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# Variability of preferred environmental conditions for Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the Gulf of Mexico during 1993–2011

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## ABSTRACT

The Gulf of Mexico (GOM) is the primary spawning ground for western Atlantic bluefin tuna *(Thunnus thynnus)*. In this work, information reported by previous studies about the preferred environmental conditions for the occurrence of bluefin tuna larvae in the GOM is integrated into a dimensionless index, the BFT_Index. This index is used to evaluate the spatial and temporal variability of areas with favorable environmental conditions for larvae within the GOM during 1993–2011. The main findings of this work are that: (i) the proposed index successfully captures the spatial and temporal variability in the *in situ* occurrence of bluefin tuna larvae; (ii) areas with favorable environmental conditions for larvae in the GOM exhibit year-to-year spatial and temporal variability linked with mesoscale ocean features and sea surface temperature; and (iii) comparison of the BFT_Index-derived variability with recruitment of age-0 fish estimated from recent stock assessment indicates that changes in environmental conditions may drive a relevant component (~58%) of the recruitment variability. The comparison with the recruitment dataset further revealed the existence of key regions linked with recruitment in the central/northern GOM, and that the Loop Current may function as a trap for larvae, possibly leading to low survival rates. Above (below) average conditions for occurrence of larvae in the GOM during spring were observed in 2000, 2001, 2002, 2006–2008, and 2011 (1994, 1996, 1998, 1999, 2003 and 2010). Results reported here have potential applications to assessment of bluefin tuna.

**Key words**: environmental index, fisheries oceanography, fronts and eddies, ichthyoplankton distribution, loop current, mesoscale features, satellite altimetry

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## INTRODUCTION

The Gulf of Mexico (GOM) is the main spawning location for the western stock of Atlantic bluefin tuna (*Thunnus thynnus*) (Richards, 1976). Bluefin tuna larvae have been collected throughout the GOM during boreal spring (Richards and Potthoff, 1980; McGowan and Richards, 1986; Rooker *et al.*, 2007; Muhling *et al.*, 2012), and mostly in the northern GOM in late May (Muhling *et al.*, 2010). Collected larvae were typically small, with mean lengths of ~4 mm (~7 days or less of age), suggesting that they were collected within the same water mass where they were spawned (Muhling *et al.*, 2010). *In situ* observations indicate that adults target specific habitats or oceanographic features as spawning grounds (Reglero *et al.*, 2014), as they can detect and respond to oceanographic gradients (Humston *et al.*, 2000; Wilson *et al.*, 2005; Fromentin *et al.*, 2014). For example, bluefin tuna larvae have been consistently collected in the Loop Current

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front (Richards *et al.*, 1989) and were generally more abundant within the boundary of mesoscale anticyclonic features in the GOM (Lindo-Atichati *et al.*, 2012). Similarly, bluefin tuna larvae are also more commonly collected within the boundaries of anticyclonic features in the Mediterranean Sea (Garcia *et al.*, 2005; Alemany *et al.*, 2010).

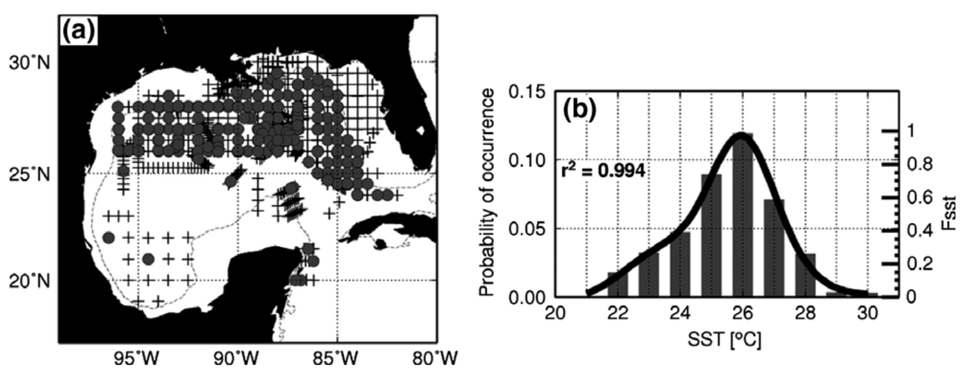
In addition to specific types of mesoscale features, there are certain environmental conditions under which bluefin tuna larvae and adults are more commonly found in the GOM. During spring, tagged adults were located preferentially in lower continental slope waters (2800–3400 m), in areas with a sea surface temperature (SST) of approximately 24–27°C, and relatively low chlorophyll concentrations (<0.16 mg $m^{-3}$) (Teo *et al.*, 2007). Larvae have been collected in areas with SSTs between ~24 and 28°C, sea surface salinity between ~35.5 and 37.0 and temperature at 200 m depth between ~15 and 22°C (Muhling *et al.*, 2010). Previous studies demonstrated that, among different environmental parameters, SST is the most important parameter defining areas where spawning may be observed (Muhling *et al.*, 2011) for bluefin tuna and other tunas (Rooker *et al.*, 2013). In fact, the probability of bluefin tuna larvae occurrence derived from *in situ* surveys shows a consistent relationship with SST (Fig. 1b).

Areas with favorable conditions for occurrence of bluefin tuna larvae during spring may exhibit variability on different temporal and spatial scales. For instance, changes in the ocean circulation and in the distribution of oceanographic features revealed by satellite observations indicate that the Loop Current (the main feature in the GOM) extends northward preferentially during the spring, reaching maximum northward intrusion in the summer, and that rings are shed mostly from July to September (Alvera-Azcárate *et al.*, 2009; Vukovich, 2012; Lindo-Atichati *et al.*, 2013). In addition to seasonal variations, these studies also reported year-to-year variability in the Loop Current dynamics during the past two decades: the Loop Current has been consistently located more to the north during the past 10 yr.

The GOM SST also showed substantial variability during the past decades. For example, warming SST trends have been reported for the GOM during 1985–2004 (Good *et al.*, 2007). In addition, changes in the net surface heat flux induced by atmospheric teleconnections with El Niño-Southern Oscillation (ENSO) are known to drive year-to-year variability in the region (Enfield and Mayer, 1997). Modeling studies suggest that cooler SSTs are observed in the northern GOM during winter/spring after a peak of ENSO (Alexander and Scott, 2002). Long-term SST variability in the GOM is also linked with changes in the strength of the Atlantic Meridional Overturning Circulation (AMOC; Liu *et al.*, 2012) and in the Atlantic Multidecadal Oscillation (Wang and Zhang, 2013). Therefore, areas with preferred environmental conditions for occurrence of bluefin tuna larvae may have experienced substantial temporal and spatial variability during the past decades.

While certain environmental parameters, such as temperature, may provide the baseline for a successful spawning season and for how long it takes for eggs to hatch (Medina *et al.*, 2002; Gordoa and Carreras, 2014), the actual spawning behavior, survival of larvae and subsequent recruitment of bluefin tuna is determined by multiple processes. Drivers of bluefin tuna larvae survival are not generally well known, and it is assumed that mortality during early life is primarily due to starvation and predation (Rooker *et al.*, 2007),

**Figure 1.** (a) Distribution of *in situ* stations (+) sampled by SEAMAP surveys during 1982–2010. Stations that captured bluefin tuna larvae are marked by gray circles. (b) Probability of bluefin tuna larvae occurrence as a function of sea surface temperature (SST) based on 8208 larval-fish collections in the Gulf of Mexico (GOM). Overlaid in the plots is the best fit spline function (black line), which is normalized to values between 0 and 1 (Fsst, right axis) and used in the computation of the BFT_Index.



both of which are dependent on various biophysical processes. Increased larval growth has been previously associated with warmer temperatures, and enhanced quality of microzooplankton prey in the Mediterranean (García *et al.*, 2013). Other studies (Jenkins *et al.*, 1991), however, found that larval growth of southern bluefin tuna was mostly linked with the feeding rate, and not linked with temperature. Therefore, temperature conditions may not be directly linked with bluefin tuna larval growth in the GOM, and may only reflect when and where spawning is initiated by the adults. In addition, mesoscale features can provide spatial heterogeneity in water mass conditions, which can produce better conditions for larval feeding, as proposed by Bakun (2006). This may explain why bluefin tuna larvae are mostly found in the boundary of anticyclonic features in the GOM (Lindo-Atichati *et al.*, 2012) and Mediterranean Sea (Garcia *et al.*, 2005; Alemany *et al.*, 2010). Hence, mesoscale eddies may be important for larval feeding and survival.

