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BLUE CRAB LARVAL DISPERSION AND RETENTION IN THE MISSISSIPPI BIGHT: TESTING THE HYPOTHESIS

Harriet Perry, Donald R. Johnson, Kirsten Larsen, Christine Trigg and Fred Vukovich

ABSTRACT

An hypothesis relating physical forcing to dispersion and retention of blue crab larvae was tested in the area of the Mississippi Bight. Seasonal circulation patterns derived from a 3-dimensional, primitive equation, sigma-coordinate model of the Gulf of Mexico (GOM) indicate favorable conditions for offshore dispersal of larvae and their return to nearshore waters as megalopae occur between April and October. Large basin-scale events, such as Loop Current intrusions into the GOM with spin-off eddy generation and anomalies in average wind stress may interrupt this circulation pattern and change the settlement success rate. Meteorological and hydrological factors thought to influence settlement were compared to daily records of megalopal abundance in Mississippi Sound for the years 1991 through 1999. Wind stress was strongly correlated with settlement success. Eastward wind stress during the months of July and August, when the larvae are at sea, and westward wind stress during recruitment in September and October were important in retaining larvae in the general area and subsequently returning them near shore as megalopae, respectively. Northward intrusion of the Loop Current and warm core ring detachment during late summer altered circulation patterns and decreased settlement success.

In Gulf of Mexico (GOM) estuaries, eggs of the blue crab *Callinectes sapidus* hatch near offshore barrier islands and are immediately transported to open ocean environments in the seaward flowing waters (Perry and Stuck, 1982; McClintock et al., 1993). Rapid seaward dispersal of zoeae may increase larval survival by reducing predation rates (Christy and Morgan, 1998). Subsequent development in offshore surface waters as buoyant free-drifting plankton includes seven or, occasionally, eight zoeal stages with an at-sea duration of approximately 30 to 50 days (Costlow and Bookhout, 1959; Costlow, 1967; Bookhout and Costlow, 1975; Sulkin, 1978). Toward the end of this planktotrophic phase, which is under the influence of prevailing currents, metamorphosis to the megalopal stage occurs. Blue crabs recruit to GOM estuaries as megalopae and settle in nearshore habitats (Stuck and Perry, 1981; Perry and Stuck, 1982; Perry et al., 1995; Morgan et al., 1996). Onshore winds enhance return of megalopae to estuaries (Perry et al., 1995; Morgan et al., 1996); however, once in the estuary, distribution is facilitated by tidal transport (Olmi, 1994; Morgan et al., 1996; Christy and Morgan, 1998). Johnson and Perry (1999) traced the at-sea stage of hypothetical larvae spawned in the Mississippi Bight with a climatologically driven numerical model. They noted that seasonality of spawning coincided with climatological inner shelf circulation patterns that transport zoeae offshore initially, but then act to retain the larvae within the Mississippi Bight and to bring them back to shore at the appropriate stage. Results of this model exercise suggested that inter-annual variations in wind stress patterns together with basin-scale events, such as Loop Current spin-off eddies generated during critical periods of larval development, were both influential in establishing recruitment success.

Coastal climatology of the northern Gulf is largely dictated by the subtropical Azores-Bermuda High (Eleuterius and Beaugez, 1979; Ward, 1980). Onshore and eastward blowing winds are most prevalent in the summer when the High is strongest and farthest northwest. As the High weakens in early fall, coastal areas become subject to the westward and southwestward blowing trade winds. Low

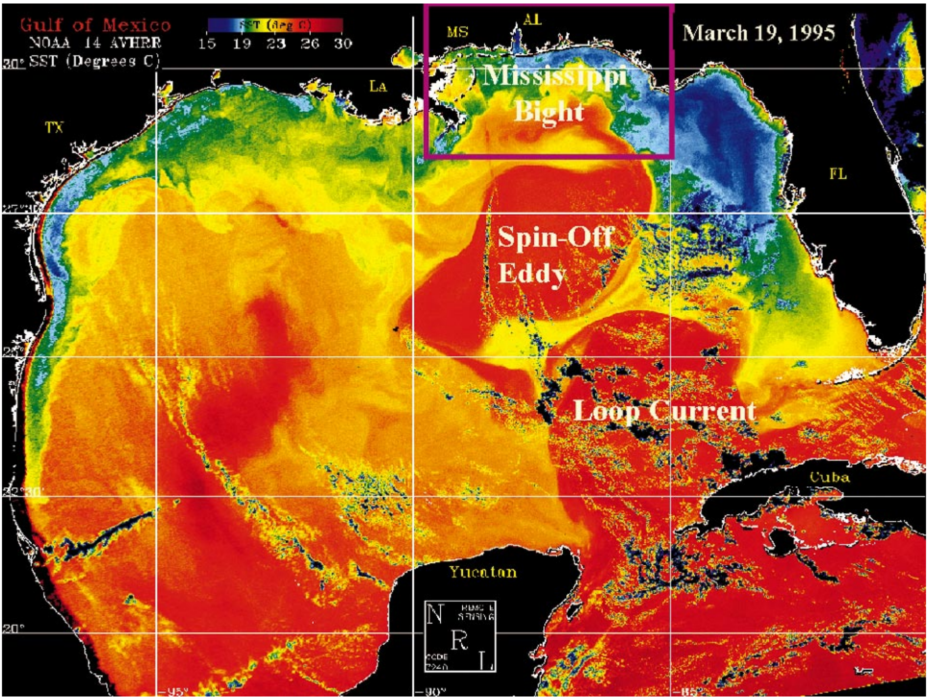

Figure 1. NOAA-14 AVHRR thermal image of the Gulf of Mexico. Winter temperatures between warm Caribbean Waters and cooler Gulf of Mexico waters clearly outline the intruding Loop Current and a recently formed spin-off eddy. The Mississippi Bight study area (Apalachicola to the Mississippi River Delta) is outlined in the upper center of the image.

tidal amplitude in conjunction with a broad shallow shelf in the northern and eastern Gulf contribute to meteorological forcing of coastal processes (Smith, 1977; Chuang et al., 1982; Schroeder and Wiseman, 1986; Schroeder et al., 1987). Circulation in the Mississippi Bight follows seasonal wind patterns. There is a general surface drift toward the west within the Bight for most of the year, countered by light eastward winds during summer, but reversing to westward in early fall. Optimal retention of planktotrophic larvae within the Bight would occur during spring and summer, a time period coincident with spawning peaks of *C. sapidus* in the northern GOM (Perry et al., 1995; Rabalais et al., 1995; Morgan et al., 1996).

