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ARTICLE

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Abstract

The potential for Red Snapper *Lutjanus campechanus* on Campeche Bank to contribute to regional fisheries in the Gulf of Mexico through larval transport was studied using numerical circulation model data. A tracking algorithm was applied at an array of starting locations over Campeche Bank and simulated larval propagules launched every 3 d during the spawning seasons of four model years within the period 2003–2010. Successful recruitment was defined as arrival in water depths less than 200 m after 31 d of planktonic drift, regional recruitment being defined as a percentage of propagules launched. It was found that successful natal retention to Campeche Bank was high, varying between 67% and 73% of all launched propagules. However, successful recruitment to other regions around the Gulf of Mexico (GOM) was sporadic and extremely low. Robustness of the methodology was examined in a set of experiments involving larval depth and subgrid scale diffusion. The results suggest that larvae from Campeche Bank can contribute to homogenization of the gene pool throughout the GOM but may be insufficient to restore depleted regional populations.

This study addresses dispersion of Red Snapper *Lutjanus campechanus* from Campeche Bank (off the Yucatan Peninsula; Figure 1) to regions throughout the Gulf of Mexico (GOM) by advective larval transport. An understanding of the connectivity of populations in the GOM is important for management of the species throughout its range. Study goals are to determine potential larval pathways for connecting Campeche Bank with the rest of the GOM, determine the seasonal influence on pathways, and make a general estimate of the effectiveness of the pathways for larval spread. While our focus is on Red Snapper, applications can be made to other species with similar early life histories.

The GOM is an international body of water, bounded by the United States, Mexico, and Cuba, and is narrowly linked to the Caribbean Sea through the Yucatan Channel and to the North Atlantic through the Straits of Florida. Since the mid-19th century, the GOM Red Snapper fishery has undergone significant changes in area fished and the size and status of the commercial harvest (Porch et al. 2007; Shipp and Bortone 2009). The U.S. fishery has been declared overfished (Fitzhugh et al. 2004; SEDAR 2005; Porch 2007), and the Mexican fishery on Campeche Bank has been recently described as severely deteriorated (Brulé et al. 2010). High abundances of Red Snapper still occur on Campeche Bank, although catches declined by a factor of four between 1992 and 2005 (Brulé et al. 2010). Harvest of Red Snapper in the GOM is heavily skewed toward the west (SEDAR 2009), and fishery-independent surveys confirm this skewed distribution (Mitchell et al. 2004; Lyczkowski-Shultz and Hanisko 2007).

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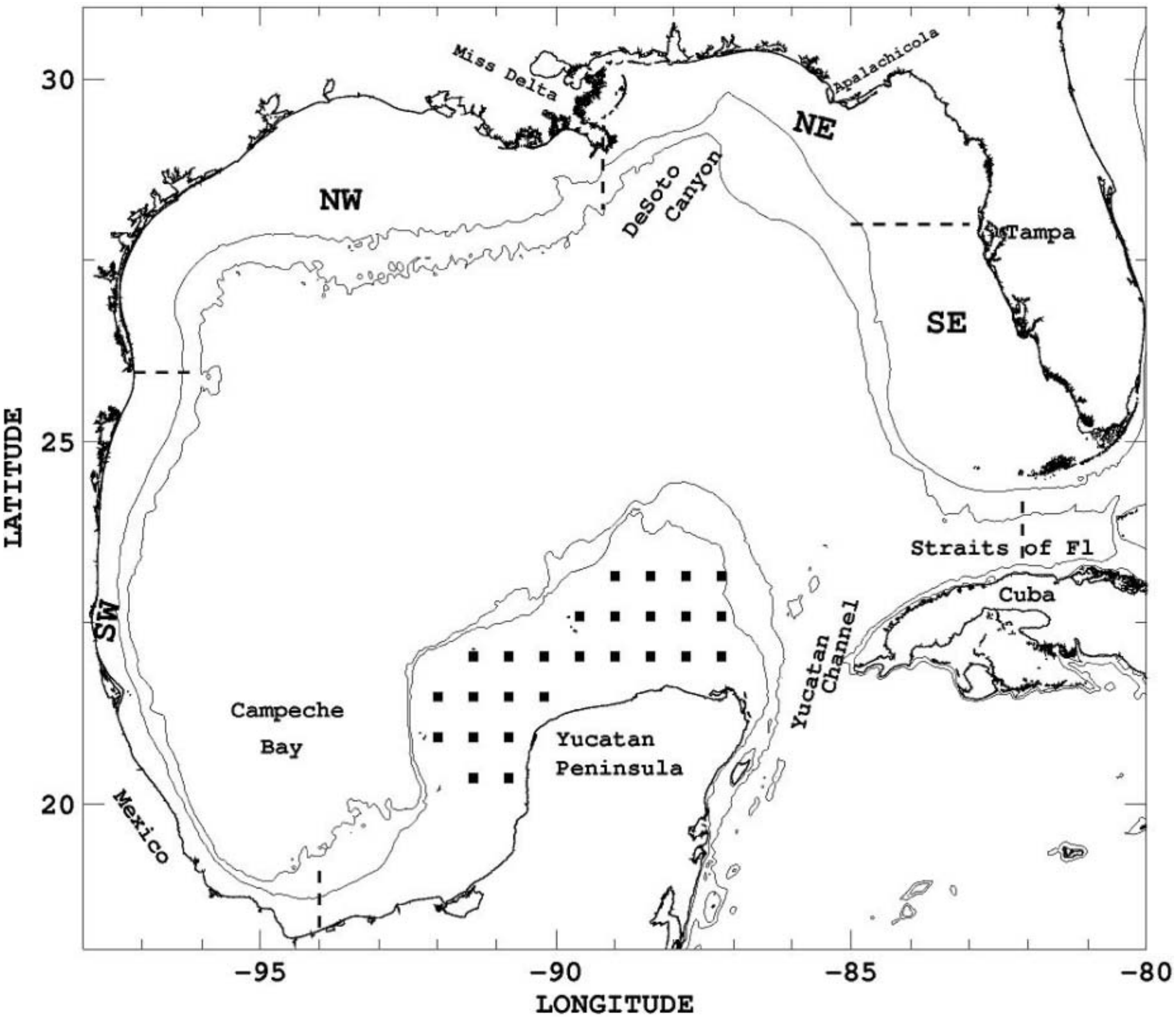

