Loop Current Spin-off Eddies, Slope Currents and Dispersal of Reef Fish Larvae from The Flower Gardens National Marine Sanctuary and The Florida Middle Grounds

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GULF AND CARIBBEAN

R E S E A R C H

LOOP CURRENT SPIN—OFF EDDIES, SLOPE CURRENTS AND DISPERSAL OF REEF FISH LARVAE FROM THE FLOWER GARDENS NATIONAL MARINE SANCTUARY AND THE FLORIDA MIDDLE GROUNDS

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ABSTRACT: Large energetic spin—off eddies from Loop Current intrusions into the Gulf of Mexico play a major role in water exchange between the continental shelf and the deep basin in the northern Gulf. Reef fish larvae, spawned on the outer shelf and planktonic during their early life history, are broadly dispersed by this mechanism, but may be lost to the cohort by transport away from suitable settlement habitat. In this study, satellite altimeter data—assimilative ocean model currents (HYCOM) from 2003—2015 are used to calculate kinetic energy of the mixed layer over the upper continental slope (200 m—1000 m) due to eddy interactions with the shelf and to track the dispersal of larvae spawned during core summer (June—August) season. Over the 13 year model period, dispersal into the deep basin from the Flower Gardens National Marine Sanctuary averaged 63.5%, with a high of 90.8% and a low of 34.6%. Dispersal from the Florida Middle Grounds averaged 9.5%, with a high of 23.1% and a low of 0.6%. 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. Between 2010 and 2011, mean kinetic energy replaced turbulent kinetic energy as the dominant dispersal mechanism.

KEY WORDS: kinetic energy, larval transport, Gulf of Mexico, climate variation, model.

INTRODUCTION

Large offshore eddies in the northern Gulf of Mexico (GOM) induce water exchanges between the continental shelf and the deep basin with potential impact on dispersal of planktonic larvae from reef fish endemic to the shelf (Lugo—Fernández 1998, Lugo—Fernández et al. 2001). However, these eddy—induced exchanges across the shelf break are highly variable in both location and time as they are driven by seasonal and inter—annual variations in Loop Current (LC) intrusions and the subsequent westward migration pathways of spin—off eddies (Vukovich 2007, 2012). The objective of this study is to evaluate this important driver of larval dispersal from selected reefs in the northern GOM and its variation over a 13 year period. The long—term objective is to provide a greater basis for understanding effects of climate changes on important fishery resources of the GOM.

The dominant oceanographic features in the deep basin of the GOM are the LC and its spin—off eddies (Figure 1A). As part of the North Atlantic western boundary current, the LC intrudes into the GOM through the Yucatan Channel, penetrating far northward before looping back and exiting through the Straits of Florida. At times, the head of the loop bends back on itself and detaches from the main flow,
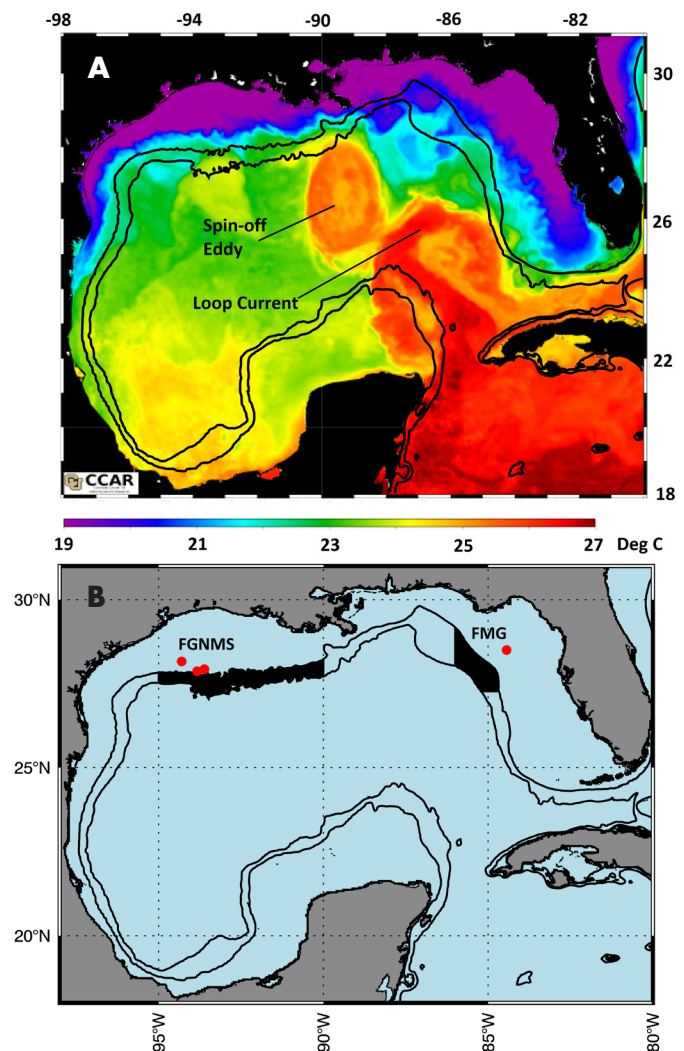
FIGURE 1. Maps of the Gulf of Mexico. A. Satellite thermal image on 5 March 2006 showing intruding Loop Current and a spin—off eddy. Bathymetric contours of 200 m and 1000 m depth define the upper continental slope. Image credit to CCAR, University of Colorado. B. Study setting. Red dots represent the Flower Gardens National Marine Sanctuary (FGNMS; 3 sites) and the Florida Middle Grounds (FMG). Bathymetric contours are 200 m and 1000 m depth. The upper slope areas fronting the 2 locations are where comparative current energy was averaged yearly.

creating a large spin—off eddy. Baroclinic instability appears to be responsible for the detachment and eddy formation (Hurlburt and Thompson 1980), making the process difficult to predict. From analysis of satellite thermal imagery and altimetry, eddy detachment occurs from 3—18 months with most detachments occurring in summer and winter (Vukovich 2007).

