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## SETTLEMENT OF BLUE CRAB POSTLARVAE IN WESTERN NORTH ATLANTIC ESTUARIES

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### ABSTRACT

We quantified variability in daily settlement of blue crab postlarvae (megalopae) on identical artificial settlement substrates at up to 6 sites concurrently over a broad geographic expanse (~1300 km) of the western North Atlantic (Delaware–South Carolina, USA). The 4-year study encompassed the blue crab recruitment season (generally July–November) from 1989–1992. Regional settlement was characterized by: (1) constant low levels of daily settlement punctuated by significantly non-random, episodic peaks of variable duration and intensity with peaks collectively accounting for at least half the total annual settlement at a site; (2) spatial and temporal variability leading to a general lack of coherence between sites in a given year and across years within a site; (3) occasional coherence in patterns between sites during a given year, suggesting linkages in regional processes affecting settlement; and, (4) significant semilunar patterns of episodic settlement pulses at the York River and Charleston Harbor sites over a 4-year period. Thus, regional settlement patterns exhibit both consistent (i.e., semilunar periodicity, episodic pulses) and variable (i.e., temporal and spatial variation) elements, which are likely due to a combination of stochastic and deterministic processes. Such patterns may impart an ecological advantage to crabs settling en masse (i.e., reduced encounter rate with predators through predator swamping) or at continuous low levels (i.e., below a density-dependent threshold) during the recruitment season. An identical study illustrated that settlement in Gulf of Mexico estuaries exhibited similarly episodic and highly variable patterns. Daily mean and total annual settlement were up to a hundred-fold greater for gulf than Atlantic Coast estuaries implying population limitation by post-settlement processes in the gulf and greater recruitment limitation in the Atlantic. These studies emphasize the merit of conducting research over a broad geographic range using standardized techniques to attempt meaningful ecological comparisons.

Recruitment success of marine species with pelagic larvae can be highly variable over space and time and cause extreme fluctuations in population abundance (Butman, 1987; Cameron, 1986; Doherty and Fowler, 1994; Gaines and Roughgarden, 1987; Hjort, 1914; Richards and Lindeman, 1987). Here, recruitment is defined as the addition of individuals to the population through settlement of postlarvae or first-instar juveniles (*sensu* Fritz et al., 1990). Fluctuations in recruitment are often characteristic of fishery species and can have important ecological and socio-economic consequences. Many commercially exploited species on the Atlantic and Gulf of Mexico coasts of the United States are dependent on estuaries during some portion of their life cycle (Boesch and Turner, 1984). Since estuaries are inextricably linked to the coastal ocean, the factors influencing this linkage can be important for understanding the causes of population fluctuations in these species.

Species that utilize estuarine and coastal waters during their life cycle commonly include a phase that involves transport of a weakly-swimming early developmental stage (i.e., larva, postlarva or young juvenile) from coastal to estuarine waters. These include estuarine and nearshore spawners such as the blue crab (*Callinectes sapidus*) and white shrimp (*Penaeus setiferus*), and species that

spawn in deeper waters of the shelf such as menhaden (*Brevoortia* spp.), Atlantic croaker (*Micropogonias undulatus*), and brown shrimp (*Penaeus aztecus*). Understanding the influence of oceanographic features on larval supply to estuarine waters in such species and thus, their impact upon recruitment variability, remains an important goal for ecologists, fisheries scientists and resource managers alike (Goodrich et al., 1989).

The various processes affecting recruitment of estuarine-dependent species with an oceanic dispersal phase include: (1) advection and mixing of eggs and larvae on the continental shelf; (2) retention of larvae and postlarvae in proximity to estuaries, (3) reinvasion of estuaries by postlarvae with subsequent migration of juveniles and adults; and (4) synchronous settlement of postlarvae in response to various environmental cues. Oceanographic features (e.g., wind forcing or semi-diurnal tides) and environmental cues (e.g., lunar stage) may affect broad areas of the coastline and therefore promote temporal coherence in settlement across geographic scales (e.g., between estuaries). In contrast, spawning seasons punctuated by downwelling-favorable winds at local scales can produce discrete events that transport large volumes of shelf water and entrained postlarvae shoreward and into estuaries (Goodrich et al., 1989; Blanton et al., 1995; Olmi, 1995). In addition, wind-driven transport processes can interact with vertical migration patterns of larvae to influence their broad distribution and fate. Moreover, local hydrodynamics (e.g., semi-diurnal tidal excursion) in combination with behavior of recruiting postlarvae may also influence settlement patterns at smaller spatial scales (Olmi, 1995).

One wide-ranging fishery species suited to a comparative study of recruitment processes is the blue crab, *Callinectes sapidus*. Despite oceanographic discontinuities at biogeographic boundaries, varying climatic regimes, and a diversity of estuarine habitats, this species is distributed across a wide geographic range from Maine in the northwestern Atlantic throughout the Gulf of Mexico and Caribbean to northern Argentina (Williams, 1984). Ovigerous females along the western North Atlantic release up to 8 million larvae (zoeae) per individual near the mouths of estuaries (Prager et al., 1990). The larvae are subsequently transported to offshore coastal waters for development lasting at least 30 days through seven or eight larval stages (Costlow and Bookhout, 1959; Provenzano et al., 1983; McConaugha, 1988; McConaugha et al., 1983). Subsequently, metamorphosis occurs to the postlarva (megalopa) stage which reinvades estuarine or lagoonal nursery habitats (Costlow, 1967; Epifanio et al., 1989; Mense and Wenner, 1989; van Montfrans et al., 1990; McConaugha, 1992). Minimal development time from postlarva to first juvenile instar under laboratory conditions is 15 d (Sulkin and Van Heukelem, 1986). In Chesapeake Bay, postlarvae settle principally in seagrass (*Zostera marina* and *Ruppia maritima*) beds prior to metamorphosis into the first juvenile instar (Orth and van Montfrans, 1987, 1990), though these processes must vary in areas devoid of vegetation. Since reinvading postlarvae represent survivors of a massive larval output (sensu Fritz et al., 1990), it is at the postlarval stage that understanding the importance of recruitment processes (Olmi et al., 1990) seems most feasible.

Blue crab populations along western North Atlantic estuaries are potentially linked via larval dispersal in the coastal ocean (Campbell and Thomas, 1981; Wiseman et al., 1988; Kjerfve et al., 1981). Development of sibling zoeae to the juvenile instar, even when cultured under similar conditions, is highly variable, taking as little as 45 d and as much as 120 d (Sulkin and Van Heukelem, 1986). Such genetic variability in development timing allows for wide-spread dispersal along the coast during the oceanic phase. The potential therefore exists that large-

scale physical oceanographic processes may, in part, govern larval transport and ultimately promote similar settlement patterns within juxtaposed estuaries.