FIGURE 1. Map of study area. Black squares represent 26 Red Snapper spawning locations over Campeche Bank. For discussion, recruitment areas are defined by dashed lines: SW (southwest), NW (northwest), NE (northeast), and SE (southeast). Recruitment to Cuba and the U.S. Atlantic coast is also considered. The isobaths are 200 and 1,000 m.

Red Snapper tend to be sedentary, associating with bottom structure and exhibiting high site fidelity (Beaumariage and Bullock 1976; Szedlmayer and Shipp 1994; Topping and Szedlmayer 2011); these characteristics limit the movement of adults into depleted areas. They are highly fecund batch spawners (Collins et al. 1996; Collins et al. 2001; Woods 2003) and are capable of repeatedly spawning batches of eggs every few days over the course of the spawning season. In a recent comparison of the literature on Red Snapper reproduction throughout its range, Brulé et al. (2010) noted that Red Snapper have a more protracted spawning season (over 10 months) off Campeche Bank than in the northern GOM (5–6 months). Spawning on Campeche Bank takes place between February and November, peak spawning occurring in early fall (Brulé et al. 2010). Red Snapper eggs are buoyant, drift toward the surface, and hatch in 1 d (Rabalais et al. 1980). Larvae have a planktonic larval duration (PLD) of 27–30 d (Szedlmayer and Conti 1999; Drass et al. 2000; Rooker et al. 2004). Transport by advective currents can, therefore, potentially disperse Red Snapper to distant settlement areas (Goodyear 1995; Johnson et al. 2009).

It is important to know where in the water column Red Snapper larvae reside in order to predict transport pathways using hydrodynamic modeling techniques. Until recently, there has been little information on the depth distribution of snapper larvae. In a 2-year survey of snapper larvae in the Straits of Florida (D'Alessandro et al. 2010), eight of the most abundant species of snapper larvae were found in the upper 50 m of the water column, seven of the species being most concentrated in the upper 25 m. There was little information on Red Snapper larvae from this study since only two specimens were collected. Under the National Marine Fisheries Service (NMFS) Southeast Area Monitoring and Assessment Program (SEAMAP), discrete plankton samples have recently been collected using a 1-m multiple opening–closing net and environmental sensing

