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Red Snapper Larval Transport in the Northern Gulf of Mexico

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Abstract.—This study examines the advection of red snapper *Lutjanus campechanus* larvae in the northern Gulf of Mexico. The potential for repopulating the eastern Gulf stock through larval transport from the more populous western stock is addressed. Transport pathways across topographic features that inhibit alongshelf flow (e.g., the Mississippi River delta, DeSoto Canyon, and the Apalachicola peninsula) and interregional larval transport are considered. An advective field of currents is developed from a large database of drifter and moored currents, augmented by an operational model to fill gaps. The starting points for larval transport are the locations and day of the year of larval captures from the Southeast Area Monitoring and Assessment Program ichthyoplankton surveys. Because the field of currents is derived from near-surface observations and the depth distribution of larvae is uncertain, findings are expressed in terms of maximal transport pathways. Transport pathways were principally vectored toward the west during September, October, and May under the influence of relatively strong climatological westward wind stress. Eastward pathways occurred in June, July, and August under the influence of weaker shoreward wind stress. Westward transport pathways past the Mississippi delta were found near the delta, whereas eastward transport pathways were found in deeper waters beyond the continental shelf break, away from typical juvenile settlement habitat. Water movement from east to west across the Apalachicola peninsula occurred in the fall, suggesting the potential for genetic exchange from the eastern to the western Gulf. Eastward water movement across the Apalachicola peninsula occurred in July, but only along the outer shelf.

Red snapper *Lutjanus campechanus* is one of the most important food fishes in the Gulf of Mexico (GOM), its annual U.S. commercial landings averaging 3,145 metric tons between 1950 and 2005 (National Marine Fisheries Service, Fisheries Statistics Division, personal communication). During this period, a dramatic shift occurred in landings by geographical area. In the 1950s, commercial landings of red snapper from Florida's Gulf coast were nearly twice as great as those from the rest of the U.S. GOM combined (Texas, Louisiana, Mississippi, and Alabama). By 2005, however, the Florida west coast landings amounted to only about 17% of the rest of the U.S. GOM harvest. Currently, the abundance of red snapper in the western GOM is estimated to be three times greater than that in the eastern GOM (SEFSC 2005; Porch 2007).

There are two principal mechanisms for the dispersion of red snapper populations: adult migration and larval transport. The movement of adult red snapper has been studied extensively. Early tagging studies (Beaumariage 1969; Beaumariage and Bullock 1976; Szedlmayer and Shipp 1994) found that red snapper were sedentary, associated with bottom structure, and exhibited site fidelity (generally moved <5 km). A more recent study by Patterson et al. (2001) off the Alabama coast found that adult red snapper moved further than previously thought when hurricanes occurred between tagging and recapture. When a hurricane intervened, the mean distance of movement was 42.4 km and the farthest distance moved was 352 km, even though 36% of all tagged and recaptured fish were still taken within 2 km of the release site. These authors concluded that red snapper movement over time was sufficient to maintain a single, genetically homogeneous stock in the northern GOM. This conclusion was in agreement with the results of genetic data provided by Camper et al. (1993), Gold et al. (1997), and Heist and Gold (2000), who found little genetic diversity among sites off Texas, Louisiana (west of the Mississippi River delta), and Alabama. The genetic studies did not include fish taken from the West Florida continental shelf.

The second mechanism for the dispersion of red snapper involves larval transport by ocean circulation. Rough scaling, using characteristic shelf currents of 20 cm/s, suggests that eggs and larvae could be carried as far as 480 km during a 4-week planktonic stage.

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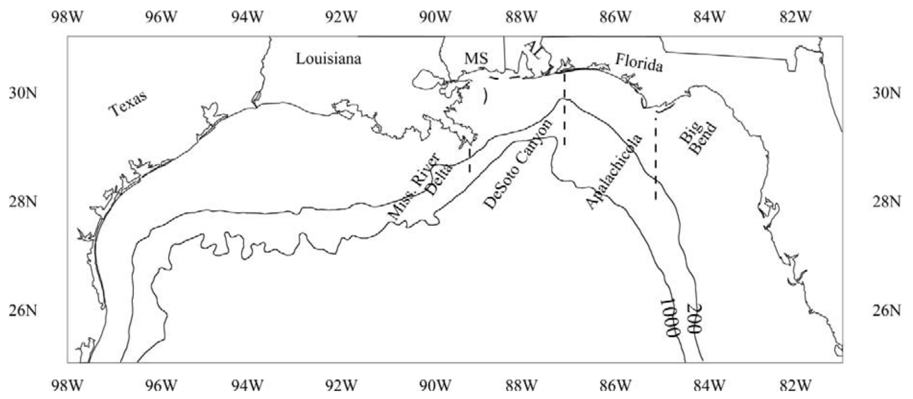

FIGURE 1.—Area in which the transport of larval red snapper was studied. The dashed lines delineate topographic impediments to alongshore flow.

Although larval transport may play a role in dispersion into recruitment-depauperate areas and the maintenance of stock homogeneity, little attention has been paid to this mechanism. In the northern GOM, the continental shelf is broken by several topographic features that narrow the shelf width and potentially inhibit alongshore transport over large distances, namely, the Mississippi River delta, DeSoto Canyon, and the Apalachicola peninsula (Figure 1). Fortunately, an extensive set of ocean current observations in the northern GOM, derived from satellite-tracked drifters and fixed current meters, is available to address some of the questions involving larval dispersion. In this study, a field of currents derived from this data set was used to estimate larval transport from location of capture during ichthyoplankton surveys to locations of potential recruitment.

One of the difficulties in the present approach is the lack of information on the depth distribution of later-stage larvae. Because small larvae are consistently observed in neuston samples taken during the day and at night, it seems reasonable to assume that they are subject to surface currents for some portion of their presettlement life history. Most of the larvae captured in the Southeast Area Monitoring and Assessment Program (SEAMAP) samples were in the notochord flexion stage (11–17 d posthatch; Drass et al. 2000), when their swimming capability is developing rapidly. During the latter part of presettlement development, one might expect vertical migration to occur, although there is no reason to expect active regulation of depth for transport. Because currents are generally strongest at the surface and taper with depth, the computed surface transport path length would represent maximal distance. The computed propagule trajectories then are expected to be "optimal"; actual pathways are expected to be shorter and to show broader dispersion around the pathways because of current veering below the surface. The existence of pathways that pass topographic impediments and provide a mechanism for supplying the eastern GOM is of major interest. Interannual variations in wind strength and storm-scale events can produce variations along these pathways. The goals of this study are to estimate the potential extent of larval dispersion by advective transport, the pathways of dispersion, and the implications for geographic separation of stocks.

