Variability of mesoscale structures in the Gulf of Mexico with effects on larval fish distribution during spring months

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ABSTRACT: Spatial and temporal distributions of larval fishes have been related to environmental conditions and mesoscale oceanographic structures, with subsequent effects on larvae growth and survival and, thus, recruitment to adult populations. Using satellite altimetry and \textit{in situ} larval fish densities we developed a methodology to identify regions of different circulation and to estimate links between mesoscale features and larval distributions of six fish taxa in the Gulf of Mexico (GOM), during spring from 1993 to 2007. Northward penetration of the Loop Current (LC) tended to increase during spring and reach maximum values in summer, but was highly variable from year to year. This variability was reflected in larval fish distributions, with generally higher larval abundances during years of high northward penetration. We hypothesized that the frontal position and northward excursions of the LC, and other mesoscale features in the GOM would be important for determining larval distributions. Our results showed that larvae of bluefin tuna (\textit{Thunnus thynnus}), little tunny (\textit{Euthynnus
alleteratus), Auxis spp., and snappers (Lutjanidae) were preferentially located within the boundaries of anticyclonic features (generally between 140-150 cm of sea surface height), and within GOM common waters. Our findings suggest that the position and strength of mesoscale features in the GOM is likely to dictate the temporal and spatial distribution of larval fish assemblages, possibly by influencing the area and persistence of habitat favorable for adult spawning.

KEY WORDS: Larvae distribution • Loop Current • Variability • Mesoscale features • Gulf of Mexico • Thunnus thynnus

INTRODUCTION

The Gulf of Mexico (GOM) is characterized by a complex and highly variable circulation, in time and space. Since some ecosystems are highly affected by changes in environmental conditions (Teo & Block 2010), variability of ocean properties in the GOM is expected to have a direct effect on ecosystems in this region. The GOM is very diverse biologically, being the site for spawning and habitat of several pelagic and benthic fish species (Shipp 1999, Rabalais et al. 1999).

The mesoscale circulation in the GOM is dominated by two main features: the Loop Current (LC) and the rings shed by the LC (Fig. 1). The LC extends northward into the GOM from the Yucatan Channel. The current forms an intense anticyclonic flow, which can extend as far north as 29.1°N and can come within close proximity to the Mississippi River delta or the Florida Panhandle coast (Molinari & Mayer 1982). Although the LC intrusion may tend to form more frequently in the spring, it may occur in any season and with periods varying from 6 to 17 months (Molinari 1980), with an average period of 10-11 months (Maul & Vukovich 1993).
LC returns to its southern location by slowly pinching off its northern extension to form large, warm-core anticyclonic rings that then propagate westward at speeds of 2-5 km day\(^{-1}\), and have lifetimes of days to approximately a year (Elliott 1982, Forristal et al. 1992, Shay et al. 1998). These large anticyclonic rings shed by the LC with radii of approximately 150 km, swirl speeds of 1.8-2 m s\(^{-1}\), and around 800 m depth (Oey et al. 2005) are generated aperiodically, with an average shedding time of 9.5 months and a range of 3 to 21 months between consecutive sheddings (Sturges & Leben 2000, Zavala-Hidalgo et al. 2006). The annual fluctuations in LC flow were apparently due to wind forcing (Sturges & Evans 1983).

**Fig. 1.** Example of general circulation through the Gulf of Mexico. Gray arrows in the background represent satellite-derived geostrophic currents with red contours highlighting anticyclonic movements (mainly Loop Current, LC, and anticyclonic regions, AR) and blue contours for cyclonic movements (cyclonic regions, CR)