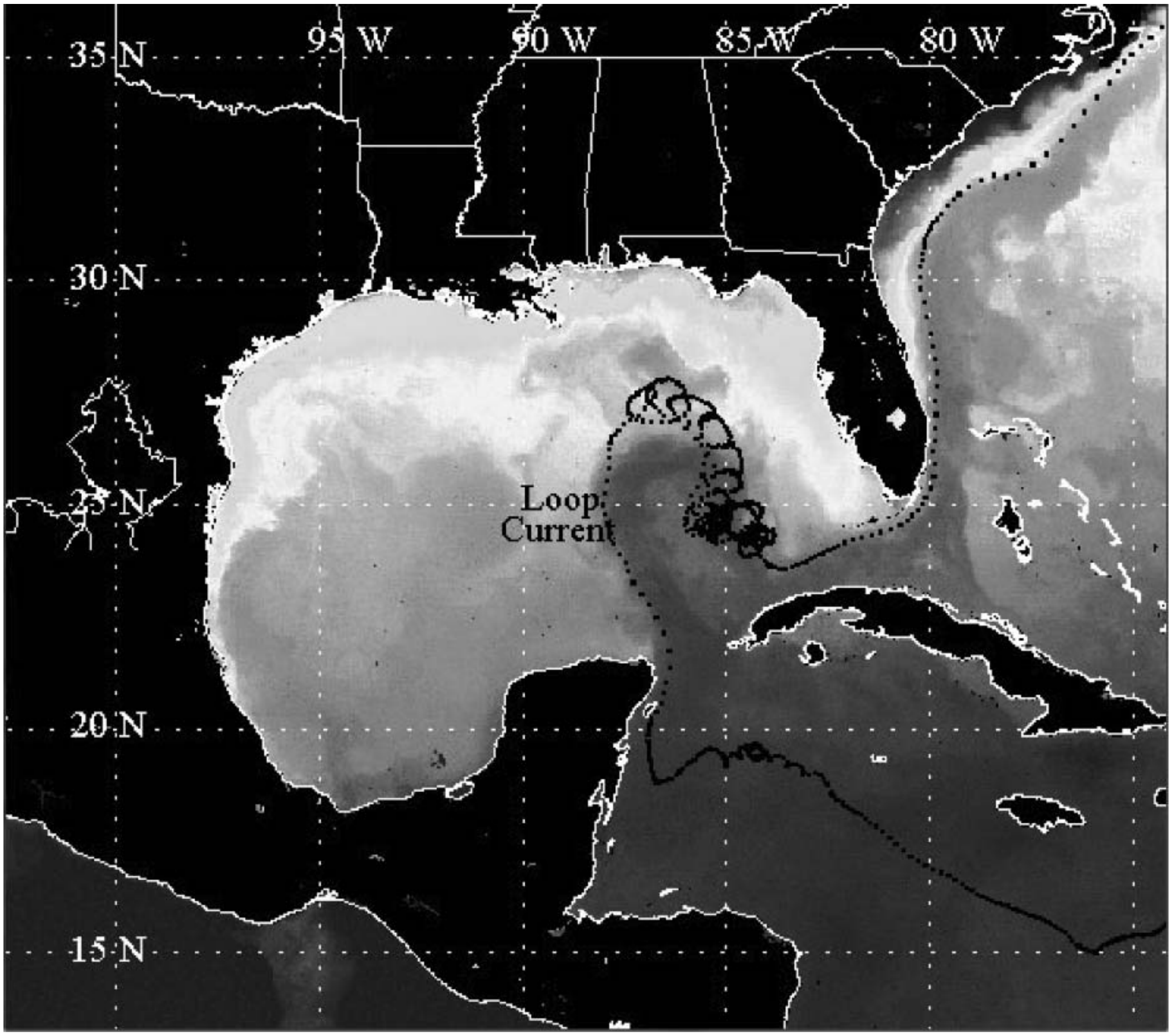

FIGURE 2. Louisian State University Earth Scan Lab GOES-12 sea surface temperature composite for March 10–16, 2004. Darker pixels represent warmer water. Concomitant satellite tracked drifter from the National Oceanic and Atmospheric Administration's Atlantic Oceanographic and Meteorological Laboratory–Drifter Data Assembly Center illustrates potential mechanism for larval transport onto the West Florida shelf through eddy motions on eastern flank of the LC.

system. These samples were taken in the northern GOM in 2009 and 2011 at locations where Red Snapper larvae are known to be abundant. Although analysis of these samples has not been completed, Red Snapper larvae were most numerous (91% of 266 larvae captured) within the upper 30 m of the water column, and 93% of Red Snapper larvae in these collections occurred at stations where water depth was < 52 m (G. Zapfe, NMFS, unpublished data).

Circulation patterns in the GOM are dominated in the deep basin by the Loop Current (LC; Figure 2) and its spin-off eddies, and by wind stress over the continental shelves. The LC is formed when the northward-flowing Caribbean Current intensifies as it passes through the Yucatan Channel, intrudes northward into the GOM basin, and loops back southward before exiting into the Straits of Florida. At times, the head of the intruding current spins off to form a large eddy, while the main current reattaches south of the separated eddy in a shortened and flattened intrusion. The process results from dynamic instability and is not readily predictable (Hurlburt and Thompson 1980; Vukovich 1995). The LC and its spin-off eddies are deep (~800 m) and contain warm, salty, oligotrophic Caribbean water. Core current speeds are in excess of 1 m/s. The spin-off eddies can be 200–300 km in diameter. Under influence of the earth's rotation, they migrate westward across the GOM over a period of months while interacting with continental shelf waters and spinning off smaller eddies around the perimeter. The high current speeds associated with the LC and its spin-off eddies, and eddy interactions with shelf waters suggest a potential for larval entrainment from Campeche Bank and successful basin crossing transport during the Red Snapper PLD.

