Bolivar Roads on the eastern end of Galveston Island (indicated by black triangle).

intrusion of higher salinity Gulf of Mexico waters. The collector study site was located 13 km from the nearest pass. Water salinity was generally lower in 1991 than in 1992 (Fig. 3).

Mobile Bay is a submerged river valley about 50 km long from its mouth to the northern end at the Mobile River delta and averages 17 km in width. Its southern terminus is integrated with the eastern portion of Mississippi Sound. Dauphin Island forms the western boundary to Main Pass into Mobile Bay. Megalopal collectors were anchored on the eastern end of Dauphin Island (30:15.02'N, 88:04.30'W) immediately adjacent to the open Gulf of Mexico (Fig. 5). Salinity was higher in 1990, and paralleled that of Mississippi Sound in 1991. A second collector site considered in this comparison was seaward of a *S. alterniflora* marsh at the mouth of Fowl River (30:27.10'N, 88:08.02'W), 21 km

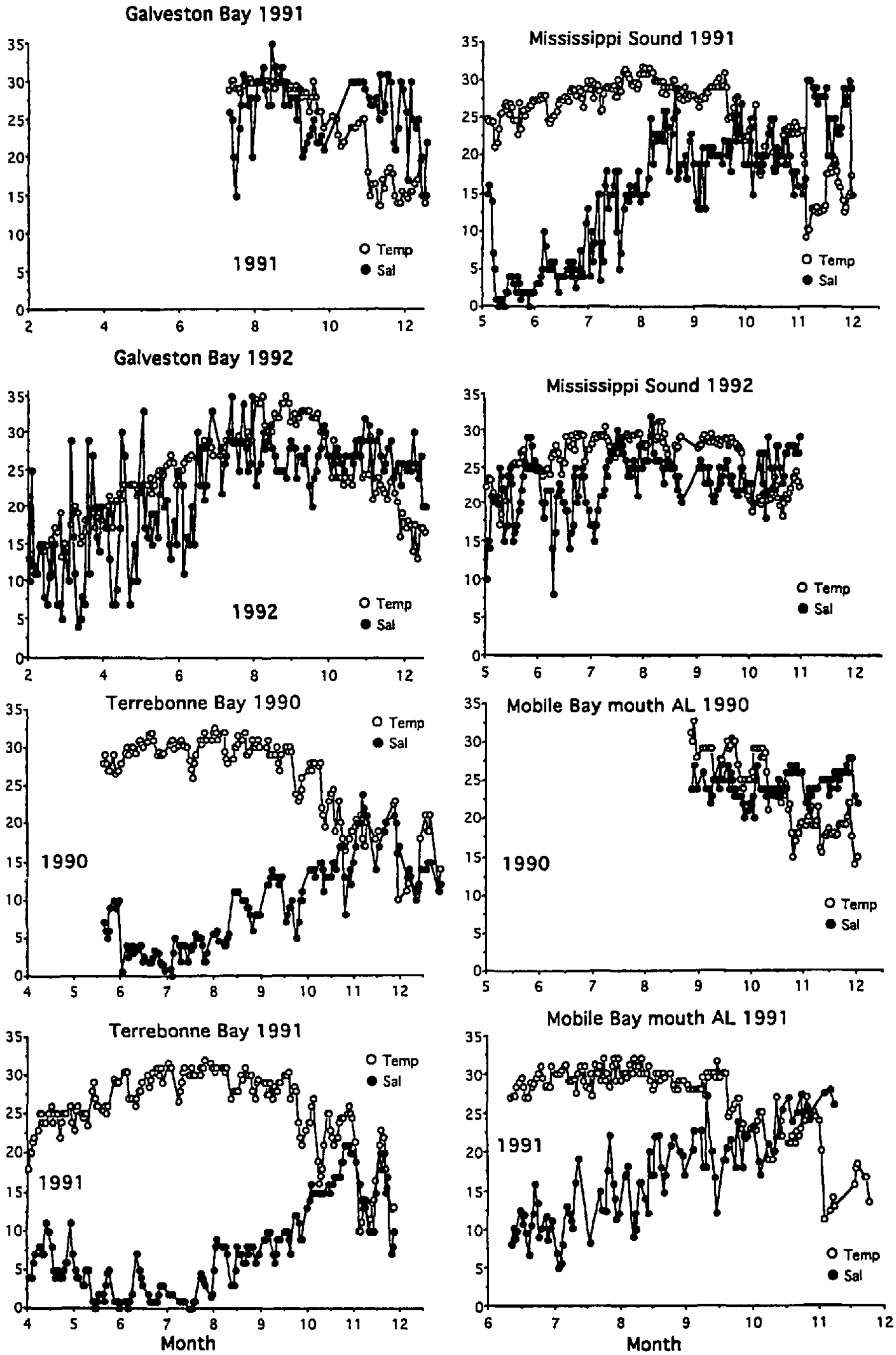

Figure 3. Water temperature (°C) and salinity (‰) for each site and year combination.