The questions of whether and how the dynamics of the GOM have a direct impact on the distribution of early life stages of some commercially important fish species are explored herein. A detailed knowledge of the temporal and spatial variability of mesoscale structures in the
eastern GOM is fundamental for understanding the environmental conditions that influence distributions of the larvae of different fish species, spawning sites, larval growth and subsequent variability in larval and juvenile survival (Richards et al. 1993, Bakun 2006). Frontal structures and rings provide necessary feeding resources by concentrating nutrients in certain areas, and therefore may influence the spawning strategies of fishes (Cabella & Wiobe 1985, Ortner et al. 1978). The influence of mesoscale eddies on larval fish transport and survival depends both on regional oceanographic characteristics, and the strategies of the fish species in question (Medina et al. 2002, Royer et al. 2004, Wilson et al. 2005). In addition, both anticyclonic and cyclonic eddies have been shown to positively affect the abundance and distribution of plankton and fish larvae by entrainment of planktonic organisms (Nakata et al. 2000, Okazaki et al. 2002). Specific influences of eddies on larval fishes depend on several factors, such as the nature of the biological environment that the eddy provides for the larvae in terms of food concentrations and planktonic predators, and the favorability of the environment where larvae are transported by eddies.

Physical and biological conditions for both larvae and adult fish in the northern GOM exhibit high spatial and temporal variability (Muller-Karger et al. 1991), which are likely linked to the patterns of spawning (Ortner et al. 1984, Bakun 2006). Variability in larval abundances of some pelagic species has previously been linked to environmental parameters such as water temperature, salinity, zooplankton abundances, water depth, day length and fluorescence (Muhling et al. 2010, Richardson et al. 2010). Therefore, adult fish would be expected to target specific habitats or oceanographic features to spawn, in order to maximize the survival of their larvae.
Larval fish assemblages of pelagic species may be enhanced by the dynamics of the LC (Richards et al. 1993). During SEAMAP surveys in the spring of 1987, transects made across the LC boundary showed higher displacement volumes of plankton and higher densities of fish larvae in the LC frontal areas (Richards et al. 1993). Therefore the LC boundaries and northern excursions of the LC are hypothesized to play a key role in larvae distribution and recruitment.

The objectives of this paper are twofold:

i) To gain a deeper understanding of the mesoscale dynamics in the GOM which are important for larval distribution and transport, by means of characterization of their properties, their spatial distribution, and their temporal evolution from 1993 to 2008.

ii) To assess the influence of mesoscale ocean features and sea surface height on the distribution patterns of fish larvae spawned in the GOM in spring months from 1993 to 2007, in order to provide a benchmark for future coupled physical and biological studies, and stock assessment models.

These two objectives have not previously been applied to the GOM, and will thus improve current understanding of the influence of mesoscale ocean features on larval fish distribution in this region.

**MATERIALS AND METHODS**

**Satellite data.** Much of the knowledge of ring shedding behavior in the GOM has been gained using sea surface temperature (SST) fields from satellite infrared data, and from a limited number of hydrographic observations. The temporal and spatial resolution of *in situ* oceanographic observations in the GOM is sparse. However, satellite derived observations of sea
height anomaly (SHA), SST and ocean color offer sufficient temporal and spatial resolution to study the evolution of the main surface mesoscale features. Although infrared data continue to be invaluable due to their unsurpassed spatial resolution, they are subject to cloud contamination and temperature limitations during summertime, when the uniformly warm SST does not allow inference of the flow field. On the other hand, altimetry measurements of SHA are not subject to this limitation. The goal of the present work included establishing links between surface ocean features and larvae of several species during the spring months, and sometimes extending the season of study to the beginning of summer. In this situation, altimetry data become more appropriate since they can be used to monitor surface ocean features year-round. For example, during the month of May 1998, SST, SHA, sea surface height (SSH), and gradient of SSH fields clearly show the LC and an anticyclonic ring (Fig. 2a, b, c, & d). Conversely, during the month of June 1998 the LC and a ring cannot be observed with SST (Fig. 2e) but are distinguishable using altimetry observations (Fig. 2f, g, & h). Altimetry observations are thus the main data set of this study, and they are used herein to locate and monitor the LC from November 1992 to December 2008.