By examining the magnitude of daily and annual settlement at various spatial scales, it is possible to infer potential relationships between sites regarding effects of stochastic (e.g., wind events) or deterministic processes (e.g., semilunar periodicity in settlement) on recruitment. Settlement patterns of various crustaceans have been quantified on artificial settlement substrates revealing temporal features of settlement (Beninger et al., 1986; van Montfrans et al., 1990; Boylan and Wenner, 1993), and year-class strength of commercial species (Witham et al., 1968; Phillips, 1972, 1986; Little and Milano, 1980; Lipcius and Cobb, 1994) with predictive capabilities of commercial harvest up to 5 years in advance for some crustaceans (Morgan et al., 1982; Phillips, 1986, 1990; Phillips et al., 1994).

Our goal was to quantify daily settlement of blue crab postlarvae along the western North Atlantic coast, examine relationships in settlement within and among sites, and infer potential influences on observed patterns. Specifically, we used standardized field methods in a coordinated investigation to quantify spatial scales of variability in postlarval settlement along western North Atlantic estuaries, with an emphasis upon understanding the relative importance of periodic (daily, tidal or lunar) and stochastic (wind) phenomena. Finally, we contrast our findings to those from an identical study conducted concurrently in the Gulf of Mexico.

#### MATERIALS AND METHODS

*Study Sites.*—Two major regions were defined along the Atlantic coast (Fig. 1). Northern region (MAB)<sup>1</sup> is bounded to the north by Cape Cod and to the south by Cape Hatteras. Immediately to the south, the Southern region (SAB)<sup>1</sup> extends southward to the Florida straits. Each of these areas is bordered eastward by the inner Gulf Stream edge and westward by barrier islands and estuaries of various sizes serving as nursery habitats for juveniles of estuarine-dependent crustaceans and finfish. The Gulf Stream, associated alongshore density-driven flow, and wind-generated surface currents are the major sources of flow potentially affecting large-scale larval and postlarval transport.

General circulation patterns within each of these regions is relatively well known (MAB: Harrison et al., 1967; Bumpus, 1973; Beardsley et al., 1976; Boicourt, 1982; Boicourt et al., 1987; SAB: Atkinson et al., 1983; Schwing et al., 1983). A wide range of physical conditions exists between Delaware Bay and South Carolina, including semi-diurnal tides varying greatly throughout the region. Tidal amplitudes range from about 0.5 m off Cape Hatteras, North Carolina to over 2 m off South Carolina (Redfield, 1958). This imposes variable vertical mixing regimes which, for a given water depth, influence the strength of cross-shelf circulation and potentially, larval transport.

Settlement was examined at six sites along the western Atlantic (Fig. 1). The northernmost site was located at the mouth of the Broadkill River on the southern shore of Delaware Bay within 8 km of the mouth [depth: 2 m at mean low water (mlw)] and was sampled from 1989–1992 (Little and Epifanio, 1991, for detailed site description). Two sites were located within Chesapeake Bay. The Tangier Sound site (depth: 4 m mlw), located 90 km north of the bay entrance, was sampled from 1989–1991. Samples were collected on the southern island of Tangier from a pier that extended into the channel separating the northern and southern islands. A second Chesapeake Bay site was sampled from 1989–1992 at the Virginia Institute of Marine Science (depth: 2.5 m mlw), which is located along the western shore of Chesapeake Bay near the York River mouth approximately 50 km from the mouth of the bay (see van Montfrans et al., 1990, for details). A fourth site was located along the western shore of Pamlico Sound at Middle Bay, NC, where water depths averaged 2.5 m (Mense et al., 1995). This site, sampled only in 1991, was approximately 7 km south of the Pamlico River mouth and 60 km west of Hatteras Inlet. Another North Carolina site, sampled from 1990–1992, was located 2 km north of Masonboro Inlet at the LaQue Research Center pier in Banks Channel, Wilmington, with a water depth of approximately 2 m at mlw (Mense et al., 1995). Samples from Charleston Harbor, SC, were collected during 1989–1992 from a pier located 12 km inside the harbor entrance

<sup>1</sup> Many authors erroneously name these regions Mid-Atlantic and South Atlantic Bights. We have retained the abbreviation but have deleted the names—Editor.

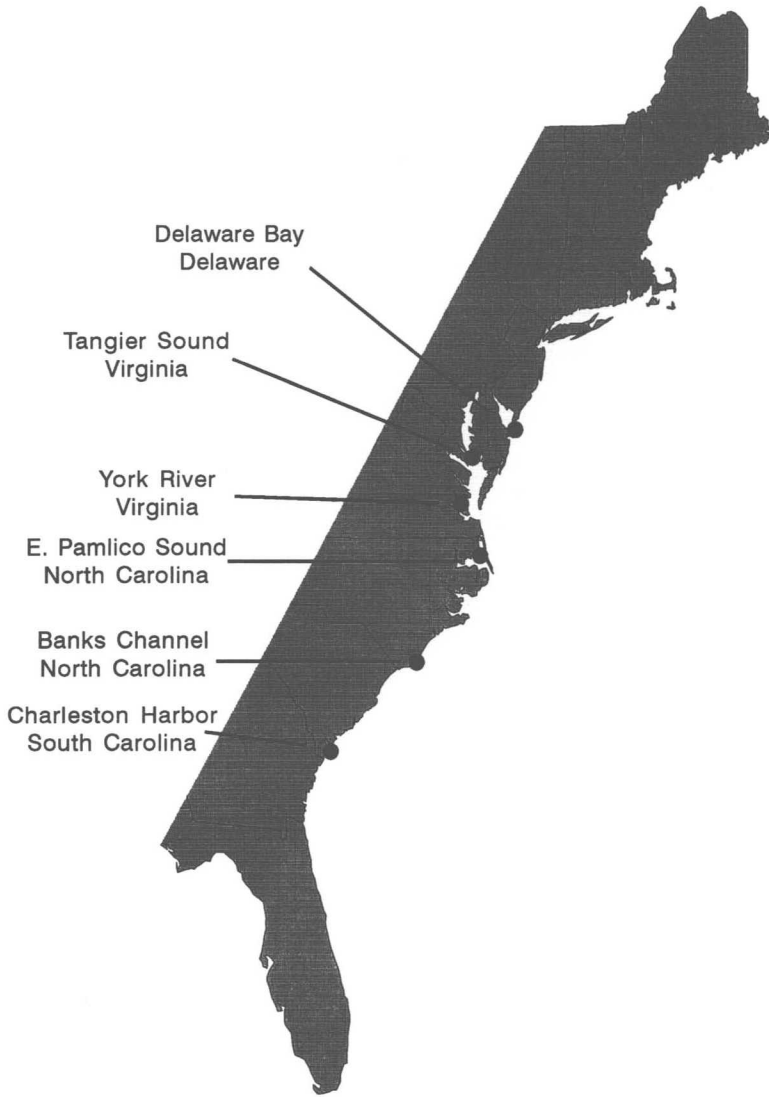


Figure 1. Locations of study sites along the Atlantic Coast of the United States.

at a water depth of approximately 3.3 m at mlw (Boylan and Wenner, 1993). Locations varied with distance from the coastal ocean and in environmental characteristics (Table 1).