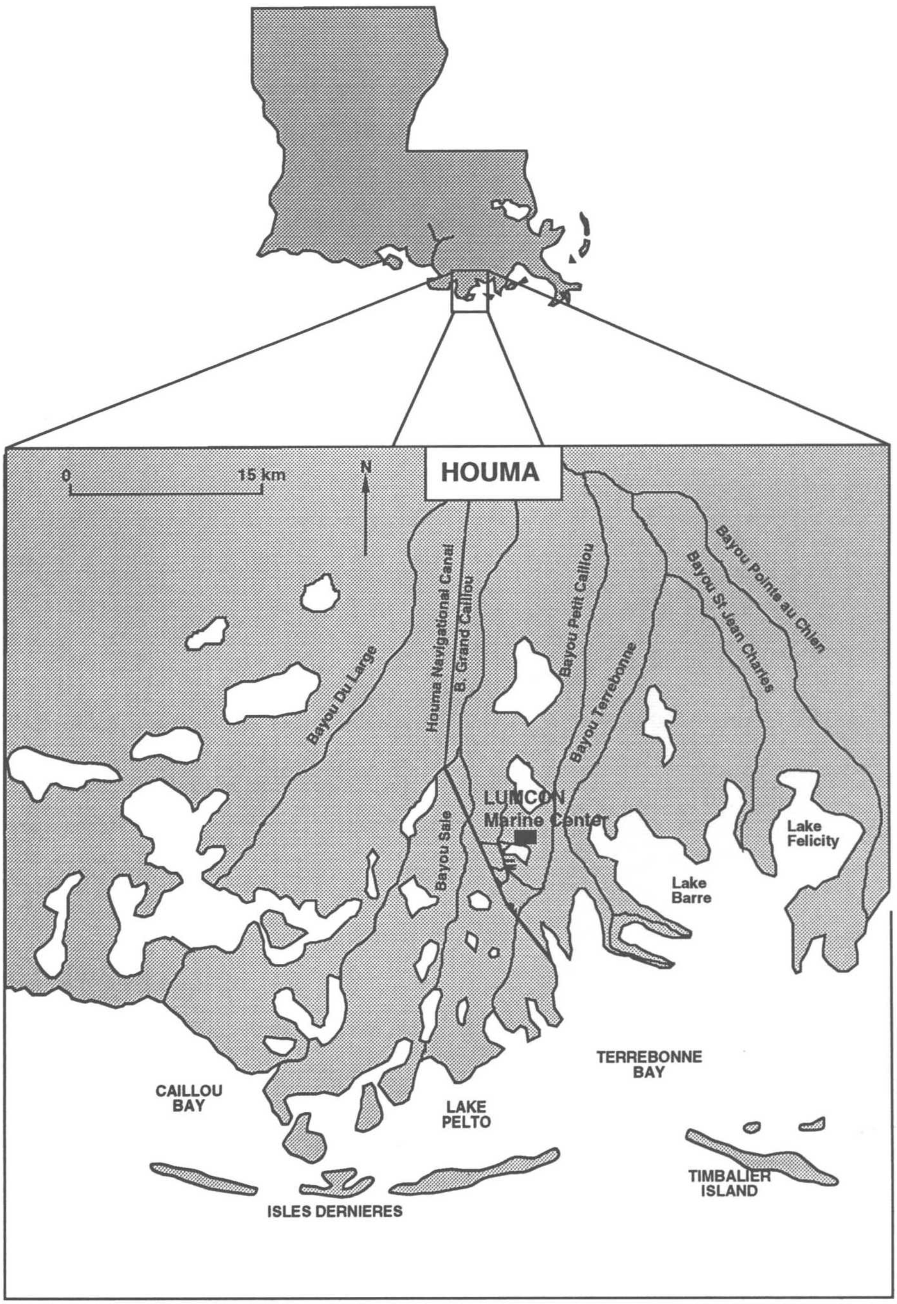

Figure 4. Location of Terrebonne Bay site within a *Spartina alterniflora* marsh bayou adjacent to the LUMCON Marine Center.

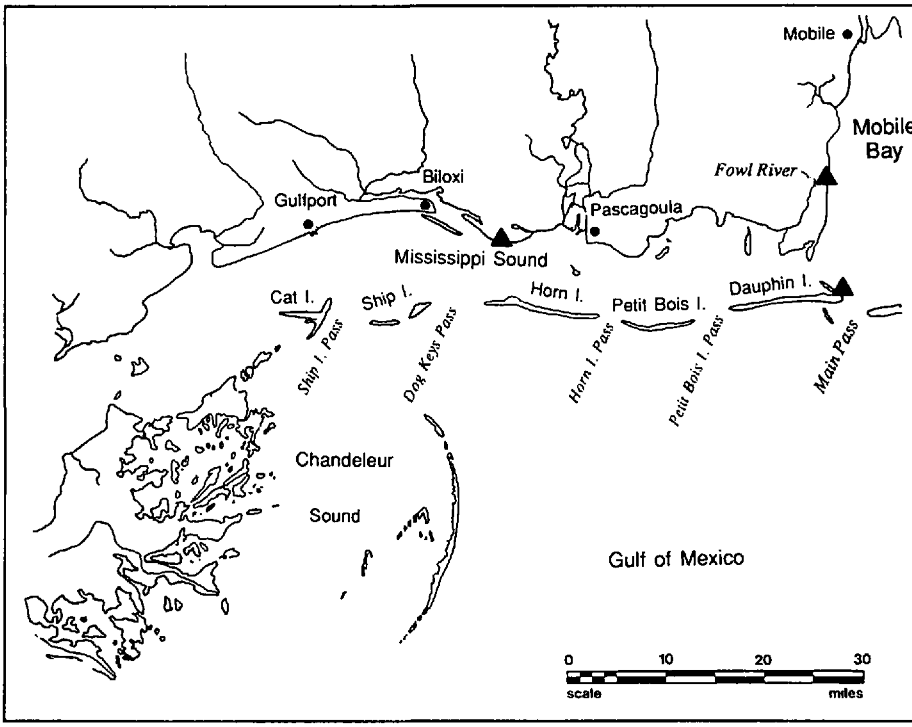

Figure 5. Location of Mississippi Sound, Mobile Bay mouth and Fowl River study sites (indicated by black triangles).

from Main Pass in Mobile Bay (Fig. 5). The distance of Fowl River from the Gulf of Mexico, and the environmental setting, was similar to that of the Terrebonne Bay site in Louisiana. Salinity data were not available for Fowl River.

The range of tide is uniformly small in the Gulf of Mexico but the type of tide differs considerably. The region from Cape San Blas, Florida, to the middle of the Louisiana coast is predominantly a diurnal tide with one high and one low water a day. On either side of this region, the tide is mixed with a semidiurnal tide around the times of the moon on the equator but diurnal around the times of maximum north or south declination of the moon. In the Gulf of Mexico, consequently, the principal variations in the tide are due to the changing declination of the moon. Study sites at Mobile Bay, Mississippi Sound and Terrebonne Bay are in the region of predominantly diurnal tides and Galveston Bay, in the region of diurnal and mixed tides.

Water levels along the Gulf coast change noticeably with changes in wind speed and direction (Ward, 1980). Normal wind stress may be sufficient to bring about a water level change of the same order of magnitude as that resulting from the periodic tide-producing forces. These non-periodic short-term wind events are superimposed on the periodic tides and can account for a substantial portion of water exchange in northern Gulf estuaries (Swenson and Chuang, 1983; Smith, 1977). The Azores-Bermuda atmospheric high pressure cell dominates wind circulation over the Gulf, particularly during the spring and summer months (Brower et al., 1972). Dominant wind fields in the summer are controlled by the more southerly position of the Bermuda high pressure cell which brings about the southeast-northwest orientation of isobars across the gulf and leads to a predominance of southeasterly winds. There are practically no northerly winds in summer and only a relatively few from the east or the west. Typical winter circulation is more easterly with few southerlies but more northerlies. During October to April, cold fronts come from the northwest or from the north at three to eight day intervals (Muller, 1977). Storm frequency increases rapidly from September to October, reaching a maximum in mid-winter.