Methods

Ichthyoplankton survey data.—For this study, observed currents were used to track the transport of red snapper larvae to and from their locations of capture, as determined from systematic ichthyoplankton surveys. Capture data were obtained from ongoing SEAMAP resource surveys in the GOM conducted by state, federal, and university participants in the program. The presence of red snapper larvae in oblique-towed bongo nets (from surface to 200 m or 2–5 m off the bottom) and surface-towed neuston nets from the SEAMAP data set was used to determine the propagule launch points in this study. Sampling was conducted at predetermined stations on a fixed, systematic grid across the U.S. Exclusive Economic Zone. Lyczkowski-Shultz and Hanisko (2007) provide a description of the methodology and the resulting seasonal occurrence, distribution, abundance, and size of red snapper larvae from these surveys.

During SEAMAP surveys, larvae identifiable as red snapper were caught at 672 stations from May through October, most larvae being captured in the months of June, July, and September. There were relatively few plankton samples from August because the primary established resource surveys are always conducted in June and July (SEAMAP Summer Shrimp/Bottomfish

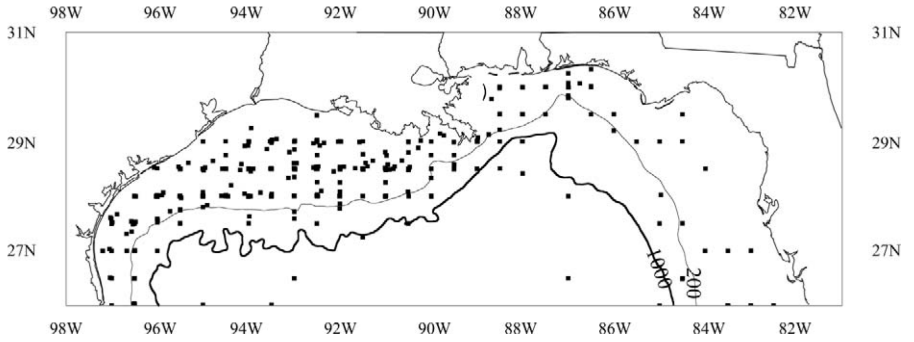

FIGURE 2.—Capture locations of larval red snapper in the SEAMAP survey.

Survey) and in September (SEAMAP Fall Plankton Survey). These two predominant sources of capture also differed in the area of the GOM surveyed. The survey in June and July is conducted from Mobile Bay, Alabama, to Brownsville, Texas, whereas the September survey is conducted across the entire GOM continental shelf from Brownsville to South Florida. Gallaway et al. (1999) described high-value habitat for juvenile red snapper as water depths between 18 and 64 m. Because both adult and juvenile (Gallaway et al. 1999) red snapper are associated with continental shelves, SEAMAP larval captures in water depths greater than 1,000 m (140 captures at 18 locations) were eliminated from this study, reducing the number of launch sites to 654. The possibility of alongshelf transport by deep-basin eddies is considered in the Discussion section. Capture locations (Figure 2) were used as the starting or launch points for advection studies, and the day of the year (hereafter, year-day) of sampling was used for the starting time.

Data on the sizes of red snapper larvae in bongo and neuston nets were taken from Lyczkowski-Shultz and Hanisko (2007). Larvae taken in bongo nets ranged from 2.4 to 12.9 mm body length (BL), with a mean size of 5.1 mm. Larvae taken in neuston nets ranged from 2.7 to 24.0 mm BL, with an average size of 4.4 mm. From monthly length–frequency distributions, the majority of larvae each month were 4.5 mm BL or smaller. The SEAMAP plankton samples also contained many smaller, undeveloped snapper larvae that could only be identified as to the family (Lutjanidae) or genus (*Lutjanus*; Lyczkowski-Shultz and Hanisko 2007). These samples were not included in our data set. In the larval developmental data of Drass et al. (2000), most of the larvae identifiable as red snapper were in the flexion stage of development. The planktonic duration of red snapper ranges from 27 to 30 d posthatch (Rooker et al. 2004). The average size of red snapper larvae in SEAMAP samples suggests that they were in the water column for approximately 11 d before capture: 1 d as eggs (Drass et al. 2000) and 10 d as larvae (Comyns 1995). A 21-d larval drift time accounts for the time interval between capture and settlement of the average size red snapper larvae in SEAMAP samples. Computations of the trajectory of each larva from the SEAMAP capture sites involved backtracking for 11 d and forward tracking for 21 d.

Near-surface currents.—The observational current data set (Figure 3) was formed from a variety of data sources covering a period of 22 years. Both satellite-tracked drifters and moored current meters were used. Drifters were drogued to a depth of 1 m. Moored currents were taken over a range of 2–27 m depth from the surface, with the deeper measurements generally taken in deeper water. The locations and times reported by the satellite-tracked drifters were interpolated to produce average daily drift directions and speeds. Near-surface current observations from current meter moorings were also averaged to daily values. Because observational data were sparse south of 26°N latitude, the study area was restricted to waters north of that latitude.

The daily averaged current vectors from the observational data set are irregular in space and time. To produce a uniformly gridded data set for tracking, each daily vector was tagged with latitude, longitude, and year-day (regardless of year); a moving window of 21 d was applied; and the current vectors within that 21-year-day window were interpolated to a uniform spatial grid. Interpolation to a one-twelfth of a degree longitude–latitude grid (approximately 8–10 km) was done with an exponentially decaying weighting scheme (objective interpolation; Bretherton et al. 1976) in which the correlation length scale was 20 km and the cutoff distance was 50 km. The 20-km-distance scale was chosen to match the typical first-mode baroclinic radius of deformation on the continental shelf (10–30

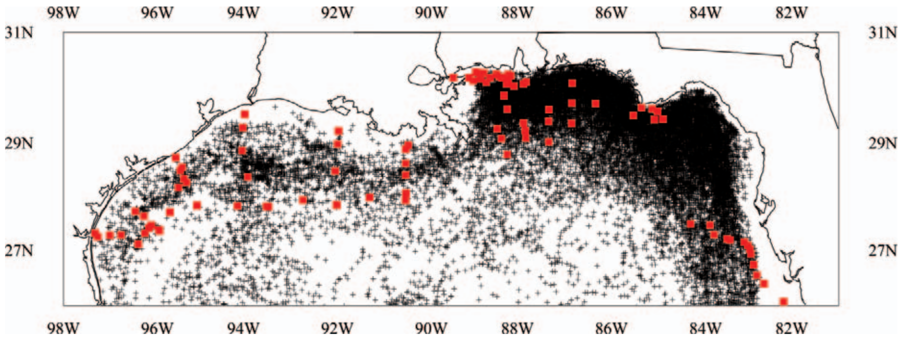

FIGURE 3.—Locations of observational currents. The small black crosses mark the locations of daily vectors from satellite-tracked drifters, the red squares the locations of moored current meters.

km; Gill 1982). The 21-year-day moving window was chosen to match the time scale of larval drift.

