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Predicting the occurrence of Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the northern Gulf of Mexico: building a classification model from archival data

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ABSTRACT

Although bluefin tuna are found throughout the Atlantic Ocean, spawning in the western Atlantic has been recorded predominantly in the Gulf of Mexico (GOM) in spring. Larval bluefin tuna abundances from the northern GOM are formulated into an index used to tune the adult stock assessment, and the variability of this index is currently high. This study investigated whether some of the variability in larval bluefin tuna abundances was related to environmental conditions, by defining associations between larval bluefin tuna catch locations, and a suite of environmental variables. We hypothesized that certain habitat types, as defined by environmental variables, would be more likely to contain bluefin tuna larvae. Favorable habitat for bluefin tuna larvae was defined using a classification tree approach. Habitat within the Loop Current was generally less favorable, as were warm-core rings, and cooler waters on the continental shelf. The location and size of favorable habitat was highly variable among years, which was reflected in the locations of larval bluefin tuna catches. The model successfully placed bluefin tuna larvae in favorable habitat with nearly 90% accuracy, but many negative stations were also located within theoretically favorable habitat. The probability of collecting larval bluefin tuna in favorable habitat was nearly twice the probability of collecting bluefin tuna larvae across all habitats (35.5 versus 21.0%). This model is a useful addition to knowledge of larval bluefin tuna distribu-

tions; however, the incorporation of variables describing finer-scale features, such as thermal fronts, may significantly improve the model's predictive power.

Key words: bluefin tuna, Gulf of Mexico, habitat modeling

INTRODUCTION

Atlantic bluefin tuna (*Thunnus thynnus*; bluefin tuna hereafter) is a large and wide-ranging species, found throughout the Atlantic Ocean (Mather *et al.*, 1995). Adult fish are highly migratory, and are capable of trans-Atlantic crossings (Restrepo, 1996; Block *et al.*, 2001; Stokesbury *et al.*, 2007; Dickhut *et al.*, 2009). In the western North Atlantic, adult fish are found from cool-water foraging grounds in New England, to temperate coastal waters of the south-eastern US, and open ocean environments (Stokesbury *et al.*, 2004; Block *et al.*, 2005; Teo *et al.*, 2007b). Spawning in the western North Atlantic has been recorded predominantly within the tropical waters of the Gulf of Mexico (GOM), in spring (April–June) (Richards, 1976; Scott *et al.*, 1993). Tagging data suggest that not all sexually mature fish make this migration every year (Lutcavage *et al.*, 1999; Block *et al.*, 2001; Stokesbury *et al.*, 2004), and it has been suggested that some spawning activity may take place elsewhere in the Atlantic (McGowan and Richards, 1989; Lutcavage *et al.*, 1999; Rooker *et al.*, 2007). Historically, bluefin tuna have been heavily exploited, and they are currently considered to be undergoing overfishing (McAllister and Carruthers, 2008). A steep decline in stocks was recorded in the 1970s, with stocks estimated to have stabilized at low levels since this time (Rooker *et al.*, 2007).

Adult bluefin tuna can tolerate ambient temperatures from approximately 3 to 31°C, which is the broadest thermal niche of any scombrid fish (Carey and Lawson, 1973; Block *et al.*, 2001). Their unique physiology allows them to tolerate colder waters than tropical tunas, and to maintain their body

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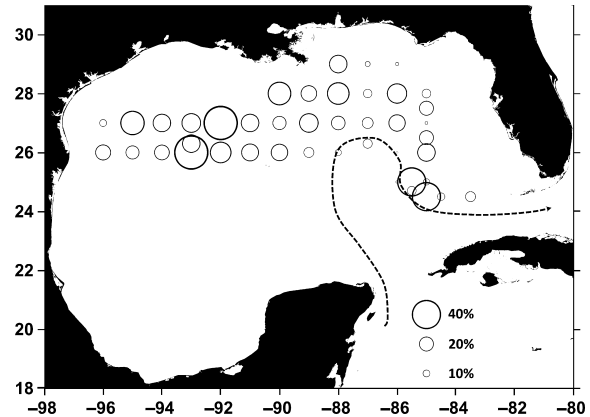
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temperatures above ambient water temperatures (Carey and Teal, 1966; Blank *et al.*, 2004). However, this endothermic ability may present challenges for the fish in warmer waters, as when ambient temperatures exceed 30°C, cardiac function in bluefin tuna is reduced (Blank *et al.*, 2004). Surface water temperatures in the GOM during the spring spawning season regularly exceed 28–29°C (Muller-Karger *et al.*, 1991; Zavala-Hidalgo *et al.*, 2002), and data from electronic tags have shown water temperatures as high as 29.8°C, with bluefin tuna body temperatures as high as 30.7°C, within the GOM (Block *et al.*, 2001, 2005). It has been proposed that the deep (>500 m depth) diving behavior shown by adult fish as they enter and exit the GOM may be to avoid heat stress from warmer waters (Teo *et al.*, 2007b).

Although the GOM can be a physiologically stressful environment for adult bluefin tuna, they often migrate large distances to reach it (Block *et al.*, 2001). It is likely that the adult fish are targeting specific habitats or oceanographic features in which to spawn, to maximize survival of larvae. Tagged adult bluefin tuna in the GOM have been shown to be preferentially located in lower continental slope waters, in areas with surface temperatures of approximately 24–27°C, and relatively low chlorophyll concentrations (<0.16 mg m⁻³) (Teo *et al.*, 2007a). This type of behavior has also been seen in bluefin tuna in the Mediterranean Sea (Garcia *et al.*, 2005; Alemany *et al.*, 2010), and in other large pelagic species such as swordfish (Tserpes *et al.*, 2008). The open GOM is warm, which would result in higher growth rates for larvae (Miyashita *et al.*, 2000), and largely oligotrophic outside of river plumes (Muller-Karger *et al.*, 1991; Gilbes *et al.*, 1996), possibly providing an environment lower in planktonic predators. Diets of preflexion larval tunas tend to be specialized, focusing on particular items such as appendicularians, and many larval tunas are piscivorous post-flexion (Llopiz *et al.*, 2010). These characteristics may represent a mechanism for larval survival in oligotrophic waters.

Physical and biological conditions for both larvae and adults in the GOM show high spatial and temporal variability, as a result of the dynamic oceanography of the GOM. The dominant feature is the Loop Current (LC), which enters the GOM through the Yucatan Channel in the south, extends northwards into the GOM, and then retroflects anti-cyclonically, exiting the GOM through the Straits of Florida (Fig. 1). The strength and degree of penetration of the LC into the GOM is highly variable, and not predictable on a seasonal basis (Sturges and Evans, 1983). On occasion, large, relatively warm eddies are shed

Figure 1. Locations of SEAMAP sampling stations for data used to construct the classification tree model. The probability of collecting at least one bluefin tuna larvae across all sampled years between 1982 and 2006 is shown, along with a schematic representation of the flow of the Loop Current.



from the LC, which can persist for months to years as they drift into the western and southern GOM (Oey *et al.*, 2005). Smaller cold-core eddies may also form, providing zones of local aggregation for zooplankton (Zimmerman and Biggs, 1999). Variability in the position and strength of these features is likely to drive the area, persistence and suitability of habitat favorable for larval bluefin tuna growth and survival, and thus recruitment to adult populations (Bailey *et al.*, 1997; Hinrichsen *et al.*, 2005). However, it is currently unknown which habitats within the GOM are more likely to contain bluefin tuna larvae.