Circulation patterns in the deep basin of the GOM are dominated by the Loop Current and the large warm core rings that separate from the Current (Fig. 1). The Loop Current is part of the Gulf Stream system that enters the GOM through the Yucatan Straits between Mexico and Cuba. It penetrates into the eastern GOM, turns anticyclonically, and exits through the Straits of Florida merging with the Florida Current. The Loop Current seldom penetrates to 28 N (Vukovich et al., 1979), and the average position of the northern boundary of the Current is about 26.4 N. After penetration into the eastern GOM, the loop eventually turns back on itself and a large (250–400 km diameter) eddy is formed and separates from the Current. Separation frequency varies from 6–17 months with an average of about 11 months (Vukovich, 1988; Sturges, 1992; Sturges, 1994; Vukovich, 1995). The Loop Current penetration and eddy shedding are the result of instability processes (Hurlburt and Thompson, 1980) hence the timing is variable and

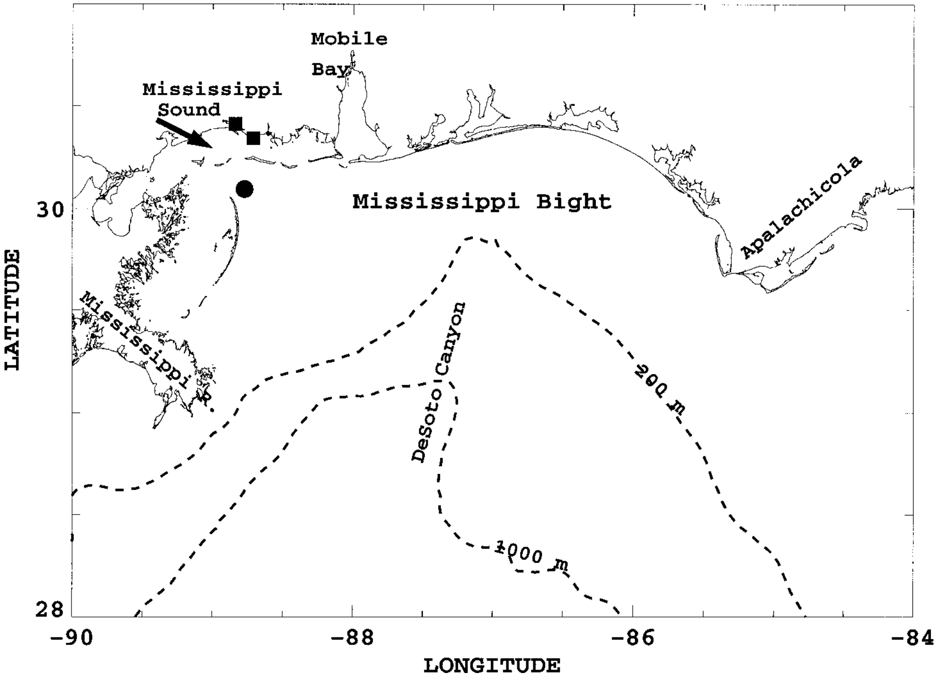

Figure 2. Mississippi Bight study area. Solid squares show settlement collectors in the Mississippi Sound (upper left). The solid circle shows the position of NDBC wind buoy #42007. The contour lines are the 200 m and 1,000 m isobaths.

cannot be readily predicted. Modeling results suggest that these instability processes appear to modulate the parabathic, shelf-break flow in the northeastern Gulf (Oey, 1995; Hetland et al., 1999) allowing greater interaction of the deep basin with the shelf itself. Although there is considerable data describing the processes of formation and movement of the Loop Current and its spin-off eddies, very little is known about the effects that these processes have on shelf circulation. There are indications, however, from satellite infra-red imagery and drifter data that the effects can be significant, especially where canyons cut across the continental shelf break or where the shelf narrows. In the Mississippi Bight these conditions occur at the DeSoto Canyon in the center of the Bight (Fig. 2) and in the narrow shelf area south of the Mississippi River Delta, which serves as the western boundary of the Bight.

Research directed toward the understanding of mechanisms of larval transport in the Mid-Atlantic Bight (MAB) provided the foundation for investigating similar strategies in the GOM. Conceptual models for dispersal and recruitment of blue crab larvae within the MAB were reviewed by Epifanio (1995). In the MAB spawning takes place on an ebbing tide with the buoyant larvae ascending into the near-surface layer (Provenzano et al., 1983; Epifanio, 1995) where they remain through the duration of zoeal and early megalopal development (McConnaugha et al., 1983). Spawning seasonality and wind patterns in the MAB provide a mechanism for dispersal while maintaining the majority of the cohorts near to the parental population. Based on this mechanism, Johnson and Hester (1989) were able to develop a wind stress index to explain variations in harvest. Winds also appear to have an important role in regulating settlement success in the northern

GOM. Both Perry et al. (1995) and Morgan et al. (1996) found peak megalopal settlement associated with onshore winds in Mississippi and Alabama, respectively. Johnson and Perry (1999) used results from a numerical model to examine the influence of seasonal circulation patterns on larval recruitment success. The numerical circulation data were from a 21 level sigma-coordinate Princeton Ocean Model (Blumburg and Mellor, 1983) driven by monthly climatological winds. They hypothesized that winds in conjunction with circulation features that prevail on the shelf during critical periods of offshore larval development were influential in determining subsequent abundance of megalopae in nearshore waters of the Mississippi Bight. The present study is an attempt to evaluate that hypothesis. Nine years of megalopal settlement data from Mississippi Sound were compared with wind and Loop Current observations for the same time period to examine the relationship between these parameters and blue crab recruitment success as measured by settlement.