Despite the large observational current data set, there were still some areas without sufficient coverage. To fill these data gaps, archived surface current data from an operational nowcast/forecast model of the GOM developed and run by Choi and Kantha (1997) were employed. This model, described in Kantha and Clayson (2000), is a three-dimensional, primitive equation-based, sigma-coordinate formulation of the Princeton Ocean model (Blumberg and Mellor 1983). The model included 21 levels in the vertical resolution and one-twelfth of a degree horizontal resolution in latitude and longitude. Observed wind stress forced the model. Data assimilation of satellite-derived sea surface height and sea surface temperature phase-locked loop current intrusions and spin-off eddies to real events. The model was run from 1993 to 2001. After dropping 1993, which was the model spin-up year, currents at depth level 3 (0.00125 times water depth) were averaged over the eight model years to produce year-day, near-surface currents. As a comparable treatment to the observed currents, the model year-day currents were smoothed over 21 d.

Whenever a grid point had one or no observed data points, model data were included as part of the data set, objectively interpolated to that grid point. Observational data were most dense in the northeastern GOM, east of the Mississippi River delta in waters less than 1,000 m deep (Figure 3). The model-augmented grid points were primarily in deep water of the western Gulf and in very shallow water, that is, the domain edge. In water less than 1,000 m, where red snapper larval advection is most important (Lyczkowski-Shultz and Hanisko 2007), only 11% of the grid points were augmented with model data; thus, the advective current field used for tracking larvae is predominantly from observed currents.

Results

Several definitive studies of circulation in the northern GOM have been made, based on the majority of observational data that contributed to our tracking field of currents (Cho et al. 1998; Yang et al. 1999; Ohlmann et al. 2001; Ohlmann and Niiler 2005; Weisberg et al. 2005). The fundamental circulation patterns during the red snapper spawning season in this study (Figure 4a–c) show agreement with those of the more definitive studies.

In previous studies, investigators concluded that alongshore current patterns on the northern GOM shelf are driven by mesoscale seasonal winds (e.g., Ohlmann and Niiler 2005). From September through May, monthly averaged wind stress is from east to west across the entire northern GOM. Cho et al. (1998) call these the nonsummer months and describe the principal circulation feature on the Louisiana–Texas shelf during this time, determined from fixed-level current meter measurements, as an elongated cyclonic gyre. This finding is visible in our field of currents (May and September [Figure 4a, c]) and is in agreement with previous work by Cochrane and Kelly (1986) and the more recent analysis of drifter observations by Ohlmann and Niiler (2005).

During the summer months of June through August, wind stress is light and directed shoreward. The resulting flow over the Louisiana–Texas shelf is eastward during summer across the entire shelf, the eastward flow being strongest during July (Figure 4b). On the Mississippi Bight shelf (Mississippi River delta to Apalachicola, Figure 1), nearshore currents tend to follow climatological wind stress patterns with westward flow during nonsummer months (Figures 4a, c) and eastward flow during July (Figure 4b). Currents on the outer edge of the northern GOM shelf appear to be driven, in part, by impinging deep-basin eddies (Hamilton et al. 2002; Ohlmann and Niiler 2005),

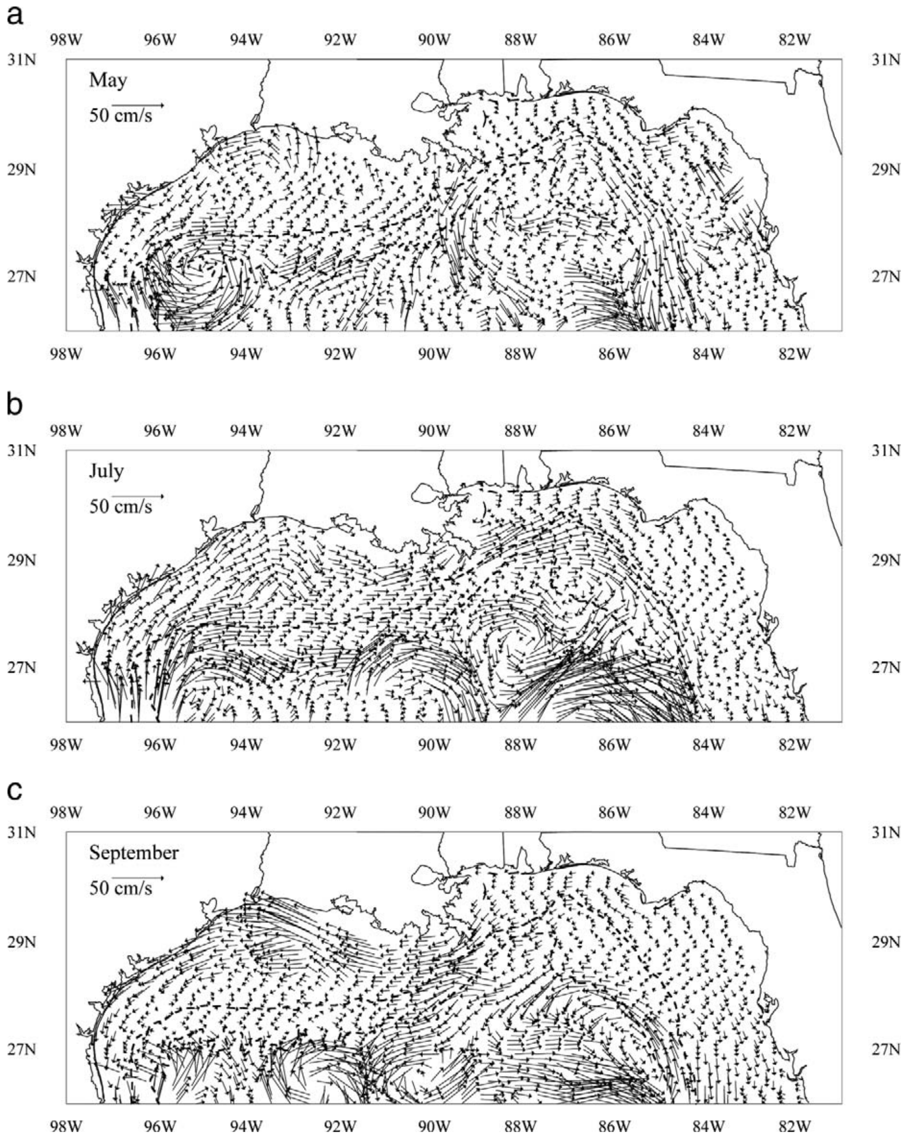

FIGURE 4.—Monthly averaged currents for **(a)** May, **(b)** July, and **(c)** September, spatially decimated by a factor of 5 for better visualization.

with a west-to-east-flowing slope current appearing at times (Figure 4a, b). At Apalachicola, this slope current continues southward and has been associated in that region with wind stress and convergent topography (Yang et al. 1999). It has also been observed in satellite images associated with an episodic chlorophyll plume (Gilbes et al. 1996). In general, the tracking field of currents that we use in our study contains the patterns of circulation observed in the more definitive physical oceanographic studies.