Spring plankton surveys targeting larval bluefin tuna have been conducted across the United States Exclusive Economic Zone in the northern GOM since 1977. Larval abundances are formulated into an index, which is used to 'tune' or calibrate the adult stock assessments, which are completed through the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Scott *et al.*, 1993; Ingram *et al.*, 2010). Larvae have been found across the northern GOM, with variable spatial and temporal distributions and high interannual variability, which has somewhat limited the usefulness of the index (Ingram *et al.*, 2010). However, it is the only fishery-independent index used in the stock assessment. While it is likely that some of this variability has resulted from interannual variability in the oceanographic environment in the GOM, these influences have not been quantitatively evaluated.

This study aimed to construct a model which would define habitat most associated with larval bluefin tuna in the northern GOM, and determine whether larvae

were found in a specific habitat envelope. We could then infer whether adult bluefin tuna spawning tended to target specific features or water masses. We hypothesized that certain habitat types, as defined by environmental variables, should be more likely to contain bluefin tuna larvae. A classification tree approach was employed to classify different habitats and conditions in the GOM in terms of their likelihood of containing bluefin tuna larvae.

METHODS

Larval bluefin tuna data were available for every year from 1982 through 2006, with the exception of 1985 and 2005, from the National Marine Fisheries Service Southeast Area Monitoring and Assessment (SEAMAP) Program. Both bongo and neuston net tows were completed across a grid of stations (the SEAMAP grid) in the northern GOM in late April and May, with sampling continuing into June in some years. Cruises were usually divided into two legs, with the grid of stations completed once on each leg. Bongo nets were fitted with 333- μm mesh, on two 61-cm-diameter round frames, and were towed obliquely as described in Scott *et al.* (1993) and Richards *et al.* (1993), mostly to 200 m depth. Neuston nets were fitted with 0.95-mm mesh on a 1 \times 2 m frame, and were towed at the surface. Samples from the neuston net, and the right bongo net only were sorted, and larvae identified to the lowest possible taxa at the Polish Plankton Sorting and Identification Center in Szczecin, Poland. The identifications of Scombridae larvae were validated at the Southeast Fisheries Science center in Miami, Florida, and occurrences of larval bluefin tuna were recorded. In all, 658 larvae from bongo net samples and 2222 larvae from neuston net samples were measured, using an eyepiece micrometer. Due to shrinkage inherent with preservation, and the high variability in age at length of small bluefin tuna larvae which have been aged in the Western Atlantic (Brothers *et al.*, 1983), length data were not included in modeling analyses. Although there was considerable variability in the number of stations sampled, and the extent of the grid from year to year, stations at whole degree intervals at least were sampled in most years (Fig. 1).

The environmental variables selected for analysis were included for a variety of reasons. Temperature and salinity data delineated water masses, to test whether bluefin tuna avoid spawning in certain oceanographic features. Wind speeds, which affect mixed layer depth and stratification (Lasker, 1975), and settled plankton volumes provided variables re-

lated to larval feeding. The time of day and moon phase were proxies for catchability, as some larval fish are caught in greater numbers at night, or when the night sky is darker, around the new moon (Hernandez and Shaw, 2003). Adult bluefin tuna have also been shown to exhibit behavioral differences with different moon phases (Wilson *et al.*, 2005). Latitude, longitude and water depth were included to test whether certain geographical locations within the GOM were more likely to contain bluefin tuna larvae, regardless of environmental conditions, and day of the year was included to test for date-related increases in spawning activity.

Hydrographic data were collected using a Seabird SBE 9/11 Plus CTD with an SBE 03 temperature sensor, SBE digiquartz pressure sensor, SBE 04 conductivity sensor, and SBE 43 dissolved oxygen sensor (Bellevue, WA, USA). Temperature and salinity at the surface, at 100 m depth, and at 200 m depth were available for the majority of stations, although the availability of environmental data was more complete in some years than in others (Table 1). Standardized settled plankton volumes (cm^3 per 100 m^3 seawater sampled) were calculated using the volume filtered data from the flowmeter fitted to the bongo net. Water depth data were inconsistently recorded over the survey period, and so station depth data were extracted from interpolated, 1-min bathymetry data from the British Oceanographic Data Centre. Interpolation was completed using kriging in SURFER 9 (Golden Software, Golden, CO, USA), and values for each station location were extracted using Spatial Analyst in ARCGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA).

Temporal variability in sampling was also considered on three different scales. The day of the year (Julian day) was included as a continuous variable, and the time of day that sampling took place was represented as a four-digit variable (e.g., 23:30 h becomes 2330). As both bongo and neuston data were included in the model, and these tows typically took place within 2 h of each other, the mean time between the two tows was used. We included the proportion of the moon illuminated as a means of quantifying moon phase, with 0 representing a new moon, and 1 a full moon. Data were downloaded from the United States Navy Astronomical Applications Department (<http://www.usno.navy.mil/USNO/>).

Data from three National Oceanic and Atmospheric Administration (NOAA) buoys in the northern GOM were used to examine wind speed data. Daily means were calculated from hourly data, downloaded from buoys #42001 (longitude -89.67 , latitude

Table 1. Details of sampled SEAMAP stations between 1982 and 2006 across the northern GOM. Some data from 1987 and 1988 were not available due to loss of archives.

| Year | Cruise start | Cruise end | No. of sampled stations (stations containing bluefin tuna larvae) | No. of stations with environmental data complete (stations containing bluefin tuna larvae) |
|------|--------------|------------|---|--|
| 1982 | 15 April | 25 May | 129 (43) | 42 (23) |
| 1983 | 22 April | 23 May | 111 (28) | 65 (21) |
| 1984 | 21 April | 16 May | 142 (13) | 30 (4) |
| 1986 | 22 April | 21 May | 147 (22) | 58 (12) |
| 1987 | 18 April | 20 May | 240 (?) | 1 (0) |
| 1988 | 19 April | 26 May | 196 (?) | 2 (1) |
| 1989 | 26 April | 19 May | 147 (28) | 45 (12) |
| 1990 | 21 April | 29 Jun | 272 (20) | 97 (11) |
| 1991 | 17 April | 10 May | 149 (16) | 30 (2) |
| 1992 | 22 April | 23 May | 166 (21) | 20 (7) |
| 1993 | 26 April | 15 June | 201 (16) | 20 (3) |
| 1994 | 28 April | 9 June | 169 (17) | 34 (5) |
| 1995 | 19 April | 7 June | 265 (34) | 88 (20) |
| 1996 | 17 April | 24 May | 189 (14) | 65 (8) |
| 1997 | 17 April | 9 June | 205 (17) | 76 (15) |
| 1998 | 26 April | 30 May | 171 (18) | 51 (8) |
| 1999 | 24 April | 31 May | 182 (16) | 68 (11) |
| 2000 | 20 April | 26 May | 170 (18) | 66 (11) |
| 2001 | 18 April | 29 May | 183 (30) | 56 (17) |
| 2002 | 19 April | 28 May | 157 (13) | 59 (9) |
| 2003 | 13 May | 30 May | 97 (24) | 37 (11) |
| 2004 | 13 May | 30 May | 86 (17) | 28 (9) |
| 2006 | 23 April | 16 July | 162 (14) | 63 (11) |