MATERIALS AND METHODS

The study area is shown in Figures 1 and 2. The Mississippi Bight is roughly bounded by Apalachicola in the east and by the Mississippi River in the west. The DeSoto Canyon is a prominent feature in the center of the Bight, cutting a trough from the deep basin onto the continental shelf. Megalopal settlement data were taken from stationary piers in central Mississippi Sound. Observations on wind direction were obtained from National Data Buoy Center (NDBC) meteorological buoy #42007 located in 13 m of water. Both the settlement stations and the NDBC buoy are located in the northwestern portion of the Bight (Fig. 2).

Megalopal settlement indices were determined using artificial settlement substrates (passive collectors) constructed of PVC pipe (16.3 cm outside diameter and 37.5 cm in length) and blue air conditioning filter material as described in Metcalf et al. (1995). These authors also established the efficacy of these collectors in quantifying relative rates of settlement. Sampling protocol followed that of Perry et al. (1995). Four replicate collectors were deployed vertically approximately 15 cm below the water surface from a stationary pier. Collectors were sampled daily between 0800 and 1000 from May through October from 1991 through 1999, weather permitting. Severe winter storms in February 1998 damaged the sampling platform and the collectors were located on a nearby pier in the spring. Sampling in 1998 was discontinued on 25 September when the pier was destroyed by Hurricane Georges. In 1999, samplers were re-located to a new pier ~3 km away. All stations were located in central Mississippi Sound. Collectors were washed in the field over plankton netting (#333 mesh) and the samples returned to the laboratory for sorting. *Callinectes sapidus* megalopae from each collector were identified, counted, and an average number of megalopae per collector per day was determined.

Records of wind speed and direction from offshore buoy NDBC #42007 in the northwestern Mississippi Bight were continuous with very few gaps. To test whether wind data from this buoy was representative of the Mississippi Bight, records from this buoy were correlated with data from a deeper water buoy off Apalachicola (NDBC buoy #42039) for concomitant periods in 1996 and 1998. The vector correlation was 0.4 at an angle of 4 degrees. The highest component correlation was between east-west wind stress at 0.5, thus the buoy winds used in this study were only moderately representative of the entire Bight. Although wind stress on the east side was somewhat different than on the west side of the Bight, the proximity of buoy #42007 to the settlement site and its continuous record length made it the most suitable for comparison with settlement. Additionally, the offshore location made it more suitable than equally long records from regional airports.

Establishing timing of Loop Current spin-off eddy generation was more difficult. The month when a major warm-core ring (WCR) separated from the Loop Current was determined for the period 1991–1999 using sea-surface temperature (SST) data from the NOAA/AVHRR, sea-surface height (SSH) data from TOPEX and ERS satellites, ocean color data from SeaWiFS, and available in-situ data. The SST data from NOAA/AVHRR was used to determine time of ring separation from fall through spring. In the summer when the mixed layer is well established, the SST data will not reflect the pattern associated with dynamic features such as the Loop Current or WCR in the GOM. Between 1991–1995 for the months of June, July, August, September, and October, when the temperature contrast was too small for feature detection, general locations were obtained from numerous ships-of-opportunity (Minerals Management Service Programs, oil companies, and various research vessels). Although anecdotal, this information allowed a reasonable means to track features when combined with the limited-value thermal imagery during summer months. From 1996–1999, information on the Loop Current and WCR was obtained from TOPEX/ERS SSH and SeaWiFS ocean color data, as well as

Table 1. Time of separation of spin-off eddy from the Loop Current.

Year	Separation month	Months from August*
1991	September	11
1992	July	1
1993	June	2
1994	September	11
1995 (2nd eddy)	March (September)	5 (11)
1996	August	0
1997	October	0*
1998	March	5
1999	October	0*

* The separation month is taken as the month in which an eddy completely detaches and moves toward the western Gulf. In 1997 and 1999, eddies detached in August, but were reabsorbed. The 'Months from August' column takes the detachment in August in 1997 and 1999 as the time critical for larvae. For the two eddies in 1995, March was chosen as the critical month of separation.

from continued analysis of ships-of-opportunity data. From these data, the month that absolute ring separation occurred was determined (the month when the WCR completed its separation from the Loop Current and moved into the western GOM). In 1997 and 1999, the ring separation initially took place in August; however, the rings were re-absorbed by the Loop Current before the end of the month or in early September, and absolute ring separation did not occur until October. In 1999, the ring that separated in August, split in two and a minor ring drifted into the western Gulf. The major part of that ring was re-absorbed by the Loop Current in September. Since the process of formation and re-attachment occurred during the critical month of August in 1997 and 1999, August was considered to be the month of formation for these two years. Table 1 lists the month of absolute separation or the month of critical separation (1997 and 1999). To quantify timing and influence of the eddy break-off, a weighting factor was established which consisted of the number of months before August (the most critical month) when an eddy was formed. This weight was subsequently multiplied against the wind stress time series (Table 1). An opportunity to examine the mechanism of ring interaction with shelf circulation occurred in 1996 when a WCR generated in August was followed using satellite-tracked surface drifters deployed in the Mississippi Bight by Mineral's Management Service (Vukovich and Müller-Karger, 2000). It allowed for comparison of circulation before and after the eddy break-off.

Previous attempts to quantitatively match settlement with local forcing parameters (Perry et al., 1995) have been marginally successful. Highly episodic settlement and low correlation with local events suggest that large scale advection patterns and patchy at-sea distributions of plankton are responsible, rather than sporadic local events operating on homogeneous plankton distributions. In this paper yearly variations and large scale forcing factors which may provide a suitable window of opportunity for patchy distributions of plankton to be returned to the near-coast areas were examined.

RESULTS

Seasonal periodicity of settlement events was similar from year-to-year; however, the magnitude of settlement was highly variable. Figure 3 shows the daily settlement for each of the 9 years, and Figure 4 shows the monthly average settlement per collector per day (a measure of effort). Initial settlement on collectors began in May with megalopal numbers low and sporadic through July. The majority of megalopae settled between August and October with September commonly the largest settlement month. Extremely high numbers of megalopae in 1991 were followed by four years of moderate abundance from 1992 through 1995 and four years of weak abundance from 1996 through 1999. In 1998, anomalously large settlement occurred in spring. However, the collection in 1998 was curtailed on 25 September due to hurricane damage, hence some uncertainty must attach to the yearly total and to the comparative effort as well.