Microwave optimally interpolated SST fields obtained from observations retrieved by the TMI and AMSR-E radiometers onboard the TRMM and Aqua satellites, respectively, were also used in this study (http://trmm.gsfc.nasa.gov/, http://nsidc.org/data/amsre/). These fields have a daily resolution on a 0.25 degree grid. This data set is complemented with gridded fields obtained using SST observations from the Advanced Very High Resolution Radiometer (AVHRR). These fields were available with a resolution of 2 days on an 18 km equal-area grid to complete the period 1993 to 1997 (Ryan et al. 1996).
The altimetry data were the optimally interpolated gridded SHA fields according to an improved objective analysis method (Le Traon et al. 1998); with spatial resolution of 0.25 degrees, and temporal resolution of 1 week. The altimetric observations used to produce these gridded fields are obtained from two to four satellites throughout the period of this study.

**Fig. 2.** Comparison between SST and SSH satellite derived fields. Fields on the left panels illustrate the spring signal of LC northward intrusion in terms of (a) SST, (b) SHA, (c) SSH, and (d) gradient of SSH on May 6, 1998. Fields on the right panels illustrate the spring signal of a ring separation event in terms of (e) SST, (f) SHA, (g) SSH, and (h) gradient of SSH on June 24, 1998.
SSH fields were derived from SHA data and a mean dynamic topography (MDT) of the ocean (Rio & Hernandez 2004), i.e:

\[ SSH (cm) = SHA (cm) + MDT (cm) \]  

Contours of constant SSH values were useful to define the locations of the LC, and cyclonic and anticyclonic rings (Fig. 2c & g). The northward LC penetration was determined by analyzing the 768 weekly fields of SSH gradient in the GOM, with SSH maximum gradient contours used to objectively characterize the northernmost position of the LC (Fig. 2d and h, for example).

**Loop Current spatial variability and local oceanographic feature identification.** The LC is characterized by a sea surface height larger than surrounding waters, and its northward penetration can be determined from the horizontal gradient of SSH.

A novel methodology using SSH and gradient of SSH fields was developed in this work to identify the main oceanographic features in the GOM, and to relate the inner and outer regions of mesoscale features to captures of fish larvae. This methodology assigned every grid point in the region to be either a) a region of anticyclonic circulation, b) a region of cyclonic circulation, c) a boundary of an anticyclonic circulation, d) a boundary of a cyclonic circulation or e) common GOM waters, defined as the background waters in between the boundary of an anticyclonic circulation and a cyclonic circulation. A location was defined as being in:

a) an anticyclonic region (AR) when:

\[ SSH \geq SSH_{max} - n \cdot \sigma(SSH) \]  

b) a cyclonic region (CR) when:
\[ SSH \leq SSH_{\min} + p \cdot \sigma(SSH) \]  

(3)

c) an anticyclonic region boundary (AB) when:

\[ SSH \geq m \cdot SSH_{\max} \quad \text{and} \quad \text{grad}(SSH) \geq r \cdot \sigma(|SSH|) \]

d) a cyclonic region boundary (CB) when:

\[ SSH \leq q \cdot SSH_{\min} \quad \text{and} \quad \text{grad}(SSH) \geq r \cdot \sigma(|SSH|) \]

e) common waters (CW) if none of the previous conditions was satisfied

where \( \sigma(SSH) \) is the standard deviation of SSH in the region, and \( \sigma(|\text{grad}(SSH)|) \) is the standard deviation of the absolute value of the gradient of SSH in the region. \( SSH_{\min} \) and \( SSH_{\max} \) correspond to the minimum and maximum values of SSH in the GOM for any given date, respectively.