METHODS

Modeled currents used in this study come from the 1/25th degree (~3.5-km horizontal resolution) Hybrid Coordinate Ocean Model (HYCOM). It is a combination isopycnal, sigma, and *z*-level coordinate model, run from 2003 through the present and archived daily with 40 levels in the vertical. A major advantage of this hybrid coordinate model (Bleck and Boudra 1981; Bleck 2002) is its smooth and dynamically sound transition from deep basin to shelf. Real-time satellite altimetry and satellite sea surface temperature data are applied in a continuous data assimilation mode. Data assimilation is important because it phase-locks the model into real oceanographic events such as the LC and its spin-off rings. The model is run with observed wind stress forcing from the Navy Operational Global Atmospheric Prediction System. To check for consistency of results, four model years were run: 2003, 2005, 2008, and 2010.

Due to the inability of models to capture subgrid scale turbulent motion, a small uncertainty exists in defining the drift of a propagule in finite-difference models. Because of the chaotic nature of ocean currents, these subgrid scale turbulent motions can lead to broadened dispersion of propagules. In order to reincorporate subgrid scale turbulent motions in the model, a random-flight algorithm (Thomson 1986; Dutkiewicz et al. 1993; Kitagawa et al. 2010) was applied to propagule tracking (Lagrangian stochastic model [LSM]). The LSM used in this application is based on multiplication of a unitary Gaussian probability density function (mean = 0; SD = 1) times a fraction of the local current (Marinone et al. 2004; Tilburg et al. 2005), expressed as

$$U_{i,j} = \tilde{U}_{i,j} + \alpha \cdot S \cdot P_{i,j}$$

where $U_{i,j}$ equals tracking current components in the east (*i*) and north (*j*) directions, $\tilde{U}_{i,j}$ equals HYCOM model currents, α is fraction of local current speed, *S* is HYCOM model local current speed, and $P_{i,j}$ is Gaussian probability density function.

The randomly generated addition represents a small turbulent adjustment to HYCOM model currents. Applied individually to 10 simultaneously launched propagules from each spawning location, the resulting ensemble of pathways represents dispersion of a cloud of spawned larvae. Time steps in tracking were at 0.1 d, random additions being applied at each step.

Several experiments were run to test the robustness of the choice of larval vertical distribution depth and the LSM. The base experiment used currents averaged over the upper 30 m, assuming snapper larvae spend equal time throughout the layer, and a LSM with α equal to 0.1 (~10% of local current speed). Experiment 1 (X-1) doubled the proportionality fraction α, and X-2 replaced *S* with $\frac{<S>}{<S^2>} \cdot S^2$. The latter suggests that turbulence is proportional to local energy. The normalization factor $\frac{<S>}{<S^2>}$ is the average of current speed throughout the domain divided by average of current speed squared. In X-2, the amplitude of noncaptured turbulence is approximately the same as in the base experiment, but it is distributed according to energy instead of momentum. In X-3 the larval vertical migration depth average is taken as 10 m, and in X-4 it is 50 m.

Since high-value settlement habitat has been characterized as being between a depth of 15 and 64 m (Szedlmayer and Conti 1999; Gallaway et al. 2009; Wells et al. 2009), simulation of larval transport into shallow water required adjustments in vertical averaging depth. Model currents were averaged over the chosen vertical migration depth (30 m, base experiment) or half the water column, whichever was smaller. This was necessary since shoreward motion by vertically averaged currents is inhibited in water shallower than the full averaging depth due to mass balance. Early tests where depths were averaged over the water column showed that propagules tended to stop shoreward motion along isobaths corresponding to the vertical averaging depth. Anticipating the results, the only place where this is important in the present study is in nearshore areas of Campeche Bank.

Twenty-six spawning locations were placed on a regular grid across Campeche Bank (Figure 1). Ten propagules were launched from each of the locations every 3 d from February through November in each of the four model years and plotted at daily intervals. Due to lack of fishery-independent distribution data for spawning Red Snapper across Campeche Bank, the spawning locations were selected to systematically cover a broad portion of the bank as potential starting positions. Additionally, the number of larvae associated with each propagule as a function of season could not be weighted as this is dependent on unknown age–weight distribution of spawning snapper. With these limitations, study goals were restricted to examining pathway connectivity and estimating relative success. For the latter, a comparison was made between the number of successful propagules and the number of propagules that were launched, and the results separated into fraction retained over Campeche Bank, fraction lost in the deep basin, and fraction ending on continental shelves outside of Campeche Bank or in the Straits of Florida.