To date, the influence of environmental parameters on the bluefin tuna stock size and variability has not yet been fully quantified. Although most fishery management assumes that fishing is the primary determinant of stock variability, there is a growing recognition of the importance, and often dominance, of environmental processes in dynamics of many stocks (Vertpre *et al.*, 2013). In fact, current stock assessment for bluefin tuna is developed under two distinct scenarios: in one scenario a relationship between recruitment and stock size is assumed; in the second scenario, environmental conditions may define limits in the production of recruits regardless of the stock size. Because bluefin tuna have been historically heavily exploited (McAllister and Carruthers, 2008), understanding the natural components driving changes in the Atlantic stock size, versus the effects of fishing, is of critical importance. Therefore, in this study, the temporal and spatial variability of favorable environmental conditions for bluefin larvae in the GOM is assessed and analyzed for the years 1993–2011 for the first time. To accomplish this, a dimensionless index (BFT_Index) is computed based on satellite data, *in situ* larval-fish collections and integrated information on the preferred environmental conditions for occurrence of bluefin tuna larvae in the GOM during spring (Muhling *et al.*, 2010; Lindo-Atichati *et al.*, 2012). It is hoped that through the analysis of such records we may be able to provide additional understanding of the relationship of the bluefin tuna stock with environmental conditions. Results are compared with estimates of bluefin tuna recruitment to investigate the role of environmental conditions during the spawning season in the subsequent recruitment of fish to the stock. The analysis performed in this study focuses on the springtime periods, which is the known spawning season for bluefin tuna in the GOM (Richards *et al.*, 1989; Teo *et al.*, 2007; Muhling *et al.*, 2010).

## DATA

### *Bluefin tuna larvae capture data*

Bluefin tuna larval capture data from Southeast Area Monitoring and Assessment Program (SEAMAP) surveys during 1993–2010 were obtained from the National Marine Fisheries Service (NMFS) database. Among different applications from this dataset, larval abundances from the SEAMAP surveys are used to formulate an index of spawning stock biomass (Ingram *et al.*, 2010), which is the only scientific measure of abundance used in the assessment of bluefin tuna (ICCAT 2014). The SEAMAP surveys follow a fixed grid of hydrographic-plankton stations in the northern GOM (Fig. 1a) sampled from mid-April to late-May of each year, which includes most of the time-frame during which spawning activity is observed in the GOM (Muhling *et al.*, 2010, 2013). SEAMAP surveys aim to complete the grid twice each year during the spring season; in a few years (e.g., 2003, 2004), however, issues with the ship caused the premature interruption of the survey, and the grid was only sampled once. Stations were sampled according to standard sampling protocols (Scott *et al.*, 1993) using bongo (333-$\mu$m mesh) and neuston (0.95-mm mesh) nets for sampling the plankton. Bongo nets were fitted within two round frames of 61 cm in diameter, and were towed obliquely to a depth of 200 m as described in Scott *et al.* (1993). Neuston nets were fitted in a 1 $\times$ 2 m frame, and were towed at the surface. Starting in 2010, a new S-10 net (505 $\mu$m mesh) was included in the SEAMAP sampling methodology. This net was attached to a standard 1 $\times$ 2 m neuston frame, and it was towed from the surface to a depth of 10 m, and then back to the surface, in an undulating pattern for 10 min. This new net targets the upper mixed layer, where bluefin tuna larvae are believed to be more abundant (Muhling *et al.*, 2012; Habtes *et al.*, 2014). The capture data provided by these different sampling methodologies were jointly analyzed in terms of positive (negative) stations, which are defined as those that captured (did not capture) bluefin tuna larvae during the surveys. The number of larvae captured at each station is disregarded in the analysis developed in this study.

Because of the change in the sampling methodology, the SEAMAP dataset is analyzed here in two separate periods (1993–2009 and 2010). These two periods are used to investigate the temporal variability in the capture of bluefin tuna larvae (1993–2009) and to assess the spatial variability of the captures (2010) in relation to the BFT_Index. The variability in the capture data from the SEAMAP surveys is reported in the Results section.

*Bluefin tuna recruitment estimates*

Estimates of bluefin tuna annual recruitment from the 2014 ICCAT stock assessment are used here to evaluate potential relationships between environmental conditions during spawning season and the stock dynamics. Estimates of recruitment are obtained from a virtual population analysis that estimated the number of age-1 fish required to produce the observed catches of adults, taking into account different indices of abundance, such as the larval index (Ingram *et al.*, 2010). We note that the possibility of Mediterranean-origin migrants in the Western catches could bias these recruitment estimates (Rooker *et al.*, 2014). Nonetheless, the stock assessment integrates as many sources of information as currently possible to provide the best available estimate of annual recruitment rather than relying upon a single index. To estimate the number of age-0 fish in the year that they were born, assessment model age-1 estimates were back-calculated using an assumed constant and density-independent natural mortality rate of 0.14 $yr^{-1}$, the same as used in the stock assessment (ICCAT 2014), however, the absolute value of this rate has no impact on our analysis. It is worth clarifying that a larval index based on SEAMAP data is used in the stock assessment model as a proxy for spawning biomass. While this index links larval captures with recruitment estimates, its practical influence on interannual fluctuations of recruitment is minor. When the larval index is removed from the assessment model, estimates of recruitment remain almost exactly the same as with the larval index in the assessment ($r^2 = 0.998$) indicating that the larval index has negligible impact upon the estimates of recruitment.

*Sea surface height*

Weekly fields of gridded Sea Surface Height Anomaly with a horizontal resolution of ¼ degree derived from satellite altimetry are obtained for the GOM during the period of 1993–2011 from AVISO (available at: http://www.aviso.oceanobs.com/). Sea Surface Height Anomaly fields are added to the mean dynamic topography (Rio *et al.*, 2011) to produce fields of Sea Surface Height (SSH). SSH fields provide information about the ocean circulation and also about the presence of oceanographic fronts in the upper layer. SSH fields are used to track mesoscale ocean features, as described in the next section.

*Sea surface temperature*

Fields of SST are obtained from NOAA's High-Resolution Optimally Interpolated SST, Version 2, for the period of 1993–2011 (available at: http://www.esrl.noaa.gov/psd/). This SST product combines SST observations from *in situ* instruments (e.g., drifters and moorings) and from satellites (e.g., AVHRR) in a gridded field with ¼ degree spatial resolution. SST data are used in the computation of the BFT_Index, which will be introduced below.

## METHODS

*Tracking mesoscale ocean features*

An altimetry-based method (adapted from Lindo-Atichati *et al.*, 2012) is used here to track mesoscale ocean features in the GOM using SSH data. Table 1 describes the criteria employed in this study to track mesoscale ocean features based on fields of SSH, and of surface geostrophic velocity magnitude ($V$), which is obtained from:

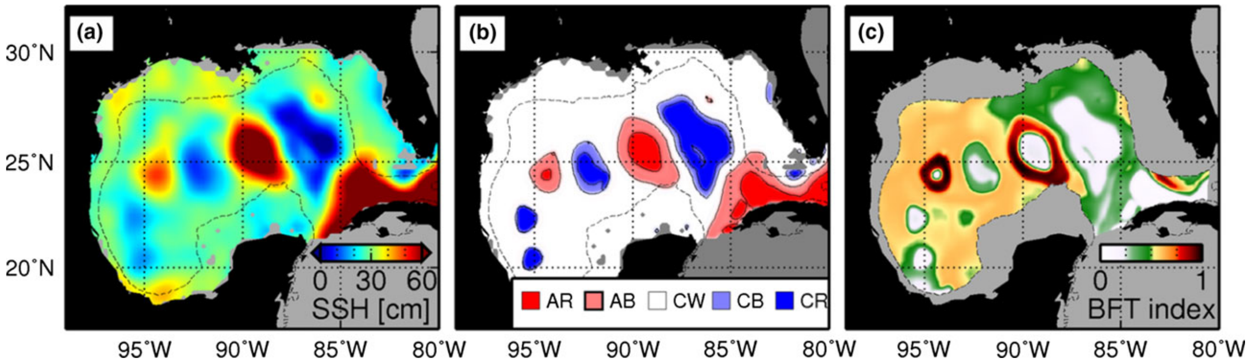
$$V = \sqrt{u^2 + v^2}, \text{with}\, u = -\frac{g}{f}\frac{\partial \mathrm{SSH}}{\partial y} \,\text{and}\, v = \frac{g}{f}\frac{\partial \mathrm{SSH}}{\partial x}, \tag{1}$$

where $u$ and $v$ are the zonal and meridional components of the geostrophic velocities, respectively, $f$ is the