The five dimensionless parameters \( m, n, p, q \) and \( r \) were determined by tuning the outputs of this methodology during summer 2009 with actual satellite-derived SSH fields and their geostrophic currents. The values obtained by the tuning for these parameters were:

\[ m = 0.91 \quad n = 3.30 \quad p = 0.60 \quad q = 1.08 \quad r = 0.67 \]  

(6)

**Biological data.** The biological data used in this work consisted of abundances of captured larvae standardized to larval densities (number of larvae per m\(^3\) of sea water filtered). Samples were collected in the GOM north of 23\(^\circ\)N, during spring months between April 1993 and June 2007. Larval fish data were available from the National Marine Fisheries Service Southeast Area Monitoring and Assessment Program (SEAMAP) database. Cruises were divided into 2 legs and
were conducted throughout the United States Exclusive Economic Zone (EEZ) in the northern GOM only (Fig. 3). Most of the sampling effort was focused on a one-degree grid of stations, and this grid was usually completed twice each year, with the exception of 2003 and 2004 when they were completed only once. Additional stations were sampled in 1994, 1995, 2005, and 2006. Between 38 and 155 hydrographic-plankton stations were carried out each year, with an average of 94 stations per survey in the 15 years covered by this study. At each station, plankton was collected with bongo and neuston nets, and CTD casts were completed.

![Fig. 3. Station locations of the NOAA/SEFSC SEAMAP annual larvae survey from 1993 to 2007. The background color is the mean SST for spring 2007. The red line indicates the limit of the US Exclusive Economic Zone. Note that since the locations are repeated every year a single circle may represent several samplings. The square bin of 2° centered at 87°W and 26.5°N illustrates a sub-area where relationship between LC excursions and larval fish collections were examined.]

Both bongo and neuston net tows were generally completed across the grid of stations in the GOM in late April and May, with sampling continuing into late June in some years. Therefore, analysis of the results presented here corresponds to periods between April and June. Bongo nets were fitted with 333 µm mesh, on two 61 cm diameter round frames, and were towed obliquely to 200 m depth or to just above the bottom at shallower stations (Richards et al. 1993). Nets were towed at 2-3 knots, and sampling took place during both day and night. Samples from bongo nets
were sorted, and larvae identified to the lowest possible taxa at the Polish Plankton Sorting and Identification Center in Szczecin, Poland.

**Larval fish data analysis.** The spring plankton surveys were originally designed to target bluefin tuna (*Thunnus thynnus*) larvae. However, larvae of more than 500 taxa were recorded over the duration of the surveys. In this study, larvae of 6 taxa from three commercially important families were analyzed. In many cases, larvae from closely related species were not distinguishable visually, and so larval groups were merged at the genus, or family, level. Larvae of *Coryphaenidae* (dolphin-fishes hereafter: likely incorporating *Coryphaenia hippurus* and *Coryphaenia equiselis*) were analysed at family level, as were larvae of *Lutjanidae* (snappers hereafter: likely incorporating up to 19 species from 6 genera: *ApsiIus*, *Etelis*, *Lutjanus*, *Ocyurus*, *Pristipomoides* and *Rhomboplites*). Within the family *Scombridae* (tunas), *Auxis* larvae (likely incorporating larvae of *A. rochei rochei* and *A. thazard thazard*) were analysed at genus level, as were *Thunnus* larvae (likely a mix of *T. albacares* and *T. atlanticus*). Larvae of both bluefin tuna hereafter and *Euthynnus alleteratus* (little tunny hereafter) were visually distinguishable from other tuna species, and were therefore analyzed at species level.

Larval distributions were related to mesoscale ocean features and their boundaries by determining when catch locations were in anticyclonic locations, anticyclonic boundaries, cyclonic locations, cyclonic boundaries or common waters. These mesoscale feature locations were identified using the values of SSH and gradients of SSH as described in the previous section.
RESULTS

Loop Current northward penetration and observations on larval fish distribution

The northernmost location of the LC varied from 24.25ºN to 28.50ºN, with marked seasonal variability and a mean value of 26.30ºN (Fig. 4). The location in summer was significantly more to the north than in the fall season, with winter and spring having values closer to the mean. August appeared to be the month with the most occurrences of the northern LC excursions (Fig. 4).

![Graph showing monthly mean location of the LC northward penetration](image)

**Fig. 4.** Monthly mean location of the LC northward penetration (blue circles). Black bars indicate one standard deviation over the 16 years of data analyzed, from January 1993 to December 2008.

