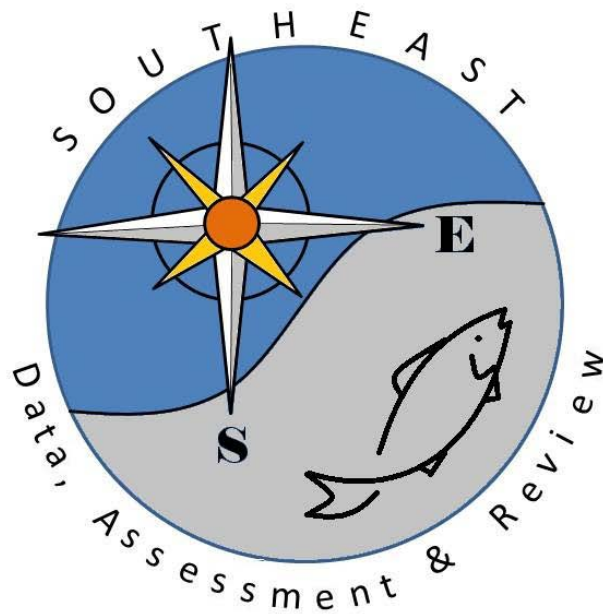# Connections between Campeche Bank and Red Snapper Populations in the Gulf of Mexico via modeled larval transport

Donald R. Johnson, Harriet M. Perry, and Joanne Lyczkowski-Shultz

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Connections between Campeche Bank and Red Snapper Populations in the Gulf of Mexico via modeled larval transport

Donald R. Johnson and Harriet M. Perry

Gulf Coast Research Laboratory, University of Southern Mississippi

703 East Beach Drive, Ocean Springs, Mississippi 39564, USA

Joanne Lyczkowski-Shultz

National Marine Fisheries Service, Southeast Fisheries Science Center

Mississippi Laboratories

3209 Frederick St., Pascagoula, Mississippi 39567, USA

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 days 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 days of planktonic drift, with regional recruitment 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 was sporadic and extremely low. Robustness of the methodology was examined in a set of experiments involving larval depth and sub-grid scale diffusion. The results suggest that larvae from Campeche Bank can contribute to homogenization of the gene pool throughout the Gulf 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, to determine the seasonal influence on pathways, and to 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 U.S., 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 as overfished (SEFSC, SEDAR7 2004, 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 *L. campechanus* in the GOM is heavily skewed toward the west (SEDAR Update Assessment 2009) and fishery independent surveys confirm this skewed distribution (Lyczkowski-Shultz and Hanisko 2007, Mitchell et al. 2004).

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); characteristics that 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 to 6 months). Spawning on Campeche Bank takes place between February and November with peak spawning in early fall (Brulé et al. 2010).   Red snapper eggs are buoyant, drift toward the surface, and hatch in one day (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 two-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, with seven of the species most concentrated in the upper 25 m. There was little information on *L.campechanus* larvae from this study since only two specimens were collected. Under the National Marine Fisheries Service, Southeast Area Monitoring and Assessment Program (SEAMAP), discrete plankton samples have recently been collected using a 1 m MOCNESS (multiple opening/closing net and environmental sensing 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 (Glenn Zapfe, 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 re-attaches south of the separated eddy in a shortened and flattened intrusion. The process results from dynamic instability and is not readily predictable (Hurlbert 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 $1/25^{th}$ 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

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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 sub-grid 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 sub-grid scale turbulent motions can lead to broadened dispersion of propagules. In order to reincorporate sub-grid scale turbulent motions in the model, a random-flight algorithm (Thompson 1986, Dutkiewicz et al. 1993, Takashi 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 of zero and standard deviation of 1) times a fraction of the local current (Marinone et al. 2004, Tilburg et al. 2005):

$$U_{i,j} = \tilde{U}_{i,j} + \alpha * S * P_{i,j}(1)$$

where $U_{i,j}$ = tracking current components in the east (i) and north (j) directions

$\tilde{U}_{i,j}$ = HYCOM model currents

α = fraction of local current speed

S = HYCOM model local current speed

$P_{i,j}(1)$ = 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

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location, the resulting ensemble of pathways represents dispersion of a cloud of spawned larvae. Time steps in tracking were at 0.1 days with random additions 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 ——— . The latter suggests that turbulence is proportional to local energy. The normalization factor —— is the average of current speed throughout the domain divided by average of current speed squared. In X-2, the amplitude of non-captured 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 between 15-64 m depth (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 near shore 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 days from February through November in each of the 4 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 day PLD (1 day egg stage + 30 days 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 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%, with 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 four years was relatively small, with the largest success 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.