Large-scale circulation in the Gulf of Mexico is influenced by the Loop Current and associated eddies, the semipermanent gyre in the western Gulf, winds, freshwater input and the density structure of the water column (Huh et al., 1981; Sturges and Horton, 1981; Sturges and Evans, 1983). The

Mississippi River exerts a major influence on the circulation and hydrology of the northern Gulf of Mexico. The birdfoot delta acts as a geographic barrier to water flow, and its discharge is a dominant freshwater source. Natural variability in systems adjacent to the outflow of the Mississippi River is due primarily to Mississippi river runoff and local climatology (Wiseman et al., 1990). Currents in nearshore waters are variable in response to large-scale circulation patterns, winds, tides, and freshwater inflow, and differ dramatically on opposite sides of the Mississippi River delta, as well as alongshore for the length of the study area west of the Mississippi River (NOAA, 1985).

METHODS

A standard artificial settlement substrate (megalopa collector) was used in each study area (Metcalf et al., 1995). The substrate matrix consisted of commercial "hogshair" air conditioning filter material of a synthetic fiber matrix over a rigid, cylindrical PVC frame (16 cm O.D., 38 cm long). A combination of floats and weights maintained the collector in a vertical position at 0 to 5 cm below the water's surface, whether deployed from a pier or anchored to the bottom.

Deployments of four subsurface megalopa collectors (N = 3 at Fowl River) were made at each of the study areas, with variability in schedules. Deployments were 7 $d \cdot wk^{-1}$ at the Mobile Bay and Mississippi Sound sites; 5 $d \cdot wk^{-1}$ at the Terrebonne Bay site; and alternating days at the Galveston Bay site (Table 1). Each deployment represented a 24-h collection, with retrieval/deployment usually occurring between 0800 and 1000. Standard protocol for rinsing collectors and collecting organisms was followed (Metcalf et al., 1995). All *C. sapidus* megalopae were identified and counted. Mean settlement is number of $megalopae \cdot collector^{-1} \cdot d^{-1}$.

Surface water temperature and salinity data were collected at the time of each recovery. Lunar data were obtained from National Ocean Service (NOAA) Tide Tables. Wind speed and direction data were obtained from the nearest weather observation station. Data available for analysis in this paper were obtained from (1) the NOAA, Local Climatological Data, Monthly Summaries for the Post Office Building, Galveston, Texas within 6 km of the Galveston Bay study site and (2) daily vector averaged wind velocity from either the Houma Municipal Airport (35 km from the Terrebonne Bay site), National Climate Data Center, National Weather Service, or the LUMCON Marine Center anemometer (within 1 km of the Terrebonne Bay site). Wind data and tidal amplitude data for Mississippi Sound and Mobile Bay mouth were analyzed by the investigators for each of these sites (Perry et al., 1995, and S. G. Morgan, unpubl. data, respectively). Tidal amplitude data were not available for the Galveston Bay and Terrebonne Bay sites.

For inter-site comparisons, data plotted were daily means of four subsurface collectors (or less, if a collector was not recovered, or it was found out of the water at the time of recovery; N = 3 for Fowl River). Pearson correlation coefficients were calculated to examine the relationship between daily megalopal settlement and water temperature and salinity (Microsoft Excel vers. 4.0). The data for each site were standardized for lunar quarter. Lunar quarter 1 was those days around the new moon (day 27–day 4); lunar quarter 3 was those days around the full moon (day 12–day 18; the intervening days were placed in lunar quarters 2 and 4. The daily settlement for those days in which settlement occurred (i.e., zero values excluded) within a lunar quarter were compared by a nonparametric one-way analysis of variance (general linear model on ranks = Kruskal-Wallis k-sample test) (SAS Inc., 1985). The number of data in each lunar quarter was unequal because full lunar months were not always sampled and because of the excluded data. Because there were unequal sample sizes, a Dunn nonparametric multiple comparison test statistic was used to test for significant differences in daily settlement between lunar quarters (Zar, 1984). Similarly, data for Galveston Bay and Terrebonne Bay were divided by wind direction (eight equal compass directions) and compared by the same nonparametric tests. Tests for significance were made at alpha = 0.05. Cross-correlation analyses among sites tested for synchrony of settlement peaks at geographically separated sites (StatGraphics vers. 6.0); these analyses were limited to two sites in 1990, five sites in 1991, and two sites in 1992.

RESULTS

Four estuaries were sampled from 1990–1992, but not all four within any 2-year period (Table 1). Blue crab megalopal settlement occurred in most months in which sampling was conducted, with the exception of January (Table 1). The month of January, however, was sampled in only one site in 1 year. Mean daily settlement varied among sites and between years for most sites (Table 1, Fig. 1). Peak settlement events ($number \cdot d^{-1}$ greater than two times mean settlement) occurred in May through December, primarily in August through October, and varied among sites within a year and within sites from year-to-year (Table 1, Fig. 6). Peak settlement events were generally episodic (Fig. 6).