**Table 1.** Criteria used in this study to classify different types of mesoscale ocean features in the Gulf of Mexico (GOM) using satellite altimetry data. The subscripts '$_{pXX}$' indicates the value of the 'XX' percentile for SSH or V in the GOM for each date.

| Mesoscale ocean feature | Acronym | Criteria |
|---|---|---|
| Cyclonic features | | |
| Cyclonic region | CR | $SSH < SSH_{p15}$ |
| Cyclonic boundary | CB | $SSH > SSH_{p5}$ & $SSH < SSH_{p15}$ & $V > V_{p50}$ |
| Anticyclonic features | | |
| Anticyclonic region | AR | $SSH > SSH_{p85}$ |
| Anticyclonic boundary | AB | $SSH > SSH_{p85}$ & $SSH < SSH_{p95}$ & $V > V_{p50}$ |
| Common waters | CW | None of the conditions above |

**Figure 2.** Maps for 20 May 1998 of: (a) Sea Surface Height; (b) type of mesoscale features; and (c) BFT_Index. Overlaid in the maps is the 200-m isobath (dashed line). In (b), AR refers to anticyclonic region, AB to anticyclonic boundary, CW to common waters, CB to cyclonic boundaries and CR to cyclonic regions.




Coriolis parameter and $g$ is the acceleration of gravity. The parameter $V$ provides information about the presence and intensity of gradients in the water mass properties. Intense gradients in the properties of water masses are key characteristics of boundaries of dynamic ocean features (or oceanographic fronts). The overlapping SSH percentiles between definitions of CR and CB (AR and AB) imply that one area that is initially classified as cyclonic region (anticyclonic region) may be later re-classified as cyclonic boundary if it complies with the geostrophic velocity criteria. This procedure is adopted to produce a spatially consistent classification of the mesoscale features. For example, it ensures that cyclonic boundaries are always classified as areas between cyclonic regions and common waters.

One example of the classification method is provided for the conditions in the GOM on 20 May 1998 (Fig. 2a,b), which shows the signature of the Loop Current, given by anticyclonic region and boundary (AR and AB on Fig. 2b) to the north of Cuba. Two additional anticyclonic features and four cyclonic features are also observed. Figure 2 provides an example of the typical distribution of mesoscale features during late spring, when bluefin tuna larvae are more likely to be found in the northern GOM (Muhling *et al.*, 2010).

*The BFT_Index and derived quantities*

In this study, a dimensionless index for monitoring favorable conditions for the occurrence of bluefin tuna larvae in the GOM is introduced. This index integrates previous knowledge about the type of mesoscale features (Lindo-Atichati *et al.*, 2012) and the SST conditions (Muhling *et al.*, 2010) where bluefin tuna larvae are more commonly found. The BFT_Index is computed from satellite-derived SSH and SST fields as follows:

$$\mathrm{BFT\_Index}(i) = \mathrm{Fsst}(i) \times \mathrm{C}_{\mathrm{meso}}(i), \qquad (2)$$

where the '$i$' indicates the location of individual grid points in the GOM. 'Fsst' is a normalized function ranging from 0 to 1 that is obtained by fitting a spline curve on the probability of catching bluefin tuna larvae as a function of the SST, derived from *in situ* observations (Fig. 1b). '$C_{meso}$' is a correction factor ranging between 0 and 1 that ranks different types of mesoscale features based on previously reported larval densities at each particular feature (table 3 of Lindo-Atichati *et al.*, 2012). Standard values for '$C_{meso}$' (Table 2) are calculated by dividing the larval density at a specific ocean feature by the largest larval density found. Both '$C_{meso}$' and 'Fsst' are functions that were derived using a combination of larval capture data from the SEAMAP surveys with other datasets of environmental conditions from *in situ* and satellite observations.

**Table 2.** Dimensionless correction factor ($C_{meso}$) based on reported larval densities at different oceanographic mesoscale features (Lindo-Atichati *et al.*, 2012).

| Oc. feature | Lindo-Atichati *et al.* (2012) (larvae/m$^2$) | $C_{meso}$ |
|---|---|---|
| Anticyclonic Region | 0.9 | 0.24 |
| Anticyclonic Boundary | **3.7** | **1.00** |
| Common Waters | 2.3 | 0.62 |
| Cyclonic Boundary | 1.4 | 0.38 |
| Cyclonic Region | 0.9 | 0.24 |

Reference values used in the calculation of Cmeso are in bold

Values of '$C_{meso}$' and of 'Fsst' are then applied to each grid point based on the type of mesoscale feature defined using weekly SSH fields, and using SST fields for the same dates, respectively. The calculation results in BFT_Index larger than 0.75 when anticyclonic boundaries have SSTs close to 26°C. For practical purposes, values of BFT_Index larger than 0.75 are defined as optimal conditions for the occurrence of bluefin tuna larvae, whereas values ranging from 0.50 to 0.75 are defined as good conditions, values between 0.25 and 0.50 are defined as intermediate conditions, and values below 0.25 are defined as unfavorable conditions. While values of the BFT_Index provide an indication of the availability of favorable conditions for occurrence of bluefin tuna larvae, it is worth emphasizing that this index is not intended for quantifying favorable conditions for larval survival, which may depend on additional environmental factors, such as the availability and quality of microzooplankton prey (García *et al.*, 2013).

Weekly fields of BFT_Index were obtained for the GOM during 1993–2011. The computation of the index is restricted to areas deeper than 200 m, as breeding phase Atlantic bluefin tuna adults and larvae are mostly observed in waters off the continental shelf (Teo *et al.*, 2007; Muhling *et al.*, 2010). Because the functions used in the computation of BFT_Index ($C_{meso}$ and Fsst) are based on *in situ* captures of bluefin tuna larvae in the GOM mostly north of 25°N, it is acknowledged here that this index may lack accuracy in regions south of this latitude. However, given that adults are observed in the southern GOM early in the spring (Wilson *et al.*, 2015), that common waters have a similar composition and that water mass variability is largely dominated by the Loop Current rings everywhere in the GOM (Behringer *et al.*, 1977; Elliott, 1982), errors introduced by the biased geographical sampling are likely small. Examples of different conditions for the occurrence of bluefin larvae are shown for 20 May 1998 (Fig. 2c). Conditions were optimal within anticyclonic boundaries located at ~95°W-25°N and at ~90°W-25°N, whereas good conditions linked with common waters are also observed throughout the western GOM. One of the main benefits of combining SSH and SST fields into the BFT_Index, is that, even although the Loop Current front has been classified as an anticyclonic boundary, SSTs larger than 27°C in this region imply an intermediate condition for occurrence of bluefin tuna larvae. Unfavorable conditions associated with cyclonic and anticyclonic regions are also observed.

Maps of the average springtime (March 20 to June 20) BFT_Index are computed for each year to evaluate the spatial variability of favorable conditions in the GOM during 1993–2011. Fields of mean springtime BFT_Index provide information on how long favorable conditions for larvae persisted at a specific location. The temporal variability is evaluated through the time-series of the overall availability of favorable environmental conditions for the occurrence of bluefin tuna larvae in the GOM for waters deeper than 200 m, which is computed as follows:

$$\mathrm{BFT\_GOM}(t) = \frac{\sum_{i=1}^{N} \mathrm{BFT\_Index}(i,t)}{N} \times 100 \qquad (3)$$

where the '$i$' indicates the location of individual grid points, '$t$' indicates the weekly time dependency during 1993–2011 and 'N' is the total number of grid points in the GOM (N = 1487). Because the BFT_Index has values ranging from 0 to 1, values of BFT_GOM can be seen as the percentage of favorable areas for the occurrence of bluefin tuna larvae in the GOM. Time-series of BFT_GOM are also computed during non-spring seasons to evaluate the relationship of long-period variability (e.g., longer than annual) with spring time conditions.

### *Statistical analyzes*

The analyzes performed in this study are evaluated statistically at the 95% confidence level. A double tail *t*-test is used to assess the significance of the correlation coefficients. For filtered time series, the degrees-of-freedom are calculated by dividing the length of the time series by the length of the low-pass filter window, where the length is defined by the number of sampling units (e.g., weeks).