Temporal settlement distribution in all years was dominated by a few days of very high numbers. Histograms of the frequency distribution of percent of days

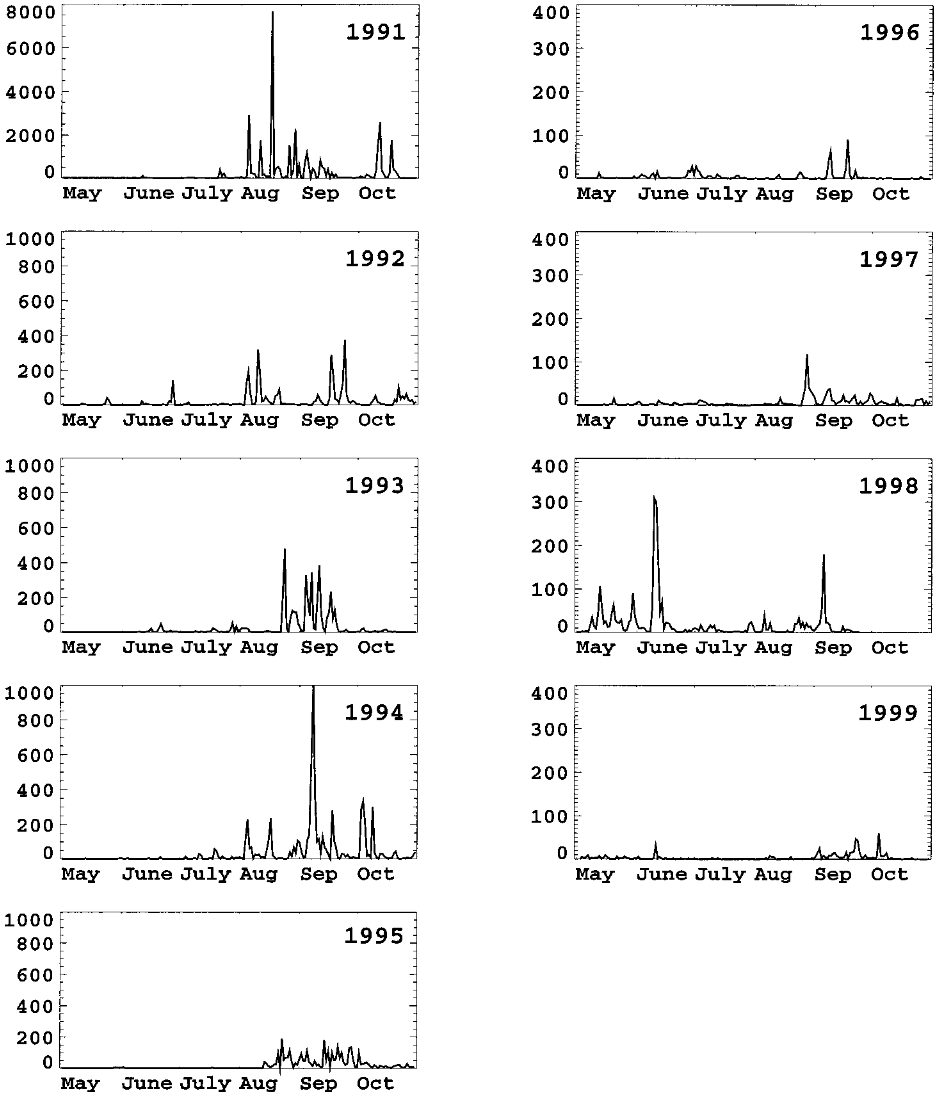

Figure 3. Daily megalopal settlement observations from May through October, 1991–1999. Note changes of settlement abundance scales.

versus average catch of megalopae per day for the August through October periods of high-settlement (1991–1999) are illustrated in Figure 5. Annual trends in abundance clustered into three groups: ~45% of the time collectors contained from 1–10 megalopae per day, ~6% of the time they contained 101–200 megalopae and ~1% of the time numbers exceeded 1,000 megalopae per day. Even though 1,000+ settlement days occurred infrequently, these events were usually responsible for elevated total yearly settlement counts. Figure 5 also compares the average settlement frequency distribution of years with high (1991), moderate (1992–1995) and low numerical abundance (1996–1999) with the baseline data of the all years combined. Years with moderate settlement closely followed the nine-year composite data (Fig. 5b). Low abundance years had high numbers of

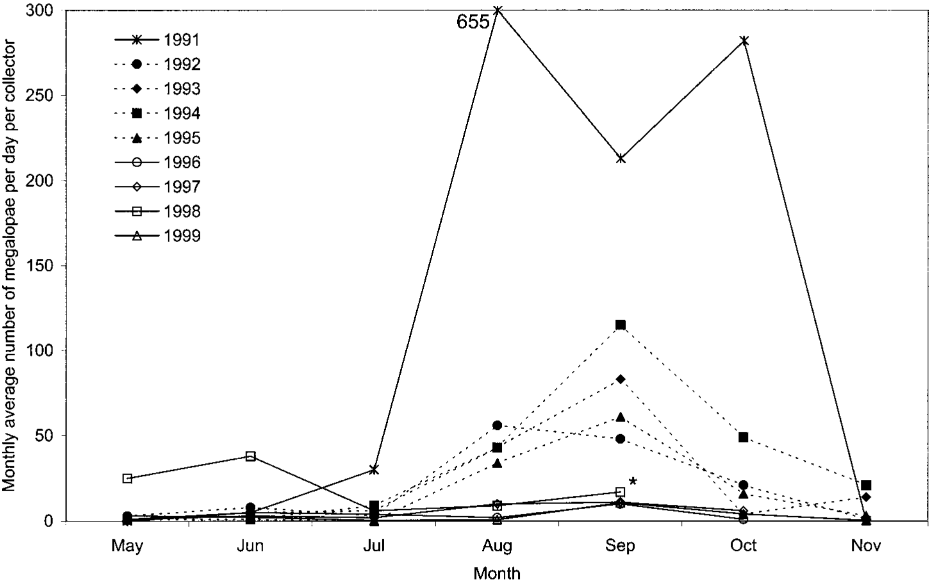

Figure 4. Monthly average number of megalopae per day per collector (reported as a measure of effort to account for variability in total days sampled).

days with 0 or ≤10 average megalopae per day (Fig. 5c). In contrast, 1991 had very few days with low settlement and 45% of the days averaged 100+ megalopae per day (Figure 5a). Additionally, 1991 had more days with average settlement values >1,000.