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 days involving propagule launches from 4 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 days, propagules from 2 spawning locations on the eastern side of Campeche Bank were entrained into the LC and then branched into the partially separated eddy

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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, with the LC and break-off eddy maintaining contact throughout the summer.

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 north 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 days, 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 to 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 4 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 (He and Weisberg 2003, Huh et al. 1981, Niiler 1976).

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 long-line 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 (Elliot 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 days post-hatch 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 to 21 days old would on average be 8.1 mm in length and range from 5.9 to 10.4 mm (Christian Jones, unpublished data). D'Alessandro et al. (2010) found only two, small (3.7-4.2 mm) *L. campechanus* in monthly larval collections in the Straits of Florida near Miami during daylight net tows. However, larvae of the size (6 to 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).

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 sub-grid scale diffusion multiplication factor and the sub-grid 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 sub-grid 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, Texas) and Campeche Bank was consistent with the hypothesis that *L. campechanus* 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.

Acknowledgements

References

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, Florida.

Bleck, R. 2002. An oceanic general circulation model framed in hybrid isopycnic-Cartesian
coordinates. Ocean Modeling 4:55-88.

Bleck, R. and D. Boudra. 1981. Initial testing of a numerical ocean circulation model using a
hybrid (quasi-isopycnic) vertical coordinate. Journal of Physical Oceanography 11:755-
770.

Brulé, T., T. Colás-Marrufo, E. Perez-Díaz and J.C. Sámano-Zapata. 2010. Red snapper
reproductive biology in the southern Gulf of Mexico. Transactions of the American
Fisheries Society 139:957-968.

Collins, L.A., A.G. Johnson and C.P. Keim. 1996. Spawning and annual fecundity of the red
snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. ICLARM
Conference Proceedings 48:174-188.

Collins, L.A., G.R. Fitzhugh, L. Mourand, L.A. Lombardi, W.T. Walling, Jr., W.A. Fable, M.R.
Burnett, and R.J. Allman. 2001. Preliminary results from a continuing study of
spawning and fecundity in the red snapper (Lutjanidae: *Lutjanus campechanus*) from the
Gulf of Mexico, 1998-1999. Proceedings of the 52nd Annual Gulf and Caribbean
Fisheries Institute 52:34-47.

D'Alessandro, E.K., S. Sponaugle and J.E. Serafy. 2010. Larval ecology of a suite of snappers (family: Lutjanidae) in the Straits of Florida, western Atlantic Ocean. Marine Ecology Progress Series 410:159-175.

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. Fishery Bulletin 98: 507-527.

Dutkiewicz, S., A. Griffa and D.B. Olson. 1993. Particles diffusion in a meandering jet. Journal of Geophysical Research 98:16,487-16,500.

Elliot, B.A. 1982. Anticyclonic rings in the Gulf of Mexico. Journal of Physical Oceanography 12: 1292-1309

Gallaway, B.J., S.T. Szedlmayer and W.J. Gazey. 2009. A life history review for red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Reviews in Fishery Sciences 17:48–67.

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.

Hare, J.A, J.H. Churchill, R.K. Cowen, 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 47:1774-1789.

He, R. and R.H. Weisberg. 2003. A Loop Current intrusion case study on the West Florida Shelf. Journal of Physical Oceanography 33: 465-477.

Heist, E.J., and J.R. Gold. 2000. DNA microsatellite loci and genetic structure of red

snapper (*Lutjanus campechanus)* in the Gulf of Mexico. Transactions of the American Fisheries Society 129:469-475.

Huh, O.K., W.J. Wiseman Jr. and L.J. Rouse Jr. 1981. Intrusion of Loop Current water onto the West Florida continental shelf. *Journal of Geophysical Research* **86:**4186–4192.