At each of the 654 stations (less than 1,000 m in depth) where red snapper larvae were found during the SEAMAP surveys, a larval "propagule" was released in the current field on the year-day it was sampled. Tests of time stepping (convergence to an end location) suggested that a 0.1-d time step was satisfactory for interpolating the temporal–spatial grid of the current field. Larvae in the SEAMAP samples were not analyzed for age determination, but the average size of sampled larvae indicated an average age of 11 d. To estimate the entire trajectory, an "average" larva at each capture location was tracked forward for 21 d and backward for 11 d. The resulting tracks (Figure 5), displayed at 1-d intervals for all 654 stations, show a

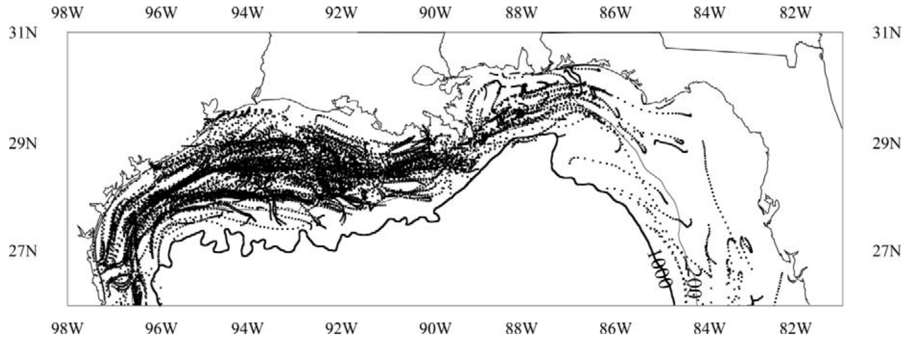

FIGURE 5.—Daily drift points from SEAMAP starting locations and dates. Drifts are computed for 21 d forward from SEAMAP capture and 11 d backward.

distinct difference in coverage from east to west. From DeSoto Canyon westward, most of the continental shelf has the possibility of receiving larvae some time during the spawning season. The western Mississippi Bight and especially the Louisiana–Texas shelf are densely covered with track points. Based on sample dates from SEAMAP and the observed surface currents associated with these dates, the region east of DeSoto Canyon, and especially in the Big Bend region, has limited potential for receiving larvae from spawning activity in the west.

The influence of subgrid scale turbulence was also tested with 10 launches from each site and a diffusive contribution calculated by multiplying the current vector by a factor of 0.1 times a probability density function with unit variance. Although the dispersion pattern broadened and filled, it had little influence on the eastward spread of launched propagules—most likely because of the broad initial distribution of launch points, in contrast to the effect of diffusive transport from a single launch site.

The distribution of tracked points separated by month of larval capture shows distinct seasonal patterns (Figures 6a–f). Captures at only a few stations were made in May and October. In June and July, surveys were conducted west of DeSoto Canyon, and the net transport pathway was found to be to the east as expected from summer wind forcing. In July, some tracks, starting in the western GOM, went eastward across the Mississippi River delta, demonstrating the possibility of larval flux around this impediment. In August, we saw some indications of westward transport pathways near the coast and eastward transport pathways on the outer shelf. In September, the track distribution west of the Mississippi River delta was dense; east of the delta and west of DeSoto Canyon, the distribution was also high. There appears to be good exchange across the Mississippi River delta during this time, most of the transport pathways going west from the Mississippi Bight onto the Texas–Louisiana shelf. This could be expected as climatological wind stress forcing in September changes from a summer northerly pattern to an autumn westerly pattern. In the eastern GOM, there were few larval capture points east of Apalachicola, and no tracks entered this area from the west; thus, enhancement of the Florida west coast shelf by recruitment from the west appears to be limited by characteristic current patterns.

To examine the effect of constricting topographic features on free exchange along the northern shelf, the shelf was divided into basins (Figure 1) according to the three major topographic impediments: the Mississippi River delta, DeSoto Canyon, and the Apalachicola peninsula. Overall, 80% of the propagules that were transported between basins traveled westward across the topographic impediments, and 20% to the east, although these numbers may be biased by the east–west distribution of captured larvae. The propagules that went eastward across the Mississippi River delta, principally during July and August, followed a path over the deeper slope region. Larvae on this deep water path are more vulnerable to deep-basin exchange events (Walker et al. 2005) and loss to the shelf environment. The propagules that went westward across the delta did so during September and in shallower water close to the delta. For all propagules, the average distance traveled was 124.8 km with a standard deviation (SD) of 86.8 km. The average speed of advection was 7.9 cm/s (SD, 4.9 cm/s). The maximum displacement was 486 km and the maximum daily speed was 72.3 cm/s.

The parameters employed in this study represent the best estimate of the advection process based on larval capture data, which are neither geographically nor seasonally uniform. The starting time for tracking was taken from the year-day of SEAMAP sampling on which red snapper larvae were found. However,

