

7-1-1999

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Johnson, D. R., Perry, H. M. (1999). Blue Crab Larval Dispersion and Retention in the Mississippi Bight. *Bulletin of Marine Science*, 65(1), 129-149.

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BLUE CRAB LARVAL DISPERSION AND RETENTION IN THE MISSISSIPPI BIGHT

Donald R. Johnson and Harriet M. Perry

ABSTRACT

A conceptual hypothesis relating physical forcing to dispersion and retention was developed for blue crab larvae within the Mississippi Bight. The spawning period for blue crabs in the northern Gulf of Mexico is protracted. Hatching of eggs occurs near the barrier islands and mouths of coastal bays from March through October. Larvae are released on ebbing tides and spend the next 30 to 50 d offshore where they develop through seven zoeal stages before undergoing metamorphosis to megalopae. Duration of the megalopal stage is variable but generally persists from 6 to 20 d. Blue crabs recruit to Gulf estuaries as megalopae. During the critical planktonic phase in their life history, larvae are subject to the vagaries of seasonal circulation patterns which can either return them to nearshore where they can successfully settle, or lose them at sea. Archived currents from a 3-dimensional, primitive equation, sigma-coordinate model of the Gulf of Mexico, driven by climatological winds and damped to surface salinity and temperature, were used to study advection of blue crab larvae in the Mississippi Bight. Data suggest that seasonal circulation patterns driven by average wind stress provide a window of opportunity for blue crab larval dispersion offshore and return nearshore during the appropriate period in their development for settlement as megalopae. In the Mississippi Bight, this window usually occurs between April and October. Large basin-scale events, such as Loop Current intrusions and spin-off eddy generation, may interrupt this circulation pattern and change the settlement success rate. Variations in the seasonal forcing, due to anomalous winds, or basin-scale events may contribute to fluctuations in levels of harvestable adult blue crabs.

The objective of this study was the development of a conceptual hypothesis relating physical forcing to dispersion and retention of blue crab (*Callinectes sapidus*) planktotrophic larvae in the Mississippi Bight. The reproductive strategy of the blue crab includes a phase which involves dispersion of larvae offshore under the control of surface advective currents. Retention of a planktonic larval stage in portunid crabs serves as a mechanism for dispersal, for gene flow between populations and for colonization of new habitats (McConaugha, 1992). Indeed, geological evidence has suggested that there is a direct positive correlation between species longevity of benthic marine invertebrates and the retention of a planktonic larval stage (Jackson, 1974; Jabonski and Lutz, 1983).

Female blue crabs molt and mate in the brackish waters of the upper estuary. Molting and mating occur from March through November in the northern Gulf of Mexico. After insemination, the female returns to more saline waters in the lower estuary, where spawning usually occurs on an ebbing tide in the spring, summer and fall (Perry and Stuck, 1981; Steele and Perry, 1990). Newly hatched larvae are transported from the estuary in seaward flowing surface waters. Subsequent development in offshore waters includes seven or occasionally eight zoeal stages with a duration of approximately 30 to 50 d before metamorphosis to the megalopal stage (Costlow and Bookhout, 1959; Costlow, 1967; Bookhout and Costlow, 1975; Sulkin, 1978). Larvae and postlarvae exhibit behavioral adaptations that promote export from coastal spawning areas and subsequent recruitment back to the estuary (Sulkin et al., 1980; Sulkin and Van Heukelem, 1982).

Recruitment to Gulf estuaries occurs in the megalopal stage (Stuck and Perry, 1981; Perry and Stuck, 1982; Perry et al., 1995).

Sulkin and Van Heukelem (1982) proposed a model for offshore recruitment based on behavioral traits of *C. sapidus* larvae and postlarvae. They noted that profound changes in behavior occur in the megalopal stage which result in a depth regulatory mechanism of high precision. Late-stage megalopae (near settlement) develop vertical migratory behaviors that favor shoreward transport. Recent studies suggest that this change in megalopal migratory behavior is mediated by chemical cues associated with settlement sites (Forward and Rittschof, 1994). Olmi (1995) noted that the change in behavior of megalopae as they approach estuarine waters was reflected in their distributions in the water column: from a surface orientation offshore to tidally-related vertical migration within the estuary. He provided direct evidence of vertical migration of megalopae by monitoring their occurrence in the water column during different stages of the tidal and diel cycles. He found that megalopae in the York River, Virginia, achieved up-estuary transport via tidally-related vertical migration. The ability of megalopae to migrate allows them to take advantage of tidal flood currents and estuary bottom compensation currents for settlement in nearshore areas that provide food and refuge from predation (Olmi, 1995). There are indications that the megalopal stage can be prolonged by changing environmental conditions which could affect dispersal and settlement success (Sulkin and Van Heukelem, 1986). Prolongation of the megalopal stage could prove advantageous in allowing megalopae more time to encounter suitable hydrographic conditions; however, it must be assumed that recruitment would be unsuccessful if the planktonic zoeal larvae were too far offshore at the time of megalopal metamorphosis.

The role that physical transport processes play in shaping population demographics of marine species with planktonic larval stages has been well established (McConnaughey et al., 1992; Olmi, 1995). Both pre-settlement and post-settlement processes are important determinants of levels of harvestable adults. Pre-settlement processes affecting recruitment success include both biotic (fecundity, behavior, predation) and abiotic (currents, winds, tides, lunar phase, water quality parameters) factors; however, abiotic variables are thought to be the initial regulators of year class strength. Wind stress is an especially attractive abiotic factor for inclusion in population predictive models (Hester, 1983) since it plays a significant role in forcing surface currents over the shallow shelf regions and it is relatively easy to monitor.

Several recent papers have provided conceptual models for dispersal and recruitment of blue crab larvae within the Mid-Atlantic Bight (MAB) and these are reviewed by Epifanio (1995). In the MAB spawning takes place on an ebbing tide with the buoyant larvae ascending into the near-surface layer where they come under the influence of wind driven surface currents (Provenzano, et al., 1983; Epifanio, 1995). Larvae remain in surface waters through the duration of zoeal and early-stage megalopae development (McConaughy et al., 1983). The joint seasonal spawning and wind patterns in the MAB appear to provide a mechanism for dispersal while maintaining the majority of the cohorts near to the parental population. In the MAB, a significant correlation was found between yearly variations in the wind patterns which drive the coastal currents and harvest of adult blue crabs in subsequent years (Johnson and Hester, 1989). It is suggested that the northern Gulf of Mexico blue crab population follows a similar pattern of dispersal and retention.

In this study the idea is tested that seasonality of spawning occurs with seasonal wind driven circulation patterns which act to retain larvae within the Mississippi Bight and to

bring them near shore after offshore dispersion. Surface currents from a climatologically forced basin-scale numerical model of the Gulf of Mexico were used to examine larval advection pathways in the Mississippi Bight and to provide a basis for relating larval success to ambient currents. Basin-scale events, such as Loop Current spin-off eddies and their effects on the coastal circulation in the Mississippi Bight may also influence recruitment success. Blue crab fisheries are characterized by large inter-annual variations in abundance attributed, in part, to recruitment success. Large-scale fluctuations in levels of harvestable adult blue crabs can cause instabilities in the fishing and processing sectors and create uncertainties in resource management. By understanding the advective pathways and the seasonal variations in forcing which drive them, we hope to develop a hypothesis relating hydrographic and meteorological conditions in the Mississippi Bight to larval success.

THE SETTING AND THE CIRCULATION MODEL

The Gulf of Mexico is a complex system with unique physiographic and hydrographic features. The Loop Current is the dominant hydrologic feature in the Gulf of Mexico and is known to shed cyclonic (Elliott, 1979; Vukovich and Maul, 1985) and anticyclonic (Cochrane, 1972; Elliott, 1982) eddies that affect circulation patterns in the eastern and western Gulf, respectively. Coastal climatology of the northern Gulf is largely dictated by the subtropical Azores-Bermuda High (Eleuterius and Beaugez, 1979; Ward, 1980). Onshore 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 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). Wind driven circulation in the Gulf generally follows seasonal patterns.