A similar study was concurrently undertaken in the Gulf of Mexico (Rabalais et al., 1995). This study served as a basis for inter-regional comparisons in settlement between western North Atlantic and Gulf of Mexico estuaries.

**Sampling Methodology.**—Standardized cylindrical artificial settlement substrates (Fig. 2) were deployed daily. Substrates were constructed from “Hog’s Hair” air-conditioner filter material formed into a cylindrical sleeve. The sleeve (surface area = 0.26 m<sup>2</sup>) was fitted over a cylinder of PVC pipe (16.3 cm diameter × 37.5 cm length) and secured with rubber straps. Each substrate was equipped with internal flotation and weighted at the bottom, thereby assuring flotation at the water surface with a vertical orientation in ambient tidal flow. Substrates were deployed from a pier at each site and sampled between 0700 and 0900 h daily by lifting the entire substrate into a 19-liter bucket. Sleeves were then removed and replaced with rinsed, sun-dried sleeves before redeployment of the substrates.

Table 1. Descriptive data for each site, by year (depths, distances from the source of postlarvae, mean and range of water temperatures, mean and range of salinities and dates sampled are shown; missing data are indicated by a dash)

	1989	1990	1991	1992
Delaware Bay	—	20.22°C (10–26°C)	21.46°C (10–28°C)	—
2 m mlw	—	26.55‰ (12–32‰)	24.31‰ (8–31‰)	—
8 km from mouth	8/24–11/01	8/20–11/02	7/01–11/06	—
Tangier Sound	19.34°C (6–29°C)	21.35°C (6–29°C)	21.15°C (6–30°C)	6/01–10/31
4 m mlw	14.73‰ (12–17‰)	16.1‰ (14–18‰)	18.79‰ (15–20‰)	
90 km from mouth	8/14–11/22	7/06–11/21	7/11–11/27	
York River	22.01°C (12–28°C)	22.96°C (10–28°C)	22.20°C (11–29°C)	21.29°C (10–27°C)
1.5 m mlw	16.88‰ (12–19‰)	19.45‰ (18–21‰)	21.38‰ (18–28‰)	19.41‰ (17–21‰)
50 km from mouth	7/24–11/22	7/06–11/21	7/08–11/26	7/13–11/20
Pamlico Sound			27.75°C (26–29°C)	
2.5 m mlw			32.93‰ (29–37‰)	
60 km from mouth			7/01–9/14	
Banks Channel			25.18°C (13–30°C)	25.51°C (17–30°C)
2 m mlw			36.08‰ (32–37‰)	32.99‰ (28–36‰)
2 km from mouth			7/08–11/02	7/07–10/31
Charleston Harbor	23.14°C (13–30°C)	24.30°C (14–30°C)	22.42°C (9–30°C)	23.48°C (12–30°C)
3.3 m mlw	20.39‰ (9–27‰)	22.31‰ (15–30‰)	21.85‰ (12–30‰)	21.28‰ (13–30‰)
12 km from mouth	8/01–11/30	7/17–12/03	7/17–12/20	7/29–11/30

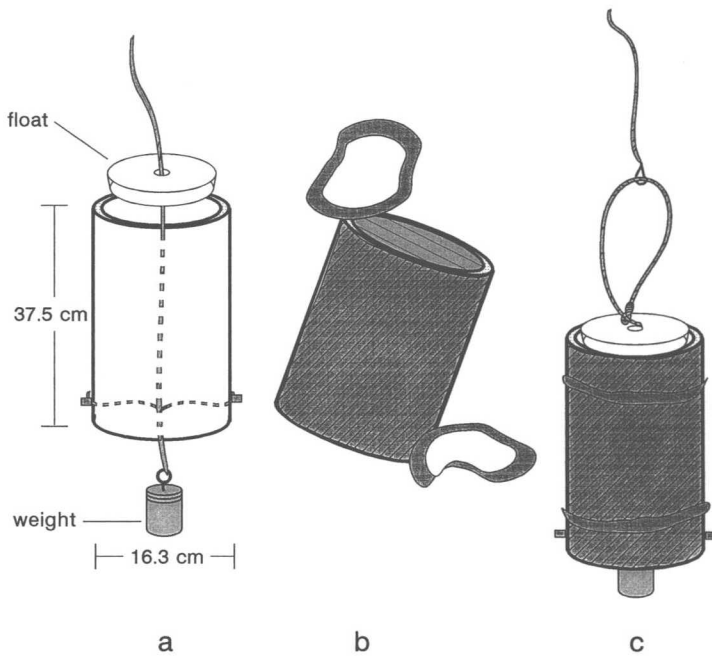


Figure 2. Construction details of the standardized artificial substrates used to quantify settlement of blue crab postlarvae throughout the region. A PVC cylinder served as a framework over which was placed a sleeve made of "Hogs Hair" air conditioning filter material fastened with rubber straps. The completed substrate floated at the water surface while maintaining a vertical orientation in the water column.

Samples were processed by rinsing sleeves in freshwater and sieving the rinse water (van Montfrans et al., 1990). Water temperature and salinity were also recorded daily at the time of substrate sampling. A minimum of four substrates are necessary to stabilize the variance in settlement magnitude and accurately assess settlement patterns in Chesapeake Bay (Metcalf et al., 1995). Therefore, four replicates were used at all sites (with the exception of Banks Channel in 1991, when three replicate substrates were sampled). Daily settlement of blue crab postlarvae was examined over the recruitment season (generally, July–November; Table 1).

*Statistical Analyses.*—We quantified settlement at each location as a function of lunar day, month and year. Data were log-transformed when necessary to meet assumptions of normality and homogeneity of variance. A Poisson test of observed versus expected daily settlement frequencies at each site determined whether settlement patterns were random for each year. Data for these analyses were grouped to maximize the number of possible time periods, while fulfilling the requirement that no expected frequency had a value of less than one and not more than 20% of the expected frequencies had values less than five (Zar, 1984).