Wind stress histograms showing the frequency of occurrence of wind stress component amplitudes for the months of July, August and September, averaged over the 9-year period are illustrated in Figure 6. In July the wind stress was light and highly variable with an average northeastward direction. This average direction drives surface waters along-coast toward the east and counter to the ambient westward drift around Apalachicola and would tend to maintain the plankton in the Mississippi Bight after large spawning events occur in June and July. In August, the wind stress components were variable with an average of nearly zero. September marked the end of the summer pattern, with more storm like conditions and average stress toward the west/southwest: a direction that would force the plankton, now more mature, back to their estuarine spawning locations. For comparison with yearly settlement values, a wind stress time series was formed by subtracting the sum of the eastward wind stress, τ^x, over July and August of each year from the eastward wind stress sum over September and October [τ^x(Jul) + τ^x(Aug) − τ^x(Sep) − τ^x(Oct)]. This reflects the hypothesis that early summer wind stress retains the larvae in the area and late summer/fall wind stress brings them back to the estuary. Although peak settlement periods were usually associated with the late summer months, anonymously high settlement occurred in June of 1998 (Fig. 3). To explain this in the context of the wind forcing hypothesis, eastward wind stress in the month preceding settlement, May, was examined for all 9 years (Fig. 7). May is the month in which the megalopae involved in the June settlement are planktonic and under the influence of winds. Over the nine year study period, 1998 was the only year with positive eastward wind stress and a settlement peak in June.

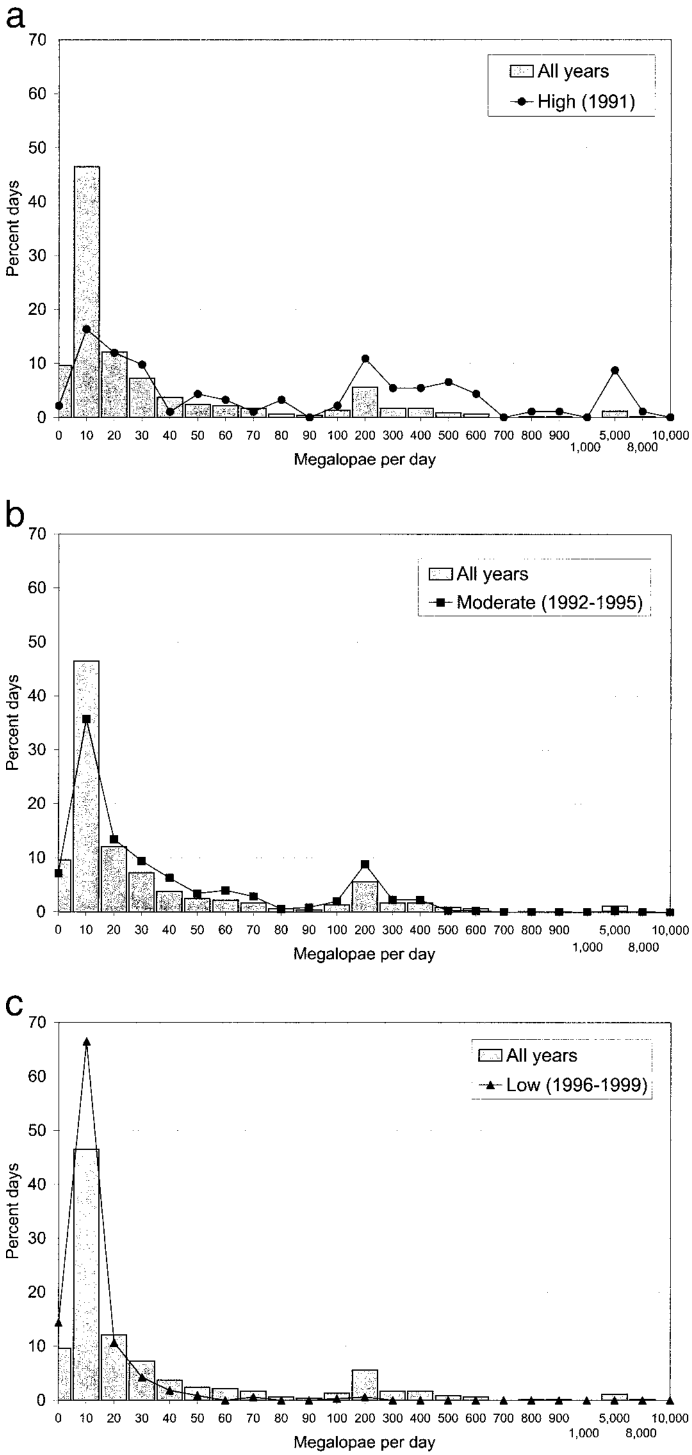

Figure 5. Histogram of frequency distribution of percent days versus average collection of megalopae per day from 1991 through 1999 (block). (a) Histogram of 1991–1999 overlain with data from the year of high abundance, 1991. (b) Histogram of 1991–1999 overlain with data from years of moderate abundance, 1992–1995. (c) Histogram of 1991–1999 overlain with data from years of low abundance, 1996–1999.