The northward penetration of the LC between 1993 and 2008 also exhibited year-to-year variability, showing a maximum in the annual northernmost location of the LC in 2005 and a minimum in the annual northernmost location of the LC in 1998 (Fig. 5).

![Graph showing annual northernmost location of the LC](image)
Fig. 5. Annual mean location of the LC northward penetration. Blue bars indicate LC location north of the mean northernmost position, and red bars indicate LC location south of the mean northernmost position. Black bars indicate one standard deviation over the 16 years of data analyzed, from January 1993 to December 2008.

Preliminary associations between the LC variability and larval distributions of bluefin tuna, little tunny, *Thunnus*, *Auxis*, snappers, and dolphin-fishes were then determined by analyzing observations in larvae distribution over background SSH fields.

Larvae appeared to be less abundant in the core regions of both cyclonic and anticyclonic mesoscale features, and more abundant at the boundaries and frontal areas. For instance, on April 17 1996, catches of *Auxis*, little tunny, and dolphin-fish were found in frontal areas of the LC but were absent when sampling the core region of the LC (Fig. 6a). Conversely, on April 24 1996, *Auxis* larvae were collected in frontal areas of the LC, and frontal areas of a cyclonic ring, and bluefin tuna larvae were found in frontal areas of an anticyclonic ring (Fig. 6b). However, both species were absent from the core region of a cyclonic ring (Fig. 6b).

Fig. 6. Spatial distribution and density of larvae of bluefin tuna (dark blue circles), little tunny (green hexagon), *Auxis* (pink diamond), *Thunnus* (light blue square), snappers (red triangle) and dolphin-fishes (inverse yellow triangle). Background is the SSH field. (a) The field on the left shows catches on frontal areas of the LC and negative stations in core regions of the LC on April 17, 1996. (b) The field on the right shows catches on frontal
areas of the LC and frontal areas of an anticyclonic ring and a cyclonic ring, and negative stations in core regions of a cyclonic ring on April 24, 1996. The size of the symbols is proportional to density of larvae.

To further analyze the relationship between LC excursions and larval fish distribution, larval fish collections were examined within a square bin of 2° centered at 87°W and 26.5°N, which represents the mean northernmost latitude and westernmost longitude of the LC during spring months (Fig. 3). In order to relate variability of larval fish captures within this sub-area to the variability of northward LC excursions, a time series of deviations from the mean northernmost location of LC in spring time was analyzed (Fig. 7).

![Fig. 7. Anomalies of the mean northernmost location of the LC in relation to spring mean density of captures. Black line shows mean larval density of captures of bluefin tuna, little tunny, Auxis, Thunnus, snappers, and dolphin-fishes, from May 1993 to June 2007. Grey line illustrates spring mean larval density of captures of Thunnus species, from May 1993 to June 2007. The mean northernmost location of the LC during spring was found to be 26.5°N. Positive red bars indicate LC location north of the mean northernmost position during spring, and negative blue bars indicate LC location south of the mean northernmost position during spring. The sub-area of study of larval fish captures is a square bin of 2° centered at 87°W and 26.5°N.](image-url)
During spring, the LC is usually to the north of its mean location at 26.31°N (Fig. 4). However, the LC northward excursions during spring months exhibit a year-to-year variability, ranging from a minimum mean latitude of 24.23°N in 2002 to a maximum mean latitude of 27.92 in 2005 (Fig. 7). Similar year-to-year variability is found in the mean density of captures of fish larvae analysed herein (Fig. 7, black line). Southern excursions of the LC usually lead to a decrease in mean larval fish densities within 86°W to 88°W, and from 25°N to 27°N. For example, in spring 2002 an extreme southern excursion of the LC translated to only 4 larvae collected within this subarea, corresponding to a mean density of 0.005 larvae m⁻³. *Thunnus* species exhibited a similar variability that other larvae did with respect to the variability in the LC excursions, with lower densities of *Thunnus* species found during southern excursions of the LC and higher densities of *Thunnus* species found in northern excursions of the LC (Fig. 7, grey line).