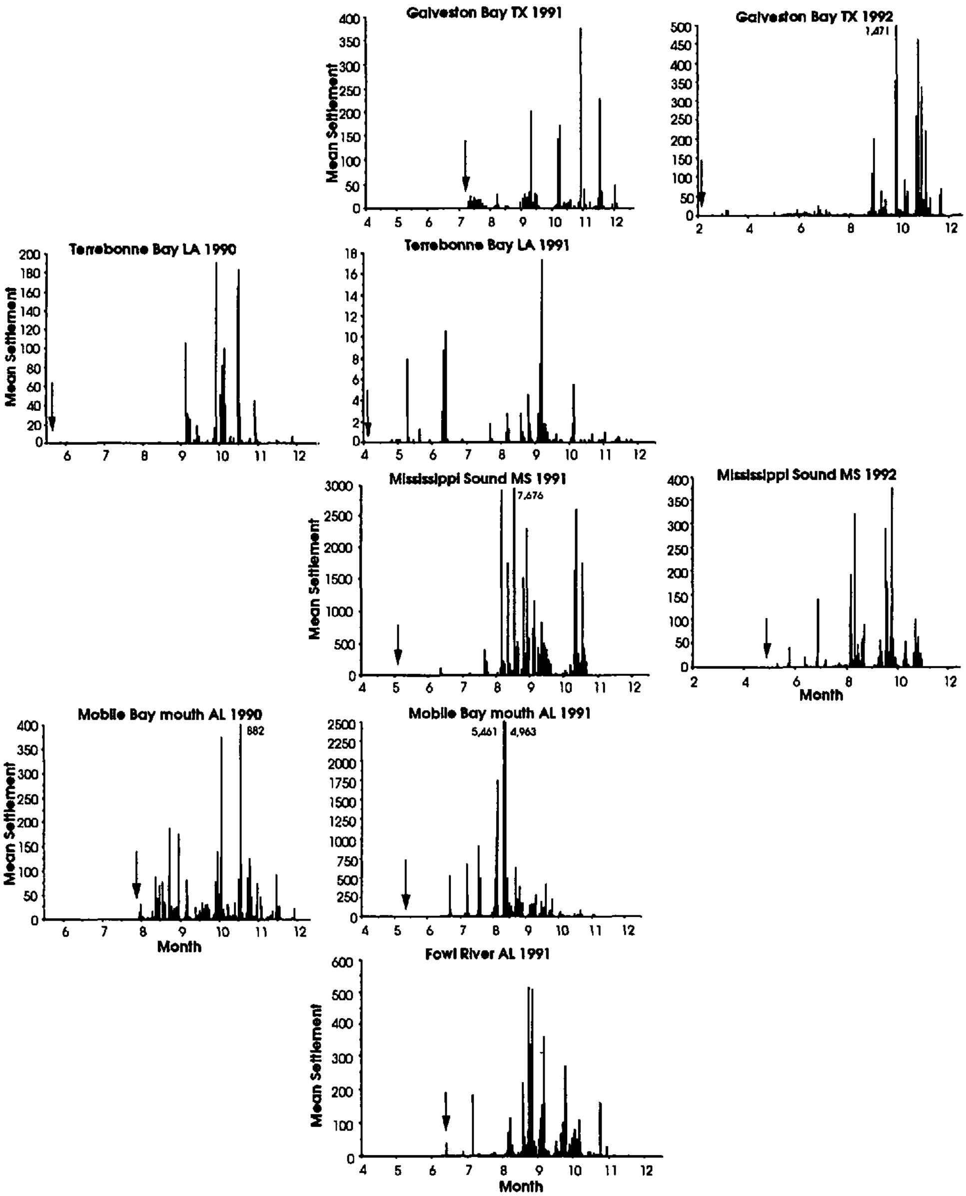

Figure 6. Mean settlement (number of megalopae·collector^{-1}·d^{-1}) of *Callinectes sapidus* megalopae for each study site and year. Collection frequency = alternating days for Galveston Bay, 5 d·wk^{-1} for Terrebonne Bay, and daily for Mississippi Sound, Mobile Bay mouth and Fowl River. Downward pointing arrow indicates first day of collection.

Galveston Bay.—Mean daily settlement was similar between 1991 and 1992 (Table 1). Peak settlement events occurred in September–December in 1991 and in August–November in 1992 (Table 1, Fig. 6). Some settlement occurred in February through June 1992 (similar dates were not sampled in 1991). More megalopae settled during lunar quarter 1 (around the new moon) in both 1991 and 1992, but the relationship was statistically significant only for 1992 (Table 2).

Table 2. Results of comparisons of daily settlement for lunar quarter within study sites by year for those days in which settlement occurred (i.e., zero values excluded). Test is a nonparametric 1-way analysis of variance (general linear model on ranks = Kruskal-Wallis k-sample test); alpha = 0.05 for significance*. Underlined lunar quarters are not significantly different from each other (Dunn's test statistic for mean rank). Mean rank and mean settlement are indicated under lunar quarter. Frequency of days with settlement within a lunar quarter is listed under mean settlement.

Site and year	Galveston Bay 1991				df = 3, N = 75 F = 1.51 *P* = 0.22	Galveston Bay 1992				df = 3, N = 124 F = 6.85 *P* = 0.0003*
Quarter	1	2	3	4		1	2	3	4	
Mean rank*	45.1	39.9	33.1	32.3		80.9	65.0	60.8	44.2	
Mean settlement†	35.1	12.0	20.5	31.6		100.8	24.4	12.6	4.1	
Frequency	28.0	25.3	24.0	22.7		26.4	24.8	20.8	28.0	
Site and year	Terrebonne Bay 1990				df = 3, N = 73 F = 1.73 *P* = 0.17	Terrebonne Bay 1991				df = 3, N = 64 F = 6.37 *P* = 0.0008*
Quarter	3	4	1	2		1	4	3	2	
Mean rank*	46.1	35.5	34.0	31.9		44.5	26.8	26.4	25.3	
Mean settlement†	27.8	4.8	24.1	13.2		3.6	0.7	2.2	0.6	
Frequency	26.8	23.9	23.9	25.4		34.4	20.3	28.1	17.2	
Site and year	Mississippi Sound 1991				df = 3, N = 142 F = 5.58 *P* = 0.0012*	Mississippi Sound 1992				df = 3, N = 122 F = 0.70 *P* = 0.56
Quarter	2	1	3	4		1	3	4	2	
Mean rank*	90.5	78.3	69.8	53.2		66.4	65.4	57.4	55.7	
Mean settlement†	568.0	249.3	183.9	111.6		38.1	32.3	26.8	23.5	
Frequency	19.6	28.0	23.7	28.7		26.9	24.3	30.1	18.7	
Site and year	Mobile Bay 1990				df = 3, N = 115 F = 1.86 *P* = 0.14	Mobile Bay 1991				df = 3, N = 148 F = 2.80 *P* = 0.042*
Quarter	1	2	3	4		2	1	3	4	
Mean rank*	65.9	63.2	54.0	47.9		88.7	80.3	70.3	61.7	
Mean settlement†	61.1	39.7	37.2	16.8		132.5	405.8	73.1	124.2	
Frequency	28.7	22.6	24.3	24.4		22.3	23.6	27.7	26.4	
Site and year	Fowl River 1991				df = 3, N = 108 F = 0.24 *P* = 0.87					
Quarter	3	1	4	2						
Mean rank*	57.1	56.0	53.0	49.9						
Mean settlement†	83.4	43.1	32.4	26.7						
Frequency	29.1	28.2	26.3	16.4						

* From Dunn's test.
† Mean of daily settlement within a lunar quarter (days with zero values excluded).

There was no statistically significant or interannually consistent relationship between daily settlement for those days with settlement and wind direction (Table 3). During 1991, most settlement occurred primarily during periods when winds were from the south and southeast, a direction which would tend to bring surface waters onshore. During 1992, most settlement occurred during periods of winds from northerly directions. Wind from the northeast (and to a lesser extent north) would be parallel to the coast. Coriolis forcing would push water toward the coast creating downwelling conditions. Winds from the northwest would blow directly offshore and probably create upwelling favorable conditions. However, northeast and north winds were associated with higher settlement of megalopae. Correlation analyses showed salinity positively related with mean daily settlement in 1992 (Table 4).