Spin—off eddies are large (300—400 km diameter) and energetic (1—2 m/s). Under the influence of the earth's rotation, they migrate from the central—east basin where they are formed to the western basin along a path partly dependent on the latitude of separation (Vukovich 2007, Lindo—Atichati et al. 2012). Both cyclonic and anti—cyclonic eddies are formed around the perimeter where there is strong horizontal current shear. If detachment occurs far to the north, the path of the spin—off eddy and its attendant eddies interact with the upper continental slope (Hamilton et al. 1999, Ohlmann et al. 2001, Teague et al. 2013) with resultant exchange of water between the shelf and deep basin. The principal impact is felt along the outer continental shelf from about 90°W (Mississippi Delta) westward, although attendant eddy exchange with the shelf has been observed east of this longitude (Niiler 1976, Huh et al. 1981). The LC itself has been noted to interact with peninsular Florida's outer shelf (Paluszkiewicz et al. 1983, He and Weisberg 2003) as it flows southward toward its exit into the Straits of Florida.

The shelf/basin coupling draws shelf spawned ichthyoplankton into deep water where they may be spread over considerable distances (Johnson et al. 2013). It may also be a source for biologically coupling with the Caribbean and a pathway for invasive species passing through the Caribbean (Johnson et al. 2005, Johnson and Perry 2008). Larvae spawned on the outer shelf are vulnerable to entrainment in the eddy—forced exchanges (Lugo—Fernández 1998, Hanisko and Lyczkowski—Shultz 2003), resulting in transport to waters over the deep basin where mortality is likely to be higher and where return to preferred habitat (Hare et al. 2002) is possible but difficult. Eddy forcing can also enhance alongshore currents on the outer shelf with subsequent dispersal to distant habitat.

Direct exchanges between the continental shelf and the deep basin in the northern GOM have been calculated using satellite radar altimetry (Ohlmann et al. 2001). The method involved computing the convergence of turbulent kinetic energy along the upper slope of the continental rise and determining onshore/offshore flow. In this study, we build on the Ohlmann et al. 2001 foundation. Variations in anomalous (turbulent) kinetic energy and the kinetic energy of the seasonal mean over the upper slope region were examined for a 13 year period using currents from a satellite altimeter data—assimilative ocean model. As a metric of the impact of this energy, larval dispersal into the deep basin from the broadcast spawn of reef fish on the outer shelf, using a simple life history stratagem, was tracked and related to temporal measures of energy over the upper slope.

MATERIALS AND METHODS

Study Area

The Flower Gardens National Marine Sanctuary (FGNMS; http://flowergarden.noaa.gov) is formed around three ancient salt domes on the mid to outer continental shelf in the GOM (Figure 1B). The sanctuary consists of East Flower Garden Bank (EFG), West Flower Garden Bank (WFG) and Stetson Bank (ST). EFG and WFG are located ~185 km offshore of the Texas coast and rise from 100—140 m water depth to within 16—18 m of the surface. These 2 banks were designated as a National Marine Sanctuary in 1992 and contain the northern—most living hard coral in the USA. Stetson Bank, located ~125 km offshore with its base in water depth of roughly 55 m, was added to the FGNMS in 1996. The Sanctuary provides important habitat for commercial reef fish. The nearness of the FGNMS to the continental shelf edge (defined herein as the 200 m isobath) raises concerns about natal retention of broadcast spawned larvae and the potential for loss from natal habitat due to sporadic eddy induced water exchanges with the deep basin.

The Florida Middle Grounds (FMG) was designated a Habitat Area of Particular Concern (HAPC; www.habitat.noaa.gov) by the Gulf of Mexico Fishery Management in the 1980s. The FMG is a prehistoric coral—reef complex with high and low relief limestone ridges (Coleman et al. 2004) lying ~150 km off the northwest coast of peninsular Florida (Figure 1B). Sporadic water exchanges (Niiler 1976; Paluszkiewicz et al. 1983; Coleman et al. 2004) with the deep basin impact this ecosystem and raise questions about planktonic larval connections across the GOM as well as with the Caribbean. Like the FGNMS, it provides important habitat for commercial as well as recreational reef fishes. Although there are many similarities between the FGNMS and the FMG, the difference in location with respect to the offshore eddies that drive shelf/basin exchanges can be significant.

Model

Currents were obtained from archived runs of the Hybrid Coordinate Ocean Model (HYCOM; Bleck 2002) from 2003 through 2015 and applied to both calculations of kinetic energy and larval dispersal. The GOM 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 GOM model is nested in a 1/12th degree global model which allows for energy exchange across external boundaries. It incorporates tides, climatological river outflow and satellite altimetry measurements of sea surface height. Atmospheric forcing is from the Navy Operational Global Atmospheric Prediction System (NOGAPS). Satellite altimeter data assimilation (Kantha and Clayson 2000, Fox et al. 2002) is important in that it

phase locks (time and location) the model to real ocean events such as location of the LC and its spin—off eddies.

Due to strong geoid variations across the upper slope and shelf combined with satellite orbital uncertainties, satellite altimeter assimilation in the HYCOM model is only included where water depths are > 400 m (Cummings and Smedstadt 2013). Eddy events, constrained on the upper slope with altimetry, are propagated onto the continental shelf by the model equations of motion. Model equations also propagate altimeter information into the areas between sparse nadir tracks.

Although yet to be documented, it is expected that a distance scale of one internal Rossby radius of deformation, R_d ~40 km in the northern GOM (Chelton et al. 1998), can be used as a basic minimum measure of eddy event influence on the shelf. In a comparable study, Muscarella et al. (2015) found that assimilation of drifters into a model of the GOM constrained the model within a distance scale of 40—60 km, suggesting that this scaling may be appropriate. The present study involves time scales of one month (larval dispersal) to 4 months (eddy energy). This mitigates somewhat the reliance on individual events for both dispersal and energy determination and focuses more properly on statistical metrics.