RESULTS

Natal retention, defined as propagules that ended a 31-d PLD (1-d egg stage + 30 d as planktonic larvae before settlement to demersal habitat) over Campeche Bank in water of depth less than 200 m, was remarkably high in all years. As a percentage of all propagules launched (26,520) in each year, natal retention was 73.3, 73.2, 67.8, and 67.5% for years 2003, 2005, 2008, and 2010, respectively. Of those propagules that were transported off Campeche Bank, ~28% were lost to the deep basin. It seems clear from the overall dispersion pattern of propagules in each of the four model years (Figure 3) that the LC and its associated eddies are important in spreading larvae throughout the eastern half of the GOM but have little impact on the western GOM.

Successful basin crossing, defined as propagules that exit Campeche Bank and end the PLD in other regions of the GOM

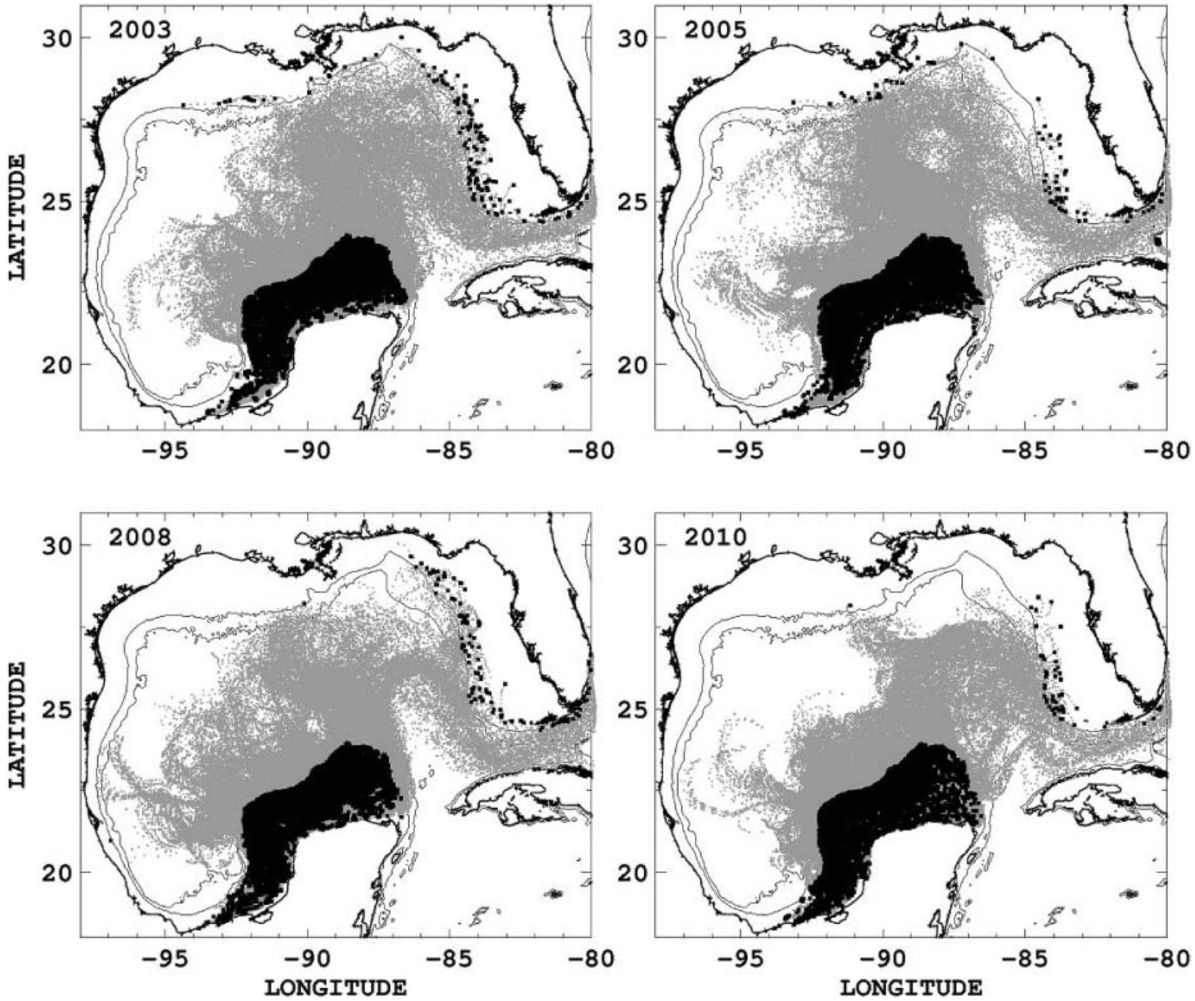

FIGURE 3. Larval dispersion from spawning locations on Campeche Bank (Figure 1) for four model years (upper left, 2003; upper right, 2005; lower left, 2008; lower right, 2010). Grey points are daily locations of propagules launched every 3 d from February to November in each model year and tracked for 31 d. Black points are end locations after 31 d where water is less than 200 m deep (defined as successful recruitment).

in water depth less than 200 m, was very low overall. As a percentage of total propagules launched, successful crossings for combined years was ∼ 0.33%, the southeast region receiving the most propagules, followed by the northeast, the northwest, Cuba, and then the southwest (Figure 4). Successful propagules that ended in the southeast region came from eastern and northern locations on Campeche Bank, where they were entrained in the LC before being transported onto the outer continental shelf along Florida.