Figure 1 shows the Gulf of Mexico and the Mississippi Bight setting for this study. Modeled surface currents from July of model year 1 are also shown in this figure, at the time of breaking off of a Loop Current spin-off eddy. The Loop Current, as part of a strong western boundary current, enters the Gulf of Mexico through the Yucatán Straits between Mexico and Cuba. It forms its loop as it turns anticyclonically in the Gulf to exit through the Straits of Florida before passing into the North Atlantic as the Gulf Stream. The distance of intrusion of the loop into the Gulf of Mexico varies slowly in time, with intrusions commonly occurring at intervals of 8–10 mo. Toward the end of a strong intrusion, the current loops back onto itself and pinches off to form a separate eddy with a diameter of 200–300 km. This eddy, with its comparatively large content of high salinity, high temperature Caribbean Water migrates into the western Gulf, under the influence of the earth's rotation, where it decays through friction and by breaking into smaller eddies. Its identification as a spin-off eddy can be retained for more than a year following break off. Hence several spin-off eddies may exist in the Gulf at the same time. After break-off occurs the original current reattaches itself across the entrance to the Gulf and begins a new intrusion.

The intrusion and eddy shedding are the result of instability processes (Hurlburt and Thompson, 1980), hence the timing cannot be readily predicted. Although much is known about the processes of formation and movement of the Loop Current and its spin-off eddies, we know very little about the effects that these processes have on shelf circulation. There are indications, however, from satellite infra-red imagery and from satellite altimetry that the effects can be important, especially where canyons cut across the continental shelf break.

The instability process of the Loop Current and its influence on shelf circulation is an intrinsic part of our study. In essence, Hurlburt and Thompson (1980) discovered that the Loop Current intrudes, grows, pinches off to form an eddy, reattaches and intrudes again in a cycle of 8–10 mo. This is done by the model even though the amplitude of the inflow through the Yucatán Straits is

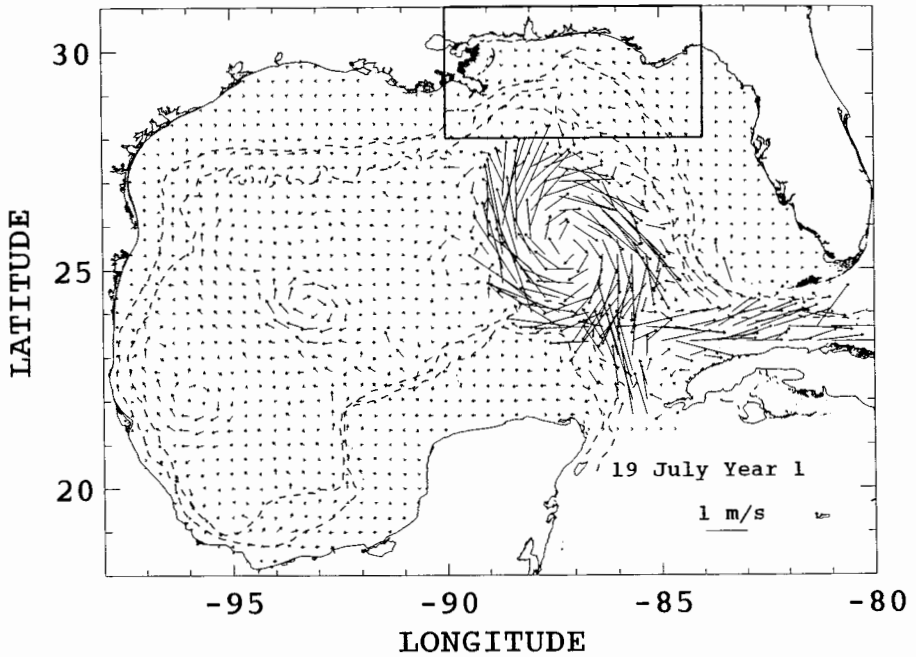


Figure 1. Study location in the Gulf of Mexico with modeled surface currents, subsampled for clarity, for July of model year 1. During this time, the Loop Current has reached maximum intrusion and is in the process of shedding an eddy. The Mississippi Bight focus of the study is shown outlined by the rectangle.

held constant; it is a process involving natural instability of the current itself. In order to determine something of the influence that this process can have on the shelf, we use a climatologically forced model (long term monthly averaged wind stress and sea surface temperature and salinity) with constant inflow conditions, and run it over four model years. Since the wind stress is repeated yearly, the principal inter-annual variations must come from differences due to the dominating deep basin Loop Current processes.

The Mississippi Bight is roughly bounded by Apalachicola in the east and by the Mississippi River in the west (Fig. 2). The DeSoto Canyon is a prominent feature in the center of the Bight, cutting a trough from the deep basin onto the continental shelf. Previous studies have observed Loop Current intrusions into this canyon (Huh et al., 1981). Numerous bays provide excellent habitat for blue crab populations. In the western part of the Bight, barrier islands separate the shelf from several sounds (Mississippi Sound, Chandeleur Sound and Breton Sound) that also provide habitat for various life history stages.

The Gulf of Mexico circulation model was developed and run on the U.S. Navy's CRAY Y-MP 8 supercomputer by Choi and Kantha (1997). It is a three-dimensional, primitive equation-based, sigma-coordinate formulation of the model originally developed at Princeton University by the Mellor group (Blumberg and Mellor, 1983). The model grid has a horizontal resolution of 1/12th degree in longitude and latitude (about 8–9 km), and 21 levels in the vertical. The vertical scale is stretched in order to resolve the surface and bottom frictional boundary layers. The model has a free surface and uses split-mode technique to solve the fully nonlinear, baroclinic governing equations (Kantha and Piacsek, 1996). It uses a two-equation second-moment closure formulation (Kantha and Clayson, 1994) to solve explicitly for turbulent mixing. The model is initialized with 1 degree Levitus annual hydrographic climatology and forced with Hellerman monthly climatological winds. The winds are linearly interpolated between mid-months to produce a smooth transition. Damping

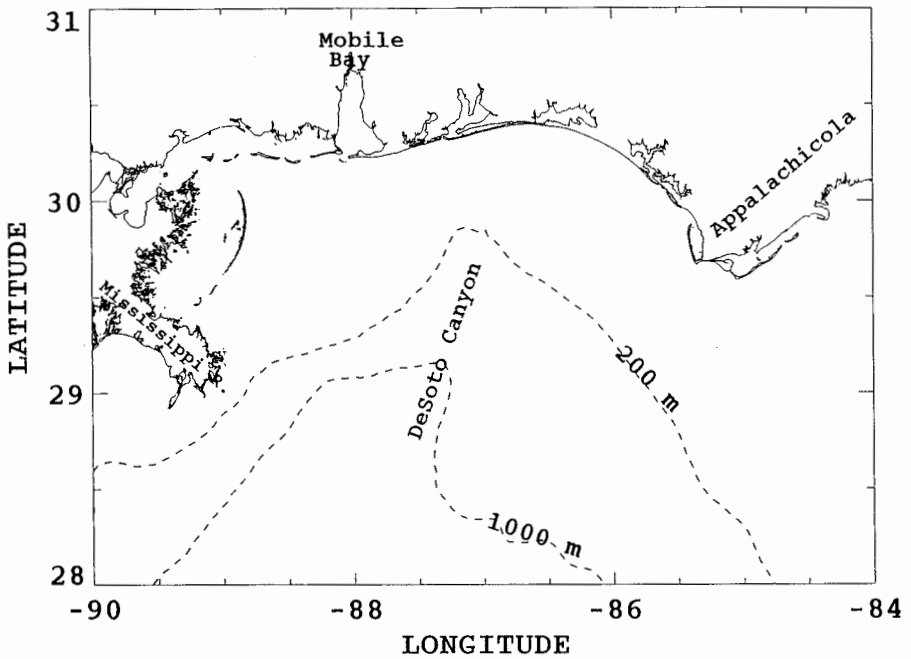


Figure 2. The Mississippi Bight extends from Apalachicola to the Mississippi River Delta. Numerous estuaries and sounds provide excellent habitat for blue crabs, and the DeSoto Canyon provides communication between shelf and deep basin dynamic processes.

to seasonal sea surface temperature and salinity is used in place of prescribing heat and salt fluxes. Special care was taken to adjust the port conditions at the Yucatán Straits and the Florida Straits in order to prevent imbalances due to mass redistribution. The model does not include tidal effects or river outflow. Although tidal currents will not be of direct advective importance for the objectives of this study due to the differences in time scales, the neglect of river outflow can potentially be more serious. This will be addressed later.