Terrebonne Bay.—Mean daily settlement was lower for this sampling site than any other (Table 1, Fig. 1). This location was furthest from the gulf (22 km) and well within a *Spartina alterniflora* marsh. Salinities were considerably lower than the other sites (<10‰ cf. 15–25‰). These habitat features, however, did not preclude megalopal settlement. Megalopae were 10 times less abundant at the collector site within Terrebonne Bay than near a major tidal pass (Port Fourchon near Belle Pass) for a limited collection period in July 1990 (N. N. Rabalais, pers. observ.). Megalopae settling at the Terrebonne Bay site were in an advanced developmental condition, and metamorphosis to first crab stage in field-collected, laboratory-reared megalopae was usually (80%) within 0.5–1 d (N. N. Rabalais, pers. observ.). Settlement patterns were very different in 1990 compared to 1991 (Fig. 6). Daily settlement was more than 10 times greater in 1990, and occurred primarily in September and October. Although numbers were reduced in 1991, there were two periods of settlement—May–June and August–October (highest in September).

More megalopae settled during lunar quarter 1 (new moon) than the other lunar quarters in 1991 ($F = 6.37$, $P = 0.0008$, Table 2). Daily settlement did not differ among lunar quarters in 1990, although highest mean daily settlement was during the full and new moon quarters (3 and 1, respectively) (Table 2). There was no statistically significant relationship between daily settlement for those days with settlement and wind direction (Table 3). However, higher settlement occurred when winds were from the south and southeast; this trend was consistent for both years. South or southeasterly winds push water into Terrebonne Bay and raise the water level in the interior marshes, perhaps delivering blue crab megalopae as well. Mean daily settlement was positively related to salinity in 1990 but not in 1991; there were no relationships with temperature (Table 4).

Mississippi Sound.—Most settlement within Mississippi Sound occurred in August–October; however, some peak settlement events occurred in June or July (Fig. 6). There was a noticeable lack of settlement in spring and early summer, even though megalopae have been collected in plankton tows in offshore waters and tidal passes at this time (H. M. Perry, pers. observ.; Stuck and Perry, 1981). Mean daily settlement was eight times greater in 1991 than 1992. Salinities were lower overall in 1991 (cf. Mobile Bay), but salinity during peak settlement was about the same for both years (Fig. 3). There were no simple relationships for peak settlement with either wind speed or direction, predicted tidal range, or lunar day (Perry et al., 1995). Daily settlement varied by lunar quarter in 1991 but not in 1992 (Table 2). Daily settlement was positively correlated with salinity in both years and with water temperature in 1992 (Table 4). Qualitative examination of hourly wind data and continuous tidal amplitude data with daily settlement in-

Table 3. Results of comparisons of daily settlement for wind direction within study sites by year for those days in which settlement occurred (i.e., zero values excluded). Test is a nonparametric 1-way analysis of variance (general linear model on ranks = Kruskal-Wallis k-sample test); alpha = 0.05 for significance*. Underlined wind directions are not significantly different from each other (Dunn's test statistic for mean rank). Mean rank and mean settlement are indicated under wind direction. Frequency of days with settlement in a wind direction is listed under mean settlement.

Site and year	Galveston Bay 1991								df = 3, N = 73 F = 1.59
Direction	W	S	SE	N	SW	NE	NW	E	P = 0.15
Mean rank*	56.0	47.3	41.0	38.1	32.9	30.5	26.9	23.1	
Mean settlement†	25.4	36.4	41.0	16.0	8.5	30.4	9.0	7.4	
Frequency	4.1	15.1	26.0	6.8	17.8	16.4	6.9	6.9	
Site and year	Galveston Bay 1992								df = 3, N = 73 F = 1.09
Direction	N	SW	SE	S	E	NE	NW	W	P = 0.37
Mean rank*	87.8	77.3	62.2	61.8	59.8	58.6	50.2	42.5	
Mean settlement†	60.4	7.2	12.9	20.0	36.8	132.5	36.9	2.3	
Frequency	8.8	2.4	25.6	36.0	8.0	11.2	6.4	1.6	
Site and year	Terrebonne Bay 1990								df = 3, N = 72 F = 1.98
Direction	S	SE	E	NW	NE	N	W	SW	P = 0.07
Mean rank*	48.9	42.6	34.1	31.3	28.7	28.6	26.8	9.0	
Mean settlement†	35.5	26.7	18.2	1.7	6.0	9.8	1.7	0.2	
Frequency	11.1	38.9	12.5	9.7	4.2	8.3	12.5	2.8	
Site and year	Terrebonne Bay 1991								df = 3, N = 63 F = 0.88
Direction	W	SE	S	NW	NE	E	N	SW	P = 0.53
Mean rank*	43.4	34.7	34.4	30.8	27.5	27.1	22.4	14.5	
Mean settlement†	2.3	1.9	2.6	0.6	0.7	0.5	0.5	0.2	
Frequency	6.4	47.6	7.9	7.9	6.4	12.7	9.5	1.6	

* From Dunn's test.
† Mean of daily settlement within a wind direction (days with zero values excluded).

Table 4. Pearson correlation coefficients for water temperature and salinity against mean settlement per day for each study site by year; alpha = 0.05 for significance*

Site and year	r Temperature	ν	r Salinity	ν
Galveston Bay 1991	0.002	77	0.056	81
Galveston Bay 1992	0.074	160	0.254*	160
Terrebonne Bay 1991	0.012	155	0.186*	155
Terrebonne Bay 1992	0.120	168	0.046	169
Mississippi Sound 1991	0.107	213	0.163*	213
Mississippi Sound 1992	0.218*	185	0.186*	185
Mobile Bay 1990	0.113	100	−0.106	86
Mobile Bay 1991	0.197*	150	0.020	105
Fowl River 1991	0.041	113	nd	

dicated that settlement occurred under a variety of conditions; however, tropic tides coupled with onshore winds were associated with the majority of high settlement events (Perry et al., 1995).

Mobile Bay.—Megalopal settlement occurred at the mouth of Mobile Bay during all months that collectors were deployed (Table 1) and most frequently in August–October 1990 and July–September 1991 (Fig. 6). Settlement was much greater in 1991 when salinities were lower than 1990. Onshore winds and tides delivered megalopae to Mobile Bay (S. G. Morgan, unpubl. data). In 1990, megalopae entered Mobile Bay after peak onshore winds, especially near minimum amplitude equatorial tides (S. G. Morgan, unpubl. data). In 1991, onshore winds were light and settlement was not correlated with onshore wind stress, but blue crab megalopae continued to recruit biweekly during minimum amplitude equatorial tides. Seven biweekly pulses of megalopae entered Mobile Bay from mid-June to mid-September (Fig. 6). Settlement was not correlated with alongshore wind stress during either 1990 or 1991 (S. G. Morgan, unpubl. data). Daily settlement for Mobile Bay was positively correlated with water temperature in 1991 (Table 4). Daily settlement also varied by lunar quarter in 1991 (highest in lunar quarter = 1), but there was considerable overlap among the quarters (Table 2).