Variation in successful basin crossings among the 4 years was relatively small, the largest success occurring in 2003 and the lowest in 2010 (Figure 5). Peaks in monthly recruitment (Figure 6) occurred in August and September (∼0.8% of propagules launched for those months), when seasonally lighter trade winds reduced the near-surface westward flow over Campeche Bank, allowing relatively greater entrainment in the LC.

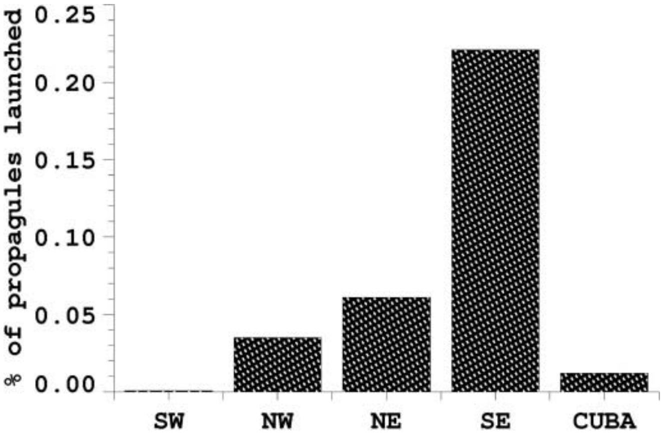

FIGURE 4. Successful recruitment throughout GOM as a percentage of propagules launched over the four model years.

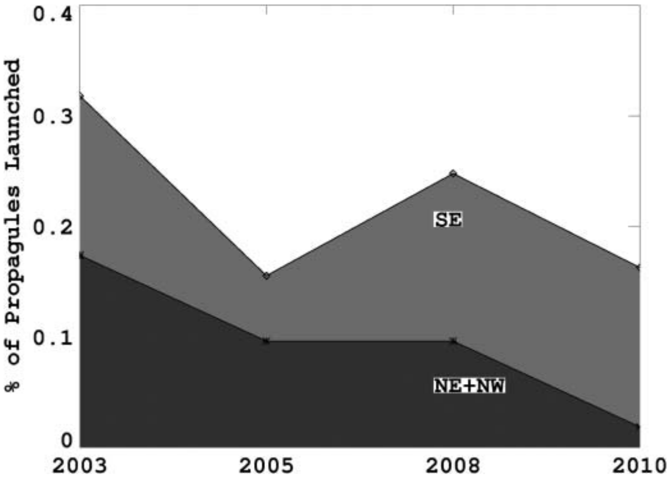

FIGURE 5. Successful recruitment to the SE and combined NE and NW (NE + NW) areas as a percentage of propagules launched over the four model years.

Several of the propagules ended in waters shallower than 200 m along the northern coast of Cuba. This happened in July 2008 over a period of 10 d and involved propagule launches from four different spawning locations on Campeche Bank, suggesting that the landings were not due to the stochastic nature of the LSM alone. During this period, the eastern branch of the LC (south flowing) penetrated uncharacteristically far to the south, impacting the northern coast of Cuba and bringing propagules onto the narrow shelf.

Propagules that ended on the shelf in the northwest area did so during both 2003 and 2005. In 2003, the LC had extended unusually far to the north. By late July, the northern half appeared to have separated but maintained contact with the reformed loop through the fall. During a period of 9 d, propagules from two spawning locations on the eastern side of Campeche Bank were entrained into the LC and then branched into the partially separated eddy, where they were transported onto the shelf west of the Mississippi River delta (Figure 7). In 2005, a similar intrusion and break off occurred in March, the LC and break off eddy maintaining contact throughout the summer.

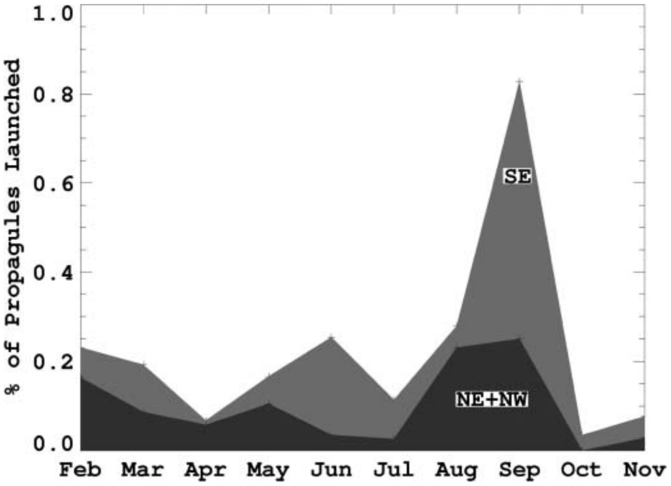

FIGURE 6. Successful recruitment as a percentage of propagules launched and averaged by month over the four model years (2003, 2005, 2008, and 2010).