Hurlbert, H.E. and J.D. Thompson. 1980. A numerical study of Loop Current intrusions   and eddy shedding. Journal of Physical Oceanography 10:1611-1651.

Johnson, D.R., H.M. Perry, J. Lyczkowski-Shultz and D. Hanisko. 2009. Circulation in the northern Gulf of Mexico and its limiting effects on distribution of red snapper populations. Transactions of the American Fisheries Society 138:458-470.

Lee, T.N., W.-J. Ho, V. Kourafalou and J.D. Wang. 1984. Circulation on the Southeast U.S. continental shelf, Part I - subtidal response to wind and Gulf Stream forcing. Journal of Physical Oceanography 14: 1001-1012.

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 II, 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.

Marinone, S.G., O.Q. Gutiérrez, A. Parés-Sierra. 2004. Numerical simulation of larval shrimp dispersion in the Northern Region of the Gulf of California. Estuarine, Coastal and Shelf Science 60: 611-617.

Maul, G.A., and F.M. Vukovich. 1993. The relationship between variations in the Gulf of Mexico Loop Current and Straits of Florida volume transport. Journal of Physical Oceanography 23: 785-796.

Mitchell, K.M, T. Henwood, G.R. Fitzhugh, R.J. Allman. 2004. Distribution, abundance and age structure of red snapper (*Lutjanus campechanus*) caught on research longlines in the US Gulf of Mexico. SEDAR7-DW-9.

Niiler P.P. 1976. Observations of low-frequency currents on the West Florida continental shelf. *Memoirs of the Royal Society of Sciences Liege* **6**: 331–358.

Oey L-Y. 1996. Simulation of mesoscale variability in the Gulf of Mexico: sensitivity studies, comparison with observations and trapped wave propagation. Journal of Physical Oceanography 26: 145-175.

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.

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.A. Nieland, editors. Red Snapper Population Ecology and Fisheries of U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Porch, C.E., S.C. Turner, and M.J. Schirripa. 2007. Reconstructing the commercial landings of red snapper in the Gulf of Mexico from 1872 to 1963. Pages 337–354 *in* W. F. Patterson III, J.H. Cowan Jr., G.R. Fitzhugh, and D.A. Nieland, editors. Red Snapper Population Ecology and Fisheries of U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Rabalais, N.N., S.C. Rabalais, and C.R. Arnold. 1980. Description of eggs and larvae of laboratory reared red snapper (*Lutjanus campechanus* Poey). Copeia 1980:704-708

Rooker, J.R., A.M. Landry, Jr., B.W. Geary, and J.A. Harper. 2004. Assessment of a shell bank

and associated substrates as nursery habitat of postsettlement red snapper. Estuarine, Coastal and Shelf Science 59: 653-661.

SEDAR7-DW-35. 2004. Characterization of red snapper (*Lutjanus campechanus*) reproduction: for the 2004 Gulf of Mexico SEDAR. NOAA, NMFS, Panama City Laboratory. Contribution Series: 04-01. Addendum. Fitzhugh, G.R., M.S. Duncan, L.A. Collins, W. T. Walling Jr., D.W. Oliver.

SEDAR Red Snapper Update. 2009. Stock assessment of red snapper in the Gulf of Mexico. Gulf of Mexico Fishery Management Council's Science and Statistical (SSC) and Reef Fish SSC Committee. 224 pages.

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

Shipp, R.L. and S.A. Bortone. 2009. A perspective of the importance of artificial habitat on the management of red snapper in the Gulf of Mexico. Reviews of Fishery Sciences 17: 1064-1262.

Szedlmayer, S.T., and J. Conti. 1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, Lutjanus campechanus, in the northeast Gulf of Mexico. Fisheries Bulletin 97:626-635.

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

Takashi K., Y. Kato, M.J. Miller, Y. Sasai, H. Sasaki, S. Kimura. 2010. The restricted spawning area and season of Pacific bluefin tuna facilitate use of nursery areas: A

modeling approach to larval and juvenile dispersal processes. Journal of Experimental

Marine Biology and Ecology 393:23-31.

Thomson, D. J. 1986. A random walk model of dispersion in turbulent flows and its

application to dispersion in a valley. Quarterly Journal of the Royal Meteorological

Society 112: 511–529.