In addition, a wavelet transform (Grinsted *et al.*, 2004) is applied to the BFT_Index-derived time-series to quantify the associated temporal variability. The wavelet transform technique decomposes the signal into dominant modes of variability as a function of time, providing information about temporal changes in the spectral characteristics of the time-series by capturing the variations in variance with time. The wavelet transform analysis yields the spectral power of the time-series at each time-frame (abscissa) and for each period associated with the signal (ordinate). In this analysis, areas inside the cone of influence (thick black line) indicate the times and frequencies that are not subject to aliasing owing to edge effects, which corresponds to numerical artifacts inherent to this type of analysis that can be introduced at the beginning and at the end of the period of interest. The spectral significance is evaluated at the 95% confidence level against a null hypothesis that corresponds to red noise (univariate lag-1 autoregressive process).

## RESULTS

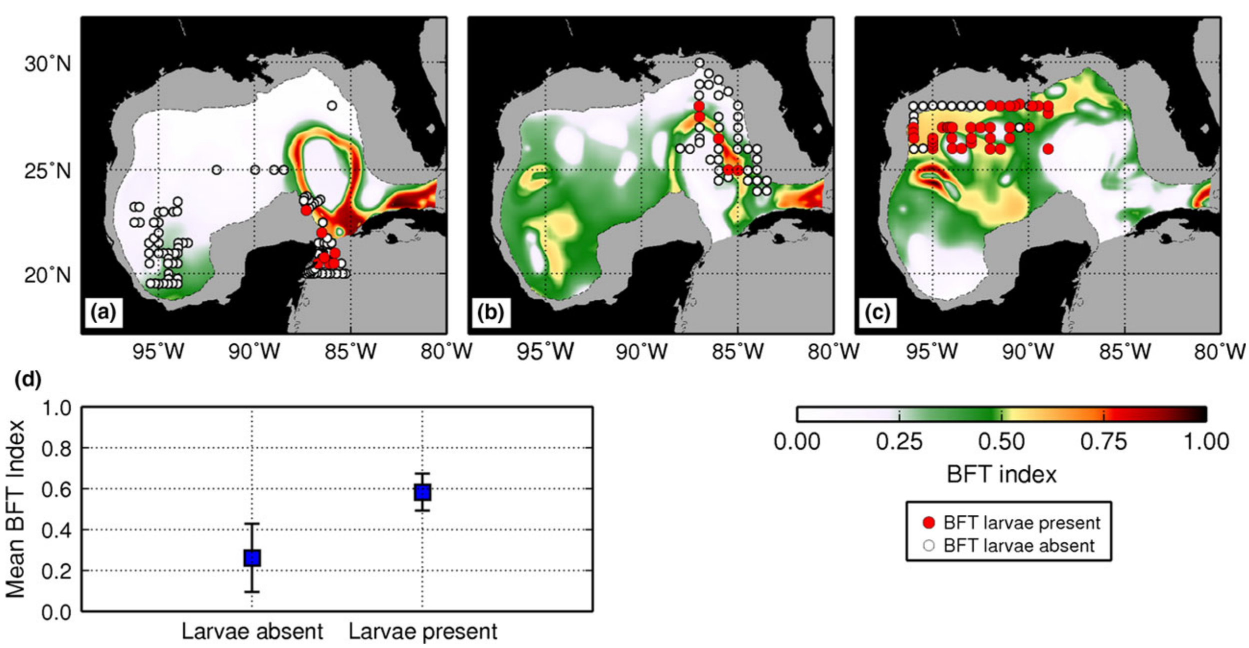
### *In situ* larvae capture versus BFT_Index

In this section, fields of BFT_Index and derived quantities are verified against *in situ* larval capture data from SEAMAP surveys. The objective of this analysis was to evaluate the relationship of BFT_Index with actual *in situ* larval captures, and also to examine the suitability of BFT_Index for additional variability assessments performed in this study.

Verification of spatial variability: for visualization purposes, the *in situ* data from the 2010 SEAMAP survey were divided into three segments between: (i) April 7 and April 27 (Fig. 3a); (ii) April 28 and May 12 (Fig. 3b); and (iii) May 13 and May 22 (Fig. 3c). This division is performed because over the full period of the survey large intraseasonal changes were observed in the GOM SST, which can be identified by inspecting the time-averaged BFT_Index for these three periods (Fig. 3a–c). Over the period of the full survey, between 7 April and 22 May, bluefin tuna larvae were collected at only a few stations in the GOM (Fig. 3a–c). From the 197 stations sampled, only 53 stations collected bluefin tuna larvae. Bluefin tuna larvae were mostly collected along the Loop Current front and in the northwest GOM. The geographical distribution of the time-averaged BFT_Index for these same periods shows consistency with the observed distribution of positive and negative stations. Positive stations generally coincide with large values of BFT_Index, whereas negative stations generally coincide with small values. The average BFT_Index at the location of the 53 positive stations (BFT_Index = 0.58 ± 0.09) is significantly larger ($P < 0.05$) than the average BFT_Index at the location of 144 negative stations (BFT_Index = 0.26 ± 0.16) (Fig. 3d).

Between 28 April and 12 May, good to optimal values of the BFT_Index were found at the location of the five positive stations sampled (Fig. 3b), which results from a combination of ideal SST conditions (Fig. 1b) with an anticyclonic boundary at the Loop Current front. Anticyclonic boundaries correspond to the mesoscale feature where bluefin tuna larvae are more commonly captured (Table 2). In contrast, areas where the remaining 36 negative stations were sampled were associated with an unfavorable BFT_Index

**Figure 3.** Stations from the 2010 SEAMAP overlaid on the average BFT_Index for sampling periods between: (a) April 7–April 27 (b) April 28–May 12, and (c) May 13–May 22. Stations where bluefin tuna (BFT) larvae were captured are marked by red circles, whereas stations that did not capture bluefin tuna larvae are marked by white circles. (d) Comparison between the mean BFT_Index at the location of stations that captured bluefin tuna larvae, with the mean BFT_Index at the location of stations that did not capture larvae.



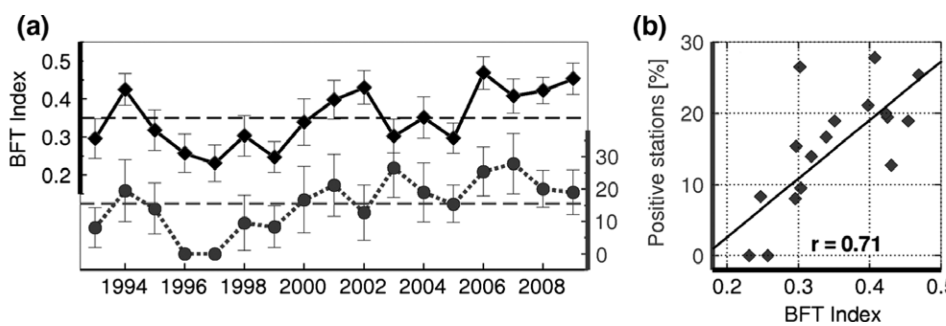
outside the Loop Current front. An unfavorable BFT_Index in these locations was mostly as a result of: (i) cold SSTs (<25°C) outside the Loop Current, and (ii) the combination of warm SSTs (>27°C) with an anticyclonic region inside the Loop Current meander (not shown). The relatively low capture of larvae and low percentage of areas with favorable environmental conditions (low BFT_Index) in the eastern GOM is partially because these stations were sampled earlier in spring. Better environmental conditions were generally available in late May, when the peak in spawning activity is usually observed (Muhling *et al.*, 2012). Figure 3 provides a useful overview of typical intraseasonal changes in the availability of favorable conditions for the occurrence of bluefin larvae during spring: (i) early in the spring, favorable conditions for occurrence of bluefin tuna larvae are only found at the Loop Current front (Fig. 3a); (ii) in the middle of the season, conditions become favorable in the southwestern part of the GOM (Fig. 3b); (iii) later in the spring, favorable conditions are mostly found in the northern part of the GOM, and the Loop Current front is no longer suitable for occurrence of bluefin tuna larvae (too warm).