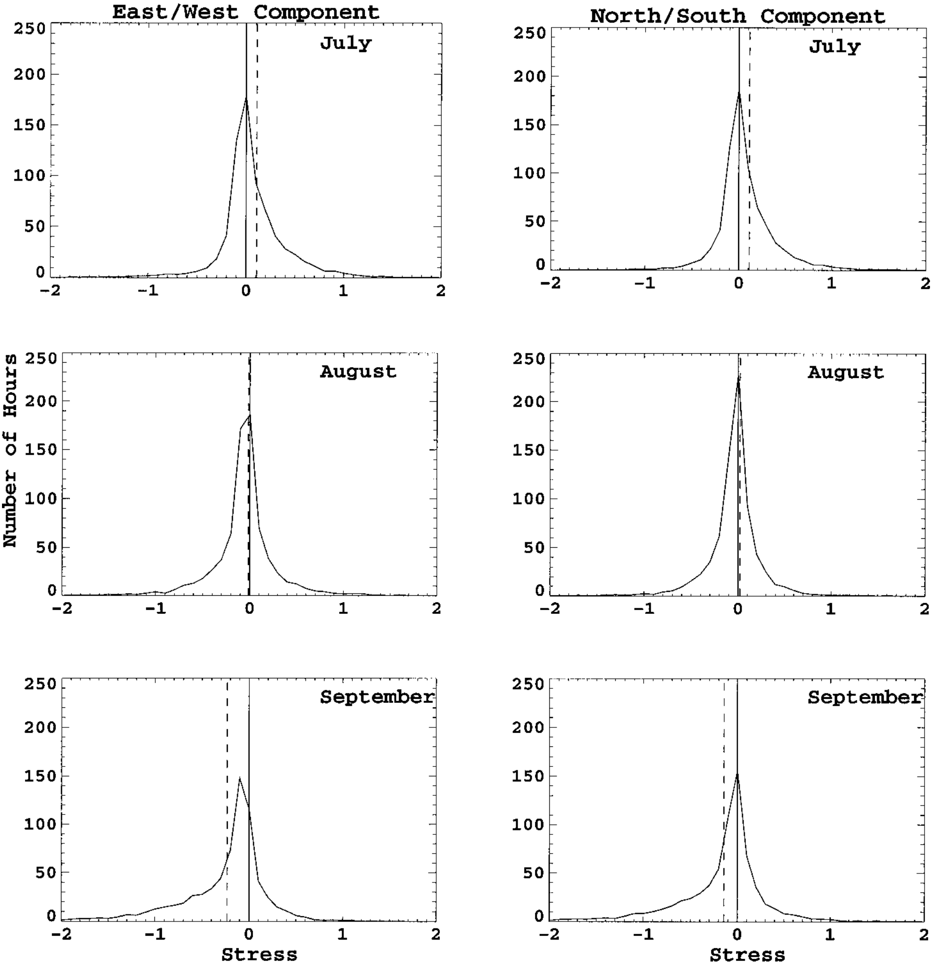

Figure 6. Wind stress histograms for the components of wind stress (dynes/cm^2) from July through September, averaged over 1991–1999. Positive is east and north. The vertical dashed lines are the monthly averages in each component and for each month.

Johnson and Perry (1999) hypothesized that if changes in circulation at the shelf break and on the shelf, which may take place during formation of a Loop-Current spin-off eddy, occur during the time in which most of the larvae are at sea, these circulation changes may seriously impact megalopal return to the estuary. During 1996, in situ surface current measurements in the Mississippi Bight were available to test the effects of a mid-summer spin-off eddy observed from satellite data. Sea surface height in the GOM, determined from satellite altimeter anomaly data referenced to a numerical model, is illustrated in Figure 8. A spin-off eddy has clearly been formed by mid-August, 1996, the critical at-sea month for planktonic larvae. Concomitant circulation in the Mississippi Bight in July and August, 1996, determined from satellite tracked surface drifters is shown in Figure 9. In July the surface drift is lightly eastward across the Mississippi Bight, with a fairly strong eastward jet along the slope. In August, after the spin-off eddy has formed, the flow has reversed to westward, with an interruption in the slope jet and removal of Bight waters around the Mississippi River Delta. The

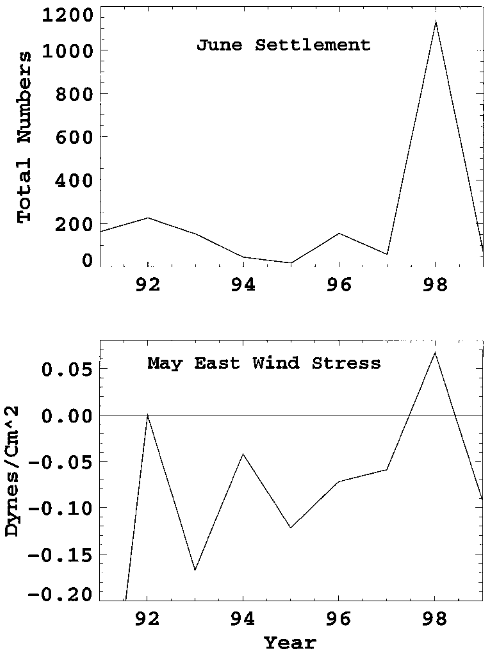

Figure 7. Megalopal settlement in June, 1991–1999 (upper). Eastward component of wind stress during May, when the June megalopae are at sea (lower).

numerical model used by Johnson and Perry (1999) showed a similar streaming of water out of the Bight in mid-summer that occurred at the same time an eddy separated from the Loop Current. Larvae caught in this flow would not be able to return to estuaries in the Mississippi Bight. Settlement in 1996 was the lowest of all 9 years.

The relationship between annual average settlement values and physical parameters over the shelf was evaluated by examining the settlement time series for July through October from 1991–1999, the composited wind stress time series, months from August of spin-off eddy formation, and a prediction index formed from weighting winds with spin-off eddy formation timing (Fig. 10). The annual settlement time series shows an exceptionally large value in 1991, followed by a smaller peak in 1994 and a very weak peak in 1998. The composited wind stress time series also shows a downward trend during the decade and similarly placed peaks, with the exception of 1996. Correlation between settlement and the composited wind stress was $r = 0.64$. The correlation between the adjusted (Table 1) spin-off eddy timing and settlement was $r = 0.69$. The two forcing factors were combined to form an ‘Index’ series in the following manner: the composited wind stress time series was multiplied by the spin-off eddy timing as a ‘weighting’ factor and the resulting Index correlated with settlement. The new correlation, $r = 0.74$, meets the 95% confidence limit for a null hypothesis with 9 data points. This correlation suggests that 55% of the variance (r^2) in the yearly settlement time series can be explained by the two environmental forcing factors.