Development of this model was undertaken for the Minerals Management Services for the purpose of oil spill risk assessment in the Gulf of Mexico. This model was an early stage, base version which served for comparison with later more complex versions involving observed forcing (non-climatological). Our approach to the problem was first to form a conceptual understanding of how blue crab strategy involves the general (average) wind patterns and then to test how inter-annual variations in the patterns affects harvestable populations. For this approach, the climatologically forced model is appropriate since it supplies the average wind patterns. In this study we are exploiting an expensive computational project by using the archived resulting model currents, not by running the model as a trajectory following model. From a practical point of view, the model current data could only be archived at 10-d intervals due to storage limitations. With observed forcing, this temporal spacing would highly alias larval trajectories, but with climatological forcing (smoothly ramped monthly averages) it is appropriate to the scales. The disadvantage, as we will discuss later, is that dispersion cannot be as broad as it would be under non-averaged conditions.

Although spawning usually begins in March and ends in October, we tested the relationship between species strategy and environmental conditions by spawning larvae at given points at 10-d intervals during the entire year. The model was run for four model years including spin-up from climatological rest. We estimate that spin-up was reasonably complete after three model months, hence we had 3.75 yrs of model currents to determine larval trajectories. Although climatological

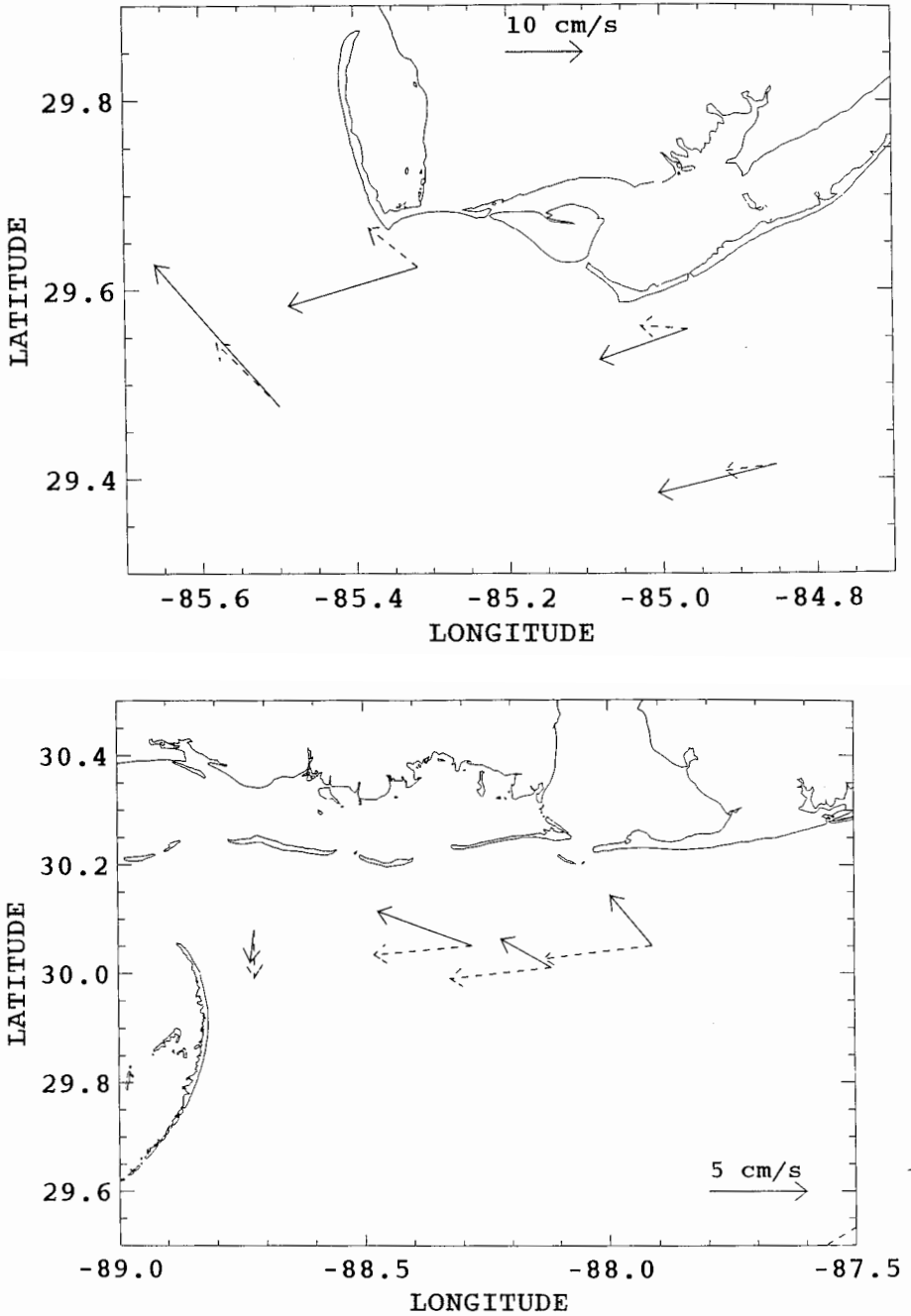


Figure 3. (a) Comparison of modeled surface currents (dashed) during April/May with observed surface currents (solid) during the same time period off Apalachicola. (b) Same for the northwestern Mississippi Bight but averaged over several periods during spring, late summer and winter (Dinnel, 1988).

forcing was the same during each model year, the non-linear nature of the Loop Current and its spin-off eddies impose an unpredictable variability.

A simple scheme was used for estimating trajectories. After spawning, each model-larva advectioned with the currents of that day to a new location, and the process repeated for subsequent days. Each model-larva was treated as a point so that diffusion (Power, 1996), which would normally occur with a patch of newly hatched larvae, was not reproduced. Currents were linearly interpolated between 10-d intervals and between grid points. We expect that, in the gulf, larval metamorphosis through the megalopal stage occurs between 40–50 d. Hence, a model-larva that has not approached to within 10 km of the coast within that time is deemed unsuccessful. This scheme clearly does not address the important subject of larval patch size and horizontal diffusion but is simply a first effort to determine if wind forced circulation during the summer months favors planktonic larval success.

Versions of this model for the Gulf of Mexico have previously been assessed for skill with mixed results. The model appears to produce many mesoscale flow structures similar to those observed by satellite and in-situ surveys. The dynamics of the Loop Current and its spin-off eddies appear to be well represented. However, it was determined that a comparable model with realistic winds (using 1993 wind stress at 12-h intervals) did not well describe shelf circulation events over the Louisiana/Texas shelf (Kirwan, 1997). The difficulty was ascribed to errors in the wind field which masked underlying problems in the model's ability to describe dynamics on the shelf. In our case, we are interested in the general pattern of flow and not in specific events, hence we expect that our model with climatologically averaged wind stress will provide a reasonable foundation for understanding larval trajectories.

A comparison between modeled and observed surface currents in two locations of the Mississippi Bight; off Apalachicola and in the northwestern part of the Bight south of the Barrier Islands, is presented in Figure 3. Off Apalachicola, the strength of the observed currents is greater than the modeled currents by a factor of about 2. The directions are consistently reproduced, with the exception of the comparison closest to Cape San Blas. At that point the observed currents are swinging around a shallow bank, (not shown) which extends outward from the Cape, while the modeled currents are flowing across the Cape. The reason for this discrepancy is that the bathymetry in the model does not resolve this bank, hence the local modeled currents are not adequately reproduced. The stronger observed currents are probably due to the more variable instantaneous winds in comparison to the climatologically smoothed winds in the model run.