Data for each site were standardized by lunar month (i.e., by the same time periods corresponding to successive lunar months throughout the recruitment season). General linear models were used in an orthogonal analysis to examine the effects of year and lunar quarter (1 = the week of the new moon beginning on the day of the new moon; 2 = the week of the waxing moon; 3 = the week of

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Figure 3a–e. Settlement records for the (a) Delaware Bay (1989–1992), (b) Tangier Sound (1989–1991), (c) York River (1989–1992), (d) Pamlico Sound (1991) and Banks Channel (1990–1991) and (e) Charleston Harbor (1989–1992) sites. Large, open circles indicate full moon and small circles new moon. The horizontal dashed line above the x-axis marks settlement levels equivalent to twice the annual mean. Periods of missing data are indicated for respective sites (e.g., Delaware Bay, 1990; Tangier Sound, 1989–1991; Banks Channel, 1991 and 1992; etc.) as a dashed line below the x-axis. Note that the y-axis scale and sample initiation and ending dates vary.

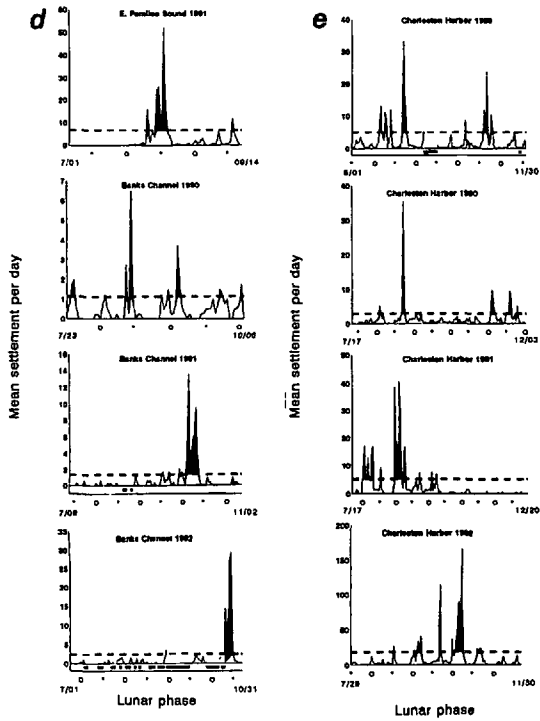
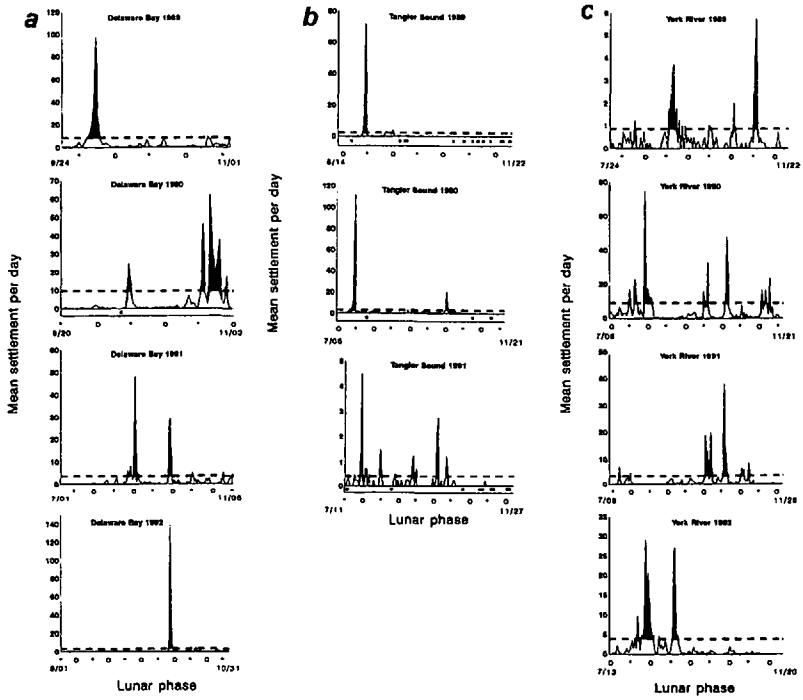




Table 2. Results of Poisson test for randomness (significant *P* values indicate non-random rather than random settlement)

	1989	1990	1991	1992
Delaware Bay	$\chi^2 = 95.389$ df = 3 $P < 0.001$	$\chi^2 = 95.389$ df = 4 $P < 0.001$	$\chi^2 = 17.731$ df = 2 $P < 0.001$	$\chi^2 = 413.910$ df = 5 $P < 0.001$
Tangier Sound	$\chi^2 = 15.759$ df = 2 $P < 0.001$	$\chi^2 = 27.174$ df = 2 $P < 0.001$	$\chi^2 = 0.044$ df = 1 $P < 0.90$	
York River	$\chi^2 = 0.666$ df = 1 $P < 0.5$	$\chi^2 = 65.348$ df = 4 $P < 0.001$	$\chi^2 = 22.11$ df = 2 $P < 0.001$	$\chi^2 = 14.303$ df = 2 $P < 0.001$
Pamlico Sound			$\chi^2 = 90.200$ df = 4 $P < 0.001$	
Banks Channel		$\chi^2 = 36.602$ df = 3 $P < 0.001$	$\chi^2 = 49.493$ df = 3 $P < 0.001$	
Charleston Harbor	$\chi^2 = 11.071$ df = 2 $P < 0.005$	$\chi^2 = 4.73$ df = 2 $P < 0.1$	$\chi^2 = 47.599$ df = 2 $P < 0.001$	$\chi^2 = 184.310$ df = 6 $P < 0.001$

full moon starting on the day of the full moon; and 4 = the week of the waning moon) on settlement magnitude ( $\log(N + 1)$ ) at each site (Sokal and Rohlf, 1981). Data records were truncated based on the shortest settlement record (usually Delaware Bay), to assure comparisons over the same days and comparable lunar periods across sites. Annual mean settlement for each site sampled 3 or more years was examined through cross-correlations to test for interannual consistency in settlement magnitude within each site. Cross-correlation analyses between sites within a year tested for synchrony of settlement patterns at geographic locations.

Lunar patterns in settlement for sites sampled over multiple years (i.e., Delaware Bay, Tangier Sound, York River, Banks Channel and Charleston Harbor) were analyzed collectively after standardizing the data across the same 3 consecutive lunar months and collapsing over all years sampled. That is, the data were: (1) restricted to three comparable lunar cycles of approximately 28 days each, over a 3-month period (generally, August to October); (2) standardized for annual variation in magnitude by dividing average daily values by the daily mean for the entire year; and, (3) collapsed over all years sampled. Subsequently, a standardized grand mean of daily settlement was calculated for the 3-month lunar period and analyzed by autocorrelations (0-day lag) to discern lunar patterns.

Settlement between Gulf of Mexico and western North Atlantic regions was compared with ANOVA models using daily mean and annual total settlement standardized across estuaries within each region.