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 m—40 m). Kinetic energy in ambient currents and kinetic energy associated with spin—off eddies were separated to form the kinetic energy of the mean (MKE) and turbulent kinetic energy anomaly (TKE):

East component: $U = \bar{U} + U'$

North component: $V = \bar{V} + V'$

Where $\bar{U} = \frac{1}{T}\int_0^T U dt$; $\bar{V} = \frac{1}{T}\int_0^T V dt$; $T = June - September$

MKE $= \frac{\rho}{2}\Sigma(\overline{U^2} + \bar{V}^2\ )\Delta x \Delta y \Delta z$

TKE $= \frac{\rho}{2}\Sigma(U'^2 + \ V'^2)\Delta x \Delta y \Delta z$

ρ is water density and $\Delta x \Delta y \Delta z$ is volume.

In practice, MKE and TKE were generated at each model grid point for each year of the study, with water density, factor of 2 and volume dropped as non—varying components. For simplicity, MKE and TKE are defined in units of m^2/s^2. To generate yearly time series of MKE and TKE for comparison with larval dispersal, these parameters were produced at each model grid point, but averaged over the upper slope between boundaries shown in Figure 1B.

In order to isolate the impact of LC eddies on energetics of the continental slope region, the TKE anomaly was calculated for the months of June—September, when wind

TABLE 1. *Spawning seasons of some northern Gulf of Mexico commercially important reef fish.*

Species	Common name	Spawning	Reference
Lutjanus campechanus	Red Snapper	Apr—Oct	Collins et al. 2001
Lutjanus griseus	Gray Snapper	Jul—Sep	Domeier et al. 1996
Mycteroperca microlepis	Gag	Feb—April	Koenig et al. 1996
Centropristis striata	Black Sea Bass	Dec—Apr	Hood et al. 1994
Rhomboplites aurorubens	Vermilion Snapper	May—Sep	Hood and Johnson 1999
Mycteroperca microlepis	Gag	Dec—May	Hood and Schlieder 1992
Mycteroperca phenax	Scamp	Late Feb—Jun	Coleman et al. 1996
Pagrus pagrus	Red Porgy	Jan—Apr	Hood and Johnson 2000

variability is low (e.g., Muller—Karger et al. 2015). As a metric for comparison with MKE and TKE, larval dispersal was simulated for modeled spawn during June—August (dispersal includes September). This period is a core spawning season for several commercially important reef fishes in the northern GOM (Table 1). In addition, MKE and TKE were generated for winter (December—February) in an effort to see if the interannual variations in energetics are due to changes in the dynamics or to seasonal shifts.

Simulated larval drift

Simulating the drift of a parcel of water containing larvae is relatively straight forward, but complexities occur due to uncertainties in both the modeled currents and the behavior of larvae as they age. In this study, a base stratagem (defined herein as BASE) was devised and applied over the 13 year model run. However, variations which may be applicable to different life histories were tested on a single year (2015). A metric of dispersal, defined as the percent of spawned larvae at each site that are transported off the shelf into water deeper than 200 m, serves as the basis for comparison with concomitant changes in energy of the slope currents.

The BASE stratagem assumes that larvae are equally distributed within the mixed layer (estimated to be the upper 30 m of the water column). The mixed layer was averaged in the vertical from surface to 30 m depth and this temporarily varying 2—D field of currents was used to simulate larval drift. Ten larvae were 'launched' at each of the 4 selected spawning locations (3 in the FGNMS and one in the FMG) at 6 day intervals over the months of June through August and tracked through the temporally changing model current field for a planktonic larval duration (PLD) of 30 days in steps of 0.1 day. A Lagrangian Stochastic Model (LSM) was applied at each new position along the simulated track of 9 of the larvae to better describe dispersal of a cloud of larvae. The chosen LSM simulates small scale turbulence by an increment (decrement) to the model current components:

$$\delta u = 0.1 * S * P$$

where δu is a turbulence addition to the current component, S is speed of the model current and P is a standard normal

random variable, applied separately to each component.

To test the impact of various vertical larval positioning schemes, 10 parcels were launched at each of the 4 sites for each spawn of the 2015 model year. The percentage of larvae lost to the deep—basin (> 200 m) for the following vertical position schemes was compared to the BASE scheme:

1. Larvae are only near the surface (5 m).

2. Larvae are only toward the bottom of the mixed layer (25 m).

3. Larvae spend 50% of the time at 5 m and 50% at 25 m (diurnal migration).

4. Larvae descend in 5 m increments from 5 m to 30 m depth over the 30 day PLD (ontogeny).

The metric for yearly variations in dispersal was the number of simulated larvae that were transported offshore and ended their 30 day PLD in water depths > 200 m. At this point they were defined as 'lost' from the shelf although some reef species can survive and return to the shelf by active motion as juveniles or by seeking temporal habitat in pelagic *Sargassum* (Hoffmayer et al. 2005). A second metric of fishery management interest is the retention (juvenile recruitment) of larvae in the area of spawn. Natal retention is somewhat arbitrarily defined here as reaching the end of PLD within ± 0.5 degree longitude of FGNMS and ± 0.5 degree latitude of FMG and in water with depth ≤ 200 m. Although arbitrary, it provides a metric for broadness of dispersal on the shelf and its temporal variation.