In the northwestern Bight, the amplitudes of the currents are very well reproduced, but the observed currents are directed more toward shore than the modeled currents. Other current observations taken near the barrier island passes of Mississippi Sound did not compare well with the model. Our conclusion is that the model is adequately simulating currents over most of the Bight, but that near shore, in poorly defined bathymetry, the currents are not well simulated. For our purposes, the general circulation patterns are sufficient. It is of interest to note that off Apalachicola, the steadiness of the observed currents (defined here as mean divided by standard deviation) was about 0.9, while in the northwestern Bight, the steadiness was much less, about 0.2. This implies that the northwestern Bight is more strongly dominated by wind stress variability.

RESULTS

CIRCULATION.—Climatological wind stress patterns, used to drive the Gulf of Mexico model, are shown for four seasons of the year (Fig. 4). In this climatology, there is a westerly component to the monthly averaged wind stress in all seasons (very small during summer in the Mississippi Bight). This average westerly component is probably responsible for the general surface drift toward the west within the Bight for most of the year. From April through July the wind stress also has a shoreward component, but for the

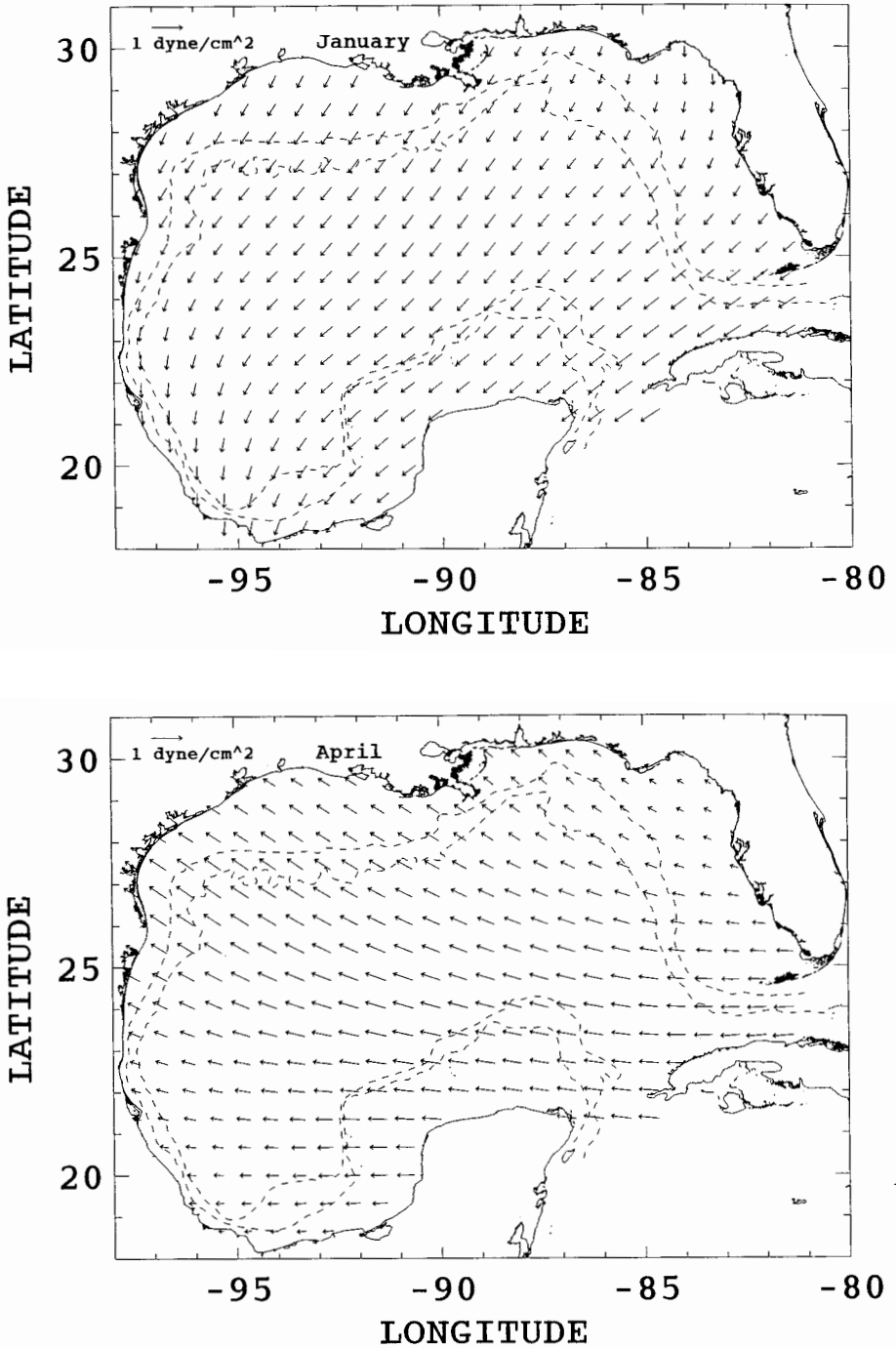
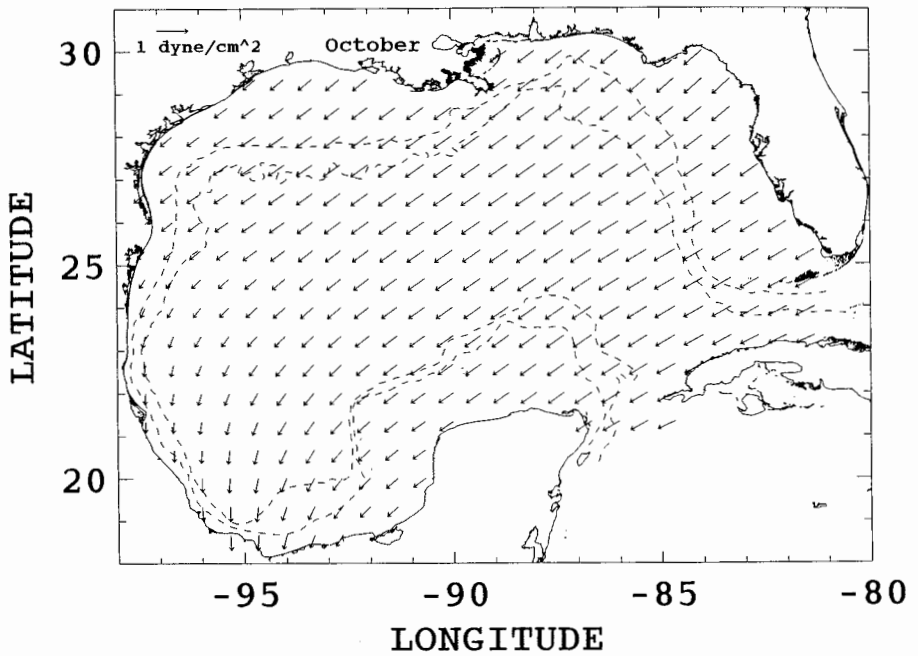
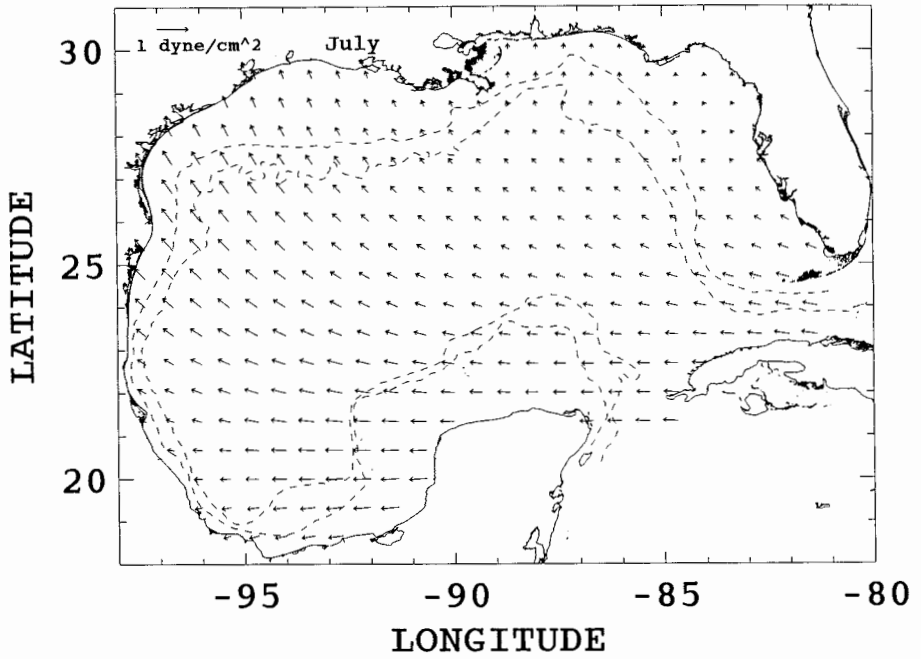