Verification of temporal variability: for the period of 1993–2009, the percentage of positive stations during the SEAMAP surveys shows large variability in the northern GOM (north of 26°N, Fig. 4), with values ranging from 0 to 27.8%. On average, 15.5 ± 8.3% of the stations captured bluefin tuna larvae during the period. The time-series of the percentage of positive stations during this period shows that below average capture of larvae occurred in 1993, 1996, 1997 and 1999, whereas above average capture occurred in 2003, 2004 and 2006–2008. The BFT_Index at the location of SEAMAP stations showed an average value of ~0.35, and an above (below) average BFT_Index is generally observed for years with an above (below) average capture of bluefin tuna larvae. The time-series of averaged BFT_Index at the location of the *in situ* stations has a significant correlation coefficient ($P < 0.05$) of 0.71 with the percentage of positive stations during 1993–2009. These results confirm that the BFT_Index largely reflects the temporal variability exhibited in the capture of bluefin tuna larvae, and shows that this index is a good habitat indicator for the distribution of larvae in the GOM during spring, explaining ~50% of the temporal variability in the percentage of positive stations during 1993–2009. Among other factors, the relative sparse and patchy distribution of bluefin tuna larvae (Richards *et al.*, 1989) and sampling gear inefficiencies during the surveys (Muhling *et al.*, 2010) may account for part of the unexplained variance. Therefore, the analyzes in the next sub-sections focus on the temporal and spatial variability derived from the BFT_Index for the entire GOM, as bluefin larvae have been captured throughout the region (Richards, 1976; Richards and Potthoff, 1980; McGowan and Richards, 1986; Rooker *et al.*, 2007).

*Environmental conditions in the GOM during 1993–2011*

The time-series of the percentage of areas with favorable environmental conditions for larvae (BFT_GOM) exhibits a well-defined semi-annual cycle during 1993–2011 (Fig. 5a). The first annual maximum of the BFT_GOM is observed during the spring (gray shaded area on Fig. 5a), which is the well-known season for bluefin tuna spawning (Richards *et al.*, 1989; Block *et al.*, 2001, 2005; Muhling *et al.*, 2010). The average BFT_GOM during spring indicates that, between April and May, approximately 20–

**Figure 4.** Comparison between *in situ* captures of bluefin tuna larvae during 1993–2009 and the BFT_Index: (a) percentage of positive stations during the SEAMAP surveys between 1993–2009 (dotted gray line, right axis), and corresponding mean BFT_Index for the same location and time of the SEAMAP *in situ* stations (black line, left axis); (b) linear regression between the two time-series plotted in (a). Error bars in panel (a) are estimated at the 95% confidence level using a bootstrap technique (Johnson, 2001).

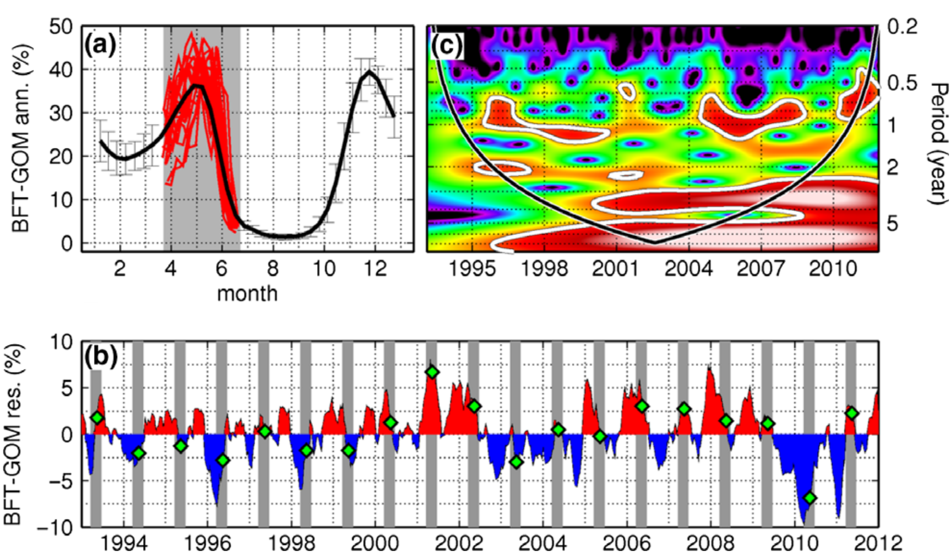


35% of the area in the GOM has favorable conditions for occurrence of bluefin tuna larvae. A secondary maximum is observed during fall, and minimum values during summer and winter. The strong seasonality of BFT_GOM is linked with the SST annual cycle in the GOM. Large values of BFT_GOM are linked with intermediate SSTs (24—28°C) observed during the spring and fall, whereas the small values of BFT_GOM are linked with low SSTs (<24°C) during winter, or high SSTs (>28°C) during summer. While favorable environmental conditions are present during the fall, very few adult bluefin tuna are present in the GOM during this time of the year, and fall spawning has not been reported. This highlights the importance of considering adult migratory behavior when modeling spawning areas. In addition, reproductive status is influenced both by the water temperature and the rate of change in temperature, with spawning condition triggered by temperature increases (Medina *et al.*, 2002). This positive rate of change in temperature is present in the GOM during the spring, but generally not in the fall.

The BFT_GOM also show large year-to-year variability for spring conditions (red lines on Fig. 5a), with peaks ranging from ~50% to ~30%. The BFT_GOM residuals (seasonal cycle removed, BFT_GOMr) range from –10% to 8% (Fig. 5b), with maximum and minimum springtime values in 2001 and 2010, respectively. Positive (negative) values in the BFT_GOMr during spring indicate that environmental conditions for occurrence of bluefin tuna larvae were above (below) the spring mean of 1993–2011. Therefore, bluefin tuna larvae were more likely to be collected during the springs of 2000–2002, 2006–2009 and 2011, and less likely to be collected during 1994–1996, 1998, 1999, 2003 and 2010. The BFT_GOMr shows strong year-to-year changes in the springtime percentage of favorable areas, which is similar to the year-to-year changes in the percentage of positive stations for 1993–2009 (Fig. 4a). These results suggest that year-to-year variability of the environmental conditions may lead to changes in the probability of occurrence of larvae.

The wavelet transform of the BFT_GOMr for the period 1993–2011 shows significant changes in the spectral characteristics of the BFT_GOMr. While 2-yr periodicity is observed during 1995–1997, 3–4 yr periodicity is observed during 2000–2011. The wavelet transform also shows semi-annual and annual periodicity during 1993–2011. The existence of longer periods (6–7 yr) is also suggested by the wavelet transform. However, most of the 6–7 yr periodicity is out of the cone of influence and subject to edge effects. Longer records would be needed to verify the 6–7 yr periodicity. Results from the wavelet transform indicate that

**Figure 5.** Observed temporal variability in the availability of areas with favorable conditions for larvae in the Gulf of Mexico (GOM) during 1993–2011: (a) average seasonal cycle of the percentage of areas with favorable conditions (BFT_GOM, thick black line) during 1993–2011 overlaid on the actual springtime percentages during each year (red lines); (b) BFT_GOM residuals (seasonal cycle removed), and its springtime mean value (green diamonds). The gray shaded areas in (a) and (b) mark the spring period. (c) Wavelet spectrum density for the BFT_GOM residuals. Overlaid in (c) are the peak-based significance levels (white contours), computed at the 95% confidence level, and the cone of influence for the analysis (black contour). The color-shading shows the decimal logarithmic of the spectral power (units = $\%^2$).



springtime conditions linked with favorable conditions for occurrence of bluefin tuna larvae can be modulated by long-period events (e.g., 2-yr periods), and also by intra-annual events (e.g., semi-annual periods).

To further investigate sources of variability in the availability of favorable environmental conditions for occurrence of bluefin tuna larvae, an analysis based on lagged correlations between BFT_GOMr and SST residuals (seasonal cycle removed) was performed for multiple frequencies (Fig. 6a). This analysis shows significant ($P < 0.05$) positive correlation coefficients centered at zero lag for all frequencies evaluated. The positive correlation coefficients indicate that better environmental conditions for catching larvae are usually linked with higher than average springtime SSTs during 1993–2011. In addition, the BFT_GOMr and the SST residual time-series are better correlated at low frequencies (~52 weeks, ~1 yr), suggesting that year-to-year changes in the availability of favorable conditions is largely influenced by the year-to-year variability in the GOM SST.

In addition, results also show intra-spring changes in environmental conditions linked with the SST variability. Although the representative figures are not shown here, during 1994, 1996, 1998, 1999, 2003 and 2010 the lower limit of 24°C for spawning activity (Masuma *et al.*, 2008) is only reached in the northern GOM on April 28 ± 9 days. In contrast, during 2000–2002, 2006–2008 and 2011 the lower limit of 24°C is reached significantly ($P < 0.05$) earlier, on April 14 ± 10 days.