Results

Validation of dispersal algorithm

Using HYCOM currents from 2015, tests were made of dispersal using the following turbulence forms (Table 2): (1) constant level of turbulence, (2) turbulence proportional to current energy (S^2) and (3) turbulence proportional to horizontal current shear. The LSM chosen for the BASE case produces small scale turbulence that is overall 10% of the root—mean—square current speed in the model domain. All 3 of the tests of turbulence form were structured so that the amplitude of the increment is at the level of BASE. A second series of tests on dispersal, also using model year 2015,

TABLE 2. *Test of Lagrangian Stochastic Model (LSM) form. Percentage of the modeled spawn in 2015 ending the planktonic larval duration in water depths > 200 m. The 3 sites in FGNMS are averaged. FGNMS — Flower Gardens National Marine Sanctuary; FMG — Florida Middle Grounds.*

LSM Function	FGNMS (%)	FMG (%)
BASE	89.8	20.0
CONSTANT	88.5	20.0
SPEED[2]	89.8	18.8
SHEAR	91.0	18.8

TABLE 3. *Test of Lagrangian Stochastic Model (LSM) amplitude. Percentage of the modeled spawn in 2015 ending the planktonic larval duration in water depths > 200 m. The 3 sites in FGNMS are averaged. FGNMS — Flower Gardens National Marine Sanctuary; FMG — Florida Middle Grounds.*

LSM Amplitude	FGNMS (%)	FMG (%)
STA	89.8	20.0
5 X STA	92.1	15.0
2 X STA	91.0	16.7
0.1 X STA	87.5	20.6

was made of turbulence amplitude (Table 3): (1) decrease the BASE turbulence increment by a factor of 10, (2) increase by a factor of 2 and (3) increase by a factor of 5. Differences in the results in both Tables 2 and 3 were not statistically significant at $p < 0.10$ using a Chi—Squared test.

The largest effect on the FGNMS spawn comes from trial #2,, where the larvae remain deep in the mixed layer (Table 4). The tendency in this case is for retention on the shelf with a 12% reduction in larvae lost to the deep basin. The largest effect on the FMG spawn comes from trial #1, (larvae are only near the surface (5 m)), resulting in a 51% reduction in larvae lost to the deep basin although it should be noted that the loss from the BASE test was also low at FMG, making this impact relatively small. These two trials are both

TABLE 4. *Test of Lagrangian Stochastic Model (LSM) amplitude. Percentage of the modeled spawn in 2015 ending the planktonic larval duration in water depths > 200 m. The 3 sites in FGNMS are averaged. FGNMS — Flower Gardens National Marine Sanctuary; FMG — Florida Middle Grounds.*

Vertical Position	FGNMS(%)	FMG(%)
BASE	89.8	21.3
5 m	94.4	9.3 (p<0.01)
30 m	37.9 (p<0.10)	14.4
50% 5 m – 50% 25 m	88.5	21.3
5–30 in 5 m increments	86.0	30.0

significant to $p < 0.01$ in the Chi—Squared test. Finding little impact on dispersal metrics from the trials of turbulent additions (LSM) and identifying those vertical positioning trials (and locations) that do influence outcome, the BASE stratagem was used to provide a simple metric of larval dispersal for the 13—year period.

Dispersal

Between 2003 and 2015, modeled larval dispersal changed dramatically at both the FGNMS and the FMG sites. Selected years (2003, 2011 and 2015) demonstrated very different spatial dispersion patterns in the eastern Gulf compared to the western Gulf (Figure 2). In 2003 and 2015, disper-

sal from the FGNMS was predominantly offshore, crossing the GOM deep basin to as far as Campeche Bank. In 2011, dispersal was predominantly alongshore toward the east. In contrast, larvae from the FMG showed remarkably little dispersal in 2003 and 2011, but substantial dispersal alongshore southward and then offshore in 2015. In general, dispersal in all years tended to follow the patterns shown in Figure 2: dispersal from the FGNMS was predominantly offshore or along–shelf toward the east, while dispersal from the FMG was either weak (natal retention) or along–shelf toward the south.

The 3 spawn sites in the FGNMS and the single site at the FMG showed similar yearly variations in numbers of larvae dispersed offshore (Figure 3) with high dispersal at the start and end of the 13 year period and low dispersal in a middle period (2010–2012). A relatively high correlation (r = 0.673; n = 13; lag = 0) between the FMG and the mean of the 3 FGNMS sites provided a measure of statistical confidence (>99%) that the same large scale deterministic processes were occurring across the entire northern GOM. Over the 13 year model period, dispersal to the deep basin from the FGNMS averaged 63.5% with a high of 90.8% and a low of 34.6%; dispersal at the FMG averaged 9.5% with a high of 23.1% and a low of 0.6%.

Dispersal of spawn from the FMG was considerably weaker than dispersal from the FGNMS and may be related to distance from the shelf edge rather than geographic location. Plotting the mean percent loss from the FMG together with each of the 3 individual sites in FGNMS against distance from the shelf edge makes it clear that distance from upper slope energy interactions was a major influence on dispersal. The nearly linear decrease (Figure 4) was in contradistinction to posited exponential scaling (internal Rossby radius of deformation), suggesting a more complex scaling would be necessary to match the complex hydrography. Overall, average loss of larvae spawned at the 3 sites of the FGNMS was high compared to loss from FMG (Figure 3, Tables 2–4). The high annual variation in larval loss was unexpected. For example, at WFG bank, nearest of the FGNMS banks to the shelf edge, the annual loss (see Figure 3) ranged from 92.5% in 2003 to a low of 37% in 2011, returning to a high of 97.5% in 2015.