Figure 4. Hellerman monthly climatological wind stress during (a) January, (b) April, (*opposite page*) (c) July and (d) October.



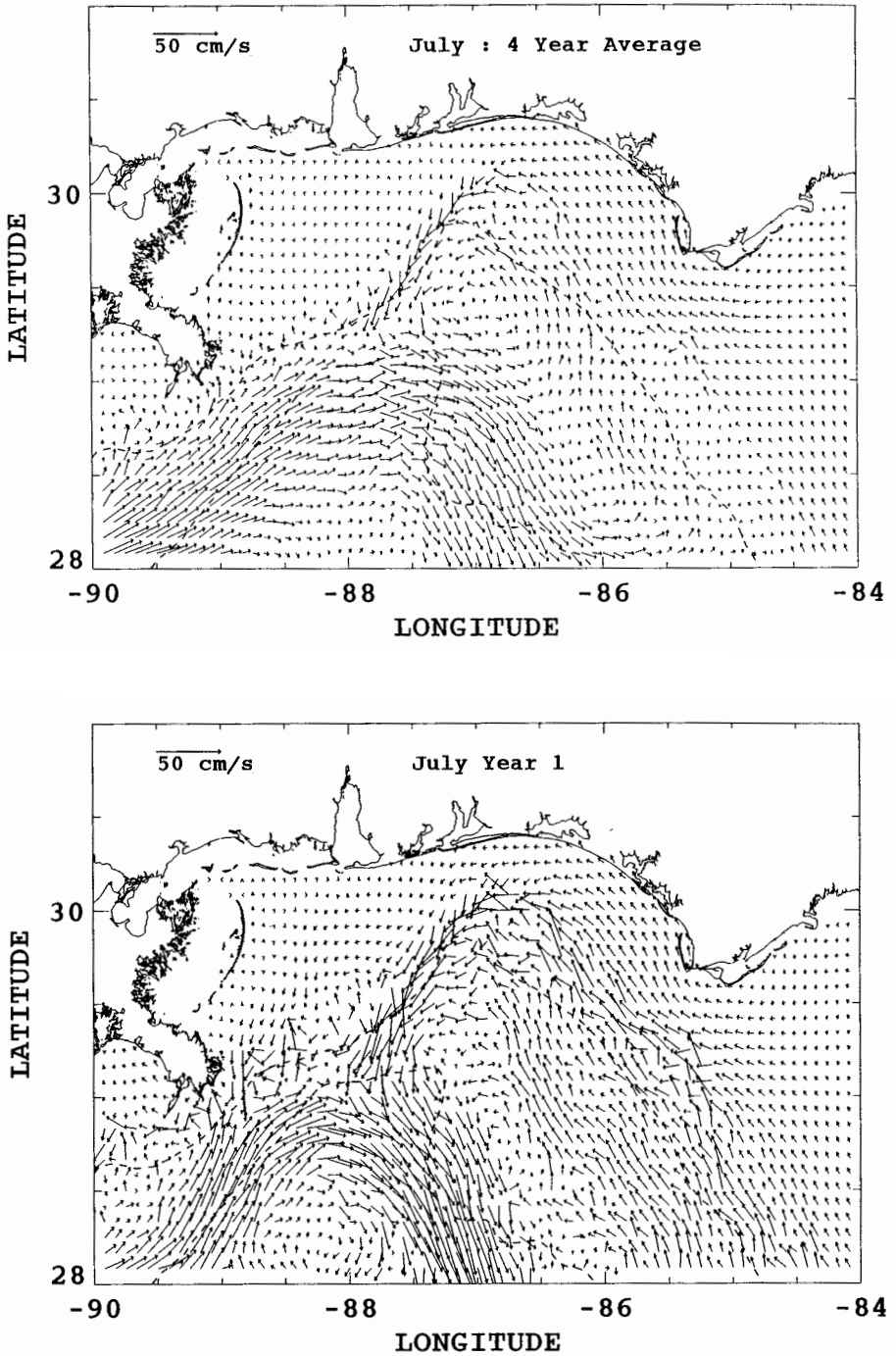


Figure 5. (a) Four year averaged model surface currents for July. (b) Model surface currents for July of model year 1.

majority of the year the component is offshore. We would expect, then that the time for optimal retention of planktotrophic larvae within the Bight would occur during spring and summer, which in fact coincides with spawning peaks.

Since the climatological wind stress applied to forcing the model does not change from model year to model year, variability in current patterns that do occur within the Mississippi Bight must come from the Loop Current instabilities and the impact that it and its spin-off eddies have on shelf circulation. These events appear to modulate the parabolic, shelfbreak flow, allowing greater interaction of the deep basin with the shelf itself (Oey, 1995).

Model current vectors for the month of July are presented in Figure 5. In Figure 5A, the 4-yr average for July shows that the characteristic currents over the eastern portion of the Bight are relatively weak ($<10 \text{ cm s}^{-1}$) and westerly. These westerly currents intensify as they round Apalachicola and enter the Bight. In the western part of the Bight, the currents are weaker still and somewhat confused in direction. All along the near shore region of the Bight, there is a weak shoreward component. This is necessary for successful larval recruitment to inshore adult populations. Further offshore, there is a cyclonic circulation established over the DeSoto Canyon and a fairly strong easterly flow along the continental shelf slope. From the averaged currents it appears that the western part of the Bight may act as a reservoir for larvae advected from the eastern side of the Bight, and that any larvae which are advected too far from shore or into the DeSoto Canyon are in danger of being unsuccessful, i.e., unable to settle in a suitable habitat.

During the first model year, the Loop Current penetrated far toward the north during the summer spawning months and an eddy was shed in July (Fig. 1). As a comparison to the averaged July currents shown in Figure 5a, the currents for July of the first model year (Fig. 5B) show a significantly stronger cyclonic motion in the DeSoto Canyon accompanied by stronger offshore flow in the middle part of the Bight, and a loss from the western Bight by southwestward flow around the Mississippi Delta. We would expect then that this disruption in the characteristic pattern by an eddy-shedding event would adversely affect larval recruitment. An AVHRR image from May, 1993, (Fig. 6) indeed shows a northward penetrating Loop Current accompanied by a cyclonic eddy over the DeSoto Canyon which appears to be pulling water from near shore into the canyon and, subsequently, further offshore. Some evidence of westward streaming around the Mississippi Delta is also implied by the sea surface temperature pattern. It should be expected, then, that northward Loop intrusions and eddy-shedding events during spawning season tend to disrupt the characteristic circulation patterns that favor retention of larvae within Mississippi Bight. And it should also be evident that the Mississippi Bight appears to be dynamically separated by the DeSoto Canyon into an east region and a west region.