Settlement at Fowl River was approximately 25% of that observed at Mobile Bay mouth, and most frequent in August-October (as was the case for Mobile Bay mouth, 1990) (Table 1, Fig. 6). Settlement was also correlated at 15-d intervals, which suggests that megalopae entered and were transported by tidal currents inside Mobile Bay (S. G. Morgan, unpubl. data). Megalopae settled 2- to 3-d later at Fowl River than Mobile Bay mouth (see below) and were a more advanced developmental stage than those entering the bay mouth (S. G. Morgan, unpubl. data).

Coherence in Settlement between Sites.—Coastwide comparisons were limited to two sites in 1990, five in 1991, and two in 1992. There was a 5- to 6-d lag in settlement in Mississippi Sound compared to the mouth of Mobile Bay (1991: $r = 0.52$). A plausible mechanism for this relationship is the alongshore movement of similar water masses carrying sources of postlarvae from offshore areas near Mobile Bay to offshore Mississippi. Summer currents (3 $cm \cdot s^{-1}$ from east to west) would likely transport parcels of water alongshore from offshore Mobile Bay to the passes off Mississippi Sound within 2+ days. Subsequent meteorological and tidal events might then bring the postlarvae to the collector site 13 km from the closest tidal pass. The period remaining, 3 to 4 days, however, is longer than the period for megalopae to reach Fowl River from Mobile Bay mouth (2 to 3 days over a longer, 21 km, distance). It is more likely that large numbers of postlarvae are present in shelf waters and are brought to shore by appropriate conditions, which differ between Mississippi Sound and Mobile Bay mouth (see above), even though the alongshore distance between the opening of Mobile Bay and the tidal pass to Mississippi Sound opposite the collector site is only 60 km.

Megalopae settled 4 days later at Galveston Bay than at Terrebonne Bay (1991: $r = 0.38$). No plausible mechanism is apparent for this relationship: (1) the distance between the two estuaries is 400 km, (2) currents during periods of peak megalopal settlement (July–September) flow from the south Texas coast back towards the north and east as far as Cameron, Louisiana (93°W) and as far eastward as the Isles Dernieres (90°50′W) off Terrebonne Bay (Kimsey and Temple, 1963, 1964) and the Mississippi River bight (N. N. Rabalais, pers. observ.), and (3) currents are not of sufficient magnitude (5 $cm \cdot s^{-1}$) to move a parcel of water 400 km in a 4-d period.

For sites within an estuary (Mobile Bay), cross-correlation analysis indicated that megalopae settled 2- to 3-d later at Fowl River (1990: $r = 0.25$; 1991: $r = 0.07$) than they did at the bay mouth (S. G. Morgan, unpubl. data) and were more morphologically advanced. This is consistent with pulses of megalopae delivered to the mouth of Mobile Bay being transported up the estuary.

Regional Comparisons.—With the exception of Mobile Bay, monthly means of daily settlement at any site (where overlap in months for each year were available) peaked at the same time each year, and lows also occurred in similar months (Fig. 7). Trends of peaks and lows at the various sites closely parallel long-term (1950–1979) monthly average water level records (Turner, 1991) (Fig. 7). Monthly means of daily settlement plotted by salinity for each site by year for months with peak settlement events showed trends of higher settlement at intermediate salinities, and lower settlement at reduced and elevated salinities. It was notable that Mobile Bay and Mississippi Sound each had higher megalopal settlement during the low salinity year (1991). An example of these comparative data for months of regionwide peak settlement is shown in Fig. 8. The individual sites showed similar curves for peak numbers during optimal salinity ranges. The comparisons among estuaries are remarkably robust ($y = -0.47 - 0.59x + 0.12x^2 - 0.006x^3 + 0.001x^4$, $F = 26.20$, $P = 0.0001$). The broad regional trends are consistent with (1) physiological constraints of larval stages, i.e., maximal growth rates and survival of zoeae within an optimal salinity and temperature range (Costlow and Bookhout, 1959), and (2) predictions of longer-term fisheries yield based on climatic conditions (=salinity and temperature of recruitment habitat) at the stage of recruitment (megalopa and early crab) (West, 1980). The relationships with optimal salinity ranges and long-term water level indicate that abiotic controls are very influential at this life stage, that many recruits are likely available, and that broader regional controls (climate and lunar periodicity) influence successful recruitment to the estuaries. To test the strength of these relationships would require additional years of settlement data.

Comparison with Atlantic Coast.—Blue crab megalopal mean settlement was much higher in northern Gulf of Mexico estuaries than in U.S. Atlantic coast estuaries (Fig. 9). Abundance over a fairly uniform length of deployment (125–150 d) during the time of the year when 50+% of the megalopae were collected (June or July through October or November) was also much greater for Gulf of Mexico sites than Atlantic coast sites. [Abundance for the Galveston Bay study site would likely be much higher than included in Fig. 9, since collections were made on alternating days; i.e., a 75-d sum compared to other Gulf estuaries with