**Effects of mesoscale structures on larval fish distributions**

Detailed associations between larval catches of bluefin tuna, little tunny, *Thunnus*, *Auxis*, snappers and dolphin-fishes, and the inner and outer regions of mesoscale features were initially assessed by means of probability bar diagrams. Capture locations were classified into five different categories: anticyclonic region, anticyclonic boundary, cyclonic region, cyclonic boundary and common waters, as detailed previously. The probability of finding larvae of taxon *i* in an oceanic mesoscale feature *j* was calculated using the following quotient:

\[
P_i(j) = \frac{c_{ij}}{e_{ij}}
\]

\[
\sum_{j=1}^{5} \frac{c_{ij}}{e_{ij}}
\]

(7)
Where $c_{ij}$ is the number of captures of taxon $i$ in feature $j$, $e_{ij}$ is the fishing effort when sampling taxon $i$ in feature $j$, 
\[ \sum_{j=1}^{5} \left( \frac{c_{ij}}{e_{ij}} \right) \] is the summation of the captures divided by the fishing effort in the five regions, $i$ is the taxa (bluefin tuna (1), little tunny (2), *Auxis* (3), *Thunnus* (4), snapper (5), and dolphin-fish (6)), and $j$ is the region (AR, AB, CR, CB and CW). As sampling effort was not equal within all mesoscale features, the captures of taxon $i$ were standardized by dividing by the effort, defined as the total number of times the feature was sampled (with or without capture).

The highest abundances of bluefin tuna, little tunny, *Auxis* and snapper were located in the boundaries of anticyclonic features and in common waters (Table 1). This pattern was more evident in the larval distribution of species (Fig. 8a, b) than in larval distribution of groups that were merged at the genus level (Fig. 8c). Little tunny was mostly likely to be collected within common waters (probability of 0.444), and anticyclonic boundary regions (probability of 0.401). Bluefin tuna, little tunny, *Auxis*, and snapper larvae were more likely to be collected within boundaries of anticyclonic features than in core regions of anticyclonic features, and were also more abundant within boundaries of cyclonic features than core regions of cyclonic features.
Table 1. Captures ($c$), efforts ($e$) and probabilities ($P$) of finding larvae in anticyclonic regions (AR), anticyclonic boundaries (AB), cyclonic regions (CR), cyclonic boundaries (CB) and common waters (CW) for bluefin tuna, little tunny, *Auxis, Thunnus*, snappers and dolphin-fishes. Calculated from altimetry derived fields and spring sampling from 1993 to 2007.

<table>
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<th>CR</th>
<th>CB</th>
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Fig. 8. Probability of finding larvae of bluefin tuna (a), little tunny (b), *Auxis* (c), *Thunnus* (d), snappers (e) and dolphin-fishes (f) in anticyclonic regions (AR, red bar), anticyclonic boundaries (AB, orange bar), cyclonic regions (CR, dark blue bar), cyclonic boundaries (CB, light blue bar), and common waters (CW, yellow bar). Calculated from altimetry derived fields and spring sampling from 1993 to 2007.
Thunnus species, which included larvae of yellowfin tuna and blackfin tuna, were frequently found within anticyclonic regions and boundaries, common waters, and also cyclonic region locations (Fig. 8d). Although dolphin-fish larvae were scarce and patchy, larval distributions were slightly higher in anticyclonic boundaries (probability of 0.310) and slightly lower in anticyclonic regions, cyclonic boundaries, cyclonic regions and common waters (Fig. 8f). Larval bluefin tuna, little tunny, Auxis, and snapper were abundant in common waters.