Tilburg, C.E., J.T. Reager, and M.M. Whitney. 2005. The physics of blue crab larval

recruitment in Delaware Bay: A model study. Journal of Marine Research 63: 471-495.

Topping, D.T. and S.T. Szedlmayer. 2011. Site fidelity, residence time and movements of red

snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring. Marine

Ecology Progress Series 437: 183-200

Vukovich, F.M. 1995. An updated evaluation of the Loop Currents eddy-shedding frequency.

Journal of Geophysical Research 100: 8655–8659.

Vukovich, F.M. *and B.W. Crissman. 1986. Aspects of warm rings in the Gulf of Mexico.*

Journal of Geophysical Research 91*: 2645–2660.*

Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in

high gene flow species. Journal of Heredity 89:438–450.

Wells, .R.J.D., J.O. Harper., J.R. Rooker, A.M. Landry, T.M. Dellapenna. 2009.   Fish

assemblage structure on a drowned barrier island in the northwestern Gulf of Mexico.

Hydrobiologia 625:207–221

Woods, M.K. 2003. Demographic differences in reproductive biology of female red snapper

(*Lutjanus campechanus*) in the northern Gulf of Mexico. Thesis. Department of Marine

Sciences, University of South Alabama, Dauphin Island, Alabama. 128 pages.

Figure Captions

1. 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 m and 1000 m.

2. LSU Earth Scan Lab GOES-12 SST composite 2004/03/10-16. Darker pixels represent warmer water. Concomitant satellite tracked drifter from NOAA/AOML/DAC illustrates potential mechanism for larval transport onto the west Florida shelf through eddy motions on eastern flank of the Loop Current.

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

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

5. Successful recruitment to the SE and NE+NW areas as a percentage of propagules launched over the four model years. For presentation, NE and NW are combined.

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

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.