## RESULTS

A key feature of postlarval settlement patterns across the entire western North Atlantic region was the characteristically constant low levels of daily settlement punctuated by significantly non-random, episodic peaks (considered here as those exceeding twice the annual mean value) of variable duration and intensity. The episodic peaks accounted for at least half the total annual settlement at each site (Figs. 3a–e). Settlement occurred almost daily throughout the recruitment season and was significantly episodic and non-random for 15 of the 18 year and site combinations (Table 2). Peaks were of variable duration lasting from 1 to 5 days with highest magnitude occurring typically over only a single day (Fig. 3).

Another consistent pattern throughout the region was the high degree of spatial and temporal variability in settlement leading to a general lack of coherence within a site across years, and between sites in a given year. Cross-correlation analysis of settlement between years within a site (Table 3) indicated that patterns during most years were dissimilar. Seven of 19 site/year combinations showed non-significant relationships, six were strongly negatively associated, implying no mean-

Table 3. Results of cross-correlation analyses between years within a site. Significant lags are indicated for each time series (Charleston 1989 and Banks Channel 1992 are not represented because of a break exceeding 8 successive days in the time series). There were no significant negative cross-correlations.

	1990	1991	1992
1989 Delaware Bay	n.s.	+6 d	+4 d
Tangier Sound	n.s.	-1, +19 d	.
York River	-14 d	+/-15 d	-2 d
1990 Delaware Bay		-17 d	n.s.
Tangier Sound		n.s.	.
York River		-2, -17 d	0 d
Banks Channel		n.s.	.
Charleston Harbor		-18 d	n.s.
1991 Delaware Bay			-2 d
Tangier Sound			.
York River			-13 d
Charleston Harbor			n.s.

ingful biological associations, and only four exhibited apparent biologically meaningful similarities as indicated by small (i.e., 0 to  $\pm 2$  day lags) time lags. These similarities occurred in Delaware Bay between the 1991 and 1992 recruitment seasons; at Tangier Sound between 1989 and 1991; in the York River site between 1989 and 1992, and between 1990 and 1991; and showed no similarity between years at Charleston Harbor (Table 3). Thus, settlement was temporally variable at a location across years with occasionally similar settlement patterns between years.

Mean annual settlement across sites for which sampling spanned at least 3 years was significantly (though negatively) correlated for only one of six site by site combinations, namely, between Delaware Bay and the York River (Table 4). Cross-correlation analyses of settlement between each site and within years revealed significant lags ranging from 0 to  $\pm 19$  days for various time series (Table 5). Coherence in settlement as indicated by short (0–2 day) time lags occurred in only six of 31 year-by-site-combinations including: in 1989 between Delaware and the York River (2-day lag); and in 1991 between Delaware Bay and Charleston Harbor (2-day lag), Tangier Sound and the York River (0-day lag), Tangier Sound and Banks Channel (1-day lag), Delaware Bay and Charleston Harbor (2-day lag), and the York River and Banks Channel (0-day lag). In 1992, coherence occurred only between Delaware Bay and the York River (2 day lag). Settlement timing at other sites was not significantly cross-correlated, indicating a lack of coupling in settlement between sites (Table 5). Therefore, settlement was not generally coherent between locations in a given year, though several sites in 1991 exhibited similarities in settlement timing.

Table 4. Results of correlation analyses using annual means for each site (\* =  $P < 0.05$ )

	Delaware Bay	Tangier Sound	York River
Delaware Bay	—		
Tangier Sound	df = 2 $r = 0.757$	—	
York River	df = 3 $r = -0.811^*$	df = 2 $r = -0.348$	—
Charleston Harbor	df = 3 $r = 0.517$	df = 3 $r = 0.173$	df = 3 $r = -0.169$

Table 5. Results of cross-correlation analyses between each site within years. Shown are significant lags for each time series (Charleston 1989 is not represented because of a break exceeding 8 successive days in the time series). Significant values are all positively cross-correlated. There were no significant negative cross-correlations.

	Delaware Bay	Tangier Sound	York River	Pamlico Sound	Banks Channel	Charleston Harbor
1989 Delaware Bay						
Tangier Sound		-8 d	-2 d			
York River			+6 d			
1990 Delaware Bay						
Tangier Sound		-18, -15 d	-16, -13 d		-10 d	n.s.
York River			+13 d		n.s.	n.s.
Banks Channel					+15 d	n.s.
1991 Delaware Bay						
Tangier Sound		-16, +5 d	+4, +19 d	+16 d	+6, +11 d	-12, +8 d
York River			0, +14 d	+16 d	-1, -6 d	+/-2, +7 d
Pamlico Sound				+17 d	0, +13 d	+3 d
Banks Channel					n.s.	n.s.
1992 Delaware Bay						
York River			-18, +2 d			+15 d
						n.s.
						+17 d
						n.s.

Table 6. Results of autocorrelations on settlement records for each year and site (Charleston 1989 is not shown because of a break in the time series). All are significantly autocorrelated at a lag of one day. Negative versus positive autocorrelations are indicated in parentheses.

	1989	1990	1991	1992
Delaware Bay	11 d (-)	n.s.	26 d (+)	17, 23 d (+)(+)
Tangier Sound	14 d (+)	n.s.	28 d (+)	
York River	n.s.	22 d (-)	14 d (+)	21 d (+)
Pamlico Sound			n.s.	
Banks Channel		8, 24 d (-)(+)	n.s.	
Charleston Harbor		23 d (-)	15, 29 d (+)(+)	9, 15, 23, 29 d (-)(+)(-)(+)

Lastly, a key finding indicated the existence of semilunar or lunar patterns in settlement at some sites. Lunar relationships became apparent primarily by examining patterns for a given site standardized over multiple years but were generally obscured over a single recruitment season at most sites. Only Tangier Sound (in 1989 and 1991), the York River (1991), Banks Channel (1990) and Charleston Harbor (1989, 1991, 1992) exhibited semilunar or lunar patterns of settlement during a particular year (Table 6). However, autocorrelation analyses over the combination of years sampled revealed significant positive relationships at approximately 14–15 and 28–30 d for both the York River and Charleston Harbor sites indicating a semi-lunar periodicity in settlement (Fig. 4). Autocorrelation analysis of settlement at the Delaware Bay site showed no significant overall lunar pattern and at Banks Channel was positive at a lag of 24 days, suggesting a possible lunar relationship (Fig. 4). Thus, settlement for two sites sampled over multiple years (York River and Charleston Harbor) showed a strong semilunar pattern while settlement at remaining sites was variable, exhibiting trends, though non-significant, of semilunar periodicity.