*Spatial distribution of favorable areas during 1993–2011*

While the section above provided an analysis of temporal changes in the overall availability of favorable conditions for bluefin tuna larvae in the GOM, this section describes changes in the spatial distribution of these areas in the GOM during 1993–2011. To accomplish this, maps of averaged springtime BFT_Index are analyzed for each year (Fig. 7), focusing on the availability of favorable conditions outside and within the Loop Current region (dashed magenta lines, Fig. 7). Here, the Loop Current region is defined as the area limited by the northernmost and westernmost extent of this current (adapted from Lindo-Atichati *et al.*, 2013).

Within the Loop Current region, intermediate (0.25 ≤ BFT_Index ≤ 0.50) to good (0.50 ≤ BFT_Index ≤ 0.75) environmental conditions were generally available during 1993–2011 (Fig. 7). Springtime conditions within this region exhibited relatively small temporal variability during the record, and favorable areas within this region corresponded to approximately 7 ± 2% of the total area of the GOM. This indicates that favorable conditions are usually available at the Loop Current front during spring. However, unfavorable conditions were observed in the Loop Current front during certain years (e.g., 2002, ~5% of total area, Fig. 7j) because of SSTs above the acceptable range for bluefin tuna larvae (not shown).

While spring conditions for larvae within the Loop Current region remained relatively stable during 1993–2011, conditions outside of this region varied remarkably from year to year (Fig. 7). For example, while intermediate to good conditions were available in most of the area outside of the Loop Current during 2001 and 2002, unfavorable conditions were mostly observed in this area during 2003 and 2010. In fact, the percentage of areas with favorable conditions outside of the Loop Current region was significantly ($P < 0.05$) larger during 2000–2002, 2006–2008 and 2011 (23 ± 3%), than during 1994, 1996, 1998, 1999,

**Figure 6.** Comparison between the residual percentage of areas with favorable conditions for larvae (BFT_GOMr) and residual SST conditions in the Gulf of Mexico (GOM): (a) correlation coefficients between the BFT_GOMr and the GOM SST residuals plotted as a function of correlation-lag (abscissa) and of low-pass filter width applied (ordinate); (b) spring mean SST during 1993–2011. Thin contours on (b) are every 0.5°C, and the 26°C isotherm is emphasized by the thick contour.

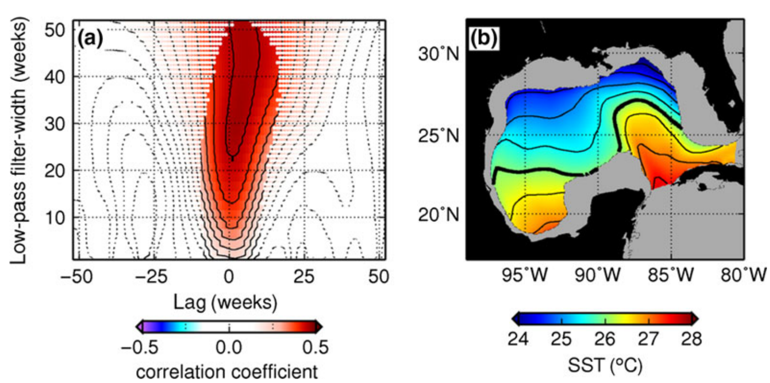
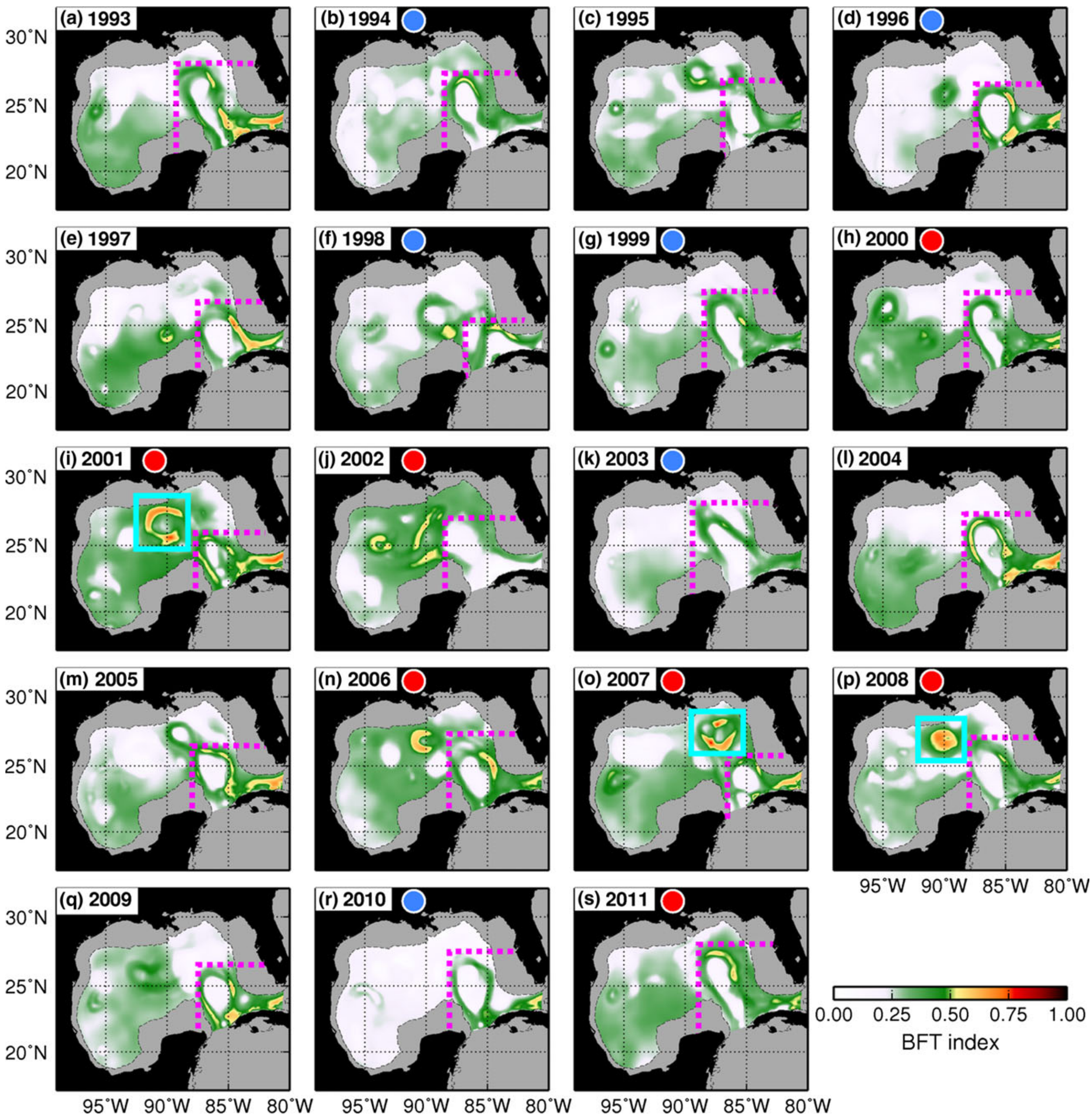


**Figure 7.** Average springtime (March 20 to June 20) conditions for larvae during 1993–2011 as defined by the BFT_Index. Years with residual springtime percentage of favorable areas for occurrence of bluefin tuna larvae in the GOM (BFT_GOMr) larger than 2.5% (smaller than –2.5%) are highlighted with a red (blue) circle. The light blue rectangles in panels (i), (o), and (p) highlight features described in the text, while the magenta dashed lines delimit the Loop Current region, which was defined following Lindo-Atichati *et al.* (2012).




2003 and 2010 (16 ± 3%). These changes in the percentage of favorable areas outside of the Loop Current region are consistent with changes in the overall conditions for larvae in the GOM described above. Therefore, year-to-year changes in conditions for larvae in the GOM are intimately associated with changes in the availability of areas outside of the Loop Current region. Potential consequences of such results will be further addressed in the Discussion.

In addition, the specific location of areas with good conditions for larvae outside of the Loop Current region was also largely linked with the mesoscale field.

For example, in 2001 and in 2008, areas with good conditions were centered around 90°W/27°N, whereas in 2007 these areas were centered around 87°W/27°N (light blue rectangle, Fig. 7i,p,o). These results show that the location of the best areas for larvae may be largely linked with the mesoscale dynamics in the GOM.