DISCUSSION

This research represents the second part of a study examining physical factors affecting larval recruitment in the Mississippi Bight. The focus has been on crit-

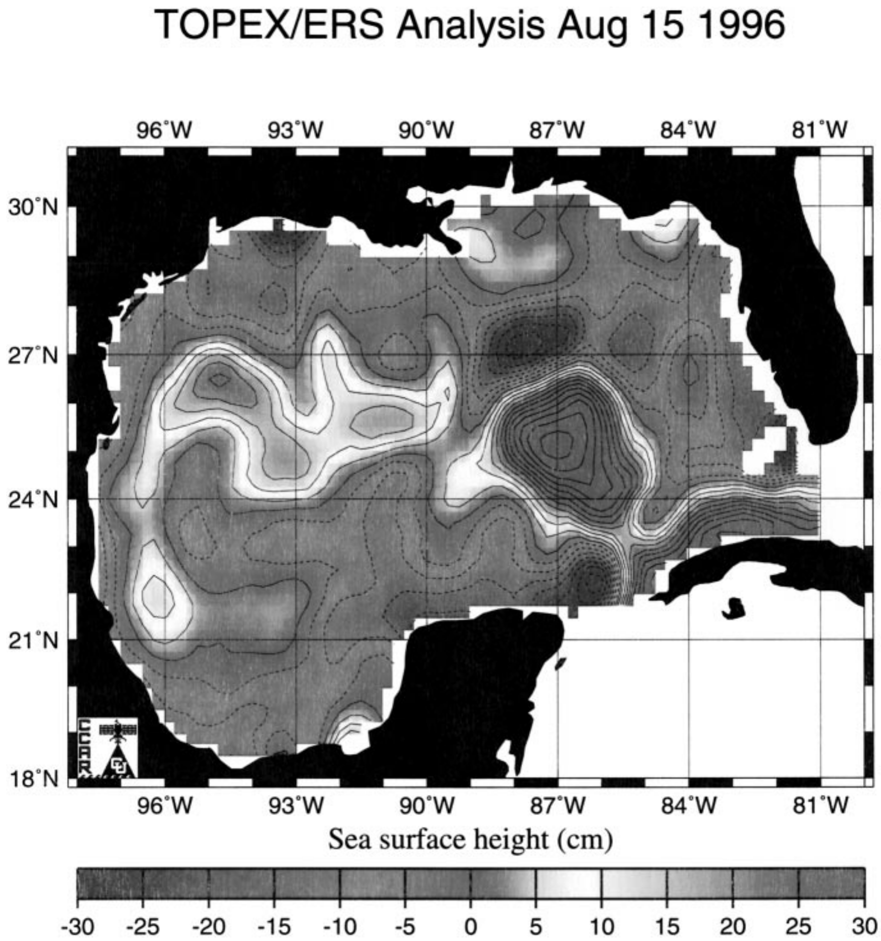

Figure 8. Sea surface height (SSH) showing Loop Current spin-off eddy formation during August of 1996. This analysis is from the Colorado Center for Astrodynamic Research (R. Leben). The SSH anomaly from full TOPEX and ERS-1/2 satellite cycles is referenced to a long-term averaged SSH from a numerical model.

ical early life history when larvae are at sea under the influence of prevailing currents and must depend on these currents both for dispersal and for return to the estuaries. Johnson and Perry (1999) used the stored results from a numerical circulation model to trace hypothetical larvae hatched at locations distributed evenly along the Mississippi Bight. The model, driven by climatological winds and damped with climatological sea-surface temperature and salinity, was run for four model years with release of larvae occurring year-round at 10 day intervals. Successful settlement was defined as return of a larva to within 10 km of the coast in the Mississippi Bight after 30–50 days offshore. Model results clearly demonstrated that a window of opportunity occurred between April and October for a successful planktonic stage. Since the principal spawning and recruitment activities fall within this window, they hypothesized that wind driven advection was a principal contributor to larval success or failure. The relation between wind driven circulation and a successful planktonic stage was earlier demonstrated for the blue crab population of the MAB. Although inter-annual variations in the