Of considerable interest is the quantity of larvae taken offshore and transported to other regions of the Gulf. Of the total yearly spawn, 4.4% (± 2.6%) were taken beyond the upper slope region (200 – 1000 m) into the deep basin and returned onto the shelf where they ended their PLD in water < 200 m deep. Larvae transported in this manner provide a modest level of connectivity and genetic homogenization over much of the Gulf. Most of the returned spawn came from the FGNMS; only 0.87% of spawn from FMG were returned to the shelf although many were streamed out of the GOM and may have grounded along the Atlantic coastline.
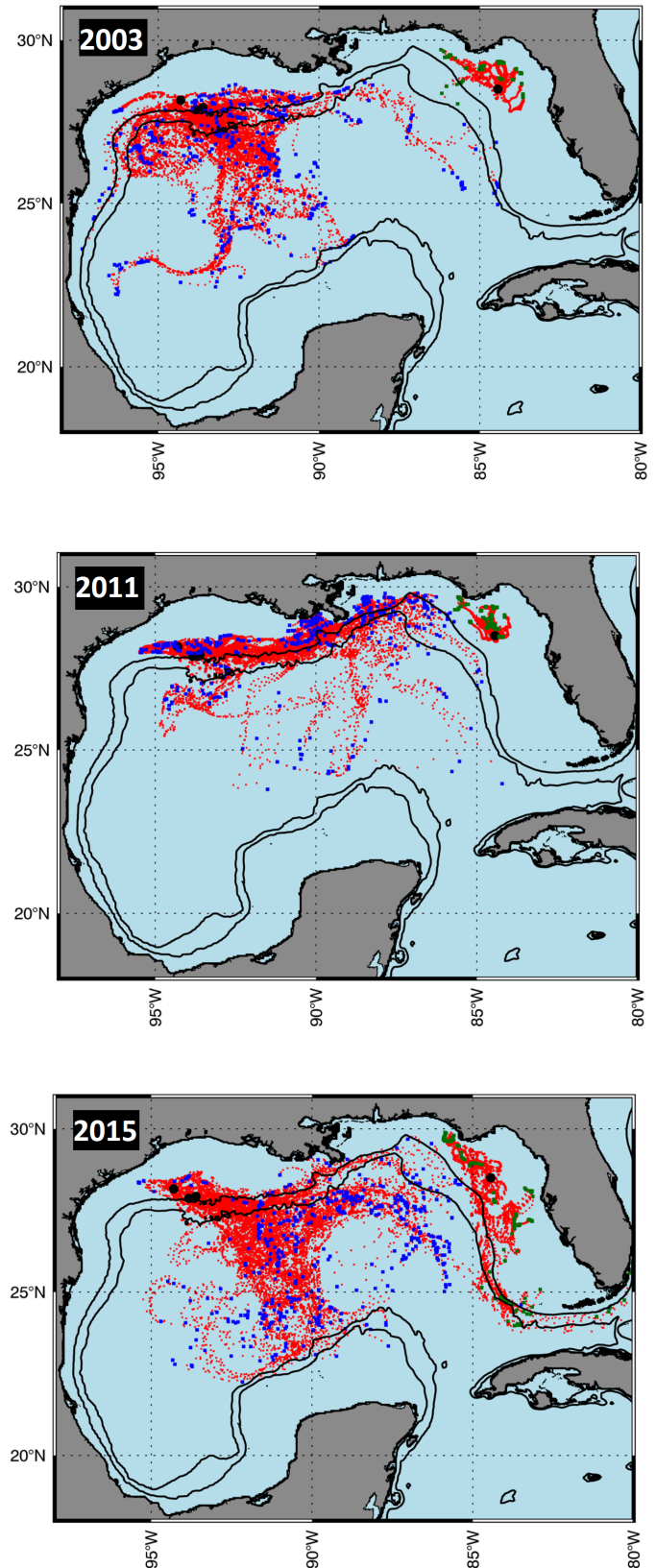

FIGURE 2. *Examples of larval dispersal from Flower Gardens National Marine Sanctuary (FGNMS) and Florida Middle Grounds (FMG). Red dots: daily positions along all tracks. Blue dots: locations of larvae from FGNMS at end of planktonic larval duration (PLD). Green dots: locations of larvae from FMG at end of PLD. Upper, model year 2003; Middle, model year 2011; lower, model year 2015.*
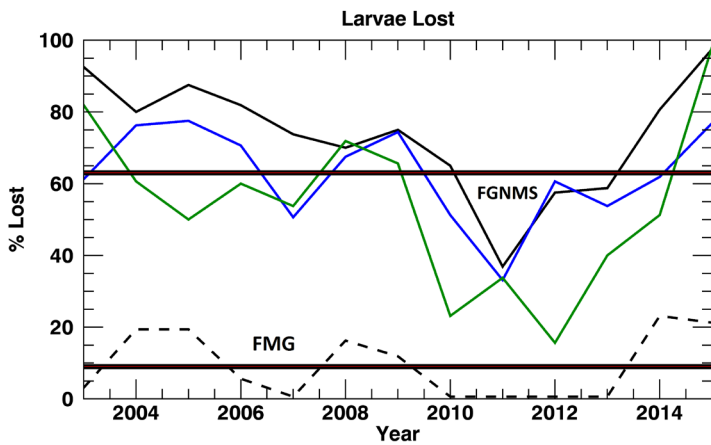
FIGURE 3. *Time series of reef fish larvae dispersed off the continental shelf (% lost) for each model year in summer (June–September) from 2003 to 2015. Black, % lost from West Flower Gardens Bank; Blue, % lost from East Flower Gardens Bank; Green, % lost from Stetson Bank; Dashed, % lost from Florida Middle Grounds (FMG); Red horizontal bars, means of Flower Gardens National Marine Sanctuary (FGNMS, upper) and FMG (lower).*
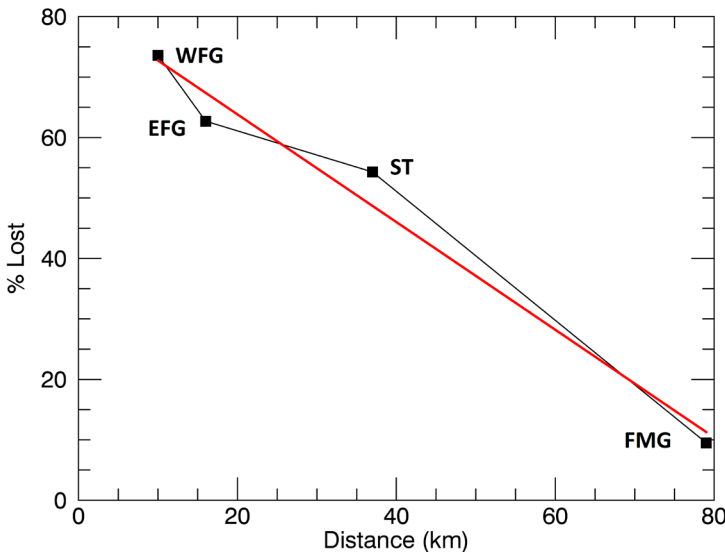

FIGURE 4. *Decreasing impact of upper continental slope energy with distance from the shelf break. Percent lost at each site is the summer mean over the 13 year period. Red line is a linear fit. WFG–West Flower Gardens Bank; EFG–East Flower Gardens Bank; ST–Stetson Bank; FMG–Florida Middle Grounds.*

Larvae returned to the shelf in this manner were not counted in the percentage lost to the basin.