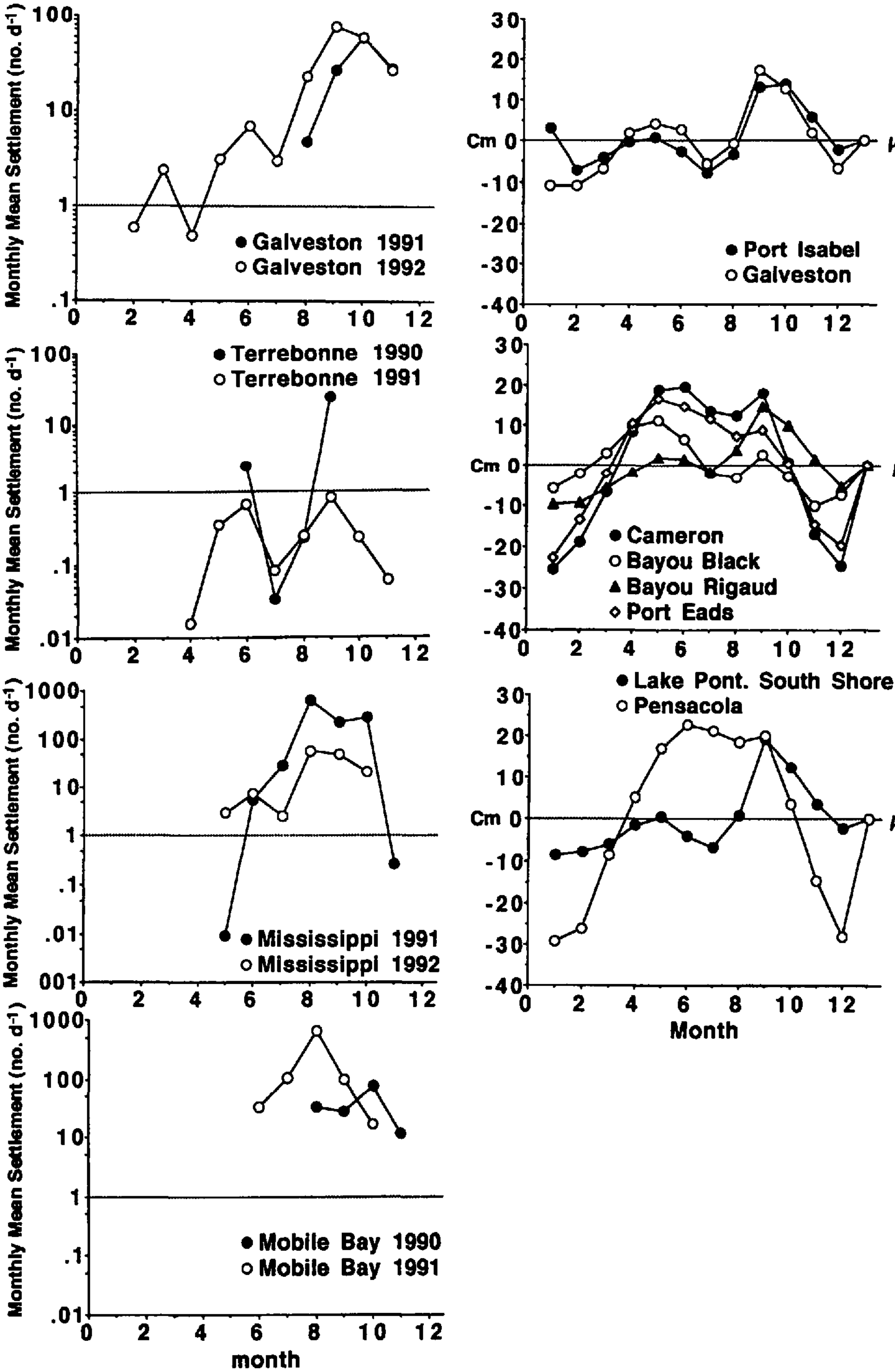

Figure 7. Left panels: monthly mean settlement for sites and years as indicated. Right panels: monthly average water levels from 1950–1979 at various Gulf of Mexico locations; (upper) lower and upper Texas coast; (middle) four locations in coastal Louisiana west of the Mississippi River delta; (lower) south shore of Lake Pontchartrain, Louisiana and Pensacola, Florida, to the west and east of Mississippi Sound and Mobile Bay, respectively. (Water level data adapted from Turner, 1991.)

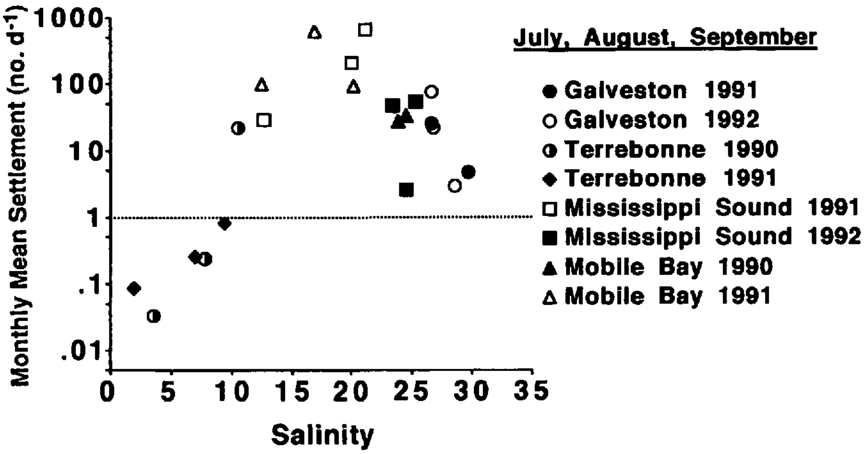

Figure 8. Comparison of mean settlement (number of megalopae·collector^{-1}·d^{-1}) for months of July, August and September for study sites and years indicated, plotted against mean salinity for the comparable month.

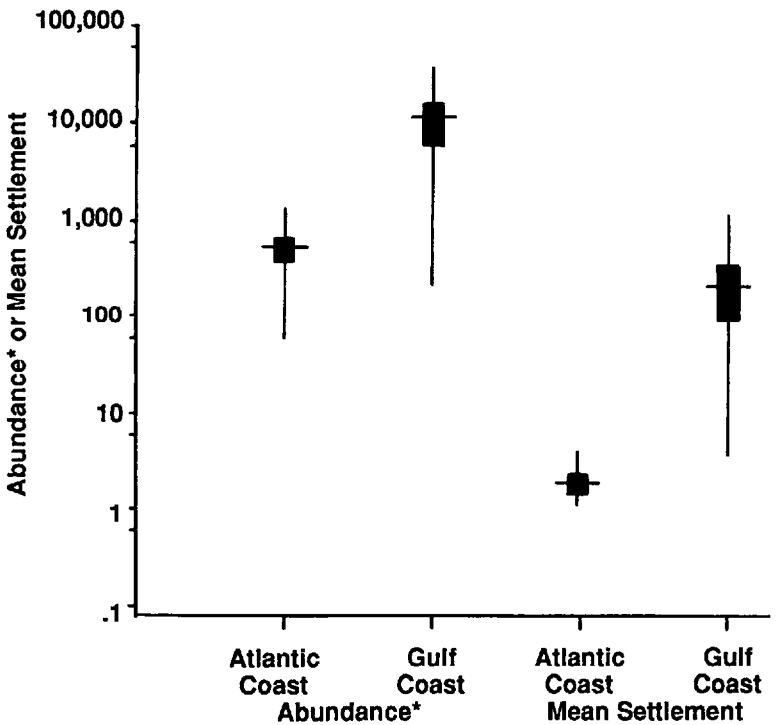

Figure 9. Comparative values (mean, standard error and range) for abundance* and mean settlement of blue crab megalopae from Atlantic coast and Gulf coast estuaries. Abundance* is the total number of megalopae collected in a 125–150 d period when 50+% of the settlement occurred, usually Jun or Jul through Oct or Nov. Mean settlement for all areas is the number of megalopae collected for the period of abundance* divided by the number of days of collections. Only those study areas (Atlantic, N = 7, or Gulf coast, N = 8) which met the >50% of total settlement within a 125–150 d period were included in the calculations. Atlantic coast data from van Montfrans et al. (1995).

data for 125 to 150 d.] Although the ranges of mean settlement and abundance overlapped for the two coasts, the values were up to two orders of magnitude greater for gulf sites than those of the Atlantic coast.