In contrast to the characteristic surface circulation patterns seen during the summer, wind stress in the fall produces a more winter-like pattern, with winds strengthening and blowing westward and offshore (Fig. 4C). Figure 7 shows four year model averaged currents for October. The resulting surface circulation pattern shows offshore flow components throughout the Mississippi Bight and a significantly strengthened outflow from the western half of the Bight. Clearly, regardless of other conditions, this circulation pattern sets the end for the yearly recruitment period.

LARVAL SUCCESS.—Spawning locations were selected at inshore grid points of the model and placed at equal longitudinal distances around the Mississippi Bight (Fig. 8). Although there are locations, such as Apalachicola Bay, the barrier islands of Alabama and Missis-

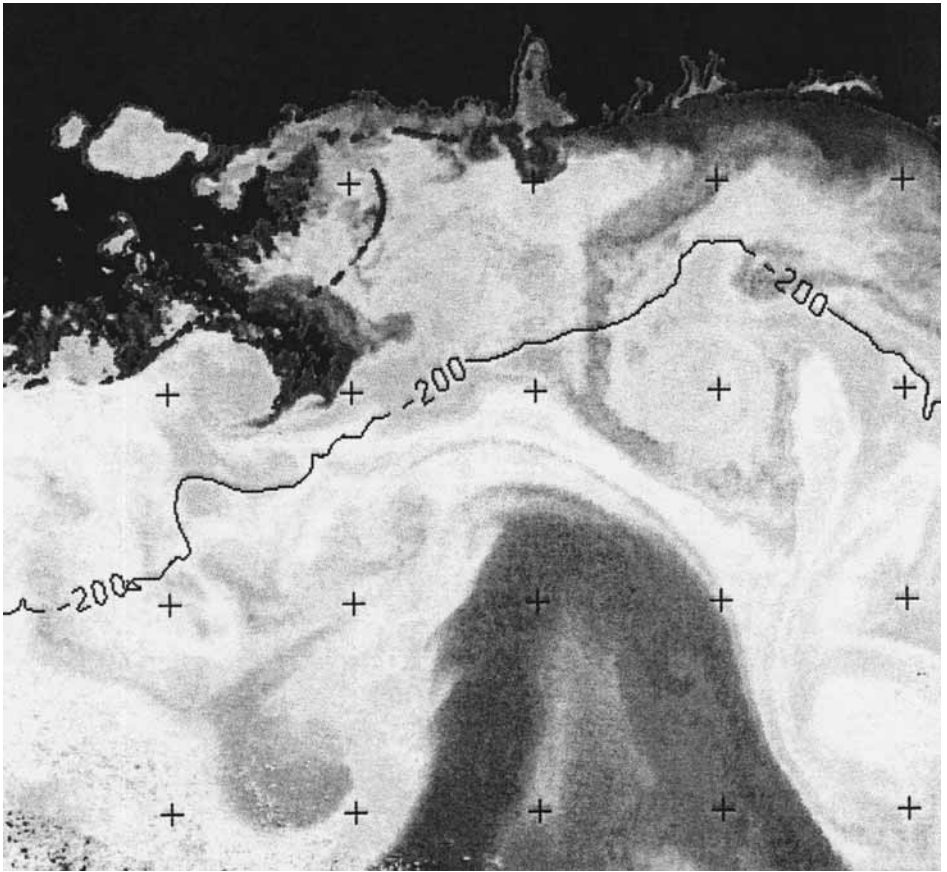


Figure 6. AVHRR sea surface temperature image from the Earth Scan Laboratory of the LSU Coastal Studies Institute. Note northward intrusion of the Loop Current and shelf interaction through the DeSoto Canyon.

sippi, and Chandeleur Sound where large quantities of spawners are known to exist, our objective at this stage of the study was to elucidate characteristic “patterns” of larval advection rather than try to mimic the actual distribution. A realistic population prediction model would certainly have to take a better account of the actual distribution of spawners.

At each of the spawning locations shown in Figure 8, a single particle was released every 10 model days for the 4-yr model run. These particles represented points (non-diffusive) of spawned planktonic larvae advected by model surface currents. The resulting positions were recorded after 50 d, or if they went ashore and were terminated before 50 d. Figure 9A shows the resulting ending locations for the summer high-settlement period of July through September, and Figure 9B shows the resulting December through February ending locations as if winter spawning actually took place. The contrast between the two is significant. In summer, a large number of ending locations are found near the shore where successful recruitment may occur. However, if winter spawning were to actually take place, very few megalopae could be recruited to the adult populations of the estuaries since they are advected too far offshore for successful return. Aside

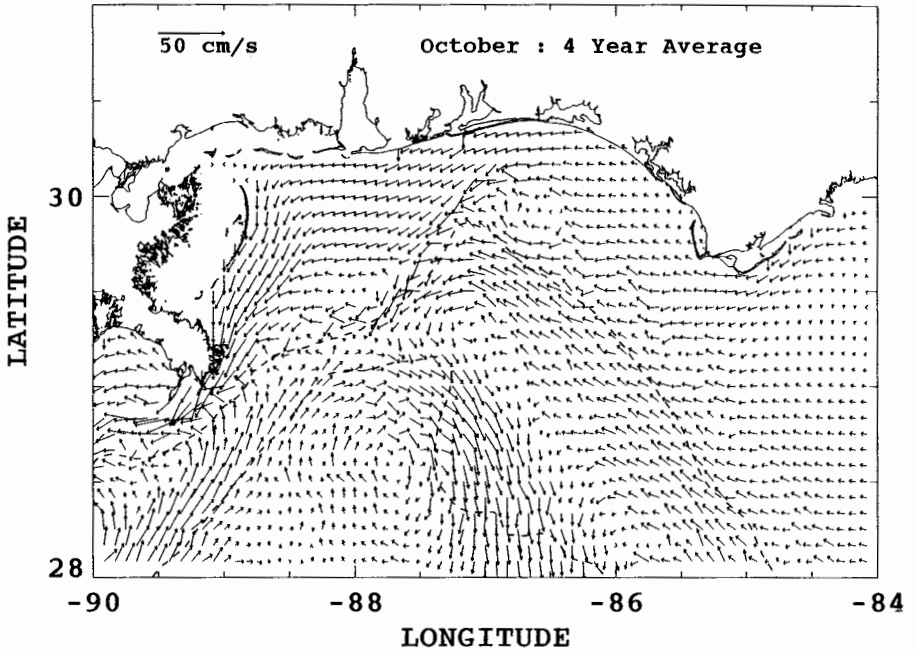


Figure 7. Four year averaged model surface currents for October.

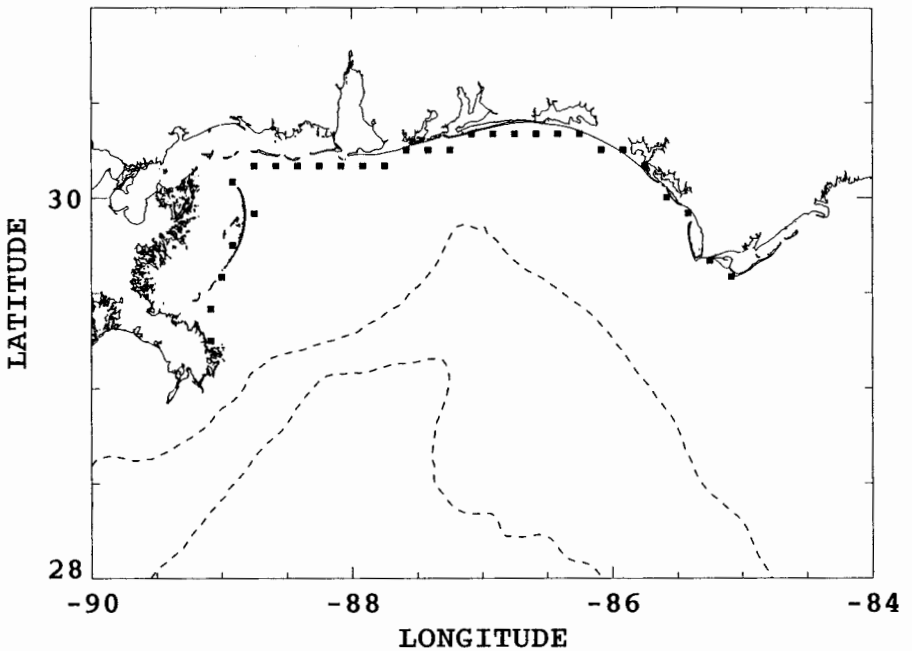


Figure 8. Larval model "spawning" points (small squares).