25.90), #42002 (−93.67, 25.79) and #42003 (−85.59, 25.97) for each year. The daily mean wind speed for the closest buoy to each sampled station, for the sampled date, was included as the last environmental variable. On the rare occasion that data were unavailable for the closest buoy to a station, data from the next closest buoy were used instead.

When they were present, numbers of bluefin tuna larvae caught tended to be variable, and were often low (<5 per tow). The model was therefore constructed to predict the presence or absence of bluefin tuna larvae only, without regard to the number of larvae collected. Data from each bongo net tow for which temperature, salinity and plankton volume data were available were collated, and the presence or absence of bluefin tuna larvae was noted (Table 1). A neuston net tow was completed at all bongo net stations considered in these analyses, and so if either or both nets at one station caught bluefin tuna larvae, the station was considered to be a 'positive' station. Both bongo and neuston net tows commonly collected the larvae of other Atlantic tunas, such as *Auxis* species, comprising either *Auxis rochei* (bullet tuna) or *Auxis thazard* (frigate tuna), *Katsuwonus pelamis* (skipjack

tuna), *Euthynnus alletteratus* (little tunny) and other *Thunnus* species. These were likely a mix of *Thunnus albacares* (yellowfin tuna) and *Thunnus atlanticus* (blackfin tuna), with small abundances of bigeye tuna *Thunnus obesus* (bigeye tuna) and *Thunnus alalunga* (albacore), but these larvae were all distinct from bluefin tuna. The presence or absence of the three most abundant species of other tunas (*Thunnus* species, *K. pelamis* and *Auxis* species) were therefore also included as three categorical variables.

As a non-statistical, exploratory tool, relationships between bluefin tuna larvae occurrences and continuous environmental variables were initially defined using a simple preference model approach (Cock, 1978). Each variable was divided into 15 bins, with an approximately equal number of observations contained in each bin. The proportion of stations within each bin which contained bluefin tuna larvae was calculated, and plotted. Although this technique does not require normally distributed data, strongly skewed variables can make interpretation difficult. Plankton volume data and depth data were strongly right-skewed, and were therefore $\log(x + 1)$ transformed before this analysis.

Table 2. Pearson product moment correlations between all continuous environmental variables.

| | | | | | | | | | | | | | |
|--------------|-------------|--------------------|--------------------|-------------|-------------|-------|--------------|------------|-------|-------|-------------|------------|-----------|
| T100 | 0.16 | | | | | | | | | | | | |
| T200 | 0.14 | <u>0.91</u> | | | | | | | | | | | |
| S0 | -0.01 | -0.03 | -0.03 | | | | | | | | | | |
| S100 | 0.02 | -0.04 | -0.08 | 0.12 | | | | | | | | | |
| S200 | 0.08 | 0.73 | <u>0.78</u> | 0.03 | 0.23 | | | | | | | | |
| Plankton log | -0.11 | -0.03 | -0.05 | -0.03 | 0.04 | -0.01 | | | | | | | |
| Depth log | 0.31 | 0.03 | 0.02 | 0.14 | 0.03 | -0.01 | -0.09 | | | | | | |
| Date | 0.62 | 0.04 | 0.02 | -0.13 | -0.04 | -0.05 | -0.05 | -0.01 | | | | | |
| Time | 0.05 | 0.03 | 0.02 | 0.001 | -0.03 | 0.02 | -0.07 | -0.01 | -0.04 | | | | |
| Wind | -0.26 | -0.04 | -0.02 | 0.03 | -0.03 | 0.01 | -0.05 | -0.04 | -0.22 | 0.004 | | | |
| Moon phase | 0.02 | 0.05 | 0.01 | -0.01 | -0.03 | -0.03 | -0.04 | 0.03 | -0.05 | 0.003 | 0.04 | | |
| Longitude | 0.2 | 0.05 | 0.03 | 0.18 | 0.08 | 0.05 | 0.12 | 0.1 | -0.09 | 0.01 | -0.17 | 0.05 | |
| Latitude | -0.37 | -0.1 | -0.09 | -0.13 | -0.08 | -0.1 | 0.13 | -0.52 | 0.02 | -0.02 | 0.07 | -0.08 | -0.11 |
| | T0 | T100 | T200 | S0 | S100 | S200 | Plankton log | Depth log | Date | Time | Wind | Moon phase | Longitude |

Temperature is abbreviated to 'T', and salinity to 'S', at the surface (0), 100 and 200 m depth. Significant correlations at $P < 0.05$ are shown in bold, and strong correlations of $r > 0.75$ are underlined.

Pearson product moment cross-correlations were generally low among all pairs of variables. However, strong ($r > 0.75$) relationships existed between temperatures at 100 m versus temperatures at 200 m, and between temperatures at 200 m versus salinities at 200 m (Table 2). As temperature at 200 m showed a slightly more cohesive trend with bluefin tuna larval occurrences than either temperature at 100 m or salinities at 200 m, this variable was retained, and the remaining two variables were excluded from the classification tree analysis. This left 15 variables as input parameters for classification tree analysis: surface temperature, temperature at 200 m depth, surface salinity, salinity at 100 m depth, standardized plankton volumes, water depth, day of the year, time of day, wind speed, moon phase, latitude, longitude, and presence or absence of larvae of the other three species of tuna. As a comparison with larval bluefin tuna associations, the sea surface temperature associations of *Auxis* species, *K. pelamis*, *E. alletteratus* and other *Thunnus* species were also calculated and displayed.

The remaining variables were input into a classification tree model, using DTREG software (Brentwood, TN, USA; Sherrod, 2003). Classification tree modeling splits a data set into increasingly small and homogeneous subsets, with each split made using the variable which provides the greatest improvement in the homogeneity of the two resulting groups (De'ath and Fabricius, 2000; Castellon and Sieving, 2006). The aim of this procedure was to define habitat conditions which had the highest likelihood of occurrence of bluefin tuna larvae. The classification tree approach was suited to our data set as it is a non-parametric procedure which

can cope with non-linear relationships and interaction amongst predictor variables (Franklin, 1998; De'ath and Fabricius, 2000; Vayssières *et al.*, 2000). Although construction of classification trees is a non-parametric technique, strongly skewed data and outliers can still affect model performance. The distributions of all continuous variables were examined, and a fourth-root transformation was applied to temperature at 200 m, and salinity at the surface, and at 100 m. The log transforms already applied to plankton volume and water depth were retained.