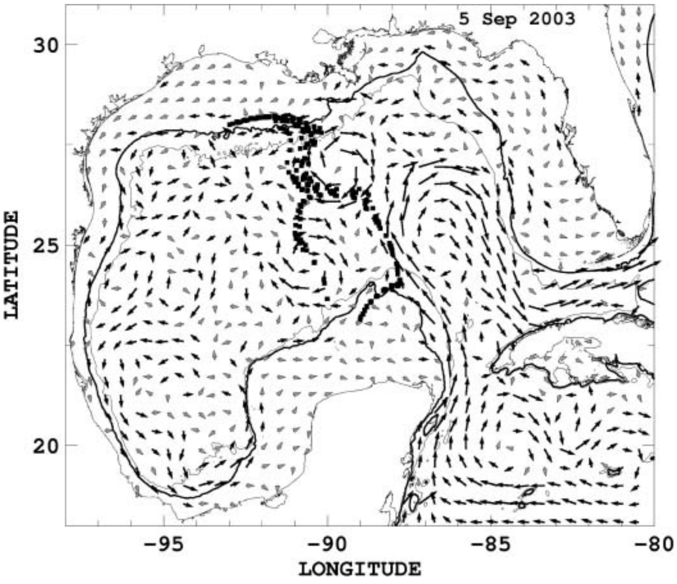

FIGURE 7. Example of pathway for successful recruitment to the NW area, September 2003. Dark squares represent tracks of 10 propagules launched from Campeche Bank. Model current vectors displayed are concomitant with propagule tracks.

Larvae from Campeche Bank can also contribute to Red Snapper populations along the U.S. Atlantic coast. A number of propagules (1.6% of propagules launched) from Campeche Bank entered the Straits of Florida entrained in the Florida Current. Studies on the U.S. Atlantic coast have demonstrated that larvae can be transported shoreward by spin-off eddies from the Florida Current up to Cape Hatteras (Lee et al. 1984) and by warm core rings from the Gulf Stream north of the cape (Hare et al. 2002). Detailed examination of the propagules that entered the Straits of Florida revealed that seven sites in the Campeche array contributed all of the propagules that passed into the Florida Current. These sites were spread along the northern and eastern side of Campeche Bank, and ranged in depth from 14 to 82 m.

DISCUSSION

In this study larval advective pathways from Campeche Bank to other regions of the GOM were modeled, with successful pathways judged to occur if, after a PLD of 31 d, the modeled propagules ended in water depths less than 200 m. It should be noted that this simplistic measure of successful recruitment depends only on the presence of the pathway from spawning location to juvenile settlement habitat and does not include other important factors such as mortality during the PLD, larval abundance associated with each propagule, or seasonal variation in spawning. Measuring recruitment as a percentage of total propagules launched provided a means of assessing the relative impact elsewhere compared with the Campeche Bank production regardless of season or distribution.

In summary, approximately 70% of all propagules remained on Campeche Bank at the end of the PLD with little yearly variation over the four model years. Only about 0.1% successfully recruited to shelf waters elsewhere in the Gulf, and about 1.6% entered the Straits of Florida entrained in the Florida Current with potential for recruitment along the Atlantic coast. This left ∼ 28.3% of the total propagules launched that did not reach suitable habitat for settlement.

The majority of propagules that successfully crossed the deep basin were transported by the LC to the southern part of peninsular Florida's outer shelf. Propagules spawned on the eastern side of Campeche Bank were entrained in the strong currents passing through the Yucatan Channel, carried relatively quickly around the head of the LC, and discharged onto the Florida shelf through eddies formed along the outer boundary of the current (Figure 2). Interactions between the LC and Florida shelf waters are well documented in the literature (Niiler 1976; Huh et al. 1981; He and Weisberg 2003).

Peak seasonal recruitment to the West Florida shelf occurred in August and September with small yearly variations. The highest percentage (>40%) of actively spawning female Red Snapper on Campeche Bank was observed (Brulé et al. 2010) to occur in September and October. This was the only time period (late summer–early fall) and region (SE) where recruitment from Campeche Bank might impact the populations in distant regions. Fishery-independent ichthyoplankton (Lyczkowski-Shultz and Hanisko 2007) and longline surveys (Mitchell et al. 2004) from the SE region indicate relatively low abundance of Red Snapper larvae and adults, suggesting that the contribution for larvae from Campeche Bank to this region is minor or at least undetectable with resource surveys.