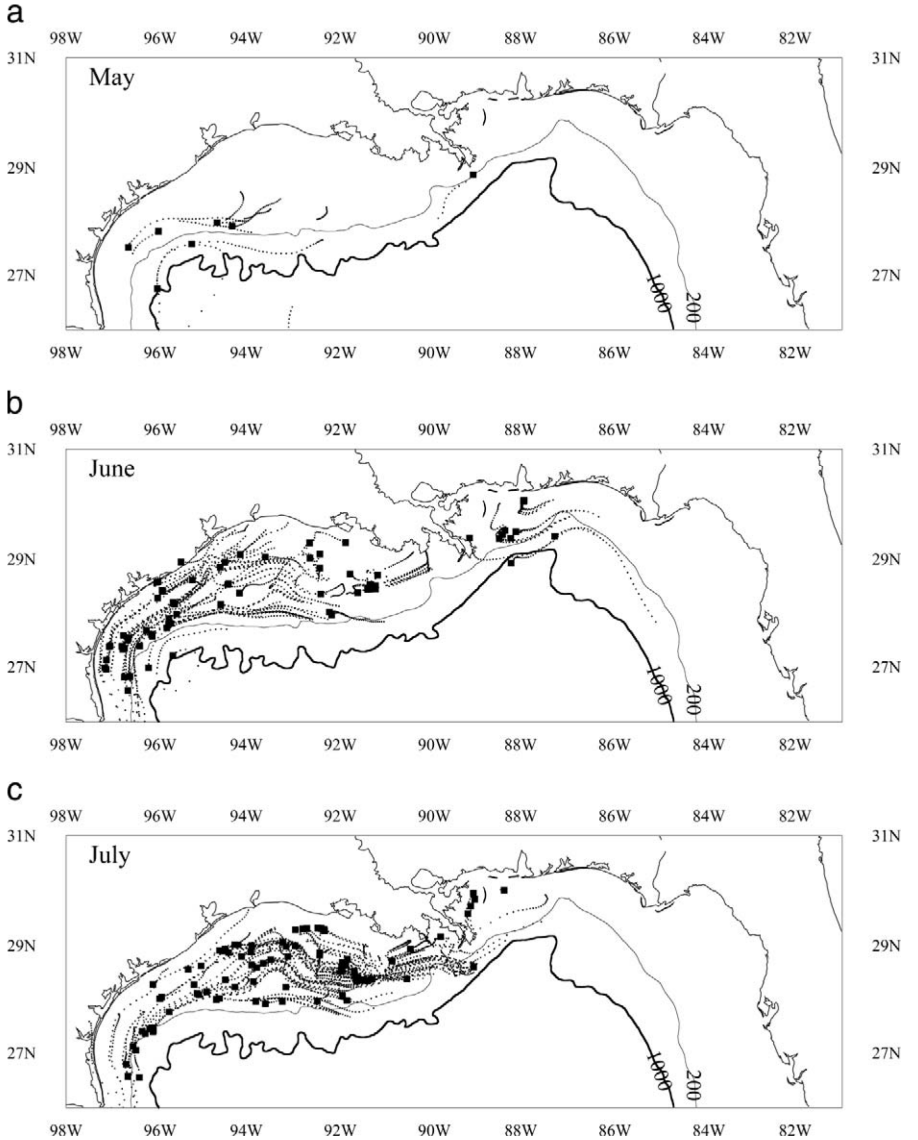

FIGURE 6.—Daily surface drift points from SEAMAP capture points during **(a)** May, **(b)** June, **(c)** July, **(d)** August, **(e)** September, and **(f)** October. Drifts are computed for 21 d forward and 11 d backward.

SEAMAP plankton sampling does not adequately cover the complete spawning period and range, especially during midsummer, when peak spawning is expected and climatological wind stress is toward the north. To account for sampling bias, larvae were launched from the same 654 capture locations but every 3 year-days during the peak spawning month of July (Figure 7). In this exercise, 90% of the propagule trajectories that passed the topographic impediments went eastward and 10% went westward. This reversal from the previous results when propagules were launched from their capture dates indicates that the east–west surface exchange across topographic impediments is seasonal, following climatological wind stress patterns.

To better qualify the transport of larvae across the topographic impediments, a series of exercises was performed with artificial launch points. Seven grid points were placed on each side of the Mississippi River delta and launches made from each of these grid points every 3 year-days from May through October and allowed to drift for 31 d. Launched from grid

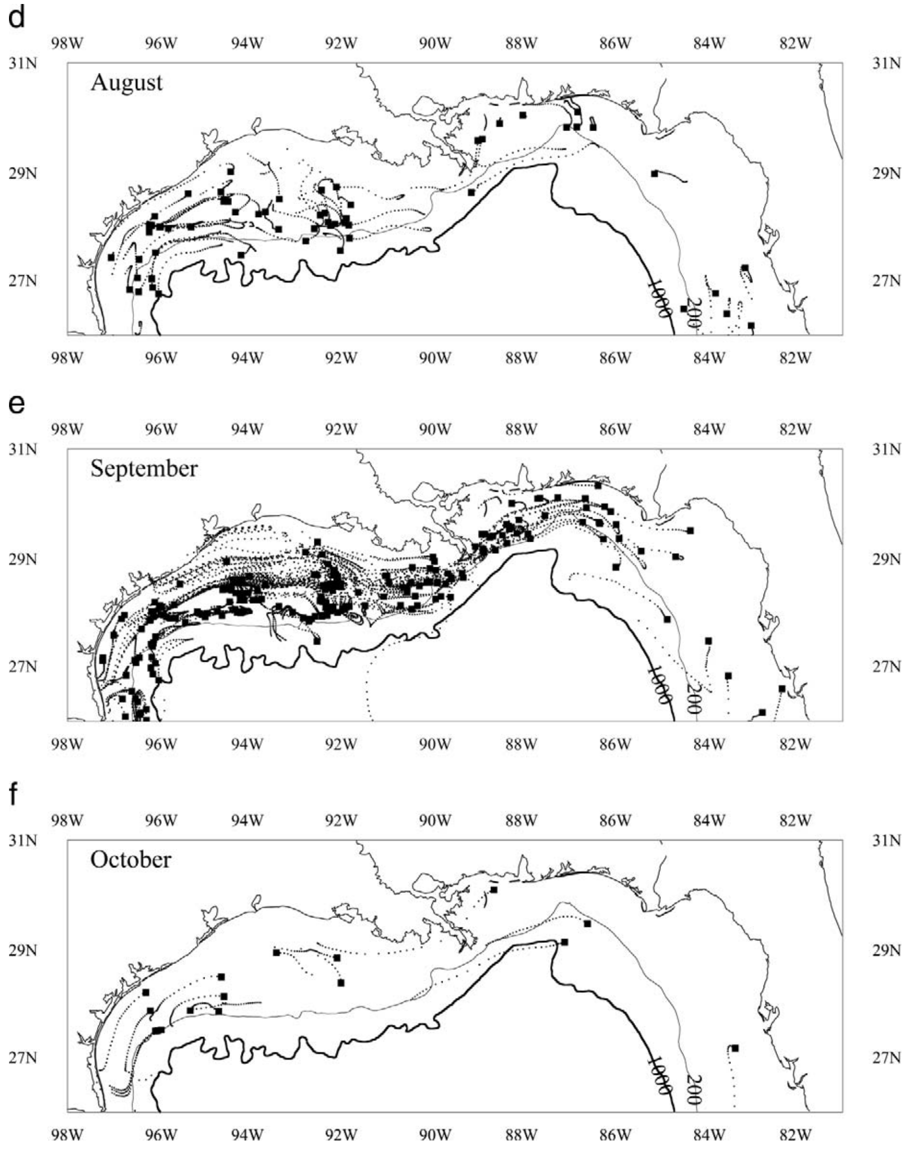

FIGURE 6.—Continued.