The Gini goodness-of-fit measure was used to determine optimum splits. To avoid model over-fitting, a minimum node size of ten observations was required to complete a split. Each continuous variable was divided by the program into 2000 categories, to make the splits of each variable as accurate as possible. V-fold cross-validation, with ten partitions, was used to validate the classification tree model (De'ath and Fabricius, 2000). The DTREG program also has the ability to set a misclassification 'cost' for the model, in order to preferentially avoid false positive or false negative, results. We used iterative analysis to find the optimum value for the misclassification cost, in terms of the number of positive, and negative, stations classified correctly by the model. To construct a model with the highest degree of generality possible, 10% of the original data set was withheld from the initial analysis as a 'test' data set. All stations from cruise leg 2 of 1995 were included in the 'test' data set, to allow us to plot the success of the model on unseen data across the GOM for one entire cruise leg. The rest of the 'test' data set was selected randomly. The

remaining 90% of the data were used as a 'training' data set. The ability of the model constructed using the training data set to correctly predict favorable bluefin tuna habitat for the test data set was then assessed, as a way of providing out of model validation. The accuracy of the model was assessed by comparing the modeled probability of larval bluefin tuna occurrence at each station to the actual observed larval data. Our aim was to define a model which would correctly classify at least 80% of positive larval bluefin tuna stations.

Throughout the larval surveys, bluefin tuna larvae were most commonly found in low numbers, signifying a sparse and patchy distribution (Richards *et al.*, 1989), and a high likelihood that sampling would miss larvae present in favorable habitat. This suggested that even after formulation of a multivariate model, a considerable proportion of favorable habitat was likely to be unoccupied by larval bluefin tuna. Our objective was to construct the classification tree model in such a way as to inclusively define the range of potentially favorable larval bluefin tuna habitat, rather than to assume that all negative stations had been located in unfavorable habitat. This was achieved by adjusting the misclassification cost of the classification tree model.

As a visual aid, the generated probabilities for four example years (1983, 1995, 1997 and 2003) were contoured, using kriging in SURFER 9, and the bluefin tuna larvae catch locations for each of these years were overlaid. These years were chosen because they represented a range through time, with contrasting oceanographic conditions, and sufficient bluefin tuna larval occurrences to test model accuracy. As two cruise legs were usually completed each year, with the same stations repeated between legs, results from one leg of each cruise only were shown in these plots. Cruise leg 2 of 1995 was chosen, as all larval bluefin tuna distributions from this leg were generated from out-of-model validation, and could be compared to predictions generated from other years.

RESULTS

Preference indices and variable selection

Between 1982 and 2006, 1101 stations with all environmental and bluefin tuna larval data were available (Table 1). Bluefin tuna larvae were found at 21% of these stations in at least one net type, and were distributed across the GOM (Fig. 1). Larvae were collected in both nets at 5.3% of stations, in the neuston net only at 6.1% of stations, and in bongo nets only at 8.6% of stations. Larvae were typically very small, with

mean lengths of 3.7 mm in bongo net samples and 5.3 mm in neuston net samples.

Data from all years were used to examine associations between bluefin tuna larvae and different environmental conditions (Fig. 2a,b). Larvae were most likely to be collected at moderate sea surface temperatures, between 25 and 28°C (Fig. 2a). In contrast, bluefin tuna larvae were associated with lower temperatures at both 100 and 200 m depth. Larvae were proportionally more abundant where salinities at 100 m depth were higher than around 36.3. However, no trend was apparent for salinities at the surface, and at 200 m depth (Fig. 2a). Bluefin tuna larvae were also more likely to be found at lower longitudes (stations farther west). Stations with higher plankton volumes were most likely to be positive for bluefin tuna larvae, as were stations of intermediate depth (Fig. 2b). In terms of temporal variables, larvae were proportionally more abundant from the middle to the end of May, and at darker (closer to the new moon) moon phases (Fig. 2b). There were no visible trends with time of day, and wind speed. Stations containing the larvae of other *Thunnus* species or of *K. pelamis* were slightly more likely to contain bluefin tuna larvae, whereas the reverse was true for stations containing *Auxis* species larvae (Fig. 2b).

The proportion of positive stations within each bin of each variable was generally no higher than 30–40%, indicating that even within the most favorable conditions for each variable, 60–70% of stations would still be unoccupied by bluefin tuna larvae. A scatterplot of temperature and salinity at the surface (as an example) showed that although bluefin tuna larvae were more common at stations with high salinities and intermediate temperatures, conditions at positive and negative stations overlapped considerably (Fig. 3).

Classification tree model

As the primary interest was in defining potentially favorable habitat for larval bluefin tuna, rather than excluding all negative stations, it was preferable that the model be constructed more to avoid false positives (bluefin tuna larvae at theoretically unfavorable stations) than false negatives (no larval bluefin tuna at theoretically favorable stations). To achieve this, the misclassification cost in DTREG was set to make false positives five times more costly than false negatives. At values lower than three, a large proportion of positive bluefin tuna stations were classified as being in unfavorable habitat. At values larger than five, the misclassification of negative stations became unacceptably high, with little improvement in correct

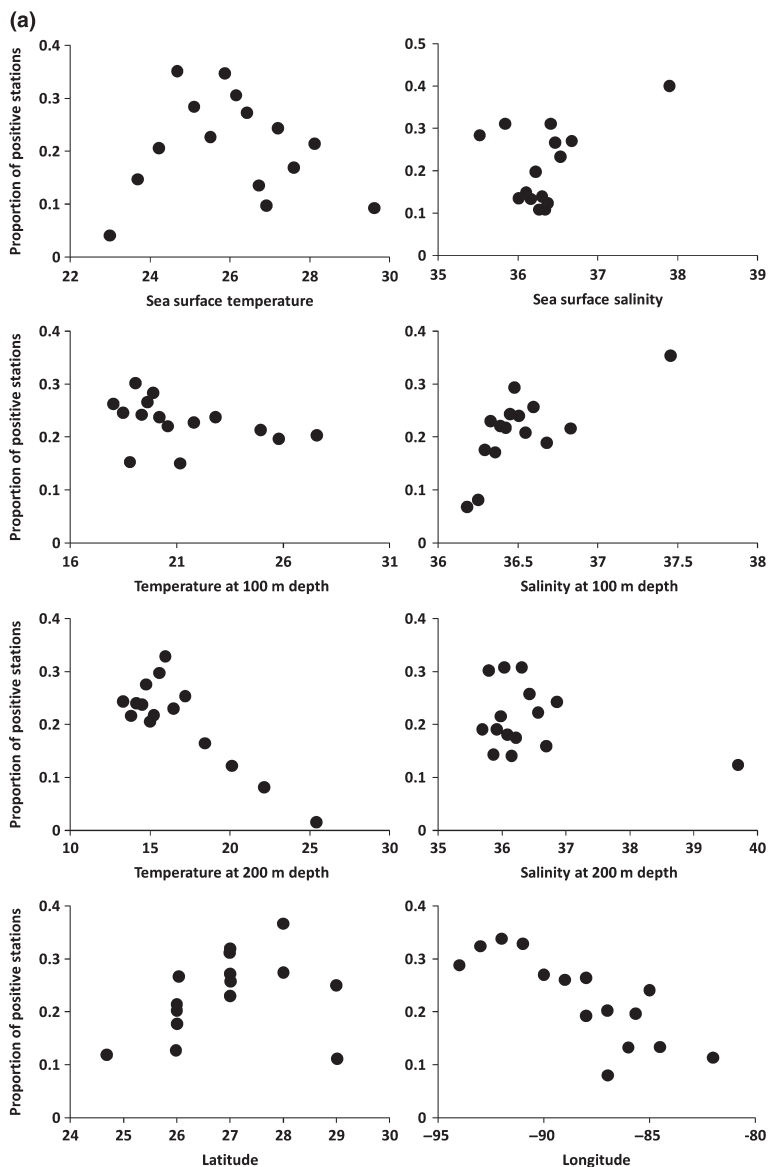


Figure 2. (a, b) Proportions of positive stations for bluefin tuna larvae for differing levels of 14 environmental variables, for all data sampled between 1982 and 2006. Both plankton volume and depth data were log-transformed.

classification of positive stations (Fig. 4). The accuracy of the model with varying misclassification costs was assessed for both the training data set used to construct the model and for the test data set used for out of model validation. The size of the classification tree for each model was also recorded (measured by the number of terminal nodes), as the structure of the tree changed to accommodate each misclassification cost. Larger trees (such as those generated when the misclassification cost was set at 3 or 4) tended to be comparatively more accurate for the training data set, but less so for the test data set, suggesting a tendency towards over-fitting, and a loss of generality. The chosen model, with a misclassification cost of 5, was 89.9% accurate for positive stations and 57.0%

accurate for negative stations using the training data set, and 82.6% accurate for positive stations and 57.5% accurate for negative stations using the test data set. This minor loss of power between the training and the test data set suggested that the model was sufficiently general, and was not overfit to the training data set.

The classification tree model chosen initially split the data by temperature at 200 m depth (Fig. 5), with temperatures above 21.0°C highly unfavorable. Samples taken after 8 May were more also likely to contain larval bluefin tuna. Earlier, larvae were still collected where sea surface salinities and sea surface temperatures were higher. For stations sampled after 8 May, larvae were more likely to be found at darker moon phases (where the fraction of the moon illuminated

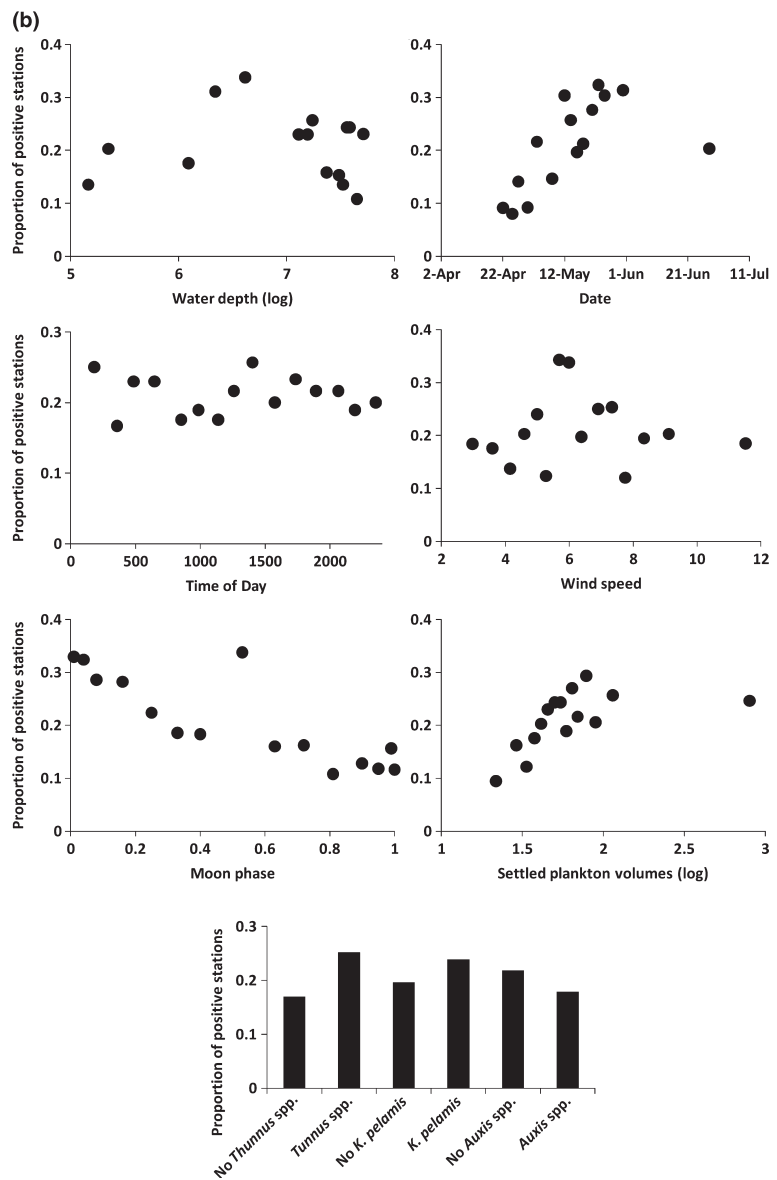


Figure 2. (Continued).

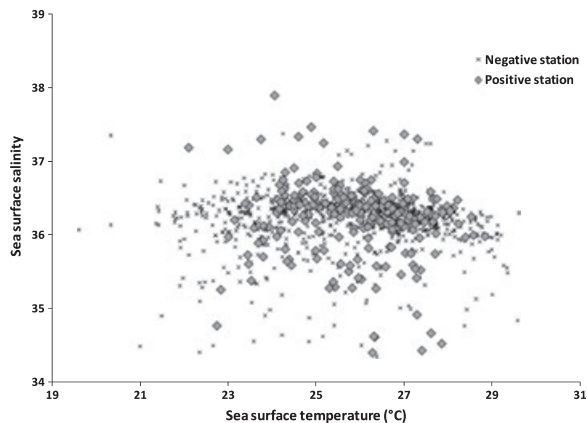
was <0.5), and where sea surface temperatures were <28.5°C. At brighter moon phases, some larvae were still collected west of 87°W, where plankton volumes were higher (Fig. 5).

To visualize the results of the model within specific years, the generated probabilities for 4 yr (Leg 2 surveys from 1983, 1995 and 1997, and Leg 1 from 2003) were contoured, and plotted, with locations of bluefin tuna catches overlaid (Fig. 6). Generally, habitat within the LC in the eastern GOM was less favorable, as were warm-core rings, and cooler water on the continental shelf. The location and size of favorable habitat was highly variable between years, which was reflected in the locations of larval bluefin tuna catches.

However, as expected, many theoretically favorable stations were negative for larval bluefin tuna.

To examine how these ‘rates of occupancy’ had changed over time, the proportion of stations which supported larval bluefin tuna were plotted for all years, except 1987 and 1988, between 1982 and 2006. Data from all sampled stations, and for all stations in theoretically favorable habitat, are shown in Fig. 7. Considering only stations in favorable habitat, there were higher occupancy rates in 1982 and 1983, with lower values thereafter. Given no habitat information, the chances of collecting a bluefin tuna larva at any sampled station over the survey period was 21.0%. However, if only stations classified as being in favorable

Figure 3. Scatterplot of sea surface temperatures, and sea surface salinities of all sampled stations, 1982–2006. Stations where bluefin tuna larvae were caught (positive stations) are shown as filled diamonds, while stations where no bluefin tuna larvae were caught (negative stations) are shown as x.



habitat were included, this probability improved to 35.5%. This improvement in probability varied among years, with some years showing up to a 200% improvement (from 14 to 44% in 1994) in the probability of catching a bluefin tuna larva if only favorable habitat was considered, and other years showing a marginal improvement (Fig. 7). The mean improvement among years was 65%. Overall, 364 (33%), of stations sampled between 1982 and 2006, and examined here, had <3.5% probability of collecting bluefin tuna larvae, based on environmental conditions.

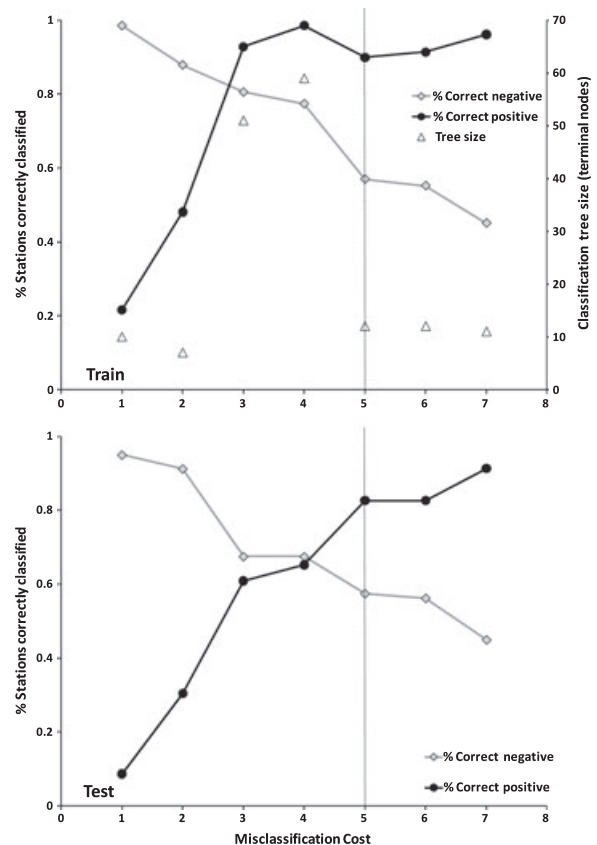
Other tuna species and sea surface temperature

The larvae of other Atlantic tunas were frequently found in much warmer water than were larval bluefin tuna (Fig. 8). *Auxis* species larvae were collected across most water temperatures, and *E. alletteratus* showed a slight association with warmer waters. However, the larvae of *K. pelamis* and other *Thunnus* species (not including bluefin tuna) showed a strong association with very warm waters.

DISCUSSION

Classification tree analysis showed that whereas bluefin tuna larvae in the northern GOM were collected in a variety of oceanographic conditions, they were very rare or absent in certain habitats. Given their small size, and thus young age of around 7 days or less (Brothers *et al.*, 1983), the larval bluefin tuna collected were likely to be located in the same water mass in which they were spawned. If larvae were largely

Figure 4. Effect of varying misclassification costs on the performance of the classification tree model. Classification successes for positive and negative stations for bluefin tuna larvae are shown for the training data set (top), and test data set (bottom). The size of the generated classification tree (measured by the number of terminal nodes) is also shown for the training data set.



absent from a habitat type, it suggests that the adults were not spawning there.

Bluefin tuna larvae were less likely to be collected where water temperatures at 200 m depth were high. Stations with higher temperatures at depth were most likely to have been in the LC, or within warm LC rings, where warmer waters penetrate to deeper depths (Schroeder *et al.*, 1974). Although high water temperatures might be most favorable for egg hatching (Miyashita *et al.*, 2000) and fast larval growth rates (Brothers *et al.*, 1983; Houde, 1989), retention conditions within the LC would be poor. Any larvae spawned within the LC would be advected out of the GOM and northwards along the south-eastern US coast within a period of days (McGowan and Richards, 1989). In addition, physiological processes of adult bluefin tuna may be compromised when they encounter very warm waters (Blank *et al.*, 2004), such

Figure 5. Classification tree model for predicting the presence or absence of bluefin tuna larvae in the northern GOM. The number of samples at each node is shown, as is the misclassification rate (percent). The importance of all included variables in the generation of the tree is also given.

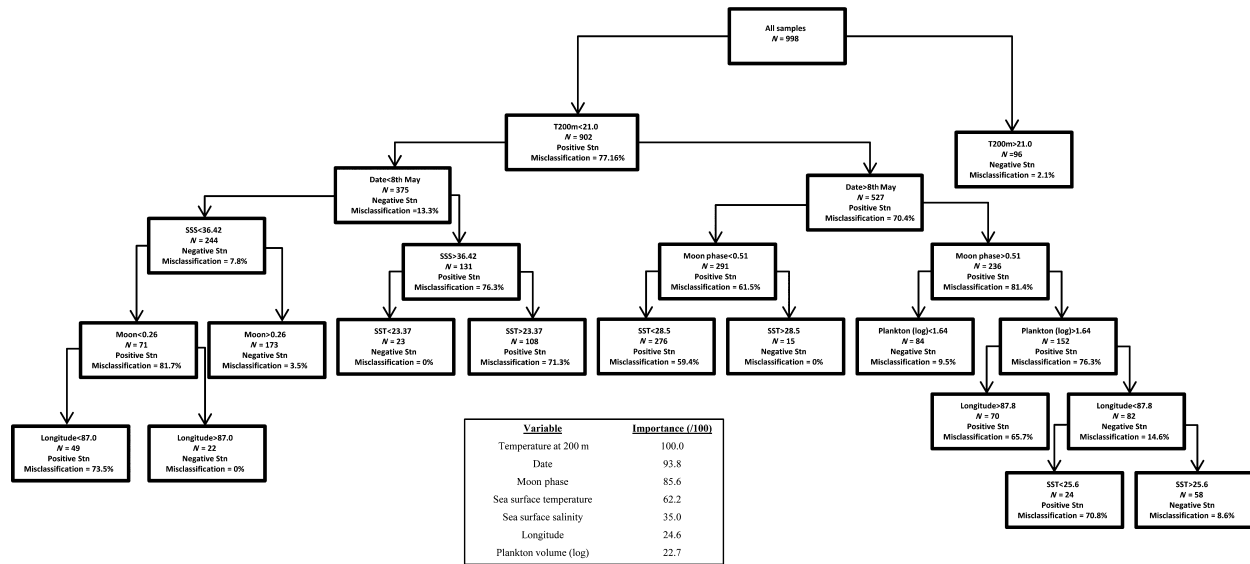


Figure 6. Predicted probabilities from classification tree analysis of collecting at least one bluefin tuna larvae across all sampled stations in cruise leg 2 of 1983, 1990 and 1997, and cruise leg 1 of 2003. All sampled stations, and larval bluefin tuna catch locations, are shown. Probabilities were kriged between stations to aid interpretation, but this should not be taken as a means to predict habitat between stations.

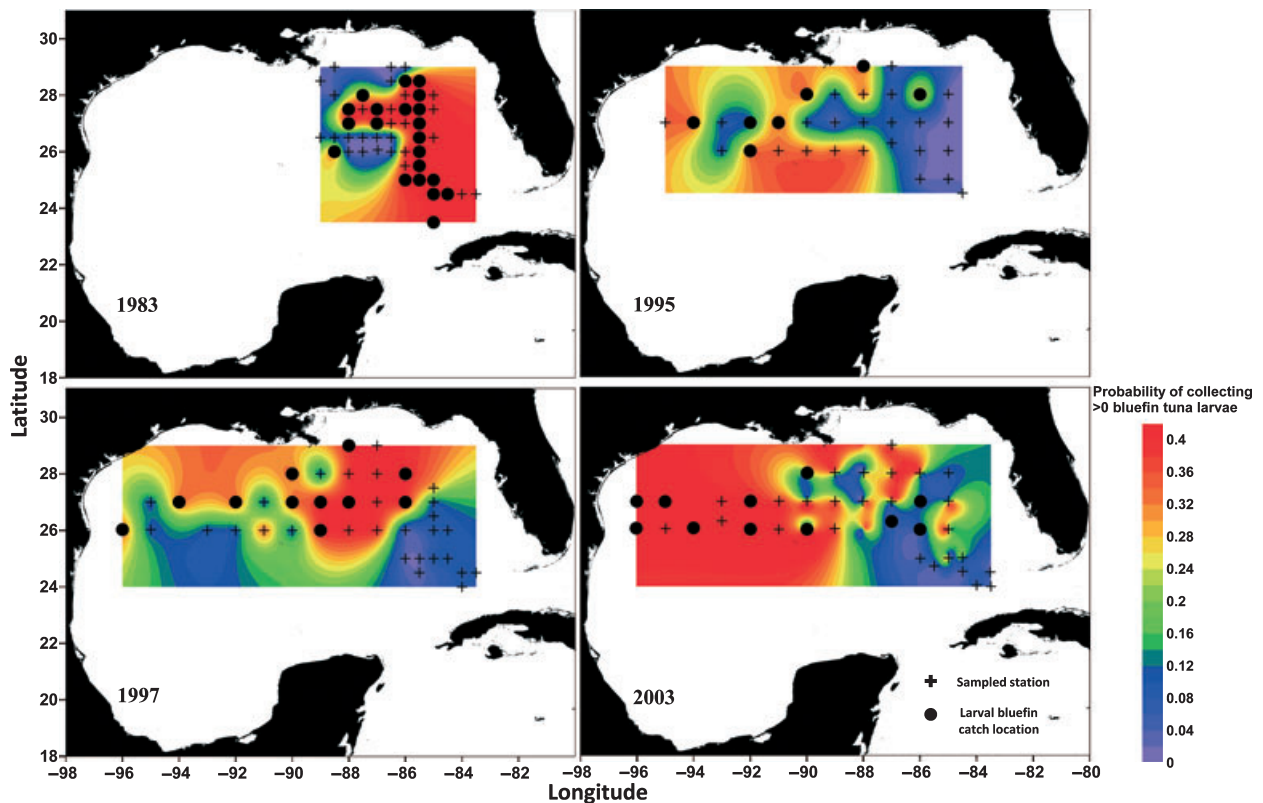


Figure 7. Proportion of stations occupied by bluefin tuna larvae in each sampled year for all habitat, and predicted favorable habitat (top). The percentage improvement in the chance of collecting bluefin tuna larvae within predicted favorable habitat, as opposed to all habitat, is also shown (bottom).

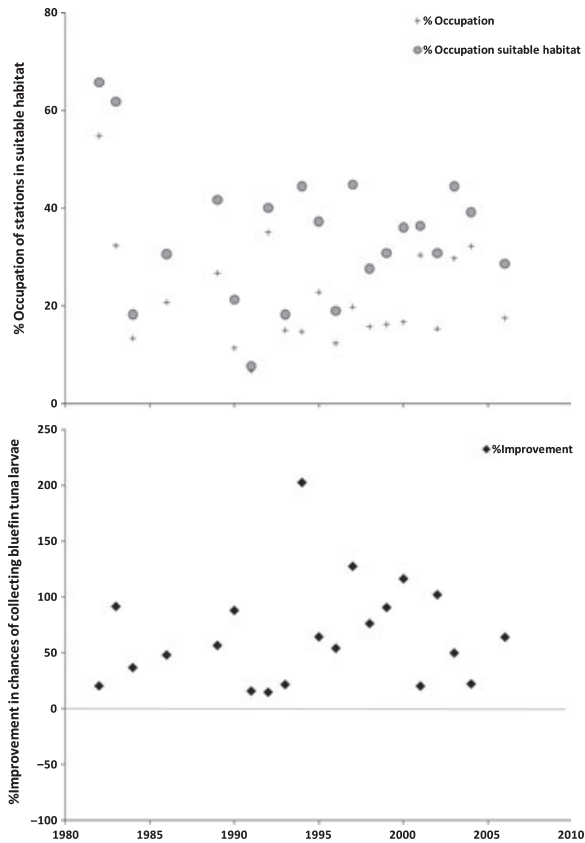
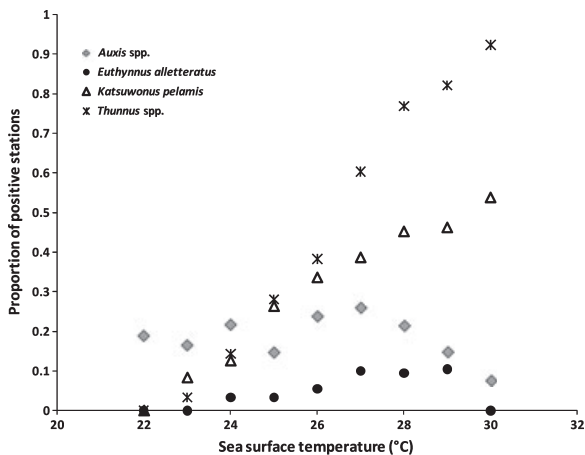


Figure 8. Proportions of positive stations for larvae of other tunas for differing levels of sea surface temperature, for all sampled years from 1982 to 2006.



as those found within LC water in late spring (Muller-Karger *et al.*, 1991; Zavala-Hidalgo *et al.*, 2002). Tagging data have shown that adult bluefin tuna do not tend to linger within the LC when migrating into the GOM (Block *et al.*, 2001), and may show deep diving behavior when crossing it, potentially to avoid very warm waters (Teo *et al.*, 2007b). A combination of poor larval retention and stressful conditions for adult bluefin tuna therefore makes LC waters a largely unsuitable spawning location.

Bluefin tuna are thought to prefer sea surface temperatures above 24°C for spawning (Mather *et al.*, 1995; Schaefer, 2001; Garcia *et al.*, 2005), and have been previously shown to prefer areas in the GOM with surface temperatures of between 24 and 27°C (Teo *et al.*, 2007a). Adult bluefin tuna are present in the GOM as early as winter; however, they are not usually in spawning condition until mid April onwards (Block *et al.*, 2001). This suggests that some environmental variable exists that may trigger spawning, such as temperature (Fitzhugh and Hettler, 1995) or photoperiod (Carrillo *et al.*, 1989), a conclusion supported by the proportional increase in catches in bluefin tuna larvae in this study at stations sampled after 8 May. However, favorable temperatures for larvae collected in the Mediterranean Sea were lower than in the GOM (24–25°C, Garcia *et al.*, 2005; 21; 5–26.5°C, Alemany *et al.*, 2010). This may suggest that although spawning is initiated by environmental thresholds, some of the upper temperature associations shown here are likely to be proxies for the avoidance of specific water masses that would result in poor larval retention, slower development or higher mortality.

Earlier in the spawning season, bluefin tuna larvae were noticeably absent from waters with low surface temperatures and salinities, which were usually on the continental shelf, or of continental shelf origin. These waters are generally higher in chlorophyll concentrations than open GOM waters (Muller-Karger *et al.*, 1991), and may be higher in nutrients and sediments, especially around the Mississippi River delta (Turner and Rabalais, 1991). Dense blooms of phytoplankton frequently occur on the continental shelf as a result of this nutrient-rich, lower salinity inflow (Lohrenz *et al.*, 1990). While these continental shelf waters may provide high concentrations of potential larval fish food items, such as zooplankton (Young and Davis, 1990), they may also contain high concentrations of planktonic predators (Bakun, 2006). Preflexion larval tuna diets are usually specialized, and many target appendicularians, before switching to piscivory at larger sizes (Llopiz *et al.*, 2010). Pelagic tunicates such as appendicularians are well adapted to oligotrophic open

oceans (Sommer and Stibor, 2002), and the reliance of larval tunas on these organisms suggests adaptation to nutrient-poor waters. Favorable habitat for bluefin tuna larvae in the GOM was therefore defined as moderately warm waters outside of the LC, and LC eddies, and outside of cooler, higher chlorophyll continental shelf waters.

Bluefin tuna larvae were more likely to be found around the new moon (between the last and first quarters) than around the full moon. Although adult bluefin tuna in the North Atlantic (Wilson *et al.*, 2005) and Pacific (Block and Farwell, 2005) adjust their feeding behavior during the full moon, there is no evidence that spawning activity is also modulated by moon phase. Instead, it is likely that the ability of larval bluefin tuna to detect, and avoid, sampling nets at night would be enhanced during a full moon, when the sky is lighter, thus contributing to lower catches of larvae (Davis *et al.*, 1990). However, further study is required to confirm this.

The precise reasons why adult bluefin tuna migrate large distances to spawn in the GOM remain unclear. Like many other large pelagic fishes, their spawning grounds are warm (Schaefer, 2001) and largely oligotrophic (Richardson, 2007). It has been suggested that natal homing may be important and that fish return to ancestral spawning grounds (Cury *et al.*, 1998). This would imply that adult fish are spawning in comparatively favorable habitats within defined spawning locations. Although similarly warm, oligotrophic regions may be found in the Atlantic and Caribbean Seas, no evidence of large-scale spawning in these areas has been found. However, it remains possible that other spawning areas exist (Lutcavage *et al.*, 1999). A few scattered larvae have previously been collected east of the Yucatan Peninsula, and off the east coast of the U.S.; some of these larvae appear likely to have originated from outside the Gulf of Mexico (McGowan and Richards, 1989; Rooker *et al.*, 2007).

The model created in this study was useful for defining broad water masses in which bluefin tuna larvae were more likely to be collected. We find that 33% of stations examined here had a <3.5% probability of positive catches. However, many stations within favorable habitat did not contain bluefin tuna larvae. Part of this result is likely to be related to catchability: larval bluefin tuna occurrences were patchy, and larvae were frequently caught in low numbers (<5). Part of this may be due to gear inefficiencies and net avoidance, so the chances of missing larvae, even if they were present, may have been considerable. However, larvae of other *Thunnus* species were collected much more commonly than bluefin

tuna larvae, and in alternative habitats, such as warmer LC water. This suggests that bluefin tuna larvae were indeed rare, possibly as a result of the depleted stock size (McAllister and Carruthers, 2008). Similar disparities between abundances of bluefin tuna and other tuna larvae have also been found in the Mediterranean (Garcia *et al.*, 2005; Oray and Karakulak, 2005).

One limitation of the current model, in terms of the data used, was the coarse resolution of the sampling stations. This factor limits our ability to correlate larval abundance to finer-scale features, such as fronts, and frontal eddies. Adult bluefin tuna are capable of detecting and responding to oceanographic gradients (Medina *et al.*, 2002; Royer *et al.*, 2004; Wilson *et al.*, 2005), and Richards *et al.* (1989) found bluefin tuna larvae concentrated along the LC front. Given the significance of finer-scale features to larval retention, feeding conditions and survival (e.g., Hinrichsen *et al.*, 2003; Richardson, 2007), this is a considerable shortcoming. However, since 2008, finer-scale sampling targeting oceanographic features has been completed as part of the annual spring GOM larval surveys, with an emphasis on the use of satellite imagery to place stations and to provide environmental data. When processed, these data will allow us to better define favorable habitat for larval bluefin tuna, and refine the current model. In addition, current research is using satellite measurements of sea surface temperature, sea surface height and chlorophyll to act as proxies for many of the environmental parameters included in this model, and to investigate the influence of ocean fronts on larval distributions.

In conclusion, we find that larval bluefin tuna were rarely collected within Loop Current waters, warm-core rings, or cooler continental shelf waters within the GOM. The extent of favorable habitat was highly variable among years, which was reflected in the spatial variability of larval bluefin tuna catches, and one-third of all stations had a <3.5% chance of collecting larvae. Given current issues with variability of data inputs, these models have high potential to significantly improve data inputs for the management of an iconic species.

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