BioOne COMPLETE

# Short-Term Habitat Use of Juvenile Atlantic Bluefin Tuna

Authors: Marcek, Benjamin J., Fabrizio, Mary C., and Graves, John E.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 395-403

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2016.1168330

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

*Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 8:395–403, 2016
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2016.1168330

NOTE

# Short-Term Habitat Use of Juvenile Atlantic Bluefin Tuna

**Benjamin J. Marcek,* Mary C. Fabrizio, and John E. Graves**
*Virginia Institute of Marine Science, College of William and Mary, Post Office Box 1346, Gloucester Point, Virginia 23062-1346, USA*

***Abstract***

**Bluefin Tuna *Thunnus thynnus* are highly sought after in commercial and recreational fisheries along the East Coast of North America. To appropriately assess and manage Atlantic Bluefin Tuna (ABT), it is necessary to understand their habitat use during multiple ontogenetic stages. We tagged 17 juvenile ABT in the northwest Atlantic Ocean with pop-up satellite archival tags (PSATs) to determine environmental factors that may affect habitat use. The PSATs were deployed off the coast of Massachusetts in August and September 2012. A generalized linear mixed model was applied to determine factors affecting the mean depth occupied by fish, and beta regression was used to understand factors affecting the proportion of time spent below the thermocline. Thermocline depth significantly affected the mean depth occupied by juvenile ABT and the proportion of time they spent below the thermocline. Time period (dawn, day, dusk, and night) also significantly affected the mean depth occupied by juvenile ABT. Additionally, the time period × lunar illumination interaction had a significant effect on the proportion of time spent below the thermocline. This study is the first to demonstrate that environmental factors such as thermocline depth, time period, and lunar illumination can significantly impact vertical habitat use by juvenile ABT and demonstrates the utility of generalized linear mixed models for investigating fish habitat use.**

Bluefin Tuna *Thunnus thynnus* support commercial and recreational fisheries along the East Coast of North America. The commercial fishery in the Atlantic Ocean targets large adult Bluefin Tuna, whereas the recreational fishery is supported by smaller fish, which are often immature (ICCAT 2014). An understanding of habitat use by Atlantic Bluefin Tuna (ABT) at multiple ontogenetic stages is essential for accurately assessing their abundance and for determining appropriate management strategies.

Although habitat use by adult ABT is well studied (Lutcavage et al 2000; Block et al. 2001; Newlands et al. 2004; Schick et al. 2004; Stokesbury et al. 2004; Wilson et al. 2005; Teo et al. 2007; Walli et al. 2009; Druon et al. 2016), less information is available regarding habitat use by juvenile ABT (Brill et al. 2002; Galuardi and Lutcavage 2012; Druon et al. 2016). Additionally, studies of juvenile ABT habitat use have focused on temporal changes in habitat use at diel and seasonal levels (Brill et al. 2002; Galuardi and Lutcavage 2012; Druon et al. 2016) and on how horizontal habitat use changes with factors like sea surface temperature and chlorophyll concentration (Druon et al. 2016); however, the manner in which environmental factors may affect vertical habitat use by juvenile ABT has not been investigated.

During summer, juvenile ABT spend the majority (>90%) of their time in the upper 30 m of the water column (Brill et al. 2002); the mean depth occupied is shallower in summer (5–12 m) than in winter (41–58 m; Galuardi and Lutcavage 2012). Juvenile fish may use deep waters as well: pop-up satellite archival tags (PSATs) have recorded individuals making vertical excursions to depths up to 800 m (Galuardi and Lutcavage 2012). Due to their extensive vertical movements, juvenile ABT may encounter a wide range of temperatures in a relatively short time interval. Although juvenile ABT are known to spend the majority of their time in waters warmer than 17°C during

Subject editor: Michelle Heupel, James Cook University, Queensland, Australia

© Benjamin J. Marcek, Mary C. Fabrizio, and John E. Graves
This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. The moral rights of the named author(s) have been asserted.

*Corresponding author: bmarcek@vims.edu
Received June 19, 2015; accepted March 13, 2016



Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

summer, they also use waters of 10°C or less for short periods (Brill et al. 2002; Galuardi and Lutcavage 2012; Druon 2016). Juvenile ABT may exploit these deeper, cooler waters in order to feed—similar to the observed habitat use of Pacific Bluefin Tuna *Thunnus orientalis*, Skipjack Tuna *Katsuwonus pelamis*, and Yellowfin Tuna *T. albacares* (Marchal and Lebourges 1996; Kitagawa et al. 2007b)—or to behaviorally thermoregulate, as seen in Yellowfin Tuna (Block et al. 1997). Although both juvenile and adult ABT have been documented as making excursions below the thermocline (Stokesbury et al. 2004; Galuardi and Lutcavage 2012), the thermocline may act as a barrier to movement for adult ABT (Wilson et al. 2005; Walli et al. 2009). However, the potential for the thermocline to act as a barrier has not been investigated for juvenile ABT.

Other factors, such as time of day and lunar illumination, are known to affect habitat use by adult ABT (Wilson et al. 2005), Bigeye Tuna *T. obesus* (Lam et al. 2014), Albacore *T. alalunga* (Cosgrove et al. 2014), and juvenile Southern Bluefin Tuna *T. maccoyii* (Bestley et al. 2009) and may affect habitat use by juvenile ABT as well. For Albacore, the percentage of time spent in shallow waters (<50 m) was typically greater at night (86%) than during the day (62%; Cosgrove et al. 2014). Adult ABT also were reported to exhibit diel variation in habitat use, maintaining a greater mean depth during the day than during dawn, dusk, or night (Wilson et al. 2005). No statistical differences in diel habitat use have been observed for juvenile ABT (Brill et al. 2002; Galuardi and Lutcavage 2012). Increasing lunar illumination (from new moon to full moon) was associated with increasing mean depth occupied by adult ABT (Wilson et al. 2005) and was significantly correlated with mean nighttime depth for adult Bigeye Tuna (Lam et al. 2014) and juvenile Pacific Bluefin Tuna (Kitagawa et al. 2007a). For juvenile Southern Bluefin Tuna, lunar phase was also an important factor in models predicting mean depth, maximum depth, proportion of time at the surface, and proportion of time at depths exceeding 100 m (Bestley et al. 2009). This relationship has not yet been examined for juvenile ABT.

As with other large pelagic predators, habitat use by juvenile ABT is likely regulated by their physiology (Brill 1994; Brill et al. 2005; Galli et al. 2009; Block et al. 2011), although other factors (e.g., prey availability) may also affect habitat use (Bertrand et al. 2002; Schick and Lutcavage 2009). To investigate how environmental factors influence short-term habitat use by juvenile ABT, we used PSATs to gather high-frequency environmental data from individual fish (Horodysky et al. 2007; Graves et al. 2009). We examined the following null hypotheses: (1) environmental factors do not affect the mean depth occupied by juvenile ABT and (2) environmental factors do not affect the proportion of time juvenile ABT spend in waters below the thermocline.

## METHODS

The experimental protocols used in the present study were approved by the Institutional Animal Care and Use Committee (IACUC-2011-07-11-7390-jegrav) at the College of William and Mary and complied with all applicable U.S. guidelines.

*Tag deployment.*—Juvenile ABT (91–119 cm curved fork length) were captured from coastal waters of Massachusetts ($n$ = 17) between August 2 and September 22, 2012 (Figure 1), reflecting the availability of fish to the recreational fishery during summer 2012. Juvenile ABT were captured via methods commonly employed in the U.S. recreational fishery (i.e., rod and reel, with a lure or lure–bait combination rigged with a large "J" hook [8/0–10/0] as the terminal tackle). A minimum of 30 min elapsed between tagging events to reduce the likelihood of sampling multiple individuals from a single school. Fish were brought onto the vessel, measured for curved fork length, and tagged with a PSAT (High-Rate X-Tag; Microwave Telemetry, Columbia, Maryland). The tag anchor was inserted into the dorsal musculature at a point directly posterior and ventral to the anterior insertion of the first dorsal fin; the fish was then released. The entire tagging process was brief (~1.5 min on average). The tag anchor (3.2 cm long × 2.4 cm wide) was a hydroscopic surgical-grade nylon assembly that was attached to the PSAT with a tether consisting of 16 cm of monofilament fishing line (91-kg breaking strength). A more detailed description of the PSAT assembly and deployment protocol is given by Marcek and Graves (2014).

The PSATs were programmed to record pressure (depth), temperature, and light every 5 min and to release after a 31-d deployment. After release, the PSATs floated to the surface and transmitted their archived data to the Advanced Research and Global Observation Satellite system. To ensure that tags would be released from moribund fish, the PSATs were programmed with two emergency release mechanisms as described by Musyl et al. (2011). The PSAT was released from a moribund fish if a constant depth was recorded for 4 d or if a maximum depth of 1,250 m was reached.

*Analyses.*—We used the data from each PSAT to (1) model the mean depth occupied by juvenile ABT and the proportion of time they spent below the thermocline and (2) explore the effects

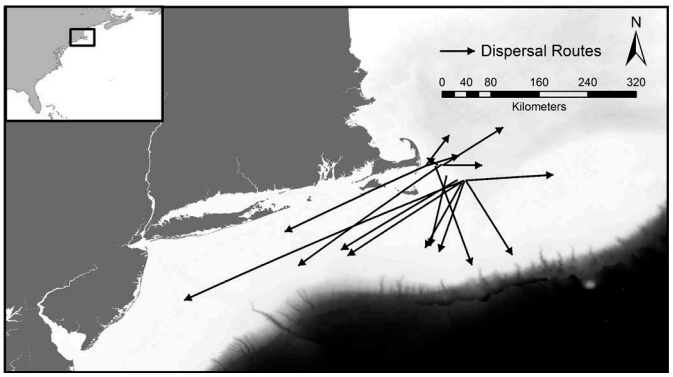



FIGURE 1. Map of the tag deployment location and dispersal routes for the 16 juvenile Atlantic Bluefin Tuna (91–119 cm curved fork length) with reporting pop-up satellite archival tags deployed in August and September 2012 off the Massachusetts coast. Fish were captured using standard trolling methods. Arrows indicate dispersal direction and distance.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

of environmental factors on habitat use by juvenile ABT. The mean depth (m) was calculated for dawn, day, dusk, and night periods, whereas the proportion of time spent below the thermocline was calculated for day and night only (as defined below). The proportion of time spent below the thermocline was calculated as the time (min) during which the fish used waters below the thermocline divided by the total time (min) in the period of interest. If there was no discernible thermocline, the corresponding data were excluded from the analysis. The predictors included in the models of mean depth and proportion of time spent below the thermocline were time period (dawn, day, dusk, or night), lunar illumination, and thermocline depth.

For the mean depth model, we defined four discrete 1-h time periods (dawn, day, dusk, and night) from each 24-h day to investigate the effects of diel and crepuscular periods on juvenile ABT habitat use. Times of sunrise and sunset from the U.S. Naval Observatory Web site (aa.usno.navy.mil/faq/docs/RST_defs.php) were used to define these periods. Crepuscular periods were defined as sunrise and sunset ±30 min, day was defined as the midpoint between sunrise and sunset ±30 min, and night was defined as the midpoint between sunset and sunrise ±30 min. One-hour intervals were used for each time period to reduce the likelihood of dampening crepuscular signals by the inclusion of observations from adjacent times and to reduce correlations among observations within a day. For the model examining the proportion of time spent below the thermocline, we defined two 6-h periods (day and night): day was defined as the midpoint between sunrise and sunset ±3 h, and night was defined as the midpoint between sunset and sunrise ±3 h. The 6-h time intervals were used to ensure that the number of observations was sufficient for calculating the proportion of time spent below the thermocline. In addition, lunar illumination data were acquired from the U.S. Naval Observatory Web site. Lunar illumination was reported as the proportion of the moon that was illuminated (0.0–1.0), where 0.0 represents the new moon and 1.0 represents the full moon.

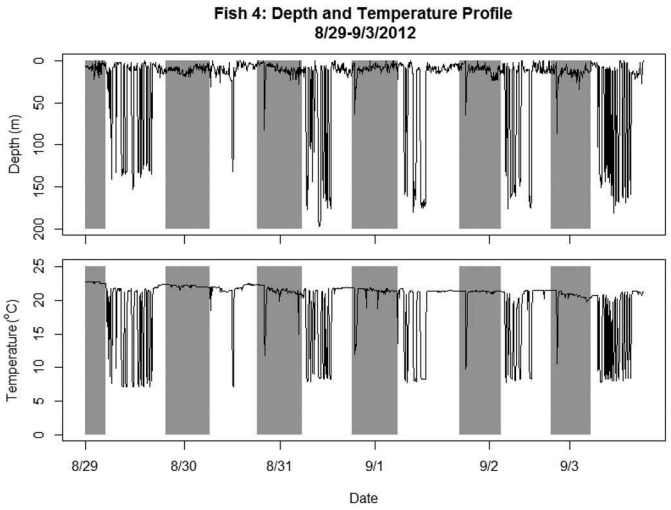



FIGURE 2. Depth and temperature profiles over 6 d in late August and early September 2012 for a juvenile Atlantic Bluefin Tuna (fish 4) that was tagged with a pop-up satellite archival tag and released off the Massachusetts coast. This individual displayed typical behavior, remaining in warmer waters near the surface for the majority of tag deployment but making periodic excursions to cooler, deeper waters. The majority of vertical excursions also occurred during the day, whereas the fish remained near the surface at night (gray-shaded bars).

We used vertical profiles of depth and temperature from tagged ABT to calculate thermocline depth (Figure 2). Depth–temperature profiles were created for each fish by aggregating data into 5-d intervals, binning the depth data into 1-m intervals, and calculating the mean temperature for each bin (±SE;

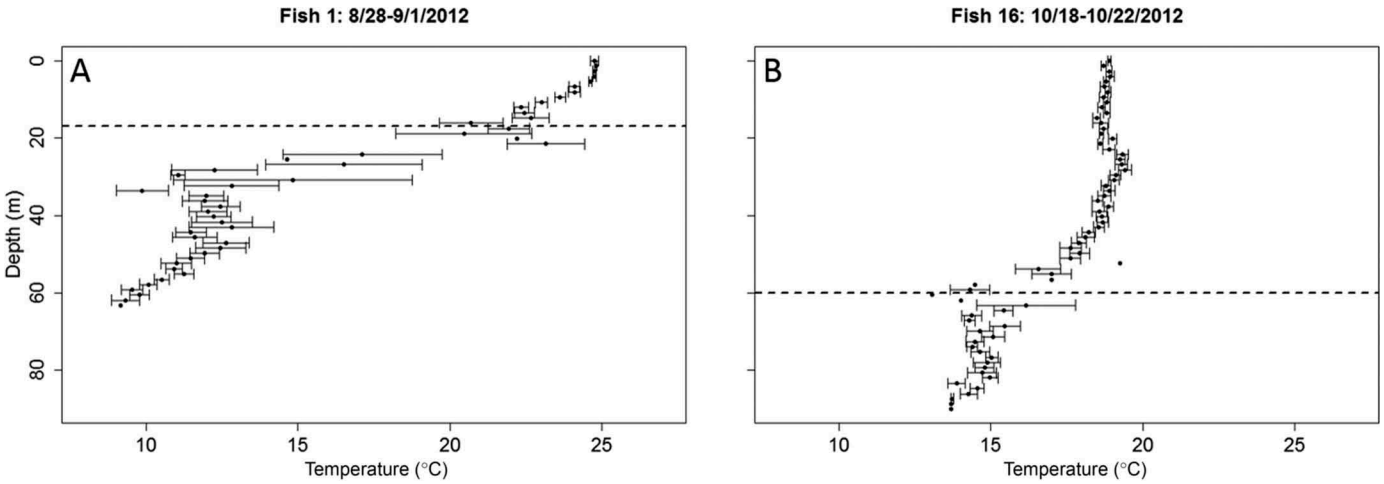



FIGURE 3. Vertical profiles of the water column occupied by juvenile Atlantic Bluefin Tuna (with pop-up satellite archival tags) from August to October 2012 offshore of Massachusetts. Examples of depth–temperature profiles for two individuals at different times during the tag deployment are shown: **(A)** fish 1 during late August and **(B)** fish 16 during mid-October. The thermocline (horizontal dotted line) was established at 15 m in August (A) and increased to 60 m in mid-October (B). The mean temperature estimate for each depth is presented with ±SE.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Figure 3). Data were aggregated over 5-d intervals to ensure that there were sufficient observations to construct depth–temperature profiles, thus allowing us to reconstruct the physical conditions of the water column in areas occupied by the fish. The depth of the thermocline was identified as the depth with the maximum gradient in water temperature. Days for which the thermocline could not be defined were omitted from this analysis.

*Mean depth occupied by juvenile Atlantic Bluefin Tuna.*—The mean depth occupied by juvenile ABT was analyzed by using a generalized linear mixed model with repeated measures (MIXED procedure in the Statistical Analysis System [SAS] version 9.3; SAS Institute, Cary, North Carolina). Mean depth was $\log_e$ transformed to meet the assumption of homogeneity of variance (Logan 2010). To allow for this transformation, 0.01 m was added to the zero observations (mean depth = 0 m when a fish was at the surface during the entire 1-h period of observation); zero observations constituted 3 (0.002%) of the 1,812 observations. Because multiple observations of depth and temperature were collected for each fish, we assumed that consecutive observations from the same fish were correlated. Therefore, we used a mixed model with repeated measures to model the mean depth occupied by juvenile ABT, with individual fish as the subject. Because individual ABT in this study represented a random sample from the population and because substantial variation in habitat use was observed among fish, we treated individual fish as a random factor; all other factors (thermocline depth, time period, and lunar illumination) were considered fixed effects. Additionally, *t*-tests were used to evaluate the significance of the factors' effects. We considered four covariance structures to describe the correlation between responses of an individual fish: variance components, compound symmetry, first-order autoregressive, and banded Toeplitz (Littell et al. 2000). Akaike's information criterion (AIC) was used to compare models that differed in covariance structure, and the best model was selected based on the lowest AIC value (Logan 2010). The covariance structure that best fit the data (eight-banded Toeplitz) was used in the final model. In addition, plots revealed potential two-way interactions (1) between thermocline depth and lunar illumination and (2) between time period and lunar illumination. Models that contained interactions were evaluated to determine whether the AIC value was lower (i.e., better performance) than that of the simpler model lacking the interactions (Hastie et al. 2009); we found that mean depth models lacking the interaction terms exhibited a better fit to the data, and therefore the interaction terms were omitted. The final model used in our analysis for mean occupied depth followed the form

$$Y_{ij} = \mu + \rho_i + \alpha + \gamma + \varepsilon_{ij}, \quad (1)$$

where $Y_{ij}$ is the mean depth occupied by individual $j$ in time period $i$; $\mu$ is the overall average mean depth occupied; $\alpha$ is the effect of thermocline depth; $\rho$ is the effect of period (dawn, day, dusk, or night); $\gamma$ is the effect of lunar illumination; and $\varepsilon_{ij}$ is the random unexplained error.

*Proportion of time spent below the thermocline.*—The proportion of time that juvenile ABT were below the thermocline during the day or night period was bounded within the interval [0, 1]; furthermore, like most proportion data, the response data were characterized by skewness. These two properties violate the assumptions of normality and homogeneity of variance, which are required for the use of general linear models (Swearingen et al. 2012). We therefore used the beta distribution to model the response in a regression framework (Swearingen et al. 2012). As before, we considered and modeled the correlations between repeated observations from the same fish.

The proportion of time spent below the thermocline was analyzed using a beta regression approach with repeated measures as implemented with the GLIMMIX (generalized linear mixed models) procedure in SAS. A generalized estimating equation (GEE) approach was used to estimate model parameters due to the correlations among repeated observations. Because the GEE in GLIMMIX uses a pseudolikelihood estimation technique, model fit could not be assessed with the typical criteria (AIC, Bayesian information criterion, etc.; Vonesh 2012). Instead, we evaluated the adequacy of the modeled covariance structure by using the variance of the Pearson residuals (Dickey 2010) and the ratio of the generalized chi-square statistic ($\chi^2$) to its degrees of freedom (df; Schabenberger 2005). If the variance of the Pearson residuals was near 1.00, the covariance structure was considered an adequate fit to the data (Dickey 2010). Additionally, a $\chi^2$:df ratio close to 1.00 indicates that the variability in the data was appropriately modeled and that there is no residual overdispersion (Schabenberger 2005). We investigated models that used either a variance components function or a first-order autoregressive function to describe the covariance structure; based on the variance of the Pearson residuals and the $\chi^2$:df ratio, we determined that the first-order autoregressive structure resulted in a better model fit. Because it was unlikely that repeated observations from each fish were completely independent of one another, the variance components structure—which assumes zero correlation—was deemed unreasonable for these data. Potential interactions (thermocline depth × lunar illumination; time period × lunar illumination) were considered. Based on inspection of the interaction plots, the time period × lunar illumination interaction was included in the final model, which followed the form

$$Y_{ij} = \mu + \rho_i + \alpha + \gamma + (\rho_i \times \gamma) + \varepsilon_{ij}, \quad (2)$$

where $Y_{ij}$ is the transformed proportion of time spent below the thermocline by individual $j$ during time period $i$; $\mu$ is the

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

overall mean proportion of time spent below the thermocline; and model predictors are as defined for equation (1) except that the period effect ρ includes only day and night. As before, individual fish were included as a random factor.

## RESULTS

Sixteen (94%) of the 17 PSATs reported between 80% and 100% of their archived data (mean ± SE = 88.3 ± 1.3%); one tag did not report (Table 1). Of the 16 reporting tags, one released prematurely at 6 d postdeployment. Additionally, one PSAT (and presumably the fish carrying it) was inferred to have been consumed by a predator 12 d after deployment (see Marcek and Graves 2014 for details). For that individual, the depth, temperature, and light profiles were consistent with normal behavior of juvenile ABT up to day 12 postdeployment; therefore, we considered data from only the first 11 d after tag deployment. Pooling across individuals, we observed that juvenile ABT occupied the upper 30 m of the water column for 81.1 ± 3.3% (mean ± SE) of their time, and waters between 17°C and 24°C were used 84.0 ± 3.3% of the time. Additionally, the pop-up locations of tags indicated a variety of dispersal patterns away from the tagging locations, with several fish moving in a generally southward direction toward winter foraging grounds (Figure 1). Minimum straight-line displacements ranged from 18 to 402 km (Table 1).

TABLE 1. Tag deployment date, curved fork length (CFL) of tagged fish, number of days the tags were deployed, the percentage of archived data recovered from each tag, and the minimum straight-line distance traveled by each juvenile Atlantic Bluefin Tuna ($n$ = 17) tagged with pop-up satellite archival tags offshore of Chatham, Massachusetts, during 2012.

| Fish | Date of tag deployment | CFL (cm) | Days deployed | % of data recovered | Minimum straight-line distance (km) |
|---|---|---|---|---|---|
| 1 | Aug 2 | 109 | 31 | 89 | 207.3 |
| 2 | Aug 2 | 107 | 31 | 85 | 44.4 |
| 3 | Aug 2 | 107 | 6 | 100 | 59.4 |
| 4 | Aug 4 | 107 | 31 | 80 | 97.9 |
| 5 | Aug 29 | 117 | 31 | 89 | 118.0 |
| 6 | Sep 12 | 114 | 31 | 86 | 134.6 |
| 7 | Sep 12 | 114 | 31 | 86 | 109.6 |
| 8 | Sep 14 | 109 | 31 | 88 | 48.6 |
| 9 | Sep 14 | 117 | 31 | 87 | 245.1 |
| 10 | Sep 15 | 117 | 31 | 87 | 402.5 |
| 11 | Sep 15 | 114 | 31 | 88 | 189.9 |
| 12 | Sep 15 | 91 | 31 | 91 | 121.3 |
| 13 | Sep 21 | 91 | 16 | 98 | 18.0 |
| 14 | Sep 21 | 119 | 31 | 89 | 169.8 |
| 15 | Sep 22 | 99 | 31 | 90 | 116.4 |
| 16 | Sep 22 | 99 | 31 | 80 | 185.8 |
| 17 | Sep 22 | 119 | | Did not report | |

TABLE 2. Parameter estimates for the model describing the mean depth occupied by juvenile Atlantic Bluefin Tuna.

| Factor | Estimate | $t$ | $P$ |
|---|---|---|---|
| Intercept | 1.56 | 6.62 | <0.01 |
| Time period | | | |
| Dawn | 0.21 | 2.05 | 0.04 |
| Day | 0.31 | 2.98 | <0.01 |
| Dusk | 0.13 | 1.25 | 0.21 |
| Night | 0 | – | – |
| Lunar illumination | 0.19 | 1.88 | 0.06 |
| Thermocline depth | 0.04 | 5.35 | <0.01 |

### Mean Depth Occupied by Juvenile Atlantic Bluefin Tuna

Variation among individual fish explained 15.4% of the overall variation in mean depth occupied by juvenile ABT. Inclusion of individual fish as a random factor resulted in a lower AIC score, indicating that differences in the behavior of individuals explained a significant portion of the variability in mean occupied depth. Fish occupied a significantly greater mean depth during dawn ($\rho_{dawn}$ = 0.21, $t$ = 2.05, $P$ = 0.04) and day ($\rho_{day}$ = 0.31, $t$ = 2.98, $P$ < 0.01) than at night (Table 2; Figure 4). The mean depth occupied by juvenile ABT also increased significantly with thermocline depth (α = 0.03, $t$ = 5.35, $P$ < 0.01). Although lunar illumination was not a significant factor in the model, the data