points east of the delta (Figure 8a), a westward flow of surface-drifting propagules crossed the delta within the 200-m isobath and penetrated the midshelf on the Louisiana–Texas side. This westward flow around the delta occurred in September and October and represented 11% of the launched propagules. Launched from grid points west of the delta (Figure 8b), the propagules flowed eastward, crossing the delta outside the 200-m isobath but remaining in deep water. This flow occurred in July–August and represented 3% of the launched propagules. The north–south bifurcation of east–west flow across the delta was first noted in drift bottle experiments by Chew et al. (1962) and provides additional evidence of the flow patterns in the current field at this critical location (Walker et al. 2005). Although westward flow during nonsummer months appeared to carry more launched propagules across the delta, spawning peaks during the summer months, when there is eastward flow across the delta. The actual interbasin flux of larvae requires better information on their seasonal abundance. Here we can only point out the existence of potential pathways.

To examine the possible eastward flow of larvae past the Apalachicola peninsula, a grid of 16 starting points

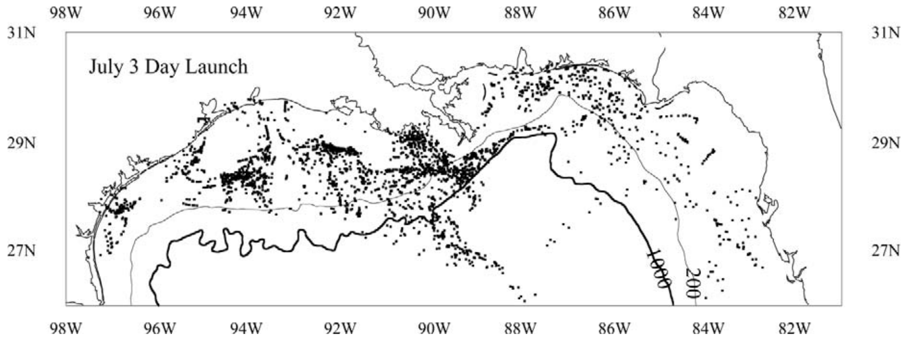

FIGURE 7.—Daily drift points from SEAMAP capture locations launched every 3 d in July. Owing to the large number of points, only the end locations after 31 d are shown.

just west of the peninsula was created. Propagules were launched every 3 d from each of these grid points from May through October and allowed to drift for 31 d. The combined tracks (Figure 9) suggested limited potential for larval transport from the west into the mid- and inner shelf of peninsular Florida. The flow from the Mississippi Bight onto the outer shelf/slope of peninsular Florida occurred from late May through mid-July. The very limited eastward penetration around the Apalachicola peninsula happened from July through mid-August. In September and October, strong westward streaming extended past the Mississippi River delta.

Discussion

As a result of continuing decreases in the red snapper population in both the western and eastern

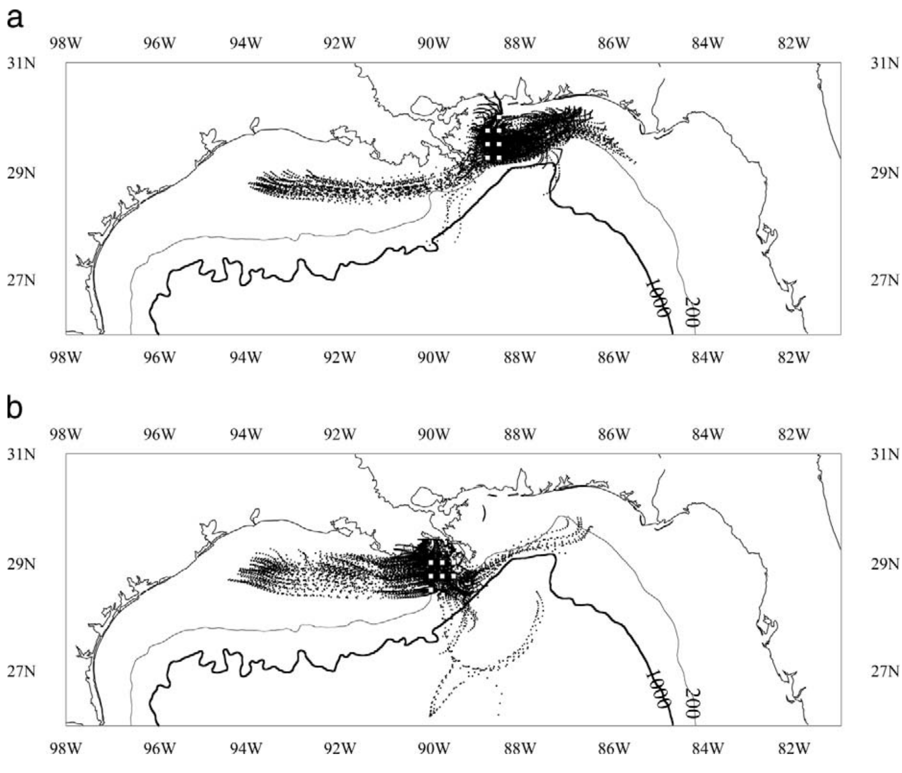

FIGURE 8.—Daily drift points launched from artificial grids (white squares) **(a)** east and **(b)** west of the Mississippi River delta. Launches were made every 3 d from May to October. Note that in (a) the tracks principally crossed within the 200-m isobath and onto the middle of the Louisiana–Texas shelf, whereas in (b) they principally crossed the delta outside of the 200-m isobath and onto the upper slope of the Mississippi Bight.

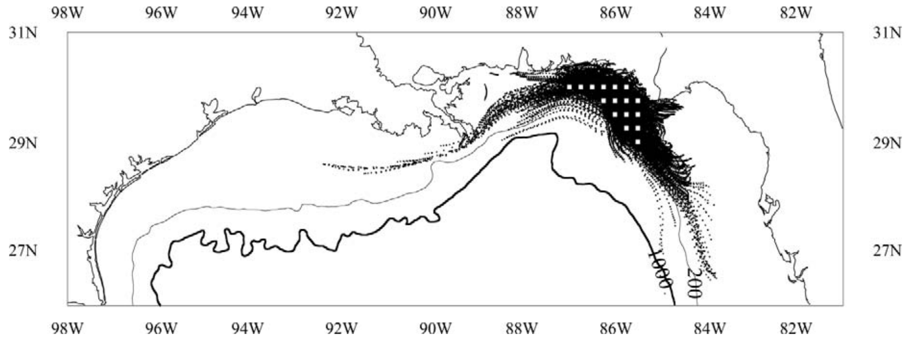

FIGURE 9.—Daily drift points launched from an artificial grid west of the Apalachicola peninsula. Launches were made every 3 d from May to October.