8. Successful recruitment to the SE and NE+NW areas for 4 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.
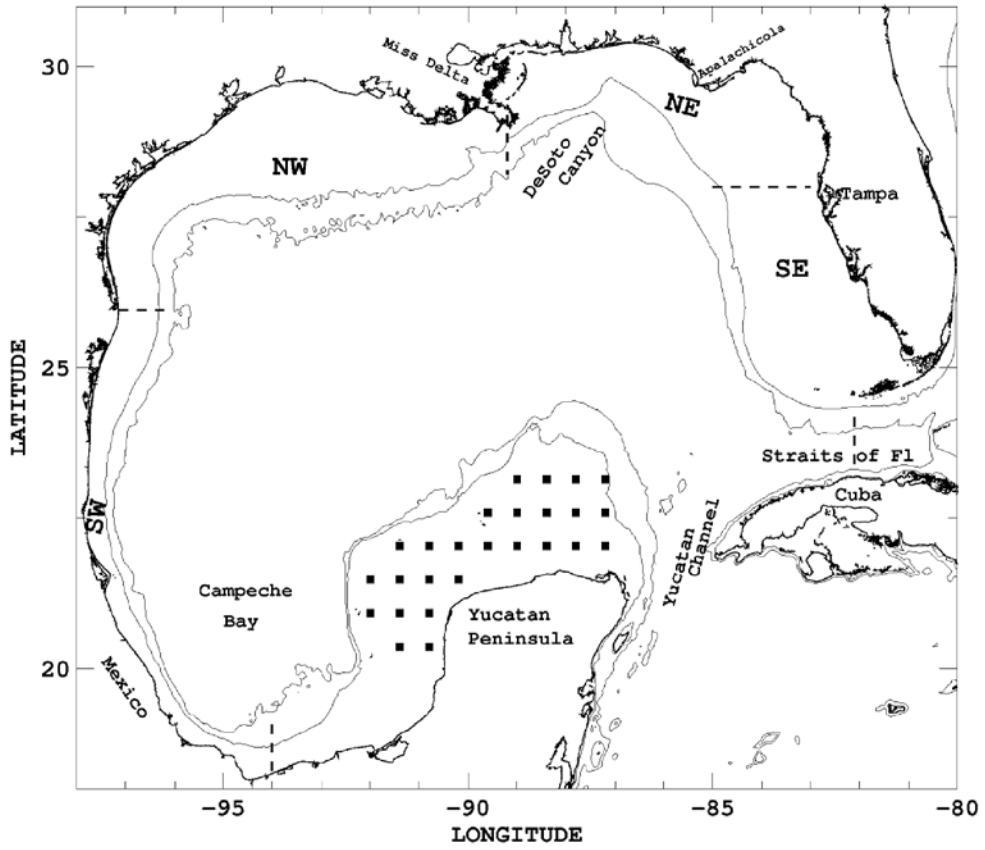