Patterns between years varied by month and lunar quarter, since there were peaks in settlement during some months, but not others (Figs. 3a–e). Significant interannual variation in settlement occurred over the four lunar quarters and between years but the patterns were temporally variable at all sites except Banks Channel, as indicated by significant interaction effects (Table 7). Lower-level ANOVA model results revealed that lunar quarters differed significantly in settlement magnitude for 9 of 15 combinations of year and lunar quarter at each of the sites and years differed significantly in 11 of 16 combinations (Table 7). At the Delaware site, settlement within a year did not differ between lunar quarters during 3 (1990–1992) of the 4 years. In 1989, however, settlement during the new moon quarter was significantly greater than during full moon. Furthermore, settlement magnitude between years did not differ significantly by lunar quarter across all years sampled. Within Chesapeake Bay, settlement at the Tangier Sound site varied significantly by lunar quarter in 1990 (full moon > new moon) and 1991 (waning moon > waxing moon), but not in 1989. Furthermore, settlement magnitude was similar across 3 years during the new and waning moon but differed significantly during the waxing moon (1989 > 1991) and full moon (1990 > 1991 = 1989). Additionally, settlement at the York River site was also highly variable by lunar quarter within and between years. In 1989, settlement was significantly greater during new moon than other lunar quarters. Magnitude in 1990

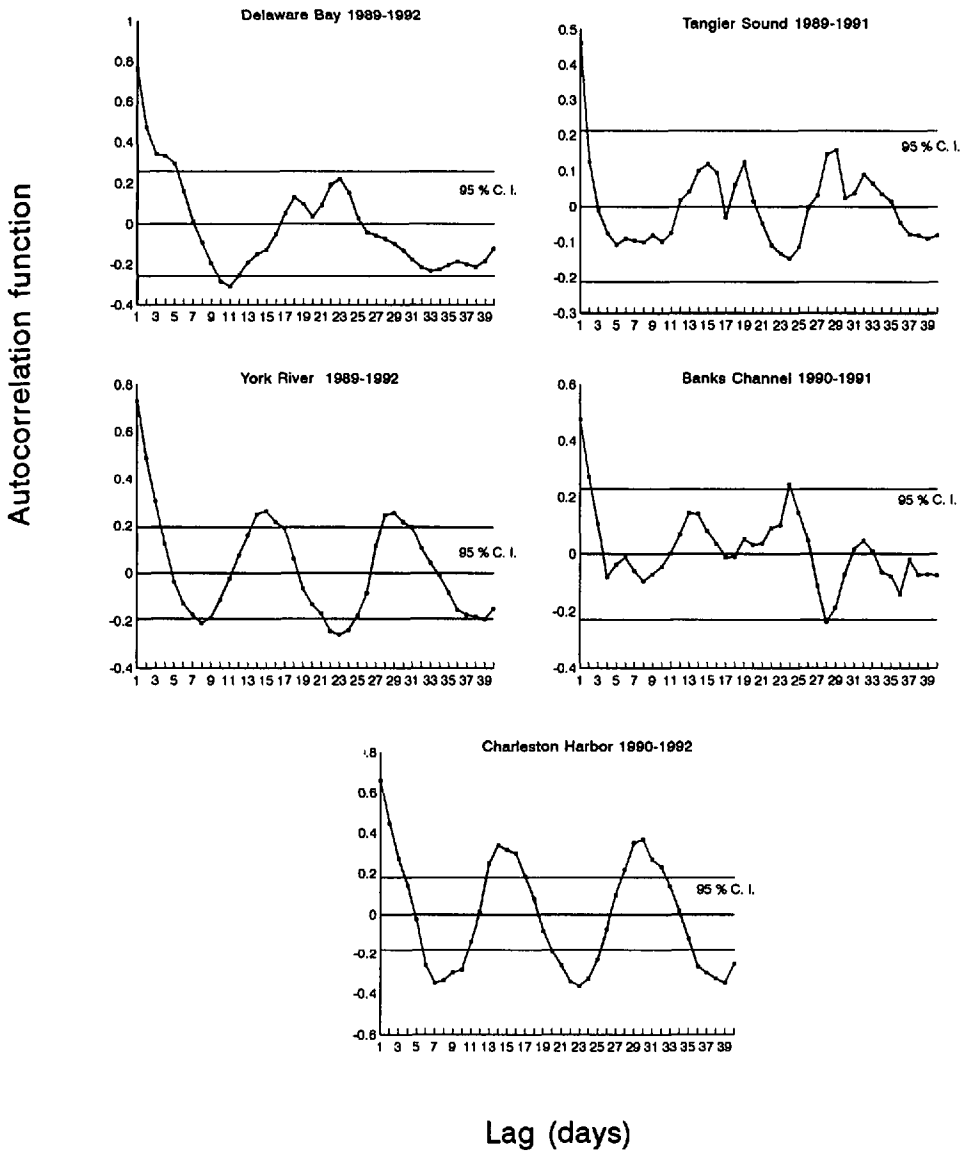


Figure 4. Plots of autocorrelation functions and 95% confidence intervals by site. Significant positive or negative relationships occur at the lag times indicated when the curve exceeds or falls below the 95% confidence interval, respectively.

was greatest during the full and new moon phase and was lowest during the waning moon. While settlement magnitude in 1991 was significantly higher during full moon, no significant differences were observed between lunar quarters during the 1992 recruitment season. Settlement magnitude was generally higher across all lunar quarters in 1990 except the waning moon. Settlement at Charleston Harbor did not differ by lunar quarter in 1989 and was variable from 1990–1992 with new moon (in combination with other lunar quarters) tending to have the highest number of settled postlarvae on substrates. Settlement across years was

Table 7. General linear models procedures show in the full model results (7a) followed by lower level analyses of each factor (7b). Results of multiple comparisons are indicated in decreasing order from left to right. Levels of a factor which are not significantly different are underlined (LQ = lunar quarter).

Table 7a.

Site	Lunar quarter	Year	Lunar quarter $\times$ year
Delaware Bay	F = 2.77, df = 3 <i>P</i> = 0.0428	F = 3.38, df = 3 <i>P</i> = 0.0190	F = 1.99, df = 9 <i>P</i> = 0.0416
Tangier Sound	F = 4.93, df = 3 <i>P</i> = 0.0024	F = 3.24, df = 2 <i>P</i> = 0.0411	F = 1.88, df = 6 <i>P</i> = 0.0037
York River	F = 1.91, df = 3 <i>P</i> = 0.0001	F = 18.18, df = 3 <i>P</i> = 0.0001	F = 2.77, df = 9 <i>P</i> = 0.0037
Pamlico Sound	F = 2.51, df = 3 <i>P</i> = 0.1388		
Banks Channel	F = 2.51, df = 3 <i>P</i> = 0.0602	F = 1.58, df = 1 <i>P</i> = 0.2103	F = 0.77, df = 3 <i>P</i> = 0.5106
Charleston Harbor	F = 7.77, df = 3 <i>P</i> = 0.0001	F = 28.57, df = 3 <i>P</i> = 0.0001	F = 2.94, df = 3 <i>P</i> = 0.0021

generally higher in 1992 during all lunar quarters. Thus, the within- and between-year variation in lunar settlement patterns was characteristic of all study sites (Table 7).