Natal retention is also of interest. For the FGNMS, natal retention averaged 15.2% for the 13 year period with a high of 32.9% and a low of 1.9%. For FMG, natal retention averaged 41.0% with a high of 86.9% and a low of 12.5%. Of equal interest are the overall trends of natal retention. For the FGNMS, natal retention decreased (linear fit) by 1% per year and FMG decreased by 1.3% per year for the period of study.

Energy on the upper slope

The strong spatial and temporal variations in dispersal patterns of outer shelf reef fish larvae in the northern GOM were the result of variations in ocean current energy over the upper continental slope. The TKE over the upper slope (attributed principally to spin–off eddies) and the MKE (attributed to seasonal upper slope currents) showed decadal scale trends with opposite tendencies (Figure 5). At both the FGNMS and FMG sites, TKE decreased over the 13 year period while MKE increased. The cross–over point where MKE reached the same level as TKE occurred in 2011 when percent loss trends (see Figure 3) changed tendencies from decreasing to increasing.

Upper continental slope currents in the northern GOM, from which the MKE is formed, were predominantly clockwise with a relatively strong increase in distribution and intensity around the entire GOM between 2003 and 2015 (Figure 6). Distribution of TKE and MKE on the upper slope also showed considerable differences between 2003 and 2015 (Figure 7), especially in the northern GOM. Inflow on the western side of the Yucatan Channel and outflow along the Florida Keys were linked to strong TKE and MKE over the adjacent slopes throughout the period (Figure 7). Over the 13 year period, energy along the upper slope of the northern GOM changed from predominantly TKE to predominantly MKE. The change–over time frame (2010–2012) from TKE to MKE coincided with the change of trend from decreasing to increasing larval dispersal.
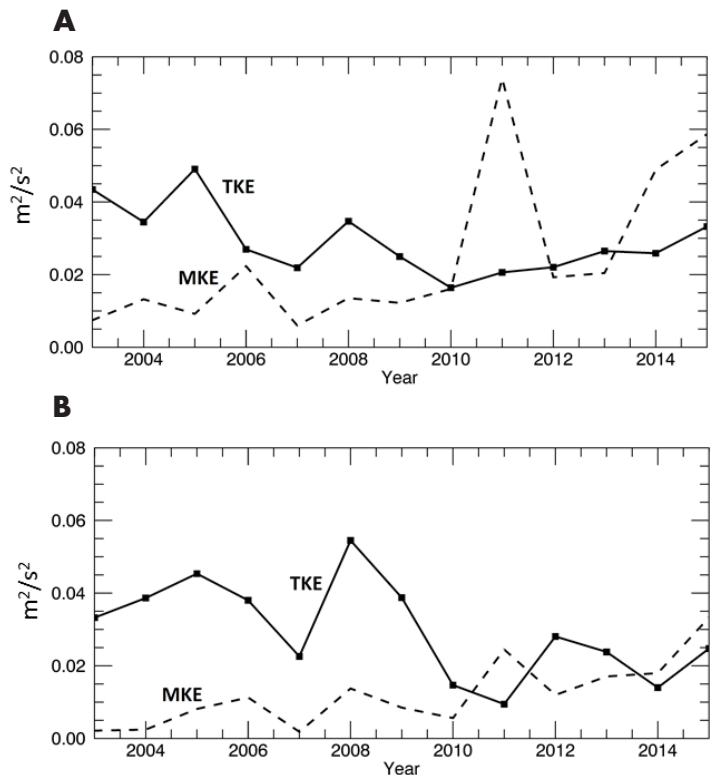

FIGURE 5. *Time series of current energy over upper continental slope fronting sites for each model year in summer (June–September) from 2003 to 2015. A. Flower Gardens National Marine Sanctuary. B. Florida Middle Grounds. Solid line, turbulent kinetic energy (TKE); dashed line, kinetic energy of the mean (MKE).*

Discussion

This study examined decadal scale changes in the kinetic energy of upper layer continental slope currents of the northern GOM and the resulting changes in dispersal of reef fish larvae spawned on the outer shelf. The FGNMS and FMG were chosen as spawn sites because of their importance to fisheries and fishery management and because of their locations with respect to LC spin—off eddies and distance to
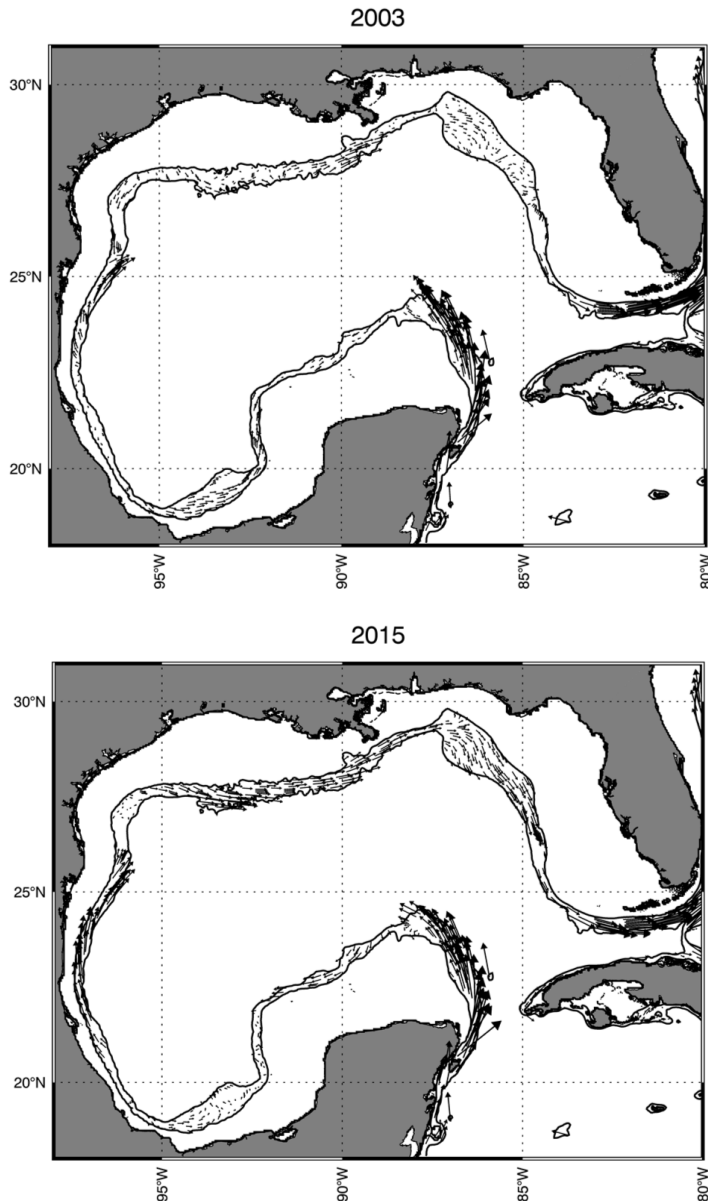
2003