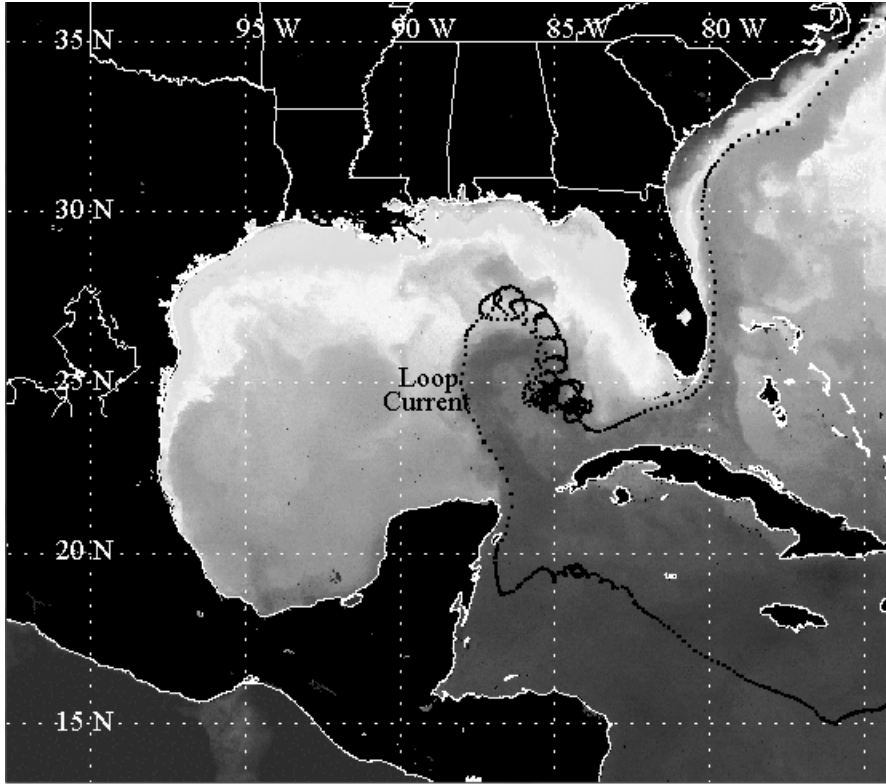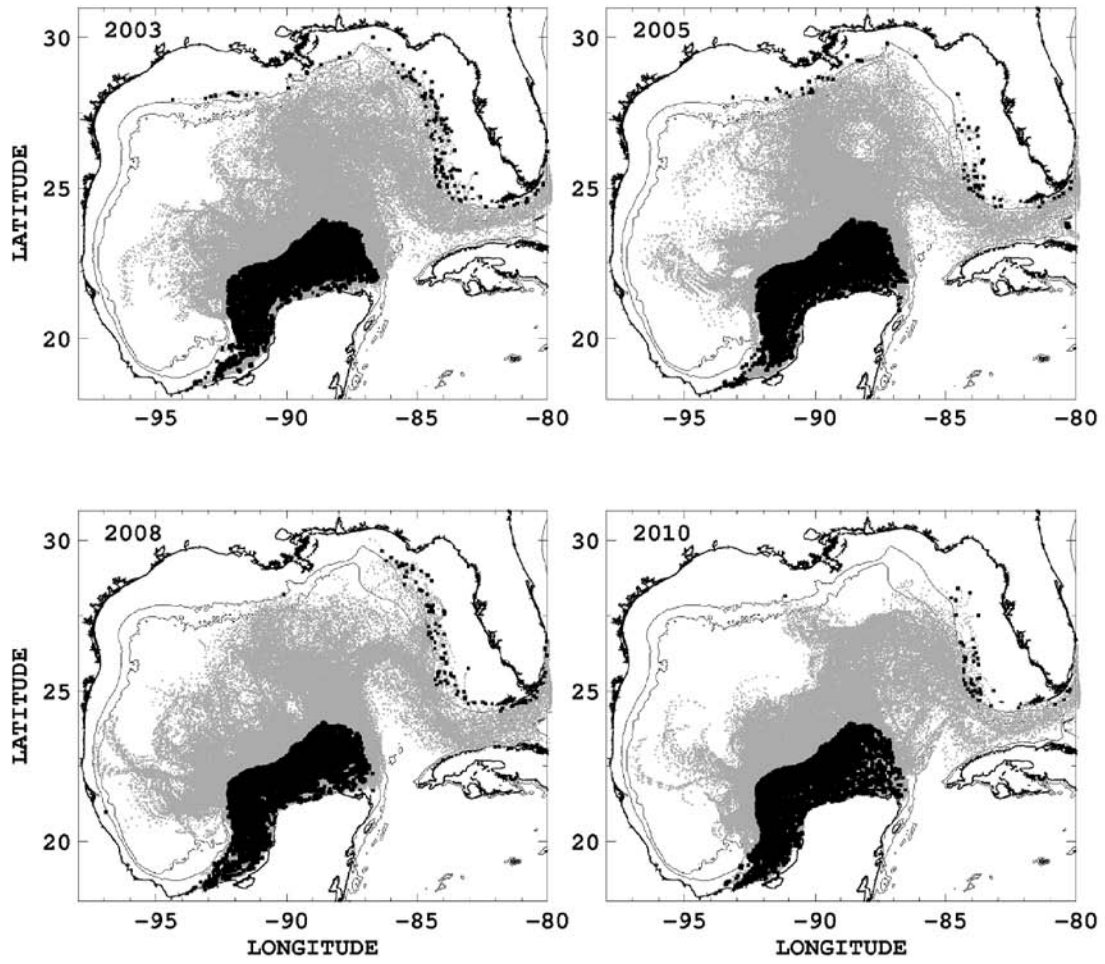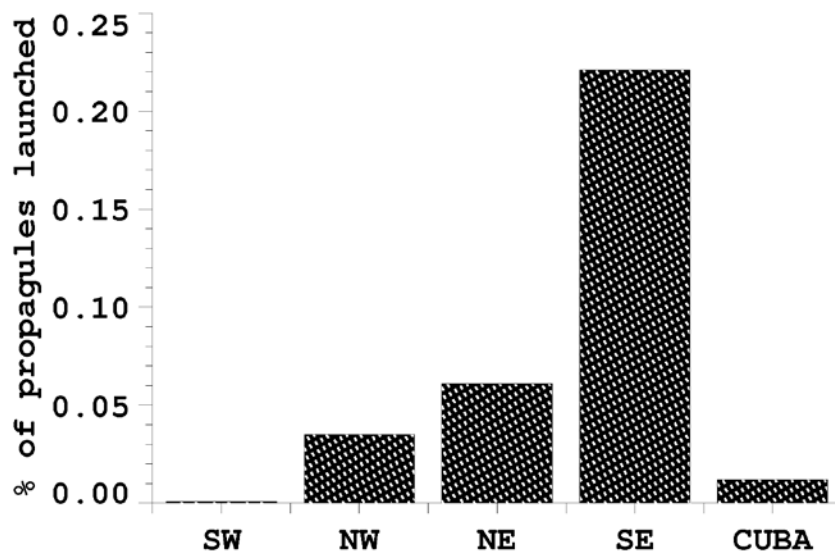