## DISCUSSION

Recruitment variability is often considered a cause of population fluctuations in exploited fisheries stocks (Witham et al., 1968; Phillips, 1972, 1986, 1990; Rothlisberg et al., 1983; Phillips et al., 1994) and other non-commercial species (Roughgarden et al., 1988; Sale, 1990; Gaines and Roughgarden, 1985; Gaines and Bertness, 1993). For the blue crab, several factors may cause population fluctuations. One demonstrated source of variability in Chesapeake Bay is a significant spawning stock-recruit relationship such that spawning stock abundance accounts for up to 82% of variability in recruit abundance (Lipcius and Van Engel, 1990). The blue crab exhibits fluctuations in population abundance over a broad geographic range throughout a variety of estuarine habitats, and it remains questionable whether such a stock-recruit relationship also pertains to other populations.

Abundance fluctuations may also derive, in part, from settlement by blue crab postlarvae (Lipcius et al., 1990; Olmi et al., 1990; van Montfrans et al., 1990), which is characterized by high variability in timing and magnitude across the western North Atlantic. The key findings from our study were that settlement across the region exhibited: (1) low levels of continuous settlement punctuated by significant, non-random, episodic peaks during most years that accounted for over 50% of the annual total; (2) semilunar periodicity at some sites; (3) a general lack of coherence between sites in a given year and within a site across years caused by high temporal and spatial variability; and, (4) occasional coherence in patterns between some sites, suggesting linkages in regional processes affecting settlement during a given year. Such highly diverse strategies may impart flexibility to deal with a variety of ecological scenarios encountered during settlement such as those influenced both by density-dependent and density-independent processes.

Settlement by blue crab postlarvae throughout the region exhibited strong tem-

Table 7. Continued  
Table 7b.

	1989	1990	1991	1992	LQ 1	LQ 2	LQ 3	LQ 4
Delaware Bay	$F = 2.94, df = 3$ $P = 0.0410$ <u>1.243</u>	$F = 2.45, df = 3$ $P = 0.0732$ <u>4.132</u>	$F = 0.53, df = 3$ $P = 0.6635$ <u>2.134</u>	$F = 2.36, df = 3$ $P = 0.0810$ <u>2.413</u>	$F = 4.71, df = 3$ $P = 0.0056$ <u>89.919092</u>	$F = 1.64, df = 3$ $P = 0.1913$ <u>89.929190</u>	$F = 1.23, df = 3$ $P = 0.3067$ <u>91.908992</u>	$F = 1.40, df = 3$ $P = 0.2539$ <u>89.909291</u>
Tangier Sound	$F = 0.75, df = 3$ $P = 0.5232$ <u>4.231</u>	$F = 6.98, df = 3$ $P = 0.0003$ <u>3.421</u>	$F = 2.93, df = 3$ $P = 0.0390$ <u>4.312</u>		$F = 0.41, df = 2$ $P = 0.6645$ <u>89.9190</u>	$F = 3.36, df = 2$ $P = 0.0420$ <u>89.9091</u>	$F = 5.22, df = 2$ $P = 0.0080$ <u>90.9189</u>	$F = 0.41, df = 2$ $P = 0.6648$ <u>90.8991</u>
York River	$F = 11.03, df = 3$ $P = 0.0001$ <u>1.234</u>	$F = 5.57, df = 3$ $P = 0.0014$ <u>3.124</u>	$F = 8.31, df = 3$ $P = 0.0001$ <u>3.142</u>	$F = 1.20, df = 3$ $P = 0.3127$ <u>3.142</u>	$F = 3.96, df = 3$ $P = 0.0103$ <u>90.919289</u>	$F = 5.02, df = 3$ $P = 0.0028$ <u>90.929189</u>	$F = 12.22, df = 3$ $P = 0.0001$ <u>90.919289</u>	$F = 3.40, df = 3$ $P = 0.0708$ <u>92.909189</u>
Charleston Harbor	$F = 0.93, df = 3$ $P = 0.4298$ <u>4.123</u>	$F = 4.71, df = 3$ $P = 0.0039$ <u>3.214</u>	$F = 4.09, df = 3$ $P = 0.0084$ <u>3.412</u>	$F = 5.81, df = 3$ $P = 0.0010$ <u>3.142</u>	$F = 9.88, df = 3$ $P = 0.0001$ <u>92.899091</u>	$F = 4.16, df = 3$ $P = 0.0079$ <u>92.849091</u>	$F = 13.18, df = 3$ $P = 0.0001$ <u>92.919089</u>	$F = 7.22, df = 3$ $P = 0.0002$ <u>92.899190</u>

poral variability at daily, monthly and annual scales similar to that reported earlier in Chesapeake Bay (van Montfrans et al., 1990) and Charleston Harbor (Boylan and Wenner, 1993). These patterns were characterized in all but three of the 18 site/year combinations by constant low levels of daily settlement punctuated by episodic peaks, with little coherence across the region. The annual magnitude of settlement over a 4-year period between Delaware and Chesapeake Bay was negatively correlated, suggesting that magnitude of potential fisheries harvest in these juxtaposed estuaries is likely decoupled. However, these indications must be tempered because substrate efficiency for quantifying settlement is unknown and spatial variability of settlement within each estuary in our study was not considered. Thus, the relationship between settlement and commercial yield awaits confirmation.

Settlement peaks often accounted collectively for more than 50% of the total annual settlement at a site, thereby suggesting their importance for setting the upper limit of population abundance within which density-dependent and density-independent processes act to regulate blue crab population size. On daily scales, settlement en masse in episodic peaks could swamp predators during the transition to a benthic existence when the associated risk of mortality is often thought to be high. Cannibalism is a major source of mortality in blue crab populations (Laughlin, 1982; Peery, 1989; Hines et al., 1990; Lipcius and Van Engel, 1990; Smith, 1990; Smith and Hines, 1991; Mansour, 1992; Moody, 1994) so settlement and metamorphosis timed to occur synchronously may greatly reduce overall mortality (*sensu* Hamilton, 1971; Reaka, 1976; but see below).

Laboratory (Moksnes, unpublished) and field (Pile, 1993) experiments on inter-cohort cannibalism in blue crabs suggest that mortality in newly settled postlarvae and early instar juvenile crabs is strongly dependent upon settlement habitat with inverse density-dependence occurring in sand and mortality independent of postlarval density in seagrass. Furthermore, Metcalf, et al., (unpublished) demonstrated a density-dependent relationship of postlarval abundance with resident fish species in nature. In any case, lowest mortality rates will occur at high postlarval densities, emphasizing the importance of episodically pulsed settlement.