*Relationships with bluefin tuna recruitment*

Time-series of recruitment are correlated with time-series of mean springtime BFT_Index at each grid point in the GOM (Fig. 8a) to identify potential spatial patterns linked with the population dynamics. Significant ($P < 0.05$) positive correlation coefficients obtained for areas outside of the Loop Current suggest the existence of key regions (contoured areas, Fig. 8a) in the central/northern part of the gulf. The positive correlation coefficients indicate that better environmental conditions for larvae (higher values of BFT_Index) within these areas are linked with increased recruitment to the adult population. In contrast, negative correlation coefficients for areas within the Loop Current region suggest that favorable conditions for larvae within this current are linked with reduced recruitment. These correlation coefficients suggest that the variability displayed by the bluefin tuna recruitment may be partially linked to environmental conditions during the spawning season.

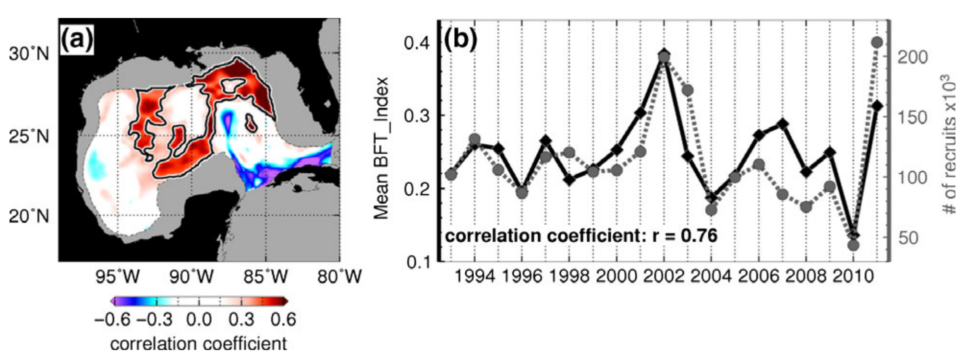
The recruitment time-series is further compared with the time-series of mean springtime BFT_Index at the key regions described above (contoured areas, Fig. 8a). These two time-series show a very close relationship (Fig. 8b), with a significant ($P < 0.05$) positive correlation of $r = 0.76$. Two distinguishable peaks (troughs) in bluefin tuna recruitment in 2002 and 2011 (2004 and 2010) coincide very well with high (low) values of BFT_Index at these key regions. A potential driving mechanism accounting for this relationship is proposed in the discussion.

It should be noticed here that in practice, the terminal 3 yr of recruitment are very poorly estimated in the assessment model and generally not reported (ICCAT, 2014). We chose to retain all years of recruitment estimates for which we had a BFT_index, but also evaluated the correlation when years 2010 and 2011 were removed, and the relationship remained significant and positive ($r = 0.68$).

## DISCUSSION

The BFT_Index proposed in this work adds to knowledge reported by previous studies (Teo *et al.*, 2007; Muhling *et al.*, 2010; Lindo-Atichati *et al.*, 2012), and provides new insights into the understanding of the preferred environmental conditions for bluefin tuna larvae during spring in the GOM. This index provides quantitative metrics for oceanographic habitat and enables the evaluation of relationships between environmental conditions and occurrence of larvae and subsequent recruitment to the population. In particular, it provides means for quantifying the relevance of ideal SST conditions and mesoscale oceanographic features for bluefin tuna reproductive biology, as previously hypothesized by other studies (Bakun, 2012).

**Figure 8.** Comparison between the BFT_Index-derived variability and the number of bluefin tuna recruits during 1993–2011: (a) correlation coefficients at each grid point (1/4 degree resolution) in the GOM between the mean springtime (March 20 to June 20) BFT_Index during 1993–2011 and the total number of bluefin tuna recruits from the 2014 ICCAT stock assessment (ICCAT 2014) for the same period; black contours emphasize regions with positive correlation coefficients that are significant at the 95% confidence level; (b) time-series of mean springtime BFT_Index for the regions contoured in (a) (black line, left axis) and of the total number of bluefin tuna recruits (dotted gray line, right axis). Note that ICCAT convention is to exclude the last 3 yr of estimated recruitment as they are unreliably estimated. If the 2010 and 2011 points were removed, the correlation between the index and model-estimated recruitment remains high at $r = 0.68$.



The reported year-to-year variability in the percentage of favorable areas (BFT_GOMr) shows a positive relationship with the SST in the GOM (Fig. 6), suggesting that better environmental conditions for larvae are generally available during years with warmer springtime SST. This is because the springtime SSTs during 1993–2011 have average values below 26°C in the northern GOM (Fig. 6b), which is the location where bluefin tuna larvae are more commonly found (Rooker *et al.*, 2007). As areas with SSTs of ~26°C have higher probability of containing bluefin tuna larvae (Fig. 1b), years with warmer SSTs are generally linked with better environmental conditions for larvae in the GOM. In addition, the variability linked with intra-spring SST changes in the northern GOM also indicated that potential year-to-year changes occurred in the timing of spawning during 1993–2011. This is because the start of the spawning behavior is believed to be triggered by environmental thresholds (Fitzhugh and Hettler, 1995), such as the SST (Rooker *et al.*, 2007). Results show that in 1994, 1996, 1998, 1999, 2003 and 2010, the lower SST limit of 24°C for spawning activity (Masuma *et al.*, 2008) was reached around 28 April ±9 days in the northern GOM because of the colder SSTs. During years with warmer SSTs, this limit was reached significantly ($P < 0.05$) earlier, around 14 April ±10 days, which may be an indication of an earlier bluefin tuna spawning in 2000–2002, 2006–2008 and 2011. Results reported by previous studies also suggested a relationship between the intra-spring SST pattern and the timing of spawning. For example, capture of bluefin tuna larvae in the northern GOM was proportionally higher after 8 May (Muhling *et al.*, 2010), when average SSTs reach the optimal value of ~26°C (not shown here). Long-term projections of GOM warming indicate that bluefin tuna may start spawning earlier in the year by the end of the 21st century (Muhling *et al.*, 2011). As the schedule of SEAMAP surveys is fixed from year to year, and the larval abundance data from these surveys are used to compute an index of spawning stock biomass (Ingram *et al.*, 2010) that is used for assessment, changes in timing of spawning could lead to biases in this index. Future surveys of bluefin tuna larvae may take into consideration potential changes in the timing of spawning and also the distribution of mesoscale oceanographic features.

One key result of this study is that the reported year-to-year variability is linked with spatial constraints in the location of areas with favorable conditions for occurrence of bluefin tuna larvae. For example, years with a low percentage of areas with favorable conditions (low values of BFT_GOM in 1994, 1996, 1998, 1999, 2003 and 2010, Fig. 7b,d,f,g,k,r) are generally linked with proportionally higher availability of favorable areas within the Loop Current. For instance, the springtime percentage of favorable areas outside of the Loop Current region was significantly smaller during these years (see Results section), whereas conditions within the Loop Current front remained relatively stable. This is because these years were associated with cold springtime SSTs outside the Loop Current (<25.6°C), which translates into unfavorable conditions for larvae in these areas. In contrast, in the Loop Current front waters are generally warmer than surrounding areas because it carries the warm Caribbean waters into the GOM (Liu *et al.*, 2012), which on some occasions produces ideal conditions for the occurrence of larvae. Indeed, bluefin tuna larvae are commonly found within the Loop Current front (Richardson *et al.*, 1989; Lindo-Atichati *et al.*, 2012), and during the cold spring of 1983, all larvae collected during the survey were captured within this feature (Muhling *et al.*, 2010). Anticyclonic regions, like the Loop Current, correspond to zones of convergence where zooplankton and other positively buoyant organisms will become concentrated, which probably provides good conditions for larvae survival (Bakun, 2012). However, Muhling *et al.* (2010) argued that retention of bluefin tuna larvae in the Loop Current is likely to be poor because larvae could be advected out of the GOM through the Florida Straits within a period of days (McGowan and Richards,1989), where feeding and predation conditions may differ. As bluefin tuna natural mortality during early life is primarily because of starvation and predation (Rooker *et al.*, 2007), mesoscale features that advect larvae to unfavorable areas may reduce their chances of survival. Changes in the ocean circulation have been previously shown to impact regional marine ecosystems (Balbín *et al.*, 2013), such as leading to changes in the retention rates of other species in the eastern North Pacific (Bailey *et al.*, 1997) and in the Baltic Sea (Hinrichsen *et al.*, 2003). In the latter, modelled hydrodynamic changes have been linked with food limitation for early life stages of Baltic cod (*Gadus morhua*), causing low rates of survival.