GOM, management strategies have been implemented to reduce nondirected and directed fishing mortality. A critical issue for management is the geographic delineation of stock structure; should snapper in the GOM be managed as a single unit or should they be treated as separate stocks in the western and eastern Gulf? Current management of the fishery assumes a single stock based on studies of population genetics (Camper et al. 1993; Gold et al. 1997). Evidence of stock mixing, however, comes from a tagging study in which significant movement of some adults were seen when a hurricane intervened between tagging and recapture (Patterson et al. 2001). Stock mixing as a result of larval transport was proposed by Goodyear (1992, 1995), but there were no data to support or refute his hypothesis. Although topographic impediments to alongshore flow, such as the Mississippi River delta, DeSoto Canyon, and the Apalachicola peninsula have the potential to foster geographic separation of stocks, the role that ocean circulation processes plays in transport of red snapper larvae had not been studied, and the potential for stock mixing by larval transport across the northern GOM was unknown.

Data on currents from a variety of sources were gathered and a field of surface currents was created to track red snapper larvae during their planktonic stage. The resulting propagule drift tracks showed a greater than expected exchange across the Mississippi River delta and DeSoto Canyon; westward crossings occurred principally in September and October and eastward crossings principally from June through August. This conforms well to climatological wind stress in the northern GOM: in summer, wind stress forcing is toward the north-northeast; in fall, it is toward the west-southwest. Around the Mississippi River delta, the westward-going propagule trajectories occurred close to the river mouth and the eastward trajectories occurred further offshore over the slope. This bifurcation in current flow represents a greater hazard to the eastward transport of larvae, as it is presumed that larvae carried out over deep water and away from nearshore juvenile settlement habitat (Rooker et al. 2004) die and are lost to the population.

The results from this study suggest that larval transport also contributes to mixing between the western and eastern segments of the GOM red snapper populations. The largest impediment to an eastward flux of larvae from the central and western GOM was the Apalachicola peninsula. Efforts to find a pathway from west to east indicated that the majority of eastward flow was directed southward along the West Florida outer continental shelf rather than around the Apalachicola peninsula into the Big Bend area. It is not clear how successful juvenile settlement on the outer shelf would be or whether migration to shallower waters from this location would occur. In the fall, however, there was movement from the east across the Apalachicola peninsula, thus raising the possibility for genetic exchange from eastern to western stocks.

It should be emphasized that this study presents climatologically smooth larval transport. An extensive observational current data set taken over many years has provided a unique opportunity to investigate large-scale transport with limited reliance on numerical models. Spatial and temporal gridding produced a field of "characteristic" currents in much the same way that surface current atlases are produced from ship drifts. The resulting current patterns do not adequately capture storm-scale (2–6-d) events or deep-basin eddies. Storm-scale events would not necessarily change the patterns of dispersion, as the drift time scale integrates over most of these events. However, such events could be expected to broaden the dispersion patterns.

Deep-basin eddies formed by Loop Current spinoffs, along with attendant cyclones and anticyclones, migrate westward from the north-central GOM and at times interact with continental shelf waters (Ohlmann et al. 2001). Only three propagules from the 654 capture sites were taken from within the 1,000-m isobath, carried alongshore, and brought back to within this isobath. This indicates that alongshore transport by deep-basin eddies (Hare et al. 2002) is possible but not important in comparison with transport over the shelf. However, storm- and eddy-scale transport current data are needed to properly address this question.

Little information is available on the vertical distribution of the early life stages of red snapper in the water column other than for the egg stage; presumably, newly hatched larvae are buoyant. Their consistent presence in neuston samples indicates that for some amount of time they are under the direct influence of near-surface circulation. Because they are spawned in water depths where they also recruit, larvae would not be expected to actively regulate their position in the water column to vector out of the water mass in which they were encountered until they reach settlement age. In general, current speeds are greatest at the surface and diminish with depth; thus, the estimates of dispersion, at least in the alongshore direction, may be maximal. During nonsummer spawning months (May, September, and October), wind stress is dominantly from east to west across the entire northern GOM. One can expect that vertical migration would broaden the dispersion pathways northward (shoreward) because of clockwise Ekman veering with depth. In summer spawning months (June, July, and August), Ekman veering associated with the northward coastal wind stress would tend to align any vertically migrating larvae with the observed eastward near-surface flow. In either case, we would not expect significant changes to the conclusions presented here.

In summary, we found that transport pathways were principally vectored toward the west during the nonsummer spawning months of September, October, and May under the influence of relatively strong climatological westward wind stress. Eastward pathways occurred in June, July, and August under the influence of weaker shoreward wind stress. Topographic impediments to alongshore larval transport in the northern GOM (the Mississippi River delta, DeSoto Canyon, and the Apalachicola peninsula) restrict the quantity of larvae crossing but do not eliminate it. Eastward flow past the impediments tends to occur in deeper water, where mortality due to the lack of optimum juvenile settlement habitat is assumed to be higher. At Apalachicola, the summertime eastward transport turns southward into deeper waters of the outer continental shelf of peninsular West Florida.

The identification of transport pathways for the larval dispersal and recruitment of red snapper are of interest to management in determining the linkages among the different regions of the GOM (SEFSC 2005). There is particular interest in the possibility of transport from areas of higher abundance in the northwestern and central GOM to areas of low abundance in the east. Larval abundance is twice as great over the Louisiana–Texas shelf as over the Mississippi–Alabama shelf and four times as great over the Mississippi–Alabama shelf as over the West Florida shelf (Hanisko et al. 2007). The results of our study suggest that only a small fraction of the Louisiana–Texas larvae have a chance of being transported eastward across the Mississippi River delta, and those that do are transported away from continental shelf into slope and oceanic waters. The eastward transport of larvae during summer months from the Mississippi Bight across the Apalachicola peninsula is diverted southward into deeper waters on the outer continental shelf. The potential for limited transport of larvae across these impediments suggests that separate management may be warranted for the eastern and western GOM.

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References

Beaumariage, D. S. 1969. Returns from the 1965 Schlitz tagging program, including a cumulative analysis of previous results. Florida Department of Natural Resources, Technical Series 59, St Petersburg.

Beaumariage, D. S., and L. H. Bullock. 1976. Biological research on snappers and groupers as related to fishery management requirements. Pages 86–94 *in* H. R. Bullis, Jr. and A. C. Jones, editors. Proceedings: colloquium on snapper–grouper fishery resources of the western central Atlantic Ocean. University of Florida, Florida Sea Grant, Colloquium Report 17, Gainesville.