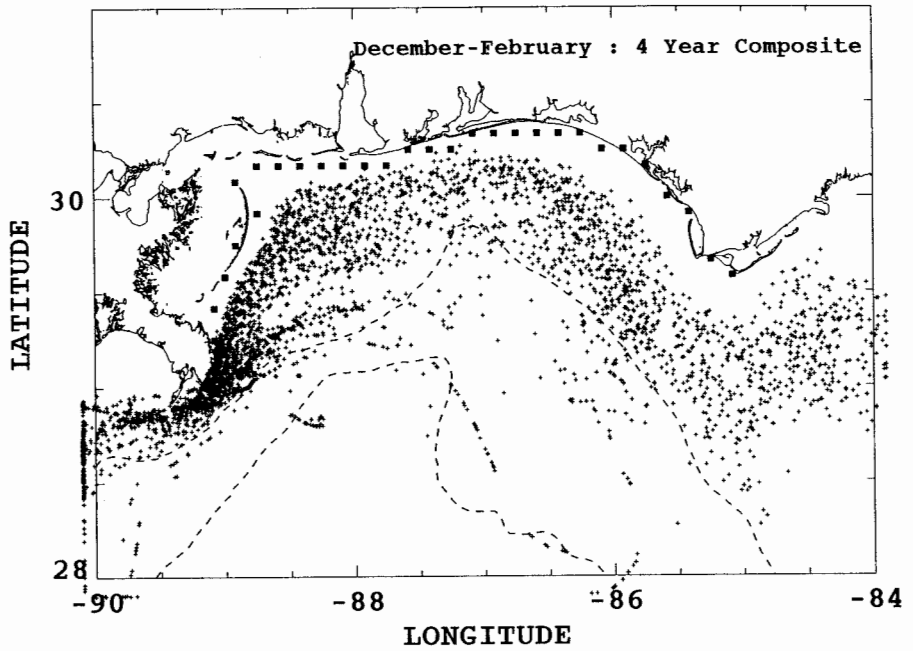
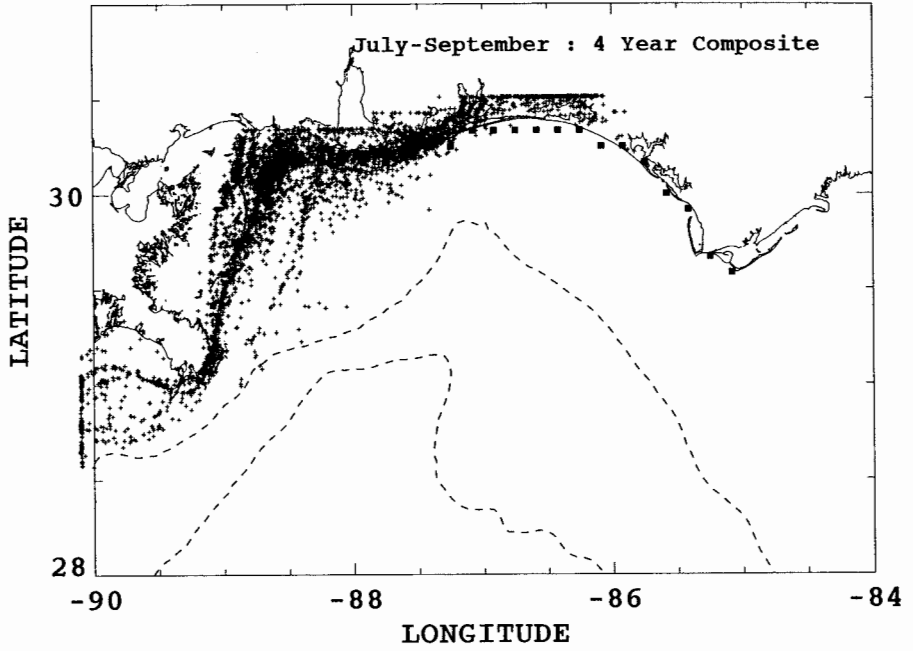


Figure 9. (a) Megalopae modeled settlement sites composited over July to September of four model years. (b) Same but for December to February.

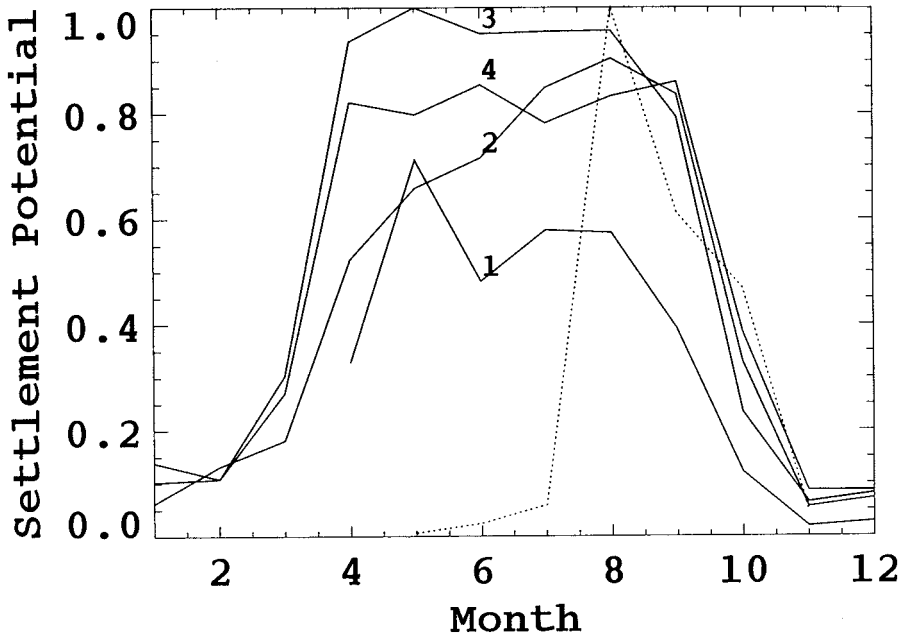


Figure 10. Normalized settlement potential for the four indicated model years (solid lines), derived from model settlement success. Dashed line is the average observed settlement for 1991–1996 at a site in the Mississippi Sound.

from other factors, such as food availability and temperature, this means that environmental conditions during the summer are indeed appropriate for evolutionary advantages associated with larval dispersement, and offers the possibility of population prediction by noting inter-annual variations in the summer patterns.

This summer environmental advantage is graphically depicted in Figure 10, where “settlement potential” is displayed versus month for each of the four model years. Settlement potential is defined as a measure of the number of model larval particles which came within 10 km of the shoreline during a period of 30–50 d after spawning, normalized by the maximum of this measure. We would like to note three points of interest from Figure 10. The first point is that even though larval particles were spawned in the model throughout the year, the success rate is clearly bounded by April–October, a function of the seasonal circulation patterns. The second point is that there is a factor of two difference between the first model year, when a Loop Current intrusion and a spin-off eddy occurred during the important summer months, and the third model year, when the Loop Current was anomalously far to the south during the summer months and the previous spin-off eddy was in the western Gulf. We suggest that this demonstrates that deep basin-scale events do indeed have a significant impact on the shelf circulation.

The third point involves comparison with observed settlement of megalopae in Mississippi Sound averaged over 1991–1996 (Perry et al., 1998) and shown in Figure 10. The major settlement occurs during August–October, with a sharp cut-off from October to November matching the cut-off from the model derived settlement potential. But the onset of intensive settlement, as measured by Perry et al. (1999) does not match the onset of

model derived settlement potential, which occurs much earlier. We expect then that the onset of spawning is more dependent on temperature and the availability of food than on the circulation pattern, but the summer circulation pattern offers a window of opportunity for long-term species survival by larval dispersion and may be responsible for the end of the local recruitment season.