Associations between altimetry fields and larval distribution were investigated by relating the number and the proportion of captures to values of sea level using satellite derived SSH fields from 1993 to 2007.
Fig. 9. Mean larval density of captures (red circles) and proportion of positive stations (blue circles) for larvae of (a) bluefin tuna, (b) little tunny, (c) Auxis, (d) Thunnus, (e) snappers, and (f) dolphin-fishes in relation to satellite derived observations of sea surface height (SSH), from 1993 to 2007. SSH values were binned to 10 cm intervals. Error bars represent one standard error. Colored blocks represent SSH intervals of cyclonic regions (CR, dark blue), cyclonic boundaries (CB, light blue), common waters (CW, yellow), anticyclonic boundaries (AB, orange) and anticyclonic regions (AR, red), calculated from the mean and standard deviation of the SSH field for each of the 5 regions.
Table 2. SSH minimum (min), maximum (max), mean, and standard deviation (stdv) of cyclonic regions (CR),
cyclonic boundaries (CB), common waters (CW), anticyclonic boundaries (AB) and anticyclonic regions (AR),
calculated from the mean and standard deviation of the SSH field for each of the five regions, from 1993 to 2007

<table>
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<tr>
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<th>min (cm)</th>
<th>max (cm)</th>
<th>mean (cm)</th>
<th>stdv (cm)</th>
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<tr>
<td>CR</td>
<td>114</td>
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<td>124</td>
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<td>121</td>
<td>147</td>
<td>137</td>
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<td>CW</td>
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<td>145</td>
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<td>138</td>
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<td>153</td>
<td>5.3</td>
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<tr>
<td>AR</td>
<td>153</td>
<td>216</td>
<td>177</td>
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Larvae of bluefin tuna, little tunny, *Auxis*, *Thunnus*, snappers, and dolphin-fishes showed both
a high mean larval density and a high proportion of positive stations at SSH of 140 cm to 150 cm. This clear association with moderate levels of SSH is in agreement previous results (Fig. 8).

Results also showed that bluefin tuna, little tunny, *Auxis*, snappers and dolphin-fishes were less
abundant at high values of SSH (Fig. 9a, b, c, e, & f). Conversely, *Thunnus* species were more
abundant at higher SSH than other species (Fig. 9d).

DISCUSSION

This study utilized a combination of satellite altimetry fields and larval fish distributions to
identify links between variability of mesoscale features, and variability in the distributions of
larval of six fish taxa.

The LC northward penetration was seasonal, with maximum values in early summer, which
was consistent with the previous study of Behringer et al. (1977). However, the mean northward
penetration of the LC during spring was highly variable from year-to-year. This variability was reflected in larval fish distributions, with generally higher larval abundances during years of high northward penetration. This could be due to a biological response by either adults or larvae to the LC feature, but also to purely physical mechanisms of northward displacement of larvae carried out by the LC. Further analysis showed that larvae appeared to be less abundant in the core regions of both cyclonic and anticyclonic mesoscale features, and more abundant at the boundaries and frontal areas. This suggests that the observed association between larval abundances and the LC excursions might be due to higher abundances within the LC frontal zone, rather than abundances within the main body of the current.

Larvae may be more common in mesoscale feature boundaries because: 1) they are concentrated by oceanographic processes; 2) feeding conditions are more favorable in convergence zones, which can concentrate planktonic fish larvae, and so larval survival is higher; and 3) adult fishes detect frontal features where they are able to spawn. We may therefore hypothesize that adult spawners of some taxa might exhibit a preference to spawn in the boundaries of anticyclonic features and in common waters. Our results also suggest that larval abundances were often highly spatially autocorrelated: i.e., if one station contained larvae of particular taxa, the neighbouring stations were likely to as well. This result is consistent throughout the various years of observations, and may suggest large-scale spawning when conditions are suitable for a particular taxa.

It is important to note that we studied the larvae of taxa with different life history strategies. For larvae to survive, and eventually recruit to adult populations, they must usually encounter favourable feeding and/or retention conditions in the ocean (Chambers & Trippel, 1997). However, for larvae of species which are benthic or reef-associated as adults, return to suitable
habitat is also crucial (e.g., Cowen et al. 2006). For example, snapper species generally live on reefs as juveniles and adults (Parrish 1989), and settlement-stage larvae must therefore locate and settle on a suitable reef habitat. Conversely, species such bluefin tuna are highly migratory as adults, and remain pelagic throughout their life cycle. Oceanographic features favourable for the survival and recruitment of one species will therefore not necessarily be favourable for another. Species-specific differences in the nature of larval retention, survival and recruitment are thus important considerations when exploring associations between fish larvae and mesoscale oceanographic structures.