Blumberg, A. F., and G. L. Mellor. 1983. Diagnostic and prognostic numerical circulation studies of the South Atlantic Bight. Journal of Geophysical Research 88(C8):4579–4592.

Bretherton, F. P., R. E. Davis, and C. B. Fandry. 1976. A technique for objective analysis and design of oceanic experiments applied to MODE-73. Deep Sea Research 23:559–582.

Camper, J. D., R. C. Barber, L. R. Richardson, and J. R. Gold. 1993. Mitochondrial DNA variation among red snapper (*Lutjanus campechanus*) from the Gulf of Mexico. Molecular Marine Biology and Biotechnology 3:154–161.

Chew, F., K. L. Drennan, and W. J. Demoran. 1962. Some results of drift bottle studies off the Mississippi Delta. Limnology and Oceanography 7(2):252–257.

Cho, K., R. O. Reid, and W. D. Nowlin, Jr. 1998. Objectively mapped stream function fields on the Texas–Louisiana shelf based on 32 months of moored current meter data. Journal of Geophysical Research 103:10377–10390.

Choi, J. K., and L. H. Kantha. 1997. Refinement and verification of a climatological and forecast model of the Loop Current and associated eddies. Colorado Center for Astrodynamics Research, University of Colorado, Report for EJIP CASE, Boulder.

Cochrane, J. D., and F. J. Kelly. 1986. Low-frequency circulation on the Texas–Louisiana continental shelf. Journal of Geophysical Research 91:10645–10659.

Comyns, B. H. 1995. Early life history of snappers in the north-central Gulf of Mexico: growth, survival, and implications to recruitment. Final technical report submitted to the National Marine Fisheries Service, Southeast Regional Office, St. Petersburg, Florida.

Drass, D. M., K. L. Bootes, J. Lyczkowski-Shultz, B. H. Comyns, G. H. Holt, C. M. Riley, and R. P. Phelps. 2000. Larval development of red snapper *Lutjanus campechanus*, and comparisons with co-occurring snapper species. U.S. National Marine Fisheries Service Fishery Bulletin 98(3):507–527.

Gallaway, B. J., J. G. Cole, R. Meyer, and P. Roscigno. 1999. Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. Transactions of the American Fisheries Society 128:713–726.

Gilbes, F., C. Tomas, J. J. Walsh, and F. E. Muller-Karger. 1996. An episodic chlorophyll plume on the West Florida shelf. Continental Shelf Research 16(9):1201–1224.

Gill, A. E. 1982. Atmosphere–ocean dynamics. Academic Press, New York.

Gold, J. R., F. Sun, and L. R. Richardson. 1997. Population structure of red snapper from the Gulf of Mexico as inferred from the analysis of mitochondrial DNA. Transactions of the American Fisheries Society 126:386–396.

Goodyear, C. P. 1992. Red snapper in U.S. waters of the Gulf of Mexico: 1992 assessment update. National Marine Fisheries Service, Southeast Fisheries Science Center, MIA-92/92-76, Miami, Florida.

Goodyear, C. P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, MIA-95/96-05, Miami, Florida.

Hamilton, P., T. J. Berger, and W. Johnson. 2002. On the structure and motions of cyclones in the northern Gulf of Mexico. Journal of Geophysical Research 107:3208–3226.

Hanisko, D. S., J. Lyczkowski-Shultz, and G. W. Ingram. 2007. Indices of larval red snapper (*Lutjanus camphechanus*) cccurrence and abundance for use in stock assessment. Pages 285–300 *in* W. F. Patterson III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Hare, J. A., J. H. Churchill, R. K. Cowan, T. J. Berger, P. C. Cornillon, P. Dragos, S. M. Glenn, J. J. Govoni, and T. N. Lee. 2002. Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. Limnology and Oceanography 47(6):1774–1789.

Heist, E. J., and J. R. Gold. 2000. DNA microsatellite loci and genetic structure of red snapper in the Gulf of Mexico. Transactions of the American Fisheries Society 129:469–475.

Kantha, L. H., and C. A. Clayson. 2000. Numerical models of oceans and oceanic processes. Chapter 14.7 *in* Nowcasts/forecasts in the Gulf of Mexico. Academic Press, San Diego, California.

Lyczkowski-Shultz, J., and D. S. Hanisko. 2007. A time series of observations on red snapper larvae from SEAMAP surveys, 1982–2003: seasonal occurrence, distribution, abundance, and size. Pages 3–23 *in* W. F. Patterson III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Ohlmann, J. C., and P. P. Niiler. 2005. Circulation over the continental shelf in the northern Gulf of Mexico. Progress in Oceanography 64:45–81.

Ohlmann, J. C., P. P. Niiler, C. A. Fox, and R. R. Leben. 2001. Eddy energy and shelf interactions in the Gulf of Mexico. Journal of Geophysical Research 106:2605–2620.

Patterson, W. F., III, J. C. Watterson, R. L. Shipp, and J. H. Cowan, Jr. 2001. Movement of tagged red snapper in the northern Gulf of Mexico. Transactions of the American Fisheries Society 130:533–545.

Porch, C. E. 2007. An assessment of the red snapper fishery in the U.S. Gulf of Mexico using a spatially-explicit age-structured model. Pages 355–384 *in* W. F. Patterson III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Rooker, J. R., A. M. Landry, B. W. Geary, and J. A. Harper. 2004. Assessment of a bathymetric high and associated habitats as nursery grounds of postsettlement red snapper. Estuarine, Coastal, and Shelf Science 59:653–661.

SEFSC (Southeast Fisheries Science Center). 2005. SEDAR 7: Gulf of Mexico red snapper. SEFSC, Miami, Florida.

Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. Bulletin of Marine Science 55:887–896.

Walker, N. D., W. J. Wiseman, Jr., L. J. Rouse, Jr., and A. Babin. 2005. Effects of river discharge, wind stress, and slope eddies on circulation and satellite-observed structure of the Mississippi River plume. Journal of Coastal Research 21:1228–1244.

Weisberg, R. H., R. He, Y. Liu, and J. I. Virmani. 2005. West Florida Shelf circulation on synoptic, seasonal, and interannual time scales. Pages 325–347 *in* W. Sturges and A. Lugo-Fernandez, editors. Circulation in the Gulf of Mexico. Geophysical Monograph 161.

Yang, H., R. H. Weisberg, P. P. Niiler, W. Sturges, and W. Johnson. 1999. Lagrangian circulation and forbidden zone on the West Florida Shelf. Continental Shelf Research 19:1221–1245.