DISCUSSION

Several previous model studies in the MAB are relevant to a comparison with the Mississippi Bight. Johnson (1985) applied a simple two-dimensional model, driven by observed winds and an along shore pressure gradient, in order to mimic the dispersal of larval point particles from Chesapeake Bay. Johnson and Hess (1990) simulated dispersal and recruitment from Chesapeake Bay with a three-dimensional, primitive equation, sigma coordinate model driven by wind stress, tides, fresh water inflows and water density gradients. Garvine et al. (1997) modeled transport and recruitment to Delaware Bay using prescribed currents based on a synthesis of the relationship between measured currents and driving by wind and river discharge. All three efforts were successful in either dispersing the larvae into position for successful return or by actually returning a fraction of the larvae by wind induced inflow. In all three cases, the efforts tried to demonstrate that realistic circulation patterns could advect larvae from a point source and return them to that point source for successful recruitment to their parent populations although they acknowledged that contributions from a broader source distribution was possible. Johnson et al. (1984) and Epifanio et al. (1989) clearly demonstrated that circulation patterns in the MAB were sufficient to retain larvae within the Bight and in many cases in the vicinity of the parent estuary.

Both Chesapeake Bay and Delaware Bay are large point sources of blue crab larvae. However, in the Mississippi Bight with its many estuaries, inlets and sounds, the distribution of spawners is more like a line source. In this case, we might expect that larval dispersion contributes to a large offshore pool from which recruitment is accomplished through vagaries of seasonal and inter-annual circulation patterns.

Using the results of a highly sophisticated climatologically forced numerical model, we have demonstrated that a window of opportunity annually occurs between April and October in the Mississippi Bight for larval offshore dispersion and inshore recruitment. Although the actual onset and termination dates of spawning and settlement are probably controlled by other factors, this window of favorable circulation patterns, must exist for larval survival strategies which include a planktotrophic stage.

The retention-favorable circulation pattern in the Mississippi Bight includes a surface drift shoreward and toward the west during late summer, with a consequential accumulation of megalopal settlements in the western part of the Bight. Interruptions of the pattern can occur with northward intrusions of the Loop Current and the generation of spin-off eddies. These events interact with shelf currents in the Mississippi Bight, disrupting the normal circulation patterns. If this disruption occurs during the critical offshore planktonic larval stage, then local recruitment to the adult populations from that year's cohorts will be in jeopardy. Although we did not have the opportunity of testing various wind patterns in the model, we expect that uncharacteristic winds during summer will also be significant in changing the settlement success rate. There are data to suggest that changes

in wind stress during critical larval development periods may affect numbers of megalopae available to settle. Perry et al. (1998) analyzed meteorological data associated with settlement in Mississippi Sound and found that the year of lowest settlement occurred in 1996, a year characterized by anomalous wind patterns and intrusion of the Loop Current onto shelf waters of the northern Gulf. In comparing years of extreme high and low settlement, they noted that major differences in the strength and direction of the east/west (along-shore) component of wind stress occurred in the 2 yrs and in the position of the Loop Current.

If the favorable circulation pattern involves a westward drift and an accumulation of megalopae in the western part of the Bight, then how are populations in the eastern part of the Bight sustained? Characteristic surface drift patterns during summer are northward along the west coast of Florida, and then westward from Apalachee Bay (Figs. 1,5). This would of course supply the eastern part of the Bight from populations to its east. But this is not an ultimately satisfactory answer since the eastern and southern sources of this flux must be resupplied sometime. As one possibility, we suggest that years with anomalously eastward wind stress patterns during the summer months produce a flux of larvae toward the east and south. This would mean, then, that blue crab larvae do not necessarily recruit to the same estuary or sound where they were spawned. Rather, it means that they become part of a pool which is dispersed over a fairly broad area and from which local recruitment is drawn.

Although the circulation model used in this study is highly sophisticated, it has some limitations, especially in its representation of near shore dynamics. In addition, our limited objectives have defined the level of complexity needed. For example, the approach that we have used to advect larvae is extremely simple and straightforward since we are interested in large scale advective processes. An approach which attempts to accurately quantify megalopal settlement should include weighted sources, relatively large spawned patches which subsequently diffuse (Power, 1996) and at-sea larval mortality (Garvine et al., 1997).

It should be noted (Fig. 9A) that some of the particles in this study ended over dry land. A 10 Nm buffer zone past the inshore grid points (currents within the buffer zone were given the same value as the last grid point) was allowed in order to cover for the fact that large scale numerical models do not represent the near shore area very well. Although it should be expected that a near shore coastal buoyancy layer, due to freshwater runoff, provides something of a barrier to prevent the larvae from going on shore too quickly (hence the buffer zone), the lack of an adequate coastal buoyancy layer (although runoff was omitted, the model was damped to climatological temperature and salinity, which produces a weak buoyancy layer) is indeed a difficulty which needs to be addressed in future work.

Runoff is at an annual low in late summer, which should partially mitigate the lack of model runoff. In addition, it should be expected that freshwater discharge, under the effects of the earth's rotation, will turn westward along the Mississippi Bight in the same direction as the offshore surface drift. Reduced wind mixing during summer will allow a strong halocline to exist with decoupling from bottom friction, which will allow greater advective influence on the buoyancy layer by wind stress. Overall, then, we would expect that the addition of a stronger coastal buoyancy layer would (1) advect larvae more readily toward the western part of the Bight and (2) provide a soft barrier to immediate inshore return. The lack of good model representation in the near shore, then, does not change our

original conclusions, but it is bothersome and may need to await improvements in near shore modeling.

A more severe limitation of this study has been the use of climatological winds rather than observed winds. We were primarily constrained by the availability of climatological model results archived at 10-d intervals. We did have the opportunity of testing archived model results from the 1993 wind field which were, of course, aliased by the 10-d archival rate and therefore not a reliable measure of individual larval success. However, this test did give an indication of differences with the climatological results on a more statistical basis. Although the fundamental results were the same, e.g., a flux of larval particles into the western basin and successful summer recruitment, there was clearly a much broader dispersion, as could be expected. Further study needs to be done with a more realistic wind field to test the concept of eastward restoration of the average western flux of larvae: whether it is done by anomalous inter-annual winds or by anomalous wind events which occur during each spawning season.

Our conceptual hypothesis, then, suggests that seasonal circulation patterns driven by climatologically averaged wind stress produces a window of opportunity for blue crab larval dispersion offshore and return near shore after 30 to 50 d for successful settlement as megalopae. This window, on average, occurs between April and October in the Mississippi Bight. Large basin-scale events such as Loop Current intrusion and spin-off eddy generation interrupt this circulation pattern and may change the settlement success rate. It also suggests that vagaries in the wind field, either through anomalous wind events during the season or by inter-annual variations, can change the success rate and can redistribute larvae from the offshore pool.

ACKNOWLEDGEMENTS

We are grateful to Lakshmi Kantha and J. K. Choi for use of the archived model results in this paper and for numerous discussions on the model setup and performance. S. Dinnel graciously provided current meter data in the northwestern Mississippi Bight. Kirsten Larsen, Christine Trigg, and Marjorie Williams aided in data collection. The Earth Scan Laboratory of Louisiana State University's Coastal Studies Institute put the AVHRR image on the internet for use by MMS sponsored investigators. The principal support for D. Johnson was provided by Mineral's Management Services under contract 2-4350-0009 with R. Labelle as manager and by the Office of Naval Research under the Naval Research Laboratory's Shelf Break Exchange Processes project. Support for H. Perry was provided by the National Marine Fisheries Service (NMFS), Interjurisdictional Fisheries Grant NA66FI0184, the Mississippi Department of Marine Resources, NMFS Grant NA76FK0428, and the Gulf Coast Research Laboratory.

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DATE SUBMITTED: March 3, 1998.

DATE ACCEPTED: February 5, 1999.

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