Many western Atlantic estuaries in which blue crabs reside are devoid of submersed vegetation or contain considerably more shallow unvegetated than vegetated habitat (Orth and van Montfrans, 1990); an episodic settlement strategy would likely reduce mortality due to cannibalism in unvegetated habitats. In the latter case, if inverse density-dependence is the rule, higher proportional mortality is experienced during low than high levels of settlement. This suggests that episodic settlement enhances survival of blue crab postlarvae in unvegetated estuaries.

Although settlement patterns were episodic at all sites, the general lack of coherence in settlement across sites can likely be attributed to the geographic extent of the study area and site-specific differences. The estuaries sampled spanned roughly 1,300 km of coastline, and exhibited considerable variability in morphology, orientation to prevailing winds, tidal amplitude and a variety of measured environmental characteristics, particularly salinity, temperature and distance from the potential source of recruiting postlarvae. Salinity and temperature impose significant variability on larval development, time to metamorphosis into the postlarva (Costlow, 1967; Costlow and Bookhout, 1959; Sulkin and Van Heukelem, 1986), and on the growth rates of early juvenile instar crabs (Leffler, 1972; Cadman and Weinstein, 1988). Postlarvae ingressing from oceanic environments to estuarine nursery habitats exhibit a progressively advanced molt state (Lipcius et al., 1990; Metcalf and Lipcius, 1992) in preparation for the metamorphic molt



to the first juvenile instar. Some variability in the rate of metamorphosis of postlarvae collected from the coastal ocean can occur in response to reduced salinity and estuarine cues (e.g., marsh water) but at time scales of less than 24 h (Wolcott and DeVries, 1994). Thus, the spatial and temporal variability in the magnitude of settlement throughout the region likely reflects differences in estuary morphology, local hydrography, the availability of postlarvae and settlement behavior (Orth and van Montfrans, 1990).

A striking feature of long-term (>3 years) patterns observed at both the York River and Charleston Harbor sites was the significant semilunar periodicity in settlement associated with new and full moon. There was also a trend towards similar patterns occurring at other sites. Such semi-lunar periodicity has been observed in numerous fish and crustaceans, and is generally caused by spawning periodicity linked with a short developmental time (Johannes, 1978; Doherty and Williams, 1988; Robertson et al., 1988; Meekan et al., 1993), physical processes associated with tides and internal waves (Shanks, 1983, 1985, 1986, 1988; Kingsford and Choat, 1986), or larval/postlarval behavior (Keough and Downes, 1982; Hadfield, 1986; Pechenik, 1990; Boudreau et al., 1993).

In the present study, observed semi-lunar settlement patterns suggest synchrony promoted by behavioral attributes of the postlarvae within the constraints of physical oceanographic processes such as tidal transport (Olmi, 1995) since: (1) egg hatching is random (Metcalf et al., unpublished); (2) lengthy larval developmental (generally 45 d or more), genetic plasticity in developmental duration (Sulkin and Van Heukelem, 1986) and vagaries associated with coastal transport would likely decouple settlement from patterns of larval release (sensu Scheltema, 1986); (3) settlement across nearby sites experiencing similar semilunar physical properties such as tides and internal waves was largely asynchronous; and, (4) patterns of nightly planktonic abundance during three recruitment seasons at one site (York River, Virginia) appear to be more protracted than and only loosely correlated with comparable records of daily settlement at the same site (van Montfrans et al., 1990, 1995, and Olmi, 1993, 1994, in press, 1995). Thus, behavior of larvae (Sulkin and Van Heukelem, 1982; Epifanio et al., 1984) and postlarvae (Brookings and Epifanio, 1985; DeVries et al., 1994; Mense and Wenner, 1989; Olmi, 1993, 1994, 1995; Tankersley and Forward, 1994) coupled with transport processes (Olmi, 1993, 1995) and, subsequently, settlement behavior likely impact population variability in blue crabs along the western North Atlantic.

Finally, settlement patterns were consistently episodic over a broad geographic range from Delaware Bay southward along the Atlantic coast (this paper) and throughout Gulf of Mexico estuaries (Rabalais et al., 1995). Moreover, settlement by postlarvae was highly variable at daily, monthly and annual scales along both coastlines where over 50% of the settlement within a recruitment season routinely occurred during 3–4 day pulses throughout the 2–3 month period of highest settlement, attesting to the generality of recruitment strategies in *Callinectes sapidus*. Significantly higher settlement magnitude (both mean settlement and abundance) of blue crab postlarvae in northern Gulf of Mexico estuaries than in Atlantic Coast estuaries (Fig. 5; Rabalais et al., 1995, and this paper, respectively) suggests that populations of blue crabs in the Gulf of Mexico are limited, in part, by post-settlement processes, in contrast to greater recruitment limitation along the Atlantic Coast.

Collectively, these studies emphasize the utility of examining one component of population dynamics (settlement) using similar techniques over a broad geographic area at appropriate temporal scales (e.g., daily) throughout the recruitment season. Without such standardization, meaningful comparisons between sites

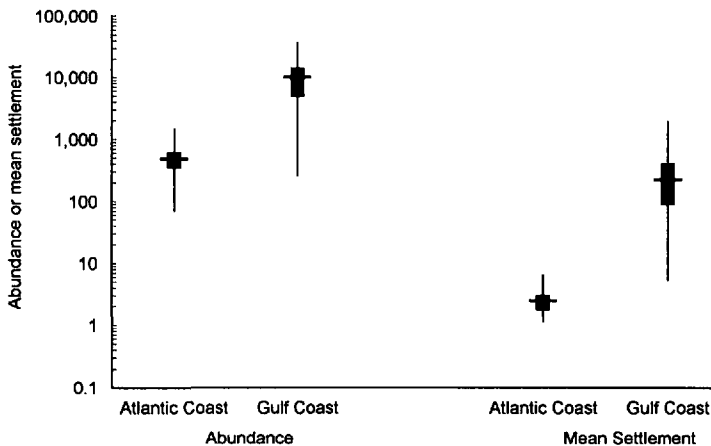


Figure 5. Comparative values (mean, standard error and range) for abundance\* and mean settlement of blue crab megalopae from Atlantic coast and gulf coast estuaries. Abundance\* is the total number of blue crab megalopae collected in a 125–150 d period when 50+% of the settlement occurred, usually during June or July through October or November. Mean settlement for all areas is the number of megalopae collected for the period of abundance\* divided by the number of days of collection. 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 calculations. Gulf coast data are from Rabalais et al. (1995).

would not have been possible. Ultimately, such collaborative and coordinated studies will be invaluable in assessing the influence of various factors including recruitment and post-settlement processes as regulators of population size.

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