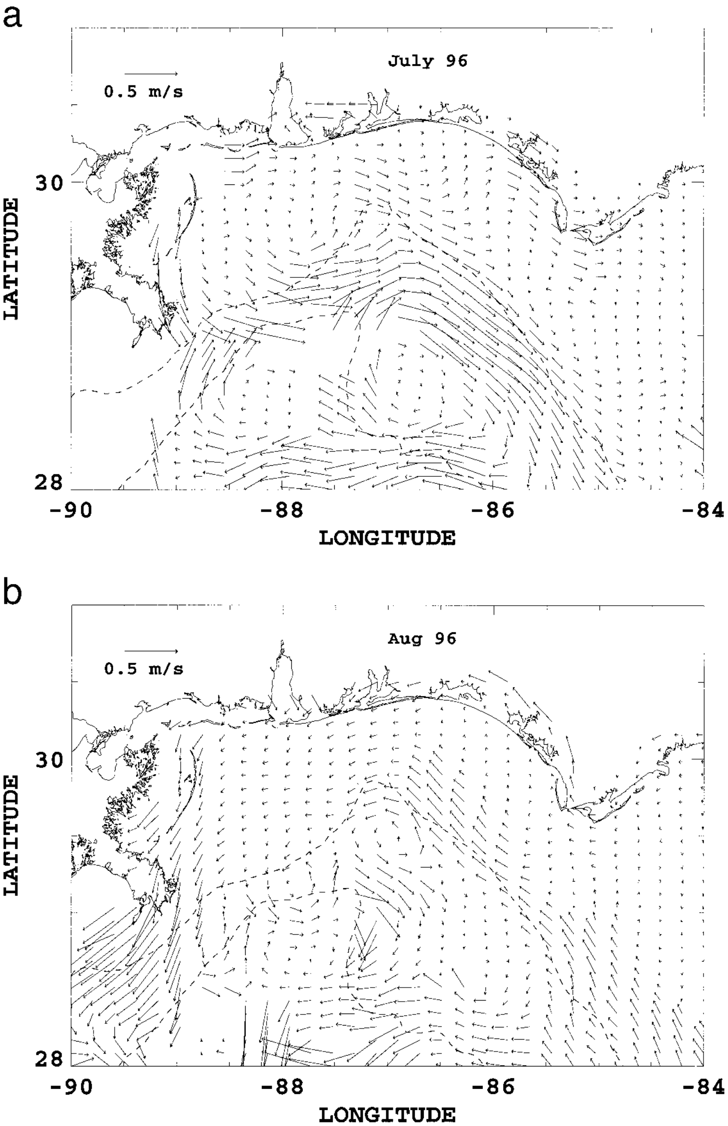

Figure 9. (a) Daily vectors from multiple satellite tracked drifters, July 1996. Vectors were smoothed by weighting with a 20 km decorrelation length scale. (b) Same for August, 1996.

seasonal wind patterns were thought to be responsible for fluctuations in settlement success, there was no opportunity to test this concept using the climatologically forced model because wind forcing was repeated exactly in each of the four years. Observed inter-annual variations in shelf circulation in model years were attributed to unstable deep basin processes associated with the Loop Current and its spin-off eddies. The lowest settlement success with the model, in fact, occurred during a year in which a Loop Current spin-off eddy was formed in July/August of the model year. From model differences between years, it was suggested that the northward penetrating Loop Current was accompanied by a cyclonic eddy over the DeSoto Canyon which pulled water and planktonic larvae from near

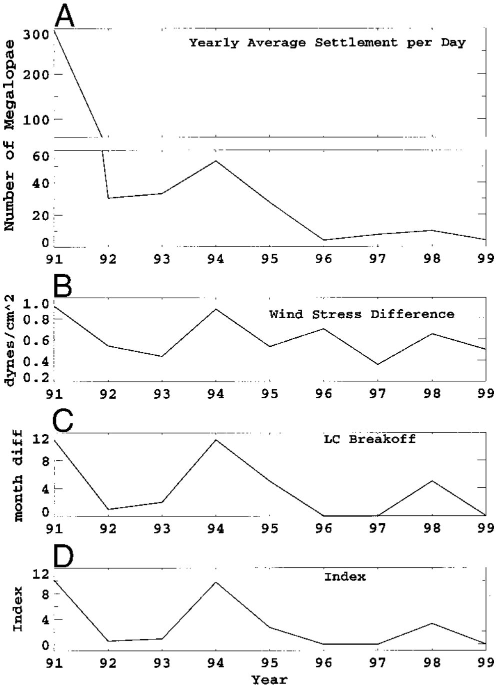

Figure 10. (a) Time series of total yearly megalopal settlement on collectors in the Mississippi Sound. Note break in magnitude of vertical axis. (b) Wind stress difference time series. Solid line represents the east/west component difference adding July and August, and subtracting September and October (positive east). (c) Time series of months before August when a break-off eddy was formed. (d) Time series of an ‘Index’ formed from the wind stress difference multiplied by the Loop Current break-off timing.

shore resulting in a loss of westward streaming larvae from the eastern Bight. Secondly, an interruption of the eastward flowing slope current along the narrow shelf south of the Mississippi River Delta allowed streaming westward flow out of the Mississippi Bight and a further loss of larvae from the western Bight caught in this flow.

In the present study, the relationship of settlement with observed inter-annual wind modulation and the timing of Loop Current spin-off eddy formation was examined. The majority of settlement commonly occurred from August to October with a peak in September. Settlement was episodic and yearly abundance totals were usually the result of a few days of high numbers. Settlement patterns appear to be related to patchiness in the at-sea distribution of larvae rather than episodic forcing events applied to a homogeneous at-sea distribution. Since previous attempts at correlating daily settlement with local forcing events, such as winds, tides and moon phases, were only marginally successful (Perry et al., 1995), efforts were directed at relating annual settlement variations with yearly wind and Loop Current activity. Eastward wind stress during July and August, and westward wind stress during September and October produced the highest correlation with settlement, thus supporting the concept of retention against the ambient westward flow around Apalachicola during mid-summer spawning, and a return to the estuaries during late summer. The relationship between the June 1998 settlement peak and eastward wind stress in May (the month in which the larvae were at sea) provides additional evidence of the importance of winds in determining settlement success.

The northward intrusion of the Loop Current and the process of WCR detachment in late summer negatively impacts settlement by altering the normal shelf circulation patterns. A Loop Current spin-off eddy was generated in August, 1996, and satellite tracked surface drifters during July and August confirmed that during this period an interruption in the eastward flowing slope current and a strong flow westward out of the Bight took place.

Settlement data were correlated with an Index computed from eastward wind stress during July and August, westward wind stress during September and October, and a weighting factor consisting of Loop Current spin-off eddy timing. The correlation ($r^2 = 0.55$) met the criteria of 95% confidence for a null hypothesis; however, the statistic was based on only 9 points. The decadal downward trend in settlement matched, in general, the downward trend of the wind stress composite. Most importantly, the statistical relationship between settlement and forcing factors was based upon testing a clearly defined hypothesis, rather than searching through environmental data sets in order to find optimal relationships.

Although favorable physical forcing factors existed in 1991, the Index does not fully explain the exceptionally high magnitude of settlement during that year. Placement of collectors and random patchiness cannot explain the difference since collectors located in the Mobile Bay estuary exhibited exceptionally high settlement in 1991 (Spitzer and Heck, this volume). Only 55% of the settlement variance was explained, thus there is still considerable uncertainty in defining the complex relationship between environment and settlement. The influence of biotic factors was not considered, but is recognized as having the potential to affect recruitment processes. The testing of this hypothesis was the fundamental first step in deciphering the complicated interplay of factors thought to influence critical early life history stages of the blue crab.

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