Another key result from this work is that years with higher availability of areas with favorable conditions for larvae (high values of BFT_GOM in 2000–2002, 2006–2008 and 2011, Fig. 7h,i,j,n,o,p,s) are linked with better conditions for larvae outside of the Loop Current front. During these years, the specific location of areas with good-to-optimal conditions was intimately associated with the mesoscale field. In the GOM, the mesoscale variability is largely dominated by the Loop Current dynamics. Previous studies (Alvera-Azcárate *et al.*, 2009; Lindo-Atichati *et al.*, 2013) showed that the Loop Current usually exhibits maximum northward intrusion during summer with rings being shed mostly from July to September. Because these rings persist from months to years as they move westward (Oey *et al.*, 2005), anticyclonic boundaries are usually created. This indicates that the particular location of areas with good to optimal conditions is largely linked with the ring shedding process by the Loop Current during years with warmer springtime SSTs. Hence, a wide variety of areas with good conditions is generally available outside of the Loop Current during these years. Bluefin tuna larvae spawned outside of the Loop Current front may grow within the GOM until they are sufficiently developed to begin their migration to feeding areas along the middle and northern U.S. east coast (McGowan and Richards, 1989), which might lead to good survival rates.

Based on these results, it is hypothesized here that the observed year-to-year variability in environmental conditions characterized by the combination of ideal SSTs with appropriate mesoscale features might be linked with year-to-year changes in bluefin tuna recruitment to the population. For example, favorable environmental conditions causing entrainment of larvae within the Loop Current front during certain years (e.g., 1983) might lead to low rates of survival and recruitment, whereas larvae spawned within oceanographic features outside of the Loop Current region may have better chances of making it into the stock population. The spatial pattern displayed by correlation coefficients between the mean springtime BFT_Index and the time-series of bluefin tuna recruitment from the 2014 ICCAT stock assessment (ICCAT, 2014) supports the hypothesis proposed here (Fig. 8a). Positive correlation coefficients between these parameters in the central/northern part of the GOM indicate that these areas function as key regions (contoured areas, Fig. 8a), where good environmental conditions during the spawning season (higher values of the BFT_Index) are linked with higher recruitment to the adult population. In contrast, negative correlation coefficients observed within the Loop Current region indicate that favorable environmental conditions for larvae in this area are linked with lower recruitment. In other words, these results suggest that favorable environmental conditions for larvae within the Loop Current region may function as a 'trap', as larvae would soon get advected out of the GOM, to areas that are likely unfavorable for their development, leading to low survival rates. This mechanism is compatible with the member-vagrant hypothesis proposed by Sinclair (1988), which states that physical oceanographic processes may play a dominant role in generating temporal variability in the abundancy of species that go through planktonic stages by driving losses from the distributional area.

Correlations between the BFT_Index and estimates of bluefin tuna recruitment further suggest that the variability of environmental conditions during the spawning season may be linked with a relevant component of the population dynamics. The correlation between recruitment time-series and time-series of mean springtime BFT_Index at the key regions indicates that ~58% of the variance in the recruitment time-series can be explained by the variability of environmental parameters described here. Therefore, the natural variability may contribute a substantial component (~58%) to the population dynamics, even though bluefin tuna have historically suffered from overfishing (McAllister and Carruthers, 2008) and are still considered overfished (ICCAT, 2014).

Nonetheless, the estimated recruitment was often comparatively smaller than the mean springtime BFT_Index (e.g., 2000, 2001 and 2006–2009). Similarly, the capture of bluefin tuna larvae during the 2002 SEAMAP survey was relatively less than high captures suggested by high values of the BFT_Index (Fig. 4a). This suggests that there may have been under-utilized spawning habitat. As it would be physically impossible for a fish to utilize all available areas with favorable conditions in time and space, it is conceivable that higher numbers of spawners could achieve higher recruitment by more fully utilizing the available spawning habitat described in this study. Thus, the correlation between the mean BFT_Index at these key regions and the recruitment could potentially increase with higher levels of spawning stock biomass. Changes in feeding conditions on foraging grounds can affect allocations of energy to growth and gamete production, which may eventually impact spawning and the overall utilization of favorable spawning habitat. For example, one study (Golet *et al.*, 2007) analyzed a dataset based on fat and oil content from fish landed between 1991 and 2004 in the Gulf of Maine, reporting an overall decline in somatic conditions of captured bluefin tuna. Such changes may partially account for the under-utilization of spawning habitat as suggested by our results. However, further studies are needed to verify this link.

Finally, observations analyzed here reinforce the importance of understanding the variability of the oceanographic mesoscale field and SST in the GOM for bluefin tuna studies. While the mesoscale variability is mostly driven by the Loop Current dynamics (Chang and Oey, 2012), the SST variability can be linked to other mechanisms. For instance, one known source of year-to-year SST variability in the GOM is caused by atmospheric teleconnections with ENSO (Enfield and Mayer, 1997). Generally, colder SSTs are expected in the northern GOM during winter/spring following a peak of ENSO (Alexander and Scott, 2002). In addition, SST variability in the GOM has also been linked with changes in the Loop Current transport (Liu *et al.*, 2012). This is because the Loop Current advects the warm Caribbean waters into the GOM while it carries the upper branch of the AMOC, which corresponds to an important component of the heat budget in the region. Other studies also acknowledged that climate-related variability could potentially drive long-term changes in the abundance of bluefin tuna. Royer and Fromentin (2006) hypothesized that a blend of environmental forcing and non-linear biological response could lead to the observed long-term fluctuations in trap catches of Atlantic bluefin tuna. They suggested that changes in oceanic mesoscale features forced by the North Atlantic Oscillation may have been linked to non-linear changes in the geographical distribution of adults, and consequentially in the distribution of spawning in the Mediterranean Sea. In the GOM, it is also likely that the availability of favorable conditions for occurrence of bluefin tuna larvae is conditioned by global-scale climate events such as ENSO and changes in the AMOC. A more detailed analysis focused on changes in spawning conditions in the GOM driven by climate-related mechanisms is left for future studies.

In conclusion, this work shows how a joint analysis that combines satellite observations with the *in situ* larval fish dataset can provide critical information on the link between mesoscale dynamic features and environmental parameters defining the availability of favorable conditions for bluefin tuna larvae. The improvements reported complement previous oceanographic and biological efforts to assess the influence of mesoscale oceanic features on the distribution of larval fish spawned in the GOM. Here, the main advances were: (i) the derivation of an index based on environmental conditions that provide information on the availability of favorable (BFT_Index > 0.5) and unfavorable (BFT_Index < 0.25) conditions for occurrence of bluefin tuna larvae in the GOM during spring months; (ii) to show that year-to-year spatial constraints in the location and availability of favorable areas are generally linked with SST; and (iii) to demonstrate that the combined effects of SST and favorable oceanographic features may contribute a substantial component (58%) to bluefin tuna productivity.

Results reported in this study have promising applications for assessment of bluefin tuna. For example, the strong correlation between larval occurrence and the BFT_Index raises the potential that favorable oceanographic features concentrate (disaggregate) larvae, making them more (less) vulnerable to capture by the larval survey. In this case, results from this study may be used to improve larval survey design. As the larval survey is used as an index of spawning biomass (rather than larval abundance), environmental conditions depicted by BFT_Index could be incorporated directly into the statistical modeling method used to construct the larval index (Ingram *et al.*, 2010) to account for differential catchability. Further, the correlation between the BFT_Index and the recruitment dataset indicates that environmental conditions likely contribute to the production of recruits, in which case this index could be used directly within integrated assessments that can utilize environmental time series (Methot and Wetzel, 2013). In this situation, the BFT_Index may be a good predictor of future recruitment and may be useful to reconcile the nature of the spawning stock/recruitment relationship, a major source of uncertainty in the bluefin tuna assessment (Rosenberg *et al.*, 2012). Ongoing and future research on the mechanisms by which these environmental conditions affect bluefin tuna larval-fish (aggregation/disaggregation, advection out of the GOM, increased growth, decreased mortality, etc.) will provide additional understanding of the population dynamics.

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