There was limited evidence of megalopal settlement for some gulf estuaries in spring and early summer related to the protracted breeding season of blue crabs in the gulf compared to the Atlantic coast. A similar period (March–June), however, was not sampled in the Atlantic coast estuaries (van Montfrans et al., 1995). In both gulf coast (data in this paper) and Atlantic coast estuaries (van Montfrans et al., 1995), megalopal settlement was mostly in episodic pulses, and settlement was highly variable within and between sites during most years. The most consistent interannual (2-yr) relationship observed for the gulf coast sites was the biweekly settlement at Mobile Bay mouth coincident with minimum amplitude equatorial tides and onshore winds (when present). Higher mean settlement related to lunar quarter was demonstrated for some gulf coast and Atlantic coast sites, but the trends were not consistent across all sites or years. Lack of comparable treatments of physical data (e.g., salinity, tidal amplitude, and wind speed and direction) across all study sites precludes identification of any of these environmental factors as being similar in effects. Occasional coherence in peaks between sites on the Atlantic coast suggested that regional processes affected settlement during a given year. Limited coherence between sites on the gulf coast was not supported by plausible mechanisms for transport, with the exception of a 2- to 3-d lag from the mouth of Mobile Bay to a mid-estuary site. Well over 50% of the megalopal settlement within a year at any gulf coast or Atlantic coast site occurred during 3–4 day episodic pulses within a 2- or 3-mo period.

Discussion

Megalopal settlement sites in this study represented a variety of habitats found within Gulf of Mexico estuarine systems: major tidal passes and more interior estuaries, those to the east and west of the Mississippi River delta, and those having semidiurnal and mixed and diurnal tides. Patterns of settlement varied across the region and showed no clear coherence among sites, with the exception of a 2- to 3-d lag from Mobile Bay mouth to the mid-estuary point at Fowl River. The lack of coherence among sites is not unexpected given the great differences in physiography, salinity regimes, distance from the open Gulf of Mexico, tidal periodicity, long-term water level cycles, wind regimes, and coastal currents among the study areas, as well as the great distances between study sites (across 700 km with the Mississippi River delta projecting into the middle of the study area). Coherence in settlement among Atlantic coast sites was limited to a single year and related to large-scale climatic and hydrodynamic conditions (van Montfrans et al., 1995). On the other hand, the lack of coherence between two close sites (60 km), Mississippi Sound and Mobile Bay, is less easily explained.

Blue crab megalopal settlement was generally episodic among gulf sites, with the exception of biweekly events at Mobile Bay mouth, which coincided with minimum amplitude equatorial tides. Megalopal settlement was higher at Mobile Bay mouth during 1990 after peak onshore winds. Similarly, the majority of high settlement events for Mississippi Sound were associated with onshore winds, but coupled instead with maximum amplitude tropic tides. The combination of higher water level and onshore winds would serve to bring megalopae into the study area with increased water movement into the estuary. Similar relationships have been observed for Chesapeake Bay (Johnson, 1985; Johnson et al., 1984; Goodrich et al., 1989; Olmi, 1995). A process for minimum amplitude equatorial tides is less evident. During 1991, most settlement events at Galveston Bay occurred primarily when winds were from the southeast, a direction which would tend to bring surface waters onshore; this is consistent with observations in Chesapeake Bay, Mississippi Sound and Mobile Bay mouth. The opposite occurred during 1992 at the Galveston Bay site but with a potentially similar effect, when most settlement was during periods of winds from variable northerly directions, which, due to Coriolis forcing, would tend to push water toward the coast and create downwelling favorable conditions. The importance of up-estuary winds was apparent at the Terrebonne Bay site, which was 22 km from the open Gulf of Mexico and well within a salt marsh. Higher mean settlement occurred when winds were from the south and southeast during both years; winds from this direction would push water into Terrebonne Bay and raise the water level in the interior marshes. Wind-induced water volume increases are a likely process for up-estuary transport of megalopae in a well-mixed, microtidal system, as opposed to the tidally-related vertical migration behavior exhibited by megalopae in Chesapeake Bay (Olmi, 1994, 1995).

Lunar periodicity was observed for several Atlantic coast sites. Boylan and Wenner (1993) found greater settlement during waning and waxing quarters, than during new or full moon quarters. van Montfrans et al. (1990), on the other hand, found greatest settlement in the York River during the full moon phase. Lunar periodicity was not evident regionwide for the Gulf of Mexico, nor was it consistent between years when observed within an estuary. This is not unexpected given the types of tides in the Gulf of Mexico (diurnal and mixed), and they are controlled more by the declination of the moon than the synodic cycle.

Within site variability was great from year-to-year in mean settlement and total numbers for most sites, but periods of peak and low settlement were usually similar. The most obvious overall, region-wide patterns were related to salinity—across sites and across years—during the months of peak settlement and to long-term water levels.

Most megalopae were collected during August–October, even though late stage larvae and/or megalopae are available all year (Stuck and Perry, 1981; Truesdale and Andryszak, 1983). Perry and Stuck (1982) found no relationship between megalopal numbers in spring nekton samples and subsequent early crab stages in Mississippi Sound, but did find that high abundances of megalopae in fall nekton samples were usually followed by increased catches of small crabs in October and November. For those estuaries sampled during the first half of the year (Galveston Bay and Terrebonne Bay), megalopae settled in May and June, but infrequently. These findings suggest that hydrographic conditions and/or circulation patterns in the spring either remove larvae from the study areas, inhibit movement of late larvae or megalopae into the estuaries, or prevent successful recruitment (i.e., suboptimal salinity and temperature ranges).

Numbers of settling blue crab megalopae declined with distance from the Gulf of Mexico (as was the case where multiple sites were sampled within an estuary along the Atlantic coast, van Montfrans et al., 1995). This trend was most obvious where five sites were sampled in Mobile Bay (S. G. Morgan, unpubl. data), but also within Terrebonne Bay (N. N. Rabalais, pers. observ.). Still, megalopae were recruiting well up into both Terrebonne Bay and Mobile Bay in fairly high numbers. Megalopae settling at Fowl River and the Terrebonne Bay site were in an advanced developmental condition.

The utility of artificial substrate collectors for defining conditions of megalopal settlement was demonstrated in this inter-regional study. Large numbers of blue crab megalopae recruit to gulf estuaries. Although settlement events were episodic, trends controlled primarily by abiotic factors (tidal amplitude, winds, water level, climate expressed as salinity and temperature) were evident within estuary and on an inter-regional basis. Eventual recruitment success as the megalopae metamorphose and occupy suitable nursery areas as juvenile crabs are likely controlled by biotic factors, such as drastic reductions in numbers due to predation (Heck and Coen, 1995).

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