A key result obtained in this study was that larvae of bluefin tuna, little tunny, Auxis and snapper were preferentially located within the boundaries of anticyclonic features, and in GOM common waters. Similarly, these taxa were likely located between 140 cm and 150 cm of SSH, which generally corresponded to GOM common water and anticyclonic boundaries. These results are in agreement with previous studies in the western Mediterranean, in which tuna spawning grounds were related to anticyclonic features, and bluefin tuna larvae were more abundant near frontal areas (García et al. 2005, Alemany et al. 2010). In contrast, we found Thunnus larvae were distributed more broadly, being collected in different regions and boundaries of mesoscale structures, and being collected at different ranges of SSH too. This result agrees with previous reports showing that adult yellowfin tuna have broader habitat preferences in the GOM in comparison to bluefin tuna (Teo & Block 2010), and higher tolerances for very warm features, such as the LC and warm LC rings. SSH is proportional to integrated vertical water temperature, and our results therefore suggest higher tolerances for warm waters for these tropical tuna species, which also is in agreement with previous studies.
showing that Thunnus spp. were more abundant in warmer waters than other species such as bluefin tuna (Muhling et al. 2010).

Some of the variability in larval abundances in GOM common waters may be due to smaller-scale oceanographic features which were not apparent from an analysis which used only altimetry data. For example, small cyclonic eddies generated at irregular intervals tend to travel along the LC edge (Zavala et al. 2003), and may influence larval distributions. Resolution of these features would require finer-scale environmental data to overlay on altimetry fields, such as SST, or chlorophyll fields.

Given the small size and small age of larvae of the six fish taxa studied herein, larval fish collected were likely to be captured in the same water mass in which they were spawned. Consequently, we may assume that our larval fish locations are relatively near to the location the adults spawned. In light of the above, the year-to-year variability of the LC might also be reflected in adult recruitment, with possibly higher adult recruitment of bluefin tuna, little tunny, Auxis, Thunnus, and dolphin-fish during years of high northward penetration of the LC. Also, we could infer that adult spawning habitat of bluefin tuna, little tunny, and Auxis were preferentially located within the boundaries of anticyclonic features, and in GOM common waters.

The significance of our findings lies in relating the spatial and temporal variability of the LC and mesoscale structures to larval fish distributions in the GOM. Previous studies based on SEAMAP surveys in the spring of 1987, had revealed higher densities of fish larvae in the LC frontal areas (Richards et al. 1993). More recent studies, had related the spatial and temporal distributions of larval fishes to environmental conditions from a classification model (Muhling et
al. 2010). We found that larval fish distributions had similar spatial and temporal variability than the intrusions and retreat of the LC system. In particular, variability in larval fish occurrences was intimately related with the boundaries of the LC and the boundaries of anticyclonic mesoscale structures, likely anticyclonic rings shed by the LC. Also larval fish distribution was related to the presence of GOM common waters. These novel results were possible thanks to the incorporation of satellite altimetry to in situ larval fish densities, since altimetry products allowed us to monitor the LC and other mesoscale structures all year round without being obscured by clouds.

In conclusion, our findings illustrate that the position and strength of mesoscale features in the GOM are likely to dictate the area and persistence of habitat favorable for larvae distribution. Interestingly, variability of the LC excursions was reflected in larval fish distributions, and larvae of some taxa were associated with anticyclonic boundaries and common water regions. The larval fish distributions in the GOM common waters regions may be investigated in future research by using other sources of satellite data to overlay on the altimetry. Tracing frontal zones from SST and ocean color data to overlay on the SSH fields, for instance, would give more detail on the 'closeness' of larvae to the features, and would complement present altimetry results. Present study and related future investigations have high potential to improve the management of iconic fish species in the GOM.

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