Interactions of the LC and its spin-off eddies with the northern GOM is more complex. Energetic large eddies formed by separation from the LC occur on time scales from 3 to 17 months (Elliott 1982; Maul and Vukovich 1993). These separated eddies migrate westward at about 60–150 km/month (Elliott 1982; Vukovich and Crissman 1986; Oey 1996). Interaction of these eddies with the northern shelf is somewhat sporadic (Ohlmann et al. 2001). Successful recruitment to the northern GOM (NW and NE areas) was low and also sporadic. Greatest recruitment occurred after the LC had intruded to unusually high latitudes and its spin-off eddy maintained contact with both the LC and the continental slope areas of the northern GOM for an extended period of time. Recruitment to the western GOM was rare as a result of the long time scale of the eddy westward drift and the relatively short PLD.

A search of daily tracking positions from propagules that entered the Straits of Florida entrained in the Florida Current suggests that these larvae would have been about 18–21 d posthatch off Miami and could reach Cape Hatteras by the end of the PLD. Although the quantity was small relative to the number of propagules launched (∼1.6%), contribution to the gene pool along the Atlantic coast seems likely. Larvae 18–21-d-old would on average be 8.1 mm in length and range from 5.9 to 10.4 mm (C. Jones, NMFS, unpublished data). D'Alessandro et al. (2010) found only two small (3.7–4.2-mm) Red Snapper in monthly larval collections in the Straits of Florida near Miami during daylight net tows. However, larvae of the size (6–10 mm) predicted to arrive in the straits from Campeche Bank would not be abundant in net collections. Larvae larger than 6 mm were rare in SEAMAP plankton collections and exceed the maximum size considered to be fully susceptible to capture in plankton nets (Lyczkowski-Shultz and Hanisko 2007).

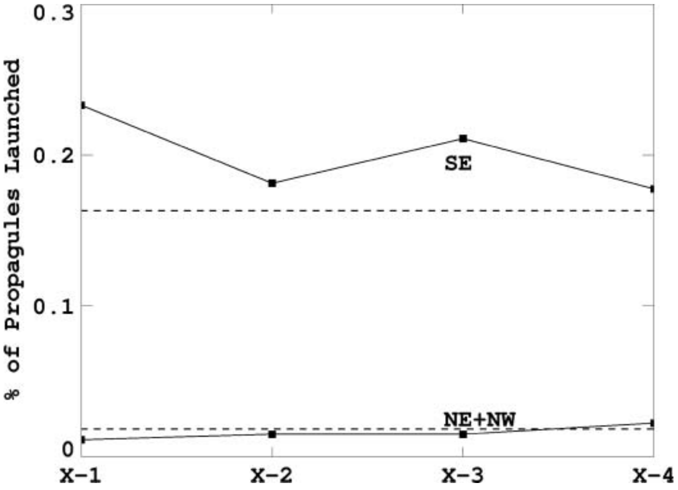

FIGURE 8. Successful recruitment to the SE and NE + NW areas for four experiments done on model year 2010 current data. X-1 doubles random turbulence ($\alpha = 0.2$); X-2 changes dependence of random turbulence from momentum (S) to energy based (S^2); X-3 changes vertical averaging depth to 10 m; X-4 changes vertical averaging depth to 50 m. For comparison, the base experiment results for model year 2010 are shown by dashed lines.

Several experiments were conducted to determine the impact of choice of model parameters on robustness of the results (Figure 8). For the model year 2010, experiments 1 and 2 changed the amplitude of the subgrid scale diffusion multiplication factor and the subgrid scale diffusion form, respectively. Doubling the multiplication factor did increase successful recruitment to the SE area (southwestern Florida shelf) but not to the NE and NW area (northern GOM). The increase was small overall and had no impact on the conclusions. Changing the subgrid scale diffusion formulation from momentum to energy had almost no impact, neither did the increase or decrease of vertical distribution depth (experiments 3 and 4). This suggests that the results are not sensitive to a reasonable range of parameters.

This study demonstrated that larvae residing in the oceanic mixed layer with PLDs of monthly scale can be successfully spread from Campeche Bank throughout the Gulf of Mexico and, potentially, along the U.S. Atlantic coast. Sporadic and limited supply to the eastern GOM, however, suggests that depleted areas such as peninsular Florida are not likely to be enhanced by larval advection from either the more abundant northwestern population (Johnson et al. 2009) or Campeche Bank.

In a study of the genetic structure of Red Snapper in the GOM, it was found that genetic variation from three localities in the northern GOM (Florida, Alabama, and Texas) and Campeche Bank was consistent with the hypothesis that Red Snapper from these locations constituted a single population (Heist and Gold 2000). Although this appears to be at variance with our findings of weak gene flow through larval transport across the GOM basin, it is consistent with the conclusion of Waples (1998) that "only a handful of individuals per generation" is sufficient to obscure most genetic evidence of stock structure.

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