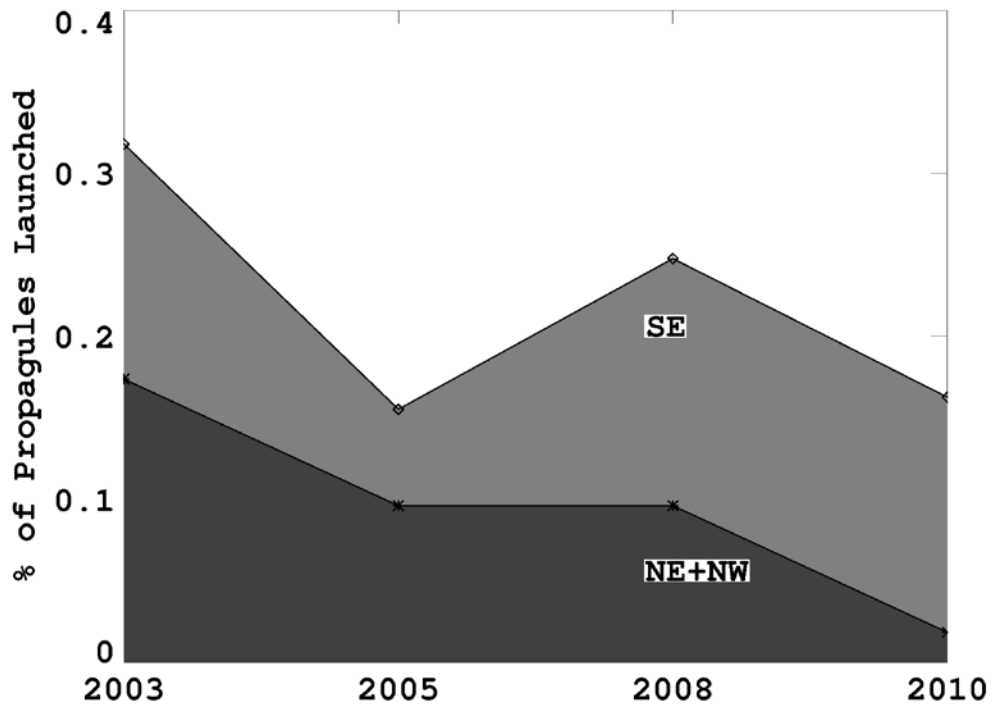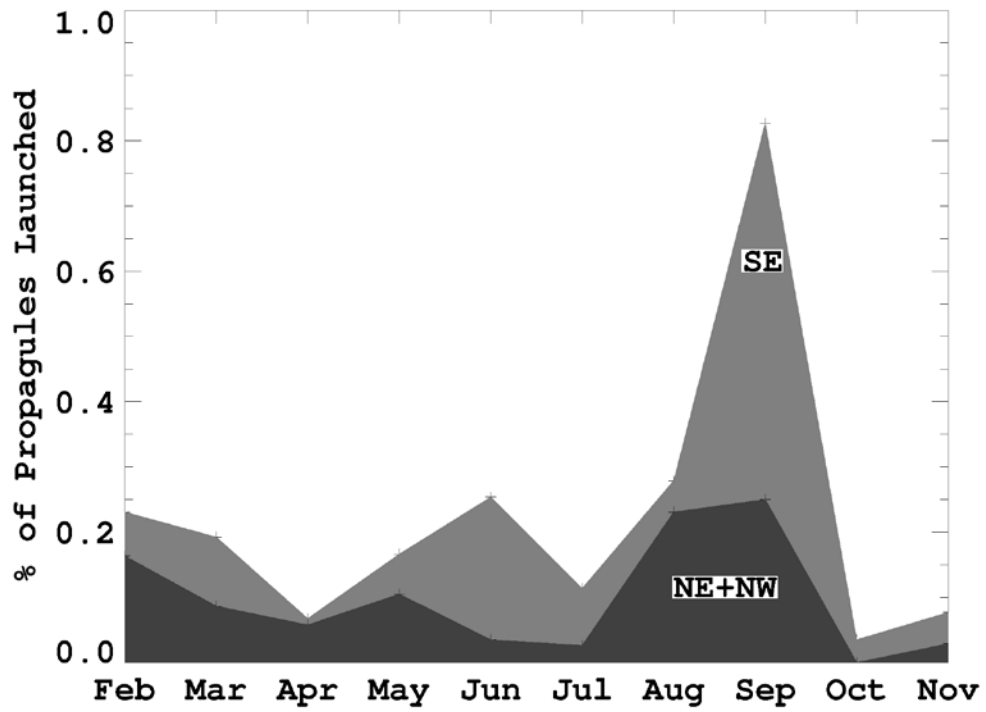
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8