2015

FIGURE 6. *Mean upper continental slope current vectors for the summer of 2003 (upper) and 2015 (lower).*

the continental shelf edge; Hare et al. (2002) suggested larvae can settle in suitable habitat after re—crossing the shelf break. Data assimilated model currents (13 year period, 2003–2015) from HYCOM were averaged over 30 m depth (estimated mixed layer depth) and used for determination of larval dispersal and calculations of kinetic energy.

Simulated larvae were tracked from the spawn sites using a base case algorithm that incorporated a simple LSM, a PLD of 30 days and larval distribution throughout the mixed layer. Changes to the LSM and vertical distribution were examined to determine if changes from the base case would fundamentally alter the metrics used for larval dispersal. It was found that there was insignificant impact except for two cases. There was better retention on the shelf from larvae spawned in the FGNMS if they stayed at the bottom of the mixed layer and better retention from larvae spawned in the FMG if they stayed at the top of the mixed layer. This mixed result suggests that care must be taken in applying the metrics of this study to some species and to specific locations.

Larval dispersal and eddy energy (TKE) along the northern GOM continental slope underwent considerable change over the study period. As dispersal to the deep basin decreased from 2003 to 2011, so did TKE as would be expected. However, between 2011 and 2015, dispersal to the deep basin increased back to its 2003 level while TKE remained low. The increase in dispersal between 2011 and 2015 corresponded to a concomitant increase in ambient (seasonal) along—slope current energy (MKE). This was unexpected and not commonly considered as important to water exchanges between the shelf and the deep basin. However, ambient slope currents (MKE) were averaged over a four month period, blurring larval entrainment and cross isobath transport on short time scales. Submesoscale processes (Luo et al. 2016) may be important at the shelf break, but will not be captured within the scales of this study.

An anticyclonic along—slope flow in the GOM has long been recognized. It is a consequence of the negative wind stress curl over much of the Gulf (Gutierrez de Velasco and Winant 1996, Ohlmann et al. 2001) and is enhanced by LC anticyclonic eddies that interact with the northern shelf. As LC eddies decay during westward migration, energy can be transferred (Hallock et al. 2009) into low frequency currents along the slope region, but it also interrupts the along—slope current along the northern boundary. The transition from TKE to MKE could just as easily be described as a restoration of the ambient wind—driven slope current due to weaker interactions of LC eddies along the northern boundary.

Summer was chosen for the principal season of study because it is a core spawning season for many reef fish species, and ambient summer wind forcing with low mean and low variance suggests that high current energy over the slope is likely due to spin—off eddies. However, the possibility that change in TKE during the study period was related to the seasonal shift from summer eddy spin—off must be considered. Although not synchronized with season, most spin—off eddy separations from the LC occur in summer and winter (Vukovich 2012). For comparison the TKE was calculated for winter. A similar decreasing trend occurred during winter (Figure 8) suggesting that the time scale associated with the
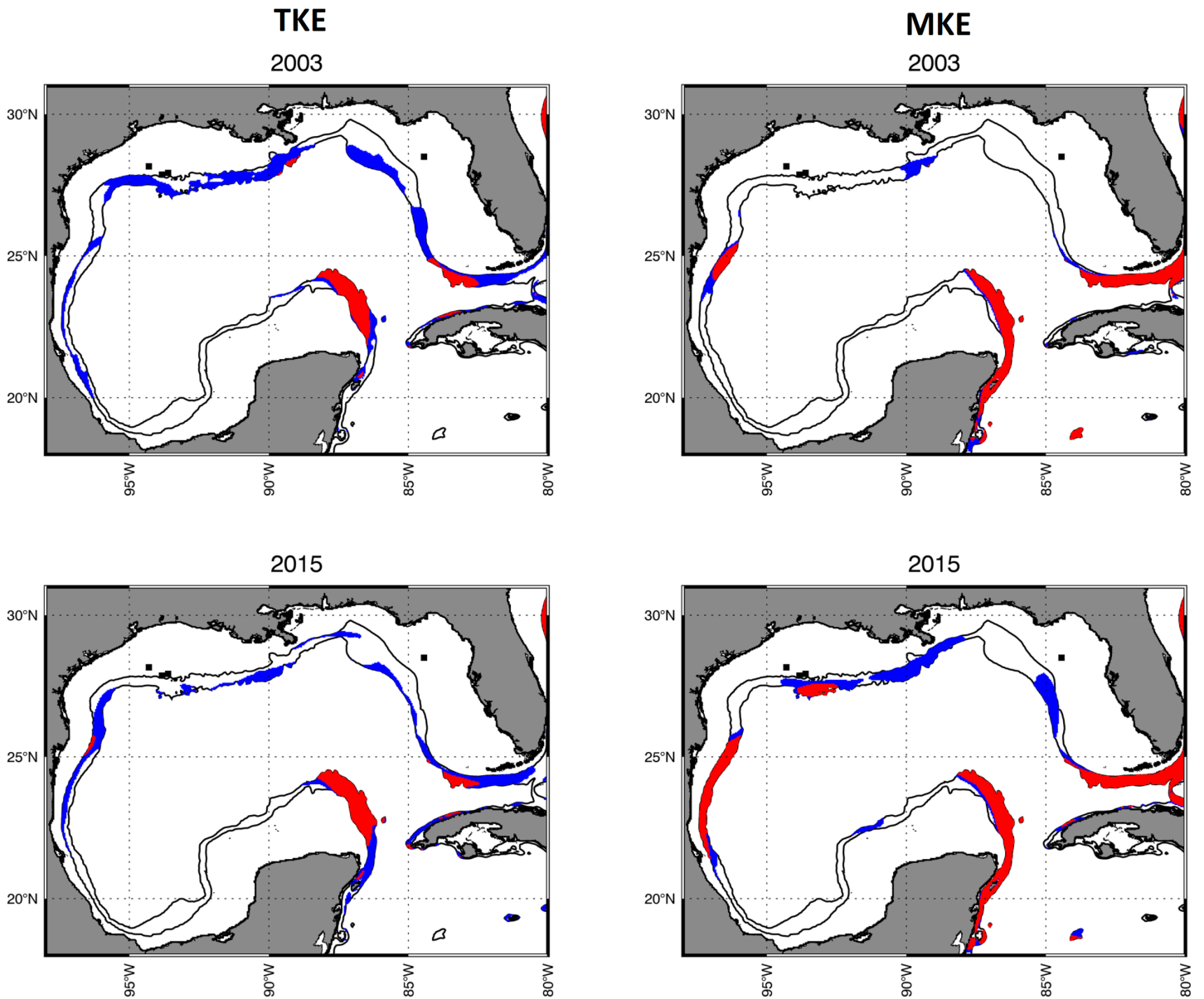
TKE

