Red snapper, *Lutjanus campechanus*, larval dispersal in the Gulf of Mexico

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RED SNAPPER BIOLOGY IN A CHANGING WORLD

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CHAPTER 2

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CONTENTS

ABSTRACT

Red Snapper, *Lutjanus campechanus*, is a demersal, nonmigratory, continental-shelf species with strong site fidelity yet an extensive latitudinal habitat range. Directly coincident with this range is the western boundary current system in the warm temperate North Atlantic Ocean, suggesting that Red Snapper range may be linked by larval dispersal. Information regarding the balances between natal retention of pelagic larvae and broad dispersal along the boundary current is fundamental to understanding variation in population abundance by natural causes. The Gulf of Mexico has a large population of Red Snapper and a long history of oceanographic observations and oceanic current modeling. In the present study, this history of

current modeling was reviewed to examine possible connections of Red Snapper populations through larval drift within the distributional limits of Red Snapper. Ocean current dynamics, driven by climatological processes, may affect larval dispersal and regional differences that occur in the Gulf of Mexico. For Red Snapper, connections were relatively weak across the Gulf of Mexico basin but sufficient to allow genetic mixing. In the southern Gulf of Mexico, the relatively large production of Red Snapper larvae on Campeche Bank was predominantly retained on the Bank, with a small portion of these larvae transported by the Loop Current both to the west Florida shelf and into the Florida Current. In the northern Gulf of Mexico, topographic barriers and degree of penetration of the Loop Current with spin-off eddies were important factors for the dispersal of larvae. Topographic features reduced connections between the eastern and western Gulf of Mexico. Eastward larval transport during high spawning months was directed from settlement areas toward deep water. Westward transport facilitates larval dispersal, but this occurred during months when spawning was reduced. Energetic Loop Current spin-off eddies negatively affected highly fecund Red Snapper populations on the outer shelf west of the DeSoto Canyon. Dispersal to the deep basin in the Gulf of Mexico was high and variable, while larval redistribution to suitable settlement habitat was weak. Ocean current modeling indicated that the more abundant Red Snapper population in the western Gulf of Mexico did not contribute substantially to stocks east of the Mississippi Delta. Also, there were areas of strong natal retention despite wide larval dispersal, but substantial loss to the deep basin over much of the Gulf of Mexico. The overall picture in the Gulf of Mexico was one of weakly connected populations with scales of roughly 100–200 km set by hydrography.

INTRODUCTION

Red Snapper, *Lutjanus campechanus*, reside near structured continental shelf habitat at depths between 10 and 190 m for most of their life span (Szedlmayer and Shipp 1994; Schroepfer and Szedlmayer 2006; Gallaway et al. 2009; Topping and Szedlmayer 2011; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016). Juveniles first recruit to low-relief, inner-shelf habitats, and as they age and grow, they disperse to increasingly larger structures over the continental shelf with no discernible migratory patterns (Szedlmayer and Conti 1999; Rooker et al. 2004; Szedlmayer and Lee 2004; Gallaway et al. 2009; Szedlmayer 2011; Syc and Szedlmayer 2012). Red Snapper, while demersal and generally nonmigratory, has a native range that extends from the equator off northeast Brazil, through the Gulf of Mexico and along the eastern seaboard of the continental United States, to past Cape Hatteras along the Mid-Atlantic Bight (Anderson et al. 2015). Records of Red Snapper from the Caribbean and South America have been attributed to the Caribbean Red Snapper, *Lutjanus purpureus* (Anderson et al. 2015). However, genetic studies indicated that the Caribbean Red Snapper was the same species as Red Snapper (Gomes et al. 2008, 2012). In addition, a lack of phylogeographic structuring in Red Snapper (Cervigón et al. 1993), morphological similarities and shared biological traits (Rivas

1966; Wilson and Nieland 2001), and geographic distributional data (Anderson et al. 2015) all support the synonymy of the two species.

The large latitudinal range of Red Snapper and its western boundary location coincide with the warm temperate western North Atlantic current system (Figure 2.1). Concurrence of the Red Snapper range with this large-scale current suggests a fundamental linkage that occurs naturally through planktonic larval dispersal (Rindone et al. 2015). The persistent western boundary current system in the North Atlantic includes the North Brazil Current, the Guiana Current, the Caribbean Current, the Yucatan Current, the Loop Current, the Florida Current, and the Gulf Stream (http://oceancurrents.rsmas.miami.edu). Although these currents flow over deep water along the continental shelf edge, interactions with shelf water and shelf-spawned ichthyoplankton occur through highly variable spatial and temporal turbulent eddy

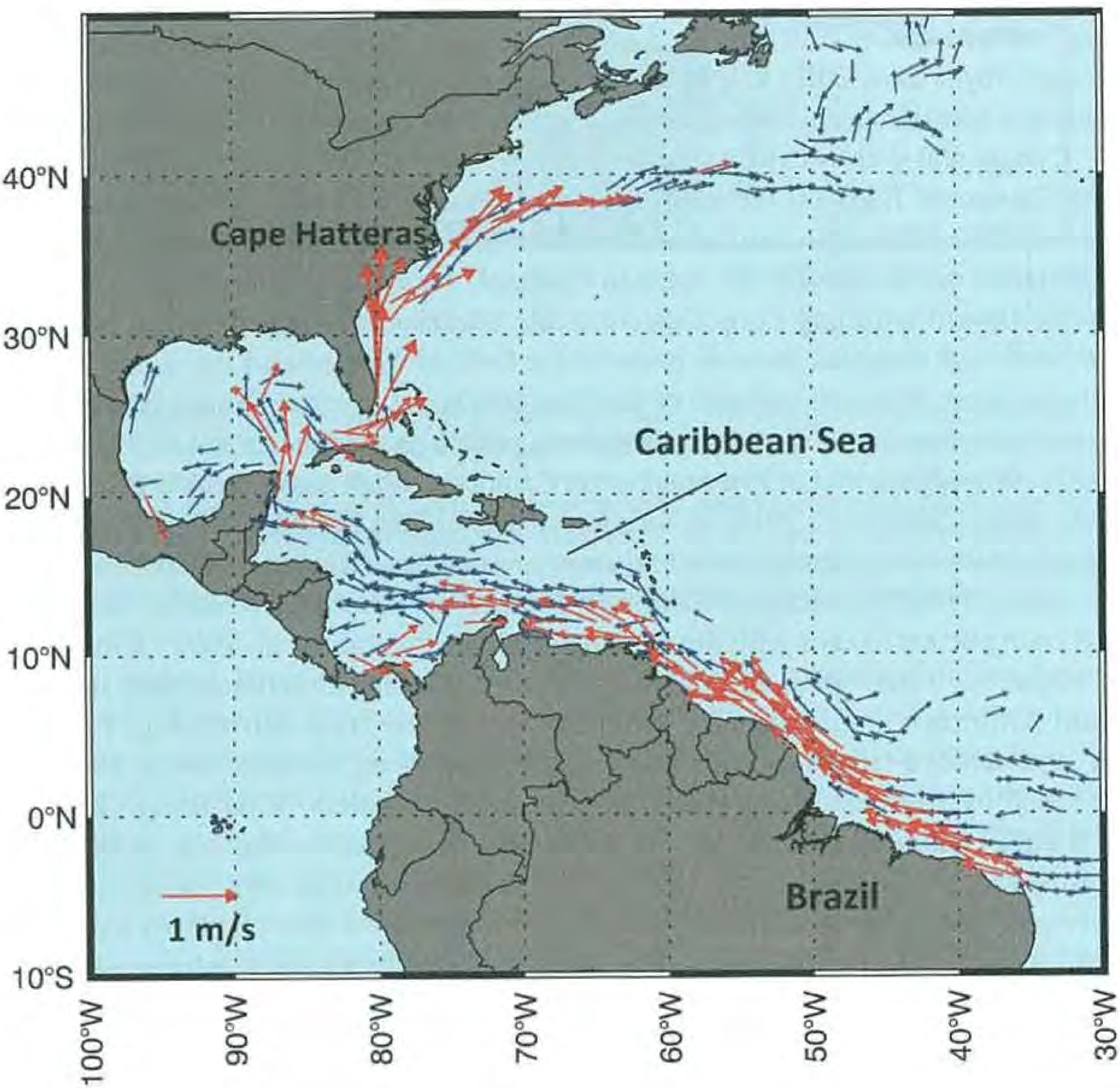

Figure 2.1 Western boundary system of surface currents in the North Atlantic, coincident with the habitat range of Red Snapper. Blue vectors: speed 0.25 to 0.50 m/s. Red vectors: speed >0.50 m/s. Currents are gridded averages from 1979 to 2017, computed from satellite-tracked mixed layer drifters from the Global Drifter Program (NOAA/Atlantic Oceanographic and Meteorological Laboratory [AOML]).

exchanges (Hanisko and Lyczkowski-Shultz 2003; Johnson et al. 2017). The dichotomy between an extensive geographic range and a relatively resident lifestyle suggested that larval drift may be associated with a persistent transport pathway for broad dispersal as an important component of Red Snapper life history strategy.

Red Snapper has a planktonic larval duration of ~30 days (Szedlmayer and Conti 1999; Rooker et al. 2004). This pelagic life-stage is sufficiently protracted to allow passive transport and entrainment into the offshore currents for broad dispersal, but is sufficiently brief to allow some degree of retention to natal areas. Both broad dispersal and natal retention are also ensured by a relatively long and intensive spawning period (May–October) that can be affected by seasonal changes in ocean flow patterns (Collins et al. 2001). In addition, the interaction of strong offshore currents with waters of the continental shelf varies greatly along the current pathway, as do regional differences in dispersal mechanisms (Hare et al. 2002). Changes in the western boundary current system (Toggweller and Key 2001) and local ocean transport conditions associated with climate change (Taylor et al. 2012) may influence future distribution of Red Snapper, although it is unclear how the specific balance of natal retention and broad dispersal will be affected.

Continental shelves (5 to 200 m deep) account for ~31% of the Gulf of Mexico area, with Campeche Bank off the north coast of the Yucatan Peninsula, Mexico, accounting for ~25% of the total Gulf of Mexico shelf area (Figure 2.2). The Campeche Bank is bounded on the east by the Yucatan Channel, where the intense Yucatan Current and northward-intruding Loop Current create a transport linkage between larvae on the Bank and dispersal to other parts of the Gulf of Mexico and the southeast U.S. Atlantic coast. A large population of Red Snapper resides over the Campeche Bank, and spawning occurs from February to November, with a peak in the early fall (Brulé et al. 2010). Although harvest of Red Snapper on Campeche Bank has decreased from earlier high values (Brulé et al. 2010), its location adjacent to the Loop Current in the Gulf of Mexico makes it a potential cross-basin source to other areas in the Gulf of Mexico.

Major drivers for currents on the shelves are river and estuary outflow, wind stress, and energetic exchanges with the deep basin winds (Sturges et al. 2005). Circulation in nearshore waters tends to flow in a counter-clockwise direction around the Gulf basin (Ohlmann and Niiler 2005). Freshwater outflow from surrounding land surfaces produces a buoyancy layer that is constrained along the coastline in width and direction by Coriolis effects (Gill 1982). In offshore waters, wind stress (direction of forcing) has a major influence on circulation. For much of the year, wind stress is westward and equatorward, producing a pattern that is stronger in the southern Gulf and weaker in the north (Figure 2.3). This westward flow results in a negative wind stress curl (Zavala-Hidalgo et al. 2014), causing clockwise circulation along the outer shelf and slope. This clockwise flow was recorded in the earliest current charts derived from ship logs and originally reported as the principal circulation in the Gulf of Mexico (Maury 1855; Sturges and Blaha 1976). During mid-summer, when Red Snapper spawning is at its peak, wind stress responds to continental heating with a light shoreward component in the northern Gulf of Mexico (Figure 2.3). Ekman drift from wind stress along coastlines counters the anti-clockwise nearshore buoyancy-driven flows, complicating larval directional tendencies (Whitney and Garvine 2005) and dispersing them into nearshore waters over the shelf (Johnson et al. 2001).

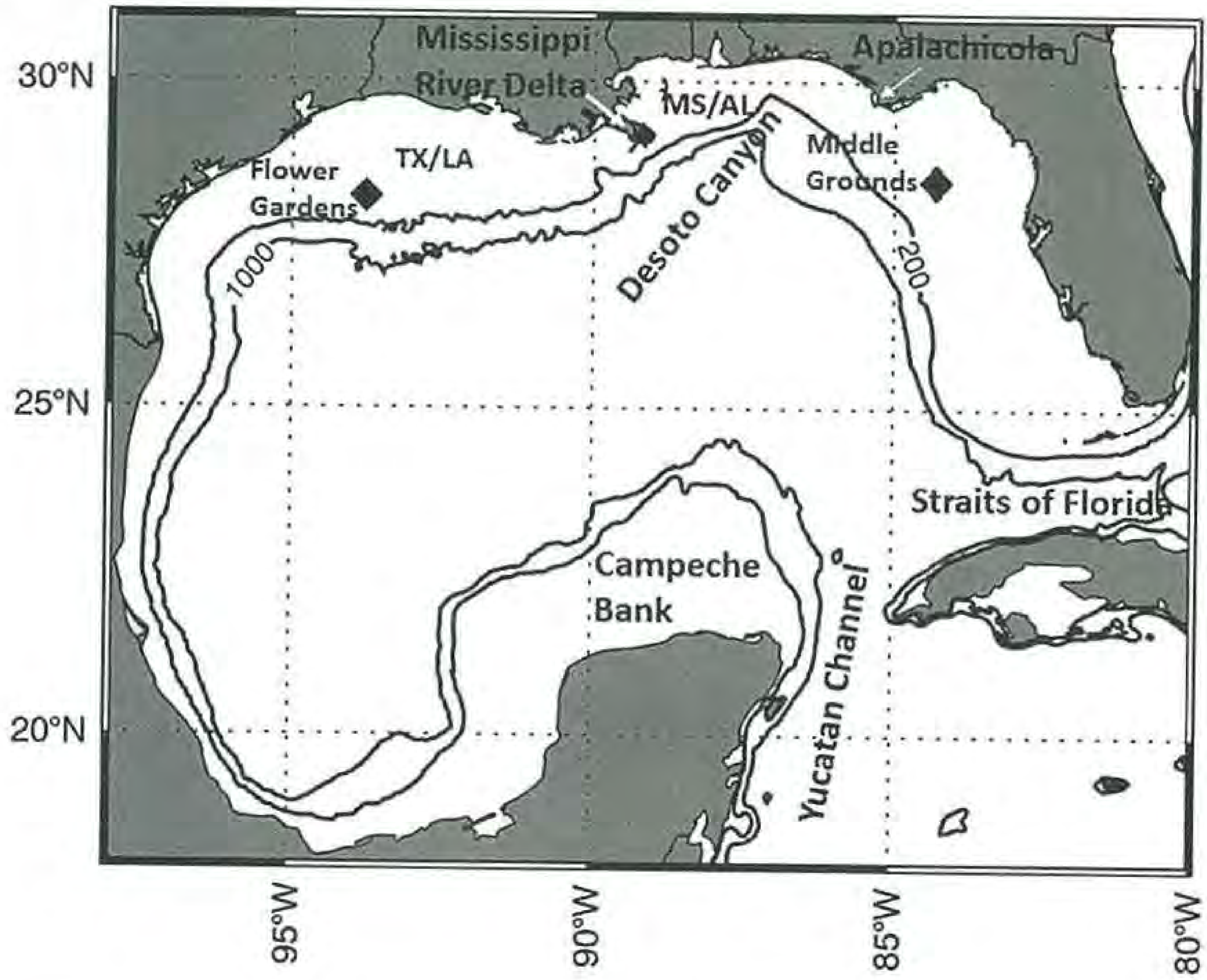

Figure 2.2 Gulf of Mexico with 200 and 1000 m isobaths. The 200 m isobath is defined as the shelf edge, and the area between the 200 and 1000 m isobaths is defined as the upper continental slope. TX/LA is the Texas–Louisiana continental shelf. MS/AL is the Mississippi–Alabama continental shelf. Major topographic barriers to along-shelf flow are the Mississippi River Delta, DeSoto Canyon, and the Apalachicola Peninsula. The Flower Gardens National Marine Sanctuary and Florida Middle Grounds Habitat of Particular Concern are noted by black diamonds.

The general tendency for surface currents to flow counter-clockwise near-shore and clockwise offshore in the northern Gulf of Mexico becomes more complex when factors such as wind stress variation, turbulent exchanges at the shelf break, and continental shelf topography are considered. Across the northern Gulf of Mexico, topographic barriers such as the Mississippi River Delta, the DeSoto Canyon, and Apalachicola Peninsula interrupt the basic current patterns, breaking the shelf into circulation regions (Ohlmann and Niiler 2005; Johnson et al. 2009; Cardona et al. 2016). The Mississippi River Delta extends close to the continental shelf edge, separating the Louisiana–Texas shelf from the Mississippi Bight (Apalachicola, Florida to the Mississippi River; Perry et al. 2003). The Mississippi Bight is separated from the peninsular west Florida shelf by the Apalachicola Peninsula and is itself separated into a western and an eastern region by the DeSoto Canyon. These regional separations create challenges for management of the Red Snapper stock, since both adults and larvae are more prevalent in the western Gulf of Mexico (Lyczkowski-Shultz and Hanisko 2007; Johnson et al. 2009; Karnauskas et al. 2017).

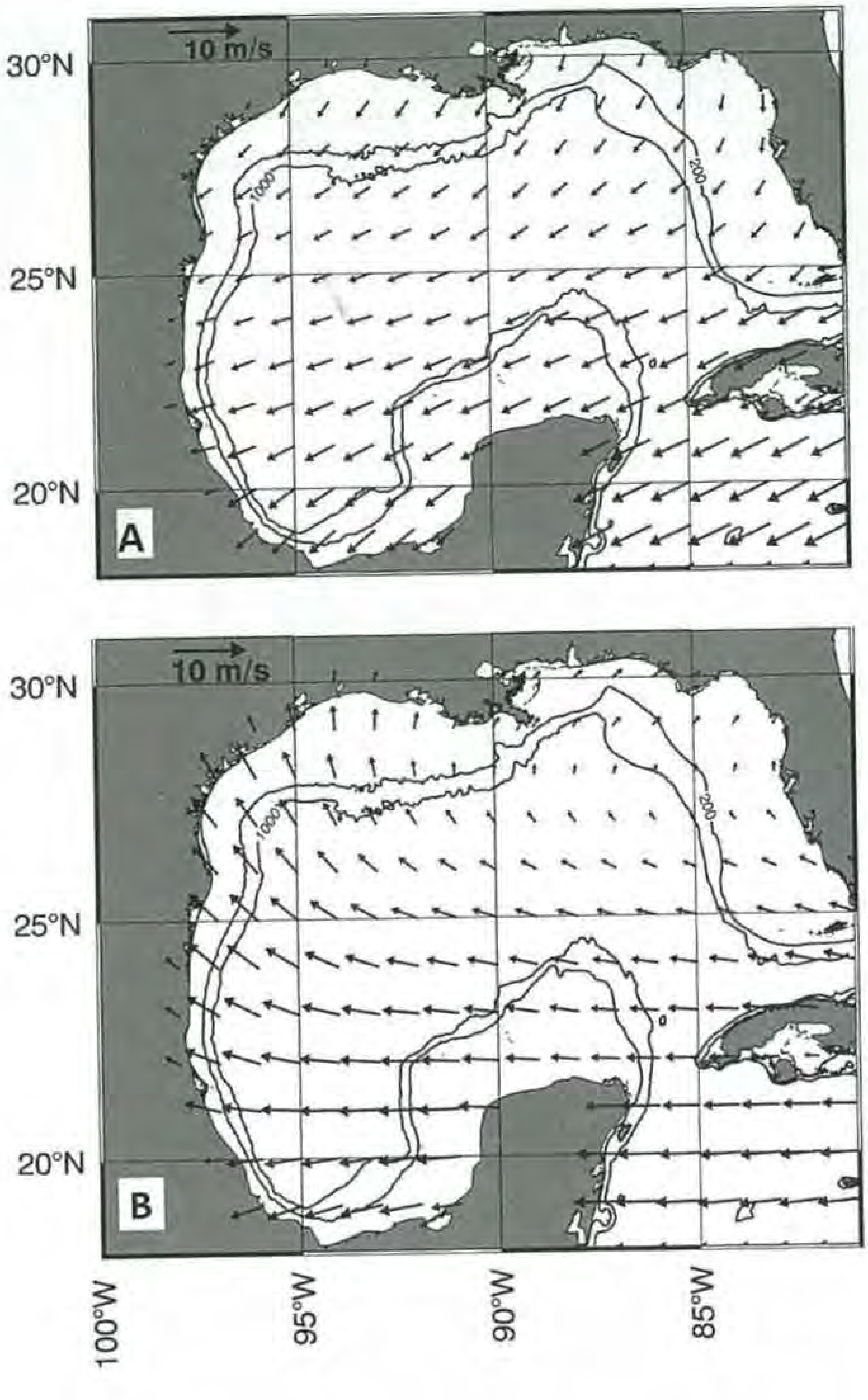

Figure 2.3 Gulf of Mexico surface wind vectors for (A) January and (B) July. Vector direction is direction of force (stress) on the ocean (oceanographic convention). Wind data from NOAA/ (NCEI) monthly blended climatology.

A natural means of bypassing hydrographic separation on the shelf can be through exchange of water with the deep basin and return to the shelf elsewhere (Hare et al. 2002). However, this deep water exchange is difficult, as the dominant flow of currents over the upper continental slope is along isobaths due to the law of conservation of angular momentum (vorticity), and buoyancy differences in the upper layer between the shelf and basin tend to be maintained. This results in density fronts at the shelf edge that inhibit cross-isobath exchange. Transport of planktonic larvae between the shelf and deep basin requires a driving mechanism in the form of turbulent eddies or wind stress. Large offshore eddies are important features of circulation in the northern Gulf of Mexico (Vukovich 2007; Alvera-Azcárate et al. 2009), and these eddies induce water exchanges across the shelf edge and upper slope with the potential to significantly affect larval dispersal from outer shelf–spawned species. Unfortunately, there is limited understanding of how important they are for larval transport, because they vary considerably over space and time (Vukovich 2007, 2012), and exchange across the shelf edge is sporadic.

Large eddies are formed in the northern Gulf of Mexico when the head of the northward-intruding Loop Current separates from the main flow. Separation is a baroclinic instability process that generally occurs with a periodicity of 3–17 months (Hurlburt and Thompson 1980; Vukovich 1995; Sturges and Leben 2000). These spin-off eddies (anticyclones) are commonly 300–400 km in diameter and contain warm, high-salinity Caribbean water with currents of 1–2 m/s. Once separated from the Loop Current, spin-off eddies tend to migrate westward under the influence of the earth's rotation and decay by shear interactions with topography and surrounding water (Vukovich 2007; Lindo-Atichati et al. 2013). If the Loop Current intrudes far northward into the Gulf of Mexico, the spin-off eddies take a westward path along the upper continental slope with resultant water exchanges and planktonic larval transport between the shelf and deep basin (Lugo-Fernández 1998; Ohlmann et al. 2001; Hanisko and Lyczkowski-Shultz 2003; Teague et al. 2013). During this westward migration, direct interactions of spin-off eddies occur along the continental slope, principally west of the DeSoto Canyon. Whether on a northern path or a more central path to the west, spin-off eddies disintegrate along the south Texas and Mexican coasts, with further exchange of water between the shelf and the western basin of the Gulf of Mexico. Energetic, smaller cyclones and anticyclones are formed around the periphery of spin-off eddies as they detach and begin to disintegrate in the central–eastern basin. These smaller eddies can affect the eastern Gulf of Mexico from the DeSoto Canyon south to the slope region off Tampa Bay (Niiler 1976). South of Tampa Bay, Florida, the Loop Current makes direct contact with the upper slope, where sub-mesoscale eddies produced from interaction of the southward-flowing current along the slope cause exchange of water between shelf and basin (Paluzkiewicz et al. 1983; Luo et al. 2016).

Several important Red Snapper populations are affected by spin-off eddies in the northern Gulf of Mexico, including populations associated with the Flower Gardens National Marine Sanctuary in the west and the Florida Middle Grounds in the east. The Flower Gardens is formed around three ancient salt domes located on the Louisiana–Texas shelf, where spin-off eddy effects have been well documented (Lugo-Fernandez 1998; Hanisko and Lyczkowski-Shultz 2003). The three sites (West Flower Garden Bank, East Flower Garden Bank, and Stetson Bank) are at approximately 10, 15, and 35 km from the respective shelf slope. The Florida Middle Grounds is located in the northeastern Gulf of Mexico at about 80 km inshore of the 200 m isobath, where both cyclonic and anticyclonic eddies spinning off the Loop Current are important contributors to slope current energetics and entrainment of shelf water (Niiler 1976; Johnson et al. 2017). Sub-mesoscale eddies from interactions of the Loop Current with Campeche Bank on the west side of the Yucatan

Channel and along the north coast of Cuba likewise result in entrainment and dispersal of shelf-spawned larvae in those locations.

The present study was based on a series of three studies conducted by the authors and provides a review of the physical oceanography of the Gulf of Mexico and dispersal mechanisms for the planktonic distribution of Red Snapper larvae. The three studies involve along-shelf dispersal, dispersal into the deep basin, and cross-basin connections. Understanding hydrography, dispersal mechanisms, and population connections is fundamental to the future management of this species.

METHODS

Shelf Dispersal

Several large physical oceanography studies were conducted in the northern Gulf of Mexico during the 1990s with satellite-tracked drifters and moored current meters (Cho et al. 1998; Yang et al. 1999; Ohlmann and Niiler 2005; Weisberg et al. 2005). These studies were used to develop operational ocean current models and oil spill risk assessments as well as to provide an understanding of regional shelf circulation. To estimate exchange across topographic boundaries and Red Snapper links between regions, data from these observational programs were used to create a gridded (1/12° longitude and latitude) and smoothed (21 year-days) 365 year-day field of currents for Lagrangian tracking (Johnson et al. 2009). The application of observational current data to larval dispersal provided spatial resolution generally reserved for more sophisticated numerical models. To test regional linkage, artificial spawning locations (Johnson et al. 2009) were placed on each side of the Mississippi River Delta (Figure 2.2) and between the DeSoto Canyon and the Apalachicola Peninsula. Particles (defined here as parcels of water containing larvae) were launched (one particle per grid) in the gridded current fields and followed with a simple tracking algorithm. Spawning was simulated at the spawn locations every 3 d from May through October and tracked for 31 d through the field of gridded currents.

Dispersal into the Deep Basin

Decadal-scale changes in the kinetic energy of upper-layer continental slope currents of the northern Gulf of Mexico and the resulting changes in dispersal of reef fish larvae spawned on the outer shelf were examined by Johnson et al. (2017). The Florida Middle Grounds and Flower Gardens National Marine Sanctuary were chosen as spawn sites because of their importance to fisheries and fishery management and their locations with respect to Loop Current spin-off eddies and distances to the continental shelf edge. Currents for this study were obtained from archived runs of the Hybrid Coordinate Ocean Model (HYCOM, GOM10.04; Bleck and Boudra 1981) from 2003 through 2015 and applied to both calculations of kinetic energy in the currents and larval dispersal. The Gulf of Mexico HYCOM is a 1/25th degree (~3–4 km) model with 27 levels in the vertical. The model dynamically changes coordinate systems as it crosses from deep basin to shallow waters, providing a more reliable transition over the continental slope. The model is nested in a 1/12th degree global model, which allows energy exchange across external boundaries. It incorporates tides, climatological river input, and satellite altimetry measurements of sea surface height. Data assimilation of sea surface height into the model phase locks it to actual eddy events (Fox 2002; Chassignet et al. 2007). Atmospheric forcing was taken from the Navy Operational Global Atmospheric Prediction System (NOGAPS). For both larval dispersal and determination of kinetic energy, currents were averaged over a mixed layer of 30 m depth (Muller-Karger et al. 2015; ~15–40 m). Kinetic energy in ambient seasonal currents (mean kinetic energy [MKE]) and kinetic energy associated with spin-off eddies (turbulent kinetic energy [TKE]) were separated by taking the mean and the anomaly of the kinetic energy over a three-month period. Simulated larvae were launched in the HYCOM model throughout the same three-month period for each of the 13 years of the study, and the dispersal was compared with the kinetic energy along the slope region fronting each spawn site. As a metric of dispersal, the distribution of end points after a pelagic period of 31 days (assumed ready for settlement as age-0 juveniles) was evaluated with respect to the 200 m isobath defined as the shelf edge. Although 31-day-old Red Snapper larvae are capable of swimming, if they remain in deep water without access to shallower seafloor habitat when they are ready to settle, they remain vulnerable to predation and may be defined as "lost" to the cohort. The percentage lost was compared over the study period with the kinetic energy (TKE and MKE) available for dispersal.

Cross-Basin Connections

To examine dispersal from spawning sources in the southern Gulf of Mexico, current data from the HYCOM GOM10.04 model were used to track simulated transport of Red Snapper larvae spawned at 26 locations spread evenly across Campeche Bank for the years 2003, 2005, 2008, and 2010 (Johnson et al. 2013). As in the Johnson et al. (2013) study, a simple Lagrangian stochastic model (random turbulent addition to smooth model currents) was applied at each time step to 10 particles launched simultaneously from each of the 26 locations, simulating the spread of spawned larvae from the launch site. Spawning in the model was simulated at each site every three days from February through November during each of the four model years. The end points of the planktonic larval drift (ready for settlement in shallow water as juveniles) were evaluated to determine the importance of the Campeche Bank as a larval source for other regions.

RESULTS AND DISCUSSION

Shelf Dispersal

Topography breaks the northern shelf into hydrographically controlled dispersal regimes with weak and asymmetric east–west connections (Figure 2.4). During peak spawning months from June through August, simulated Red Snapper larvae spawned

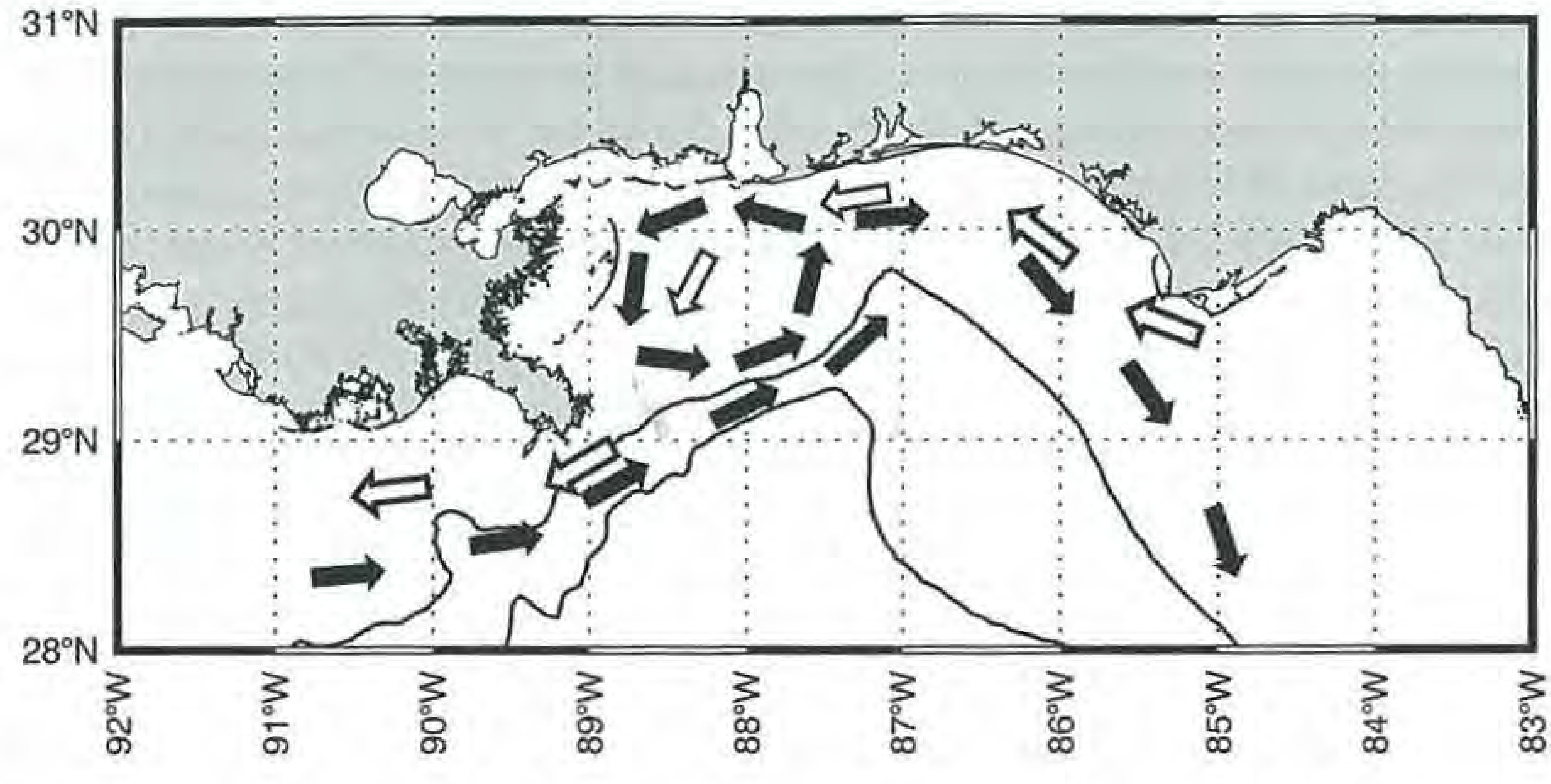

Figure 2.4 Seasonal flow patterns established through model larval dispersal studies. Black arrows = summer (June–September) currents. White arrows = nonsummer currents.

on the Louisiana–Texas shelf were transported eastward around the Mississippi River outflow and into the Mississippi Bight (Johnson et al. 2009). However, this transport pathway routed larvae into deeper waters beyond the shelf break, where they were considered lost due to greater seafloor depths. However, most larvae remained on the Louisiana–Texas shelf for the entire pelagic larval period. Similarly, larvae spawned in the Mississippi Bight were chiefly retained there, but some larvae were transported eastward to nearshore areas around the head of the DeSoto Canyon onto the west Florida shelf. Transport eastward from the west Florida shelf around the Apalachicola Peninsula to the peninsular Florida shelf was principally directed southward along the outer shelf and continental slope (Gilbes et al. 1996; Hseuh and Golubev 2002), where again larvae were considered lost due to greater seafloor depths. Transport on the middle and inner Florida shelf tended toward high natal retention of larvae.

Connections between the peninsular Florida shelf and the west Florida shelf occurred in September and October when spawning was diminished. During this time, wind stress changed to a southwestwardly direction, enhancing westward flow in the coastal buoyancy layer and offshore flow on the middle shelf (Figure 2.4). Larval transport was westward during this time. From Apalachee Bay in northwest Florida, the westward flow crossed the Apalachicola Peninsula in a narrow coastal band and connected the west Florida shelf with the Mississippi–Alabama shelf across the head of DeSoto Canyon (Figure 2.4). This narrow coastal band continued across the Mississippi Delta, ending with flow onto the Louisiana–Texas shelf.

Dispersal into the Deep Basin

Ocean model currents (HYCOM) from 2003 to 2015 were used to calculate the kinetic energy of the mixed layer over the upper continental slope (200 to 1000 m) due to eddy interactions with the shelf and to track the dispersal of larvae spawned during the summer (June–August) season (Johnson et al. 2017). Two important Red Snapper habitat areas were examined: Flower Garden Banks off Texas and the Florida Middle Grounds. Over the 13-year model period, dispersal into the deep basin from the Flower Gardens National Marine Sanctuary averaged 63.5%, with a range of 34.6% to 90.8%. Dispersal from the Florida Middle Grounds averaged 9.5%, with a range of 0.6% to 23.1%.

Temporal dispersal of larvae was associated with trends in turbulent kinetic energy and mean kinetic energy over the continental slope and varied with the North Atlantic Oscillation Index (www.esrl.noaa.gov). Between 2010 and 2011, mean kinetic energy (from ambient seasonal along-slope currents) replaced turbulent kinetic energy as the dominant dispersal mechanism. The correlation of percentage loss between the Flower Gardens and Florida Middle Grounds was surprisingly high ($r = 0.67$, $N = 13$, lag = 0, $P < 0.01$) when compared with the separation distance (~1000 km) between the two areas. This correlation provided a measure of confidence that the same Loop Current intrusion and spin-off eddy exchange processes occurred across the entire northern Gulf of Mexico, although with different regional effects.

Two important factors for Red Snapper larval dispersal were spawning location with respect to the region of major eddy–shelf interaction and the distance from the shelf edge. At the West Flower Garden Bank (10 km to the shelf edge) the mean annual loss was 79%, while at the Florida Middle Grounds (80 km to the shelf edge) the mean annual loss was only 9.5%. When all sites were compared against distance to the shelf edge (including three at the Flower Garden Banks), the mean yearly loss decreased linearly at about 1% loss per kilometer (rather than exponentially, as expected by Coriolis scaling). Spatially, loss to the deep basin was dependent on spawning locations relative to eddy influence area, distance to shelf edge, and topography of the upper slope.

Dispersal to other regions of the Gulf of Mexico through deep basin eddies was relatively low (~4.4%; i.e., into the basin in one location and return to the shelf elsewhere). Variations in frequency and northward position of the Loop Current intrusion and detachment of eddies suggested that exchange between shelf and deep basin was highly variable. Turbulent and mean kinetic energy fronting the Flower Gardens and Florida Middle Grounds study sites compared with larval dispersal percentage lost showed consistent trends over the study period (Figure 2.5). Larval percent loss was high (~60%) in 2003, low (~30%) in 2011, and high (~75%) in 2015. The turbulent kinetic energy corresponded to larval percentage loss until 2014, when it did not correspond to the rapid rise in percentage loss. The mean kinetic energy increased from a low in 2003 to a high in 2015, matched the level of turbulent kinetic energy in 2011, and thereafter provided an alternative mechanism for continued high loss in 2014 (55%) and 2015 (75%).

Cross-Basin Connections

Natal retention over Campeche Bank in water of depth less than 200 m (Figure 2.6) was remarkably high in all four years of study. As a percentage of all particles launched (26,520) in each year, natal retention was 73.3% in 2003, 73.2% in

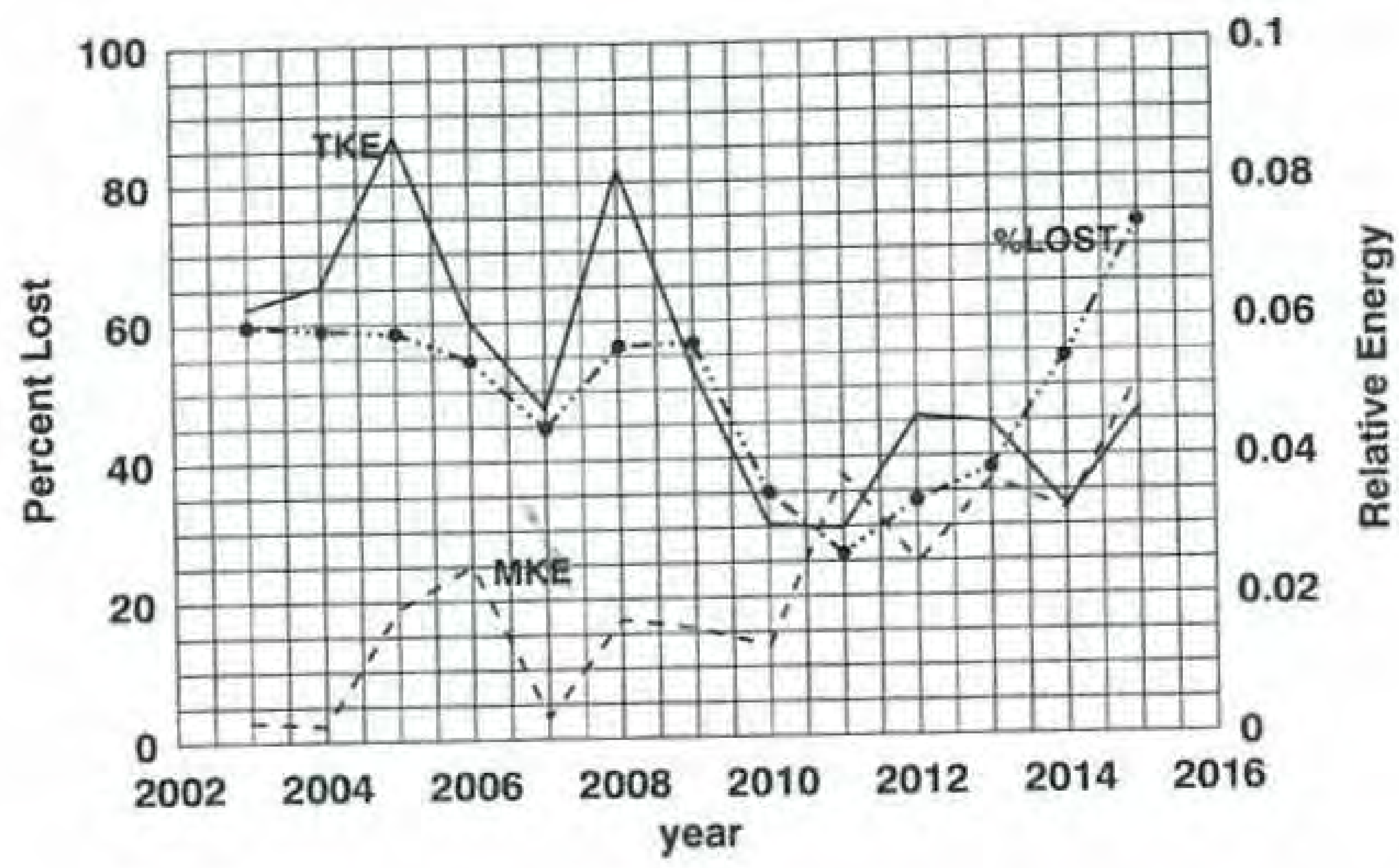

Figure 2.5 Time series (2003–2015) of larval dispersal and energy over the adjacent upper slope regions. %LOST (black line with black dots) = dispersal to the deep basin with no return. TKE (solid line) = eddy energy over the adjacent upper continental slope. MKE (dashed line) = ambient seasonal currents over the adjacent upper continental slope.

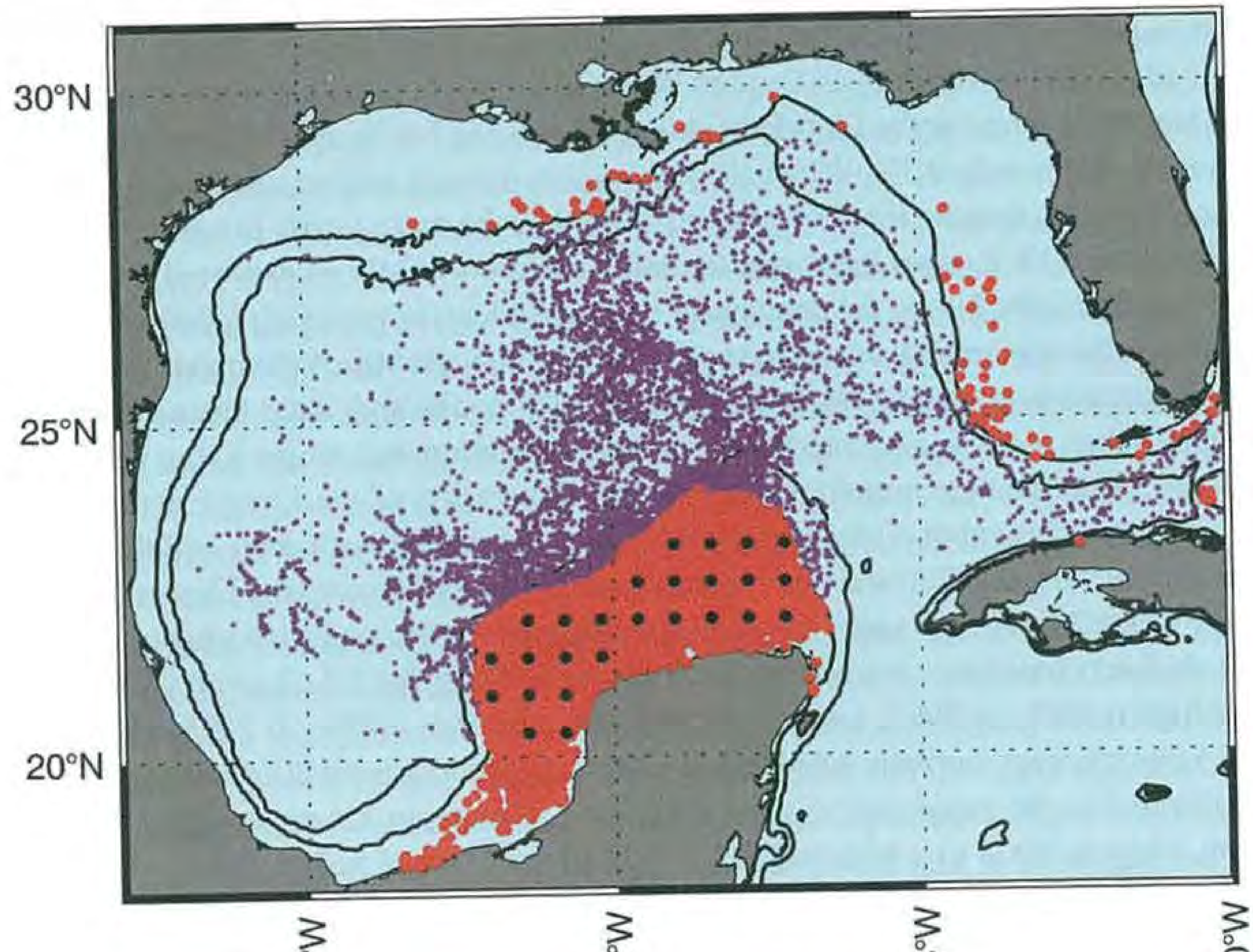

Figure 2.6 Larval dispersal from Campeche Bank in model year 2005. Black dots represent spawning locations. Red dots show locations when they are ready to settle to suitable shallow water habitat (<200 m water depth after 30 days). Purple dots show locations where they are ready to settle but remain in deep water. Note high natal retention on Campeche Bank and low cross-basin success. Some larvae are in the Straits of Florida with possible Atlantic coast settlement.

2005, 67.8% in 2008, and 67.5% in 2010. For those years, ~28% of the particles transported off Campeche Bank were lost to the deep basin. Successful basin crossing (ended pelagic drift in <200 m water depth) as a percentage of total particles launched for the combined years was ~0.33%, with most occurring on the southwest Florida shelf. Successful particles that crossed the basin came principally from eastern and northern locations on Campeche Bank, where they were entrained in the Loop Current before being transported onto the outer continental shelf elsewhere. Peaks in monthly recruitment occurred in August and September (~0.8% of particles launched for those months), when seasonally lighter trade winds resulted in greater entrainment in the Loop Current.

Several of the particles ended in waters <200 m along the northern coast of Cuba. This occurred in July 2008, over a period of 10 days involving particle launches from four different spawning locations on the Campeche Bank. During this period, the eastern branch of the Loop Current (south flowing) penetrated unusually far to the south, affecting the northern coast of Cuba and bringing particles onto the narrow shelf. Particles that ended on the shelf in the northwest Gulf of Mexico did so in 2003 and 2005 (Figure 2.6). In 2003, the Loop Current 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. Over a period of nine days, particles from two spawning locations on the eastern side of Campeche Bank were entrained into the Loop Current and then into the partially separated eddy, where they were transported onto the shelf west of the Mississippi River Delta. In 2005, a similar intrusion and break-off occurred in March, with the Loop Current and break-off eddy maintaining contact throughout the summer. A few particles (1.6% of particles launched) from Campeche Bank entered the Straits of Florida entrained in the Florida Current. Detailed examination of the particles that entered the Straits of Florida revealed that seven sites in the Campeche array contributed all particles 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 (Figure 2.6).

Conclusions

Ocean currents, driven by climatological processes and moderated by topography, were principal determinants of larval dispersal and at least partially responsible for regional differences in Red Snapper distributions observed in the Gulf of Mexico. Topographic barriers in the northern Gulf of Mexico, such as the Mississippi River Delta, DeSoto Canyon, and the Apalachicola Peninsula, separated the continental shelf in the northern Gulf of Mexico into population regions. Consistent with these larval drift patterns, genetic patterns in Red Snapper indicated a correlation at scales <~150 km and a lack of correlation >150 km across the northern Gulf of Mexico in genes associated with life history traits (Portnoy and Gold 2013). Both the Mississippi–Alabama shelf and the west Florida shelf roughly scale to ~150 km in size, supporting the present study's conclusion that topographic barriers restricted shelf circulation patterns and resulted in a metapopulation Red Snapper stock structure (Gold and Sallient 2007). Asymmetry in the alongshore directional flux of larvae occurred with seasonal changes in wind-driven, topographically moderated currents. During summer, when spawning was high, there was eastward larval transport from large western populations. However, this flow tended to be directed by topographic barriers toward deep water, where lack of suitable settlement habitat reduced the probability of juvenile recruitment success (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004; Geary et al. 2007). Westward connections occurred in a narrow coastal band, but such westward flow occurred during the fall, when spawning was reduced and there were few larvae potentially available for transport.

Turbulent kinetic energy from Loop Current–shed eddies and sub-mesoscale eddies along the shelf edge influenced Red Snapper larval dispersal on the outer shelf in the northern Gulf of Mexico, where there are large populations of highly fecund adults. Dispersal to the deep basin was strong, highly variable, and dependent on the distance of intrusion of the Loop Current into the northern Gulf of Mexico. Spin-off eddies, shed from the Loop Current, migrated westward and interacted with the outer shelf, pulling broadcast spawned larvae into the deep basin, where they were probably lost. Spawning sites in the northwestern and northeastern Gulf of Mexico were vulnerable to eddy-forced exchanges between the shelf and the deep basin. Mean percentage dispersal to the deep basin from these sites exceeded 50% of the annual larvae produced. Variation in loss from the shelf followed variation in current energy over the upper continental slope adjacent to the spawning sites. Current energy (TKE) over the upper slope was linked to the spin-off eddies, which were connected to northward intrusion of the Loop Current at the time of eddy separation. Northward intrusion appeared to be loosely linked to winds over the North Atlantic (Johnson et al. 2017).

In the southern Gulf of Mexico, Red Snapper on Campeche Bank were for the most part isolated. The strong Yucatan Current flowing along the eastern side of the Bank provided a mechanism for supply of larvae to the Florida continental shelf and to the Atlantic. Despite the strong current along the edge of the bank, most of the larvae remained on the bank until settlement age. Only 0.33% reached shelves after basin crossing in the Gulf of Mexico, and 1.6% entered the Straits of Florida.

In summary, the influence of the persistent western boundary current system on Red Snapper larval dispersal was both temporally and spatially sporadic throughout the Gulf of Mexico. Dispersal compared with natal retention was relatively high in the northwestern Gulf of Mexico and low on Campeche Bank and the peninsular west Florida shelf. Dispersal along the northern Gulf of Mexico continental shelf was limited by topography and separation into hydrographic regimes. Distance of major spawning areas to the shelf edge played a significant role in the balance between natal retention and broad dispersal. It seems clear that renewal of depleted populations by the mechanism of hydrographic dispersal is unexpectedly weak in the Gulf of Mexico; however, broad dispersal and recruitment likely contribute to genetic mixing over large scales.

There remain many unanswered questions regarding larval behavior, dispersal, settlement, and the effects of a changing climate (decadal and longer) on population connections. Of special interest would be further studies on possible links between the Caribbean and the Gulf of Mexico, and between the Gulf and the western Atlantic coast in combination with genetic studies. Gene flow among populations connected to the western boundary current pathway should be dominantly unidirectional from south to north. It is unclear how speciation may be influenced by the directionality of dispersal along this pathway.

Oceanographic conditions in the Gulf of Mexico and Caribbean have been noted to change on decadal scales (Taylor et al. 2012; Karnauskas et al. 2015; Muller-Karger et al. 2015; Johnson et al. 2017), and strong connections have been made between variations in the Atlantic and its western boundary current system (Toggweller and Key 2001). The dependence of Red Snapper distribution on larval dispersal from wind and Coriolis-driven current systems makes this species especially vulnerable to Atlantic-scale climate conditions.

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