Bluefin tuna (Thunnus thynnus) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96)

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ABSTRACT

Fishery-linked aerial surveys for bluefin tuna (Thunnus thynnus) were conducted in the Gulf of Maine (GOM) from July through October, 1994–96. Each year, from 507 to 890 surface schools were detected and their locations examined in relation to oceanographic conditions. Correlations between bluefin tuna presence and environmental variables were explored for sea surface temperature (SST), distance to a SST front, frontal density (relative density of all SST fronts seen in a given 1 km area for 2 weeks prior to each tuna sighting), and bottom depth and slope. Mean SST associated with bluefin schools was 18.1°C(±2.8). Schools were located at a mean distance of 19.7 km (±19.6) from SST fronts, and in water masses with an average frontal density of 28.2 m km–2 (±35.7). Mean bottom depth of detected schools was 139.0 m (±70.3), and mean bottom slope was 0.7% rise (±0.7). A binomial generalized linear model fit to these variables indicated that bluefin are seen closer to fronts than locations in which no tuna were seen. Using simple and partial Mantel tests, we investigated the spatial correlation between bluefin tuna presence and the environmental variables, controlling for spatial autocorrelation. For each day that schools were sighted, we performed 24 Mantel tests, on a combination of response and predictor variables. The spatial relationship between bluefin tuna and SST fronts was inconsistent. Our analysis identified significant spatial structure in the bluefin school locations that had no significant correlation with any of the measured environmental features, suggesting that other untested features, such as prey density, may be important predictors of bluefin distribution in the GOM.

Key words: bluefin tuna, fronts, Gulf of Maine, Mantel test, northwest Atlantic, sea surface temperature, spatial analysis, Thunnus thynnus

INTRODUCTION

Schools of bluefin tuna (Thunnus thynnus) occur in the Gulf of Maine (GOM) from late May through November (Fig. 1). These schools are primarily comprised of adult size classes‡, with schools consisting upwards of 5000 surface individuals (Lutcavage and Kraus, 1995). Local commercial fishermen are knowledgeable about bluefin life-history traits, and usually catch allotted quotas by season’s end, but they and fisheries managers alike have been unable to forecast shifts in interannual distribution or residency patterns. This information is relevant to stock assessments and interpretation of catch per unit effort indices of abundance for highly migratory species such as the tunas (Dagorn et al., 1995; Brill and Lutcavage, 2001), especially given that 10 of 11 indices of abundance are fishery-dependent (Polacheck et al., 1998).

Recent efforts to identify the spatial and temporal patterns of bluefin tuna in the northwest Atlantic have included ultrasonic tracking experiments (Lutcavage et al., 2000; Brill et al., 2002), aerial surveys (Lutcavage and Kraus, 1995; Lutcavage et al., 1997), individual based and population modeling (Humston et al., 2000; Newlands and Lutcavage, 2001; Newlands, 2002), and pop-up satellite tagging (Lutcavage et al., 1999; Block et al., 2001). Bluefin tuna are among the most valuable fisheries in the Atlantic, and since 1981 their population management has been the subject of intense international effort and debate (Magnuson et al., 2001). As
monitoring of a wide-ranging pelagic species is inherently difficult, increasing our understanding of the relationship between bluefin distribution and readily measured environmental correlates could provide an alternative method of predicting their distribution and relative abundance.

The migration and distribution of tuna species has been shown to be influenced by oceanographic conditions (Nakamura, 1969; Sund et al., 1981; Laurs et al., 1984). Among the tunas, bluefin tuna are notable in having the widest thermal (5–30°C), depth (>800 m) and latitudinal (8°S to 60°N) range (Tiews, 1963; Carey and Lawson, 1973; Mather et al., 1995). Although their distributions are not likely to be limited by oceanographic conditions per se, their movements and distributions have been linked to specific surface isotherms and productivity (Roffer, 1987; Humston et al., 2000; Brill and Lutcavage, 2001). Local fishermen typically seek specific water masses to successfully target bluefin, and it is likely that persistent oceanographic features in the GOM influence bluefin distribution, and that of their mobile prey (Lutcavage and Kraus, 1995).

Olson et al. (1994) explored the role of oceanic fronts on marine species at four trophic levels, noting that few available data sets allow for a definitive quantification of this relationship. The premise underlying this spatial interaction is that discontinuities in ocean structure can serve as aggregating mechanisms for less mobile prey because of the shear force between the distinct water masses (Olson and Backus, 1985; Olson et al., 1994). Predators are thought to aggregate where fronts cause concentrations of their preferred prey. Albacore and skipjack catches have been spatially correlated with sea surface temperature (SST) and chlorophyll fronts (Laurs et al., 1984; Fiedler and Bernard, 1987). Podestá et al. (1993) explored the relationship between swordfish catch rates and SST fronts, and while randomization tests indicated a significant association with fronts, the precise nature of the relationship proved difficult to identify because of the spatial uncertainty of the longline sets. Recent modeling efforts have explored relationships between bluefin tuna distributions and specific isotherms (Humston et al., 2000), as well as feeding

behavior at fronts for several tuna species (Kirby et al., 2000).

In this paper, we describe GIS-based efforts to examine surface bluefin tuna distributions in the GOM in relation to remotely sensed and interpolated variables. Specifically, we report on the quantitative relationship between bluefin school location, SST, distance to daily thermal fronts, and cumulative frontal density. We examine whether bluefin tuna aggregate near thermal gradients or areas of high frontal density in order to develop improved methods for the prediction of population distribution and relative abundance.

**METHODS**

In 1993, an exploratory survey was conducted to assess the feasibility of using fishery-linked spotter pilots to document bluefin tuna presence in the GOM (Lutcavage and Kraus, 1995). Fishery-dependent aerial surveys were flown from July through October 1994–96 (Fig. 2a–c), spanning the New England bluefin fishing season (Lutcavage et al., 1997). The surveys, while not based on line-transect methodology, were designed to provide an estimate of minimum surface biomass of schools. In addition, the objectives were to identify residency, interannual variation of distributions and aggregation patterns, and the relationship of bluefin schools to ocean conditions and prey (Lutcavage and Newlands, 1999). Spotter pilot effort totalled 309 496 km over 159 search days. Days with no sightings were less than 5% of the total days flown. Specific details on the design of the surveys and specific daily results of aircraft-based effort and effort-corrected sighting rates are given elsewhere (Lutcavage et al., 1997; Newlands, 2002). Bluefin tuna detected by aerial surveys represent schools occurring within the visual and photographic range of spotter pilots (i.e. within 3–4 m of the surface).

To explore the relationship between bluefin tuna distribution and SST fronts, a database of daily SST fronts was constructed. This database includes vector-based files of each front’s location and associated attributes, raster-based files of frontal location and interpolated raster variables of distance to fronts. Our definition of an SST front is taken from Ullman and Cornillon (1999), whereby each front represents a change in SST > 0.375°C per km, and which is longer than 10 km. These fronts are detected from the AVHRR database using a multi-image edge detection algorithm (Ullman and Cornillon, 1999). To create the daily database, we used the Distributed Oceanographic Data System (DODS) (http://www.unidata.ucar.edu/packages/dods/) to access and format SST fronts. The DODS database was queried each day on which bluefin tuna were seen. Front location data, as well as attribute information including temperature, temperature gradient and direction to warm water were extracted and formatted for coverage generation in ArcInfo (Environmental Systems Research Institute, Inc., 2000). Once a vector file was created for each day, we converted the data to a raster form, and constructed a distance-to-front data layer across the GOM study area (Fig. 3). In the latter data layer, each front was treated equally, i.e. the distance to a front was constant regardless of the strength of each front. Distance to the nearest front for each output cell in the new data layer was calculated using a Euclidean distance function in ArcInfo. To account for the presence of clouds, daily grids of cloud-masked SST were created and used to process the distance to front grids, thereby creating edited distance-to-front grids with no-data values wherever clouds were present. This process reduced the number of schools with a calculated distance-to-front value from 890 to 216 in 1994, from 796 to 516 in 1995, and from 507 to 222 in 1996.

In order to explore whether bluefin tuna are responding to fronts over a longer period, we collapsed all SST fronts seen in the 2 weeks prior to each bluefin tuna sighting into one vector layer, and a raster data layer was created by calculating the kernel-smoothed density of fronts (length of lines per unit area). Thus for each day we calculated a frontal density grid that included the density of fronts seen in the 2 weeks prior to that day. Areas that had persistent fronts in this time period yield higher density values. Once the environmental database was complete, a series of custom-written ArcInfo scripts extracted the values for each data layer for each documented bluefin school. Values for each day were then assembled into a large database for statistical analysis. We also tested for the effects of bottom depth and bottom slope, but found few significant results.

**Generalized linear model**

We fit a binomial generalized linear model (GLM) (McCullagh and Nelder, 1989) using a logit link to our presence–absence data set grouped together across all years. The GLM was run on a full model, including previously mentioned predictors, year as a categorical predictor term, and selected interaction terms. Model diagnostics were run, and the data were checked for normality, nonlinearity, skew and outliers. The distance to front and the frontal density variables were transformed with a Box-Cox transformation. The pre-
Figure 2. Distribution of the flight lines by year: 1994 (a), 1995 (b), and 1996 (c). The flight lines were fishery-linked, and thus do not follow predetermined line transects. Although the distribution of tuna schools shifts each year, and the flight lines closely mimic that shift, it is clear that some of the apparent patterns are not simply the result of flight patterns as there are overflights in each year in areas of low tuna abundance.
dictors were then centered and scaled. The full model was then run through a stepwise selection procedure using Bayes information criteria as the penalty criteria. The final model was chosen from this step, and then specified for the final GLM test using the statistical package R (Ihaka and Gentleman, 1996).

Mantel tests

To quantify the precise spatial relationship between bluefin presence and environmental data on a daily time step, we used the family of simple and partial Mantel tests, a type of multiple regression where the familiar dependent and predictor variables are replaced with distance matrices (Mantel, 1967; Legendre and Legendre, 1998). A detailed presentation of the application of the test to binary presence-absence data is given in Schick and Urban (2000). The Mantel test offers the ability to include variables of different types. A second advantage is that, unlike the GLM, geographical distance, or space, can be considered explicitly in the regression framework. Geographic distance is calculated by extracting the Euclidean distance between every pair of locations in the environmental data set. The inclusion of geographic distance allows the user to test for similarity in bluefin presence for locations that are close together. Functionally, the Mantel test is based on a linear correlation statistic (Mantel, 1967). However, the primary difference is the conversion from raw data to distance matrices. We computed the test statistic, which represents the linear correlation between two or more matrices, by unfolding the matrices and calculating the sum of the cross products (Legendre and Legendre, 1998). Because the elements of a distance matrix are not independent, the P values and confidence limits are calculated using permutations and bootstrapping, respectively. The permutation procedure is laid out by Legendre and Legendre (1998), whereby the rows and columns of the dependent matrix are randomly rearranged, and the test statistic is re-calculated. This is then repeated 10,000 times to generate the final P value. In a three matrix, or partial Mantel, framework (Smouse et al., 1986) the test can remove the effect of one or more variables and allows for the analysis of pure correlations between variables. This last step can be of major importance when one or more of the variables are spatially structured, because it removes the
potentially confounding effect of spatial autocorrelation (Legendre, 1993).

We used simple Mantel tests to explore the spatial structure of each of the biological and environmental variables. Distance matrices were constructed for the variables: species (fish presence–absence), geographic distance between locations (space), frontal density, distance to a front, and SST. Using two matrices at a time, for example, frontal density and space, we performed simple Mantel tests to test for spatial autocorrelation to find out if values that were similar in frontal density were also spatially close together. Because each of these environmental variables exhibited high degrees of spatial autocorrelation, we used partial Mantel tests to explore the quantitative relationship between bluefin distribution and each variable, while controlling for spatial structure.

Spatial correlation was examined on a daily basis (for each year) using the statistical package R. Attribute information for each school included day, time, location, school size, as well as values for five environmental variables. A custom-written spatial analysis library for R (S. Goslee and D. Urban, Duke University, Durham, NC, USA, personal communication) was used to analyze the database. At daily time steps, seven Euclidean distance matrices were created and custom scripts were used to perform different simple and partial Mantel tests. The significance value for each test was determined using 10 000 permutations, and confidence intervals were obtained using 1000 bootstrapping events. P-values were corrected for multiple comparisons using the Hochberg method (Hochberg, 1988) (as cited in Legendre and Legendre, 1998).

RESULTS

Bluefin schools were spatially varied across each of the 3 yr, but in general, tuna were most abundant in the western GOM (Fig. 4a–c). For all 3 yr, the highest number of surface schools occurred in August, when SSTs were warmest (Table 1). With the exception of the Bay of Fundy, relatively few schools were sighted in the northern Gulf, whereas the Great South Channel was the most consistent area of tuna presence. In 1994–95, schools were aggregated north of the Cape Anne peninsula and in Maine coastal waters, while in 1996 schools were located further to the south and east. One notable interannual difference is the presence of bluefin in and around the Stellwagen Bank region in 1996 (Fig. 4c) versus their absence there in 1994–95. In particular, surface schools located near Stellwagen Bank were distributed near the western edge of the bank, in areas of high topographic relief (Fig. 4c). In general, bluefin schools occurred in areas of elevated frontal density (Fig. 4a–c), and at a mean distance of 16.4 km from a front, although there was variability across each of the three seasons (Fig. 5). In 1994 and 1995, bluefin schools were seen closer to fronts than a set of random locations throughout the GOM (Fig. 6a–d). However, in 1996, this clear separation is not as readily apparent (Fig 6e,f). These differences were statistically different in 1994 (Wilcoxon rank sum test; \( P < 0.001 \)) and 1995 (\( P < 0.001 \)), but not in 1996 (\( P = 0.934 \)). These differences were not explored further because of our inability to determine whether random locations in the GOM were actually absence cells.

The results of the GLM suggest that bluefin are seen closer to fronts, in areas of lower frontal density, and in warmer waters than absence cells (Table 2). The addition of an interaction term between distance to front and temperature results in a significant reduction in the deviance table. While we tested for a year effect, none was statistically significant at the 0.05 level.

As there are over 2600 Mantel test results, we only present the results from the partial Mantel tests that tested the correlation between bluefin tuna presence and an environmental variable, controlling for the effects of spatial autocorrelation (Fig. 7). This test yields the purest correlation between bluefin and the environment. Significant results from a test that explores the correlation between bluefin presence and spatial structure, controlling for the effects of the environment, indicate a spatial residual, or that there is spatial structure in the species variable unexplained by the model. In 1994, only 5 days exhibited significant strong Mantel correlation with the environment (Fig. 7a). For example, on 8 August 1994, all three temperature-related variables (SST, distance to front, frontal density) were significantly correlated with bluefin presence. A significant warm water mass extended deep into the GOM, and was associated with strong thermal fronts and bluefin aggregations. Of the three significant correlations on this day (8 August 1994), SST had the highest partial \( r^2 \) value (0.6963, \( P < 0.002 \)).

In 1995 there were 10 days with significant Mantel correlations, but no consistent ecological story emerges (Fig. 7b). On several days, the strongest Mantel correlation was for the spatial residual, whereas distance to front was significant on one day (31 July 1995), and frontal density was only significant on 4 days. SST had the highest Mantel correlation on
Figure 4. Yearly seasonal front density maps with school symbols coded by school size: 1994 (a), 1995 (b), and 1996 (c). Each year is drawn to the same relative scale, which shows the high frontal presence in 1995. The underlying grid is the mean frontal density for a given cell across the length of each tuna season.

5 days; the highest Mantel correlation for the entire season was between bluefin presence and SST on 31 July 1995 (0.4782, \( P < 0.002 \)).

The 1996 results were more varied (Fig. 7c). Distance to a front was not significant on any of the study days in 1996, whereas SST and space were significant on 7 days (Fig. 7c). The highest Mantel correlation was for SST on 6 October 1996 (0.6917, \( P = 0.0021 \)), when surface temperatures ranged from 10.9 to 21.6°C and schools were concentrated in the Great South Channel, a region characterized by sharp fronts and strong tidal currents.

Table 1. Number of bluefin tuna (Thunnus thynnus) schools detected in aerial surveys conducted in the Gulf of Maine, July–October, 1994–96.

<table>
<thead>
<tr>
<th>Year</th>
<th>July</th>
<th>August</th>
<th>September</th>
<th>October</th>
<th>Entire season</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>315</td>
<td>414</td>
<td>154</td>
<td>7</td>
<td>890</td>
</tr>
<tr>
<td>1995</td>
<td>153</td>
<td>353</td>
<td>164</td>
<td>126</td>
<td>796</td>
</tr>
<tr>
<td>1996</td>
<td>131</td>
<td>184</td>
<td>153</td>
<td>39</td>
<td>507</td>
</tr>
<tr>
<td>Total</td>
<td>599</td>
<td>951</td>
<td>471</td>
<td>172</td>
<td>2193</td>
</tr>
</tbody>
</table>

Note that the season is closed in early October once quotas are achieved.

DISCUSSION

Several features of this database complicate an analysis of the relationship of bluefin schools to surface thermal structure and other features. First, analysis of distribution is biased by the fact that schools may spend less than 12% of each day at the surface where they could be detected by visual surveys (Lutcavage et al., 2000; Brill and Lutcavage, 2001). Thus, surface distribution alone might not portray the true extent of schools.

Another issue with this database is that surveys were fishery-linked and did not utilize line-transect methods, which yields two complications: (i) year-to-year comparisons between shifts in distribution cannot be rigorously tested without additional modeling; (ii) the absence cells are most likely biased closer in space to the presence cells as compared with random. Yet, the spotter surveys were more likely to detect more schools than traditional line transect methods, which assume a random distribution of schools with no adaptive parameters (Newlands, 2002). Although the two sampling schemes (spotter surveys and line transects) are not readily comparable, under similar conditions fishery-linked spotter surveys detected an order of magnitude of more schools than line transect surveys conducted on the same days (Hoggard, 1996;
Lutcavage et al., 1997; Polacheck et al., 1998). Thus, while we feel confident in the spotter surveys’ ability to detect surface biomass, we acknowledge the limitations the survey design places on our interpretation of these results.

We are also assuming a link between bluefin tuna and fronts because fronts are assumed to aggregate the bluefin’s prey and bluefin schools might redistribute to exploit these aggregations. In the GOM, bluefin forage on herring, mackerel, squid and sand lance (Crane,
1936; Chase, 2002), all highly mobile predators whose responses to fronts are similarly assumed, but not well researched (Sinclair and Iles, 1985). Fishermen and fish forecasters alike assume that bluefin tuna aggregate at fronts, and use conventional wisdom to locate productive fishing zones. If that were true, then we would expect to see that, on average, bluefin schools occur close to fronts; indeed, the distribution of schools in the GOM supports this relationship (Figs 4 and 6). In reality, this link is likely more complicated than the one assumed in this analysis. This complication, in turn, no doubt makes the results less consistent across each of the 3 yr.

On the other hand, a strength of our database is the accuracy with which the spatial locations of both the bluefin schools and the SST fronts are known. Unlike previous studies where the locations of Atlantic bluefin and other pelagic species were only known within a 30 km distance (Maul et al., 1984; Podestá et al., 1993), bluefin schools were located within GPS error (<100 m), and SST fronts are located within 2 km (Ullman and Cornillon, 1999), which represents a greater precision than previous studies.

Results from the GLM indicate that all three of the temperature-related variables (SST, distance to front, frontal density) are statistically significant, as is the interaction term between distance to front and SST. In this model, temperature is highly significant, suggesting that bluefin are most likely to be influenced by the presence of warm water, and indeed temperature had the highest deviance reduction. However, it should be noted that the reduction in deviance of the final model from the null model is not large (null deviance: 3080.0, residual deviance: 2993.7), suggesting that these are not the best possible set of predictors for the data. While distance to front was not the strongest predictor, GLM results, in conjunction with the random versus actual tests, suggest a significant role for fronts.

Because we saw a significant role of fronts and temperature at a broad temporal scale, and because

![Graphs showing correlation between tuna presence and environmental variables across each season.](image)

Table 2. Summary output from generalized linear model run on the binary presence–absence data using the final model.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>−0.53651</td>
<td>0.04441</td>
<td>−12.082</td>
</tr>
<tr>
<td>Distance to front</td>
<td>−0.12126</td>
<td>0.04915</td>
<td>−2.467</td>
</tr>
<tr>
<td>Frontal density</td>
<td>−0.17437</td>
<td>0.04904</td>
<td>−3.555</td>
</tr>
<tr>
<td>SST</td>
<td>0.33004</td>
<td>0.04657</td>
<td>7.087</td>
</tr>
<tr>
<td>Distance to front: temperature</td>
<td>−0.19337</td>
<td>0.05469</td>
<td>−3.536</td>
</tr>
</tbody>
</table>

Figure 7. Partial Mantel correlation between tuna presence and environmental variables across each season, removing the effects of spatial autocorrelation. The lines are plotted through time for the length of the season in 1994 (a), 1995 (b), and 1996 (c). Significant correlations (P < 0.05) on a given day are expressed with circles. P-values have been corrected for multiple comparisons using the Hochberg method. Lines are drawn as follows: distance to front (solid line); frontal density (dashed line); and sea surface temperature (dotted line). Significant spatial residuals are plotted with open diamonds (see text for further details).
space was missing from the GLM, we were interested in examining the role of fronts at a finer temporal scale using spatial statistics. These results indicate an extremely dynamic response to environmental features. For example, in each of the 3 yr there were days on which bluefin schools were seen close to the front (<10 km), yet on subsequent days the spatial correlation was absent. This can be explained in part by the presence of clouds, which inhibit the detection of SST fronts by the satellite. However, there are consecutive days with no clouds and high concentrations of tuna that show significant spatial correlation between bluefin presence and fronts one day but not the next, suggesting that fronts do not play a constant patterning role.

An example of this dynamic response can be seen on 7–9 August 1994, when large aggregations of fish in the northern GOM were spatially auto-correlated (Fig. 8). This period was characterized by high frontal density, but significant correlations between bluefin presence and the environment were only found on 8 August 1994 (Figs 7a and 8d). The previous day (7 August 1994), bluefin schools were highly clumped and in the vicinity of fronts, yet the only significant result is with space, that is, a spatial residual that suggests something other than the measured environmental variables were acting to structure surface aggregations. A close examination of 7 and 8 August 1994 indicates that although tuna were in the vicinity of fronts on 7 August, they were much closer to the fronts on 8 August. Although strong frontal features were still present the next day (9 August 1994), no schools were detected. A possible explanation is that fronts attract bluefin schools into an area (Fig. 8b) to feed (Fig. 8d), but schools may leave once their prey is dispersed, even if fronts persist (Fig. 8f).

One finding from the Mantel analysis, which is consistent with the GLM results, is that when correlation with fronts is strong, e.g. 8 August 1994, the Mantel correlation with temperature is even stronger. On this day, the vast majority of schools (92%) were seen either at the front or on the warm side of the front. Giant bluefin tracked with sonic tags also traveled along the warm side of an SST front (Lutcavage et al., 2000). This water is presumably clearer than the colder water, which may be important to a visually orienting predator. This has been previously proposed for juvenile Atlantic bluefin tuna (Mason, 1976; Roffer, 1987; Eggleston and Bochenek, 1989) and Pacific albacore (Magnuson, 1963; Laurs et al., 1984). Thus, bluefin tuna may be responding more to the incursion of warm water and associated productivity on a meso-scale (10–100 km) than to the presence of SST fronts on a smaller scale (1–10 km).

Several patterns emerge from this analysis. First, the deviance results from the GLM, and the spatial residuals from the Mantel tests, indicate there is pattern in the data that is unexplained by the model. Some reduction in deviance occurs when we include space in the model, but significant pattern remains once space is accounted for. Thus, there must be other important factors for bluefin distribution patterns in the GOM. Clearly, more comprehensive information on prey species and oceanographic conditions would be helpful. Satellite data, such as SeaWiFS, were not available for this time period, and no synoptic prey data exist for bluefin in the GOM. We suspect that shifts in prey distribution may account for some of the spatial variation, and that bluefin track prey even in the absence of consistent frontal features. Secondly, it is possible that our absence cells are biased, because spotter pilots search areas of expected abundance. Consequently, the absence cells along their track are most likely not a completely random grab of locations and associated environmental variables. Having a known set of non-biased, randomly distributed absence cells would likely strengthen some of the correlations observed herein. Thirdly, of the variables we did test, distance to front was weakly significant at the 0.05 level, but temperature was extremely significant (P < 0.001). Based on this last result, we believe that at the scale of our observations, water mass temperature is more important to bluefin tuna distributions than temperature fronts, per se, and that while fronts play a significant role, they may influence dispersal at smaller and larger time scales. However, the most important pattern is the consistency of the results across the tests. Although the spatial patterns between tuna and fronts differed from our initial expectations, it is clear they play a role. At the daily temporal scale, however, temperature seems more important, which is borne out by the GLM results as well as the Mantel results. We posit that fronts, while significant in this analysis, may play a more significant patterning role at a smaller time scales.

Our spatial analysis treats the distributions as static snapshots, yet over 48 h bluefin may travel approximately one-third to one-half the distance of the GOM (Lutcavage et al., 2000). Therefore, spatial re-distribution may create a temporal mismatch between the scale at which bluefin respond to fronts and the scale at which we are testing, which would help explain the inconsistent patterns in the daily relationships. As bluefin tuna are so mobile, it is more probable that they respond to a large-scale feature at a daily time...
Figure 8. Three days (7–9 August 1994) of tuna distribution displayed over frontal density (left column) and in relation to thermal fronts seen each day (right column). Daily flight lines are also included in the left column. Despite the presence of strong thermal fronts on 9 August (e, f), no fish were seen in the region unlike the previous 2 days. Schools symbolized as in Figure 4; fronts drawn as in Figure 3.
scale, for example, an incursion of warm water, and respond to a front at an even smaller time scale. Yet even if such a mismatch exists, our results suggest that SST fronts are important for tuna species, but that other variables, such as temperature, may be more important still.

We have examined the relationship of a highly migratory tuna species to oceanographic features in a coastal region, whereas most previous work has focused on pelagic regions and large-scale current boundary systems. Therefore the role fronts play in tuna distribution in a semi-enclosed, relatively shallow system (with bottom structure, tidal forcing, and fresh water input) has received little attention. Theory suggests that a pelagic predator will aggregate at a front if that front acts as an aggregating mechanism for less mobile prey (Olson and Backus, 1985). Olson et al. (1994) noted a discussion between Nakamura and Blackburn about whether tuna in the open ocean aggregate at fronts or use the fronts as migration cues (Nakamura and Yamanaka, 1959; Blackburn, 1965; Nakamura, 1969). How that applies to the GOM, where the magnitude and spatial and temporal natures of fronts are considerably smaller than those associated with current boundary systems such as the Gulf Stream, is unclear. It is not clear whether schools use the fronts as a cue to move toward favorable feeding locations or as a pathway to move along, which are two different mechanisms (e.g. Kirby et al., 2000) that have profoundly different implications for the distribution of fish in relation to a given front.

The availability of bluefin location data and remotely sensed temperature data at a fine spatial resolution made the present analysis possible. While the spatial interaction between bluefin and SST fronts was inconsistent, it is clear that fronts can play a significant role in explaining the observed distribution of schools. Because bluefin are present in the GOM primarily to feed, having prey data available at similar spatial and temporal scales would greatly enhance our understanding of what drives bluefin tuna distribution in the GOM. Together with predictive modeling, additional analyses examining the movements of electronically tagged bluefin tuna in response to oceanographic features at several spatial scales will improve our understanding of the ecology of this species.

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