2003

MKE

2003

2015

2015

FIGURE 7. *Distribution of upper continental slope current energy for 2003 (upper) and 2015 (lower); left column is turbulent kinetic energy (TKE) and right column is kinetic energy of the mean (MKE). Blue grid points correspond to areas where mean currents exceed 0.2 m/s; red grid points correspond to areas where mean currents exceed 0.3 m/s.*

changes is indeed decadal and not simply due to inter—seasonal shifts.

Penetration depth of the LC into the northern GOM (before eddy spin—off) and the subsequent eddy pathway westward are key factors (Vukovich 2007) in upper slope energetics, but are not fully understood. If an eddy breaks off early, its path westward may not include interactions with the northern shelf although its decay along the western shelf can contribute to the anticyclonic slope current. It has been recognized that variations in penetration of the LC can be linked to changes in volume transport through the Yucatan Channel (Molinare et al. 1978, Oey et al. 2003, Chang and Oey 2012). Yucatan Channel inflow to the GOM is part of the North Atlantic western boundary current system com-

posed of contributions from the North Atlantic Subtropical Gyre and the Atlantic Meridional Overturning Circulation (AMOC; Atlantic limb of the global ocean conveyor belt) (Johns et al. 2002). Observations of a decreasing AMOC since 2004 (Robson et al. 2014, Smeed et al. 2014) lead to expectations of a decreasing western boundary current system (Liu et al. 2012, Park and Sweet 2015), including Yucatan Channel inflow.

Several studies (Muller—Karger et al. 2015; Karnauska et al. 2015) have linked trends in oceanographic conditions and large scale ecosystems shifts in the offshore GOM to decadal trends in the sea surface temperature (SST) of the North Atlantic using the Atlantic Multi—decadal Oscillation index (detrended basin wide SST; Enfield et al. 2001). The sug-
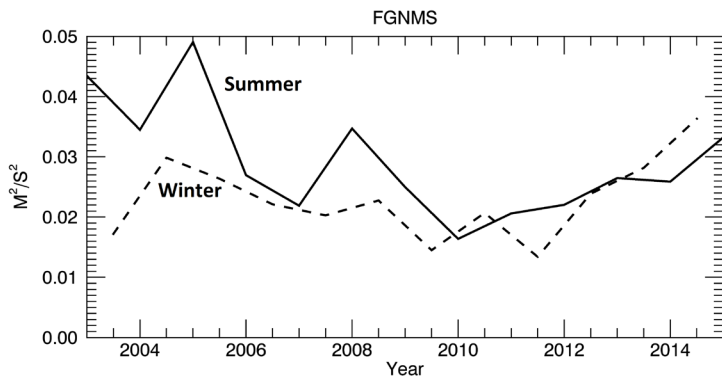
FIGURE 8. *Comparison of turbulent kinetic energy at Flower Gardens National Marine Sanctuary between summer (solid) and winter (dashed).*

gested explanation considers a link between the AMOC and heat transport into the North Atlantic. Concomitant with the decreasing AMOC has been a downward trend in the North Atlantic Oscillation (NAO) index (Smeed et al. 2013),

a measure of surface air pressure gradient and, thus, surface geostrophic winds. The NAO is a relatively simple, well monitored, surrogate for a complex system with many driving components. A simple correlation between the NAO and percent of larvae lost from the combined WFG and EFG spawning sites (nearest shelf edge) with a lag of one year (NAO leading) was significant (r = 0.72, n = 12). The lag considers the propagation time for storm generated ocean Rossby waves to impact the western boundary current system although propagation time from different distances across the North Atlantic tends to smear the impact over several years (DiNezio et al. 2009).

It is suggested that large scale climate processes are fundamentally accountable for driving strong dispersal and strong inter–annual variation in dispersal of outer shelf reef fish larvae, and that these processes vary with changing climate. For fishery management, it is important to document environmental factors that can significantly impact stock enhancement efforts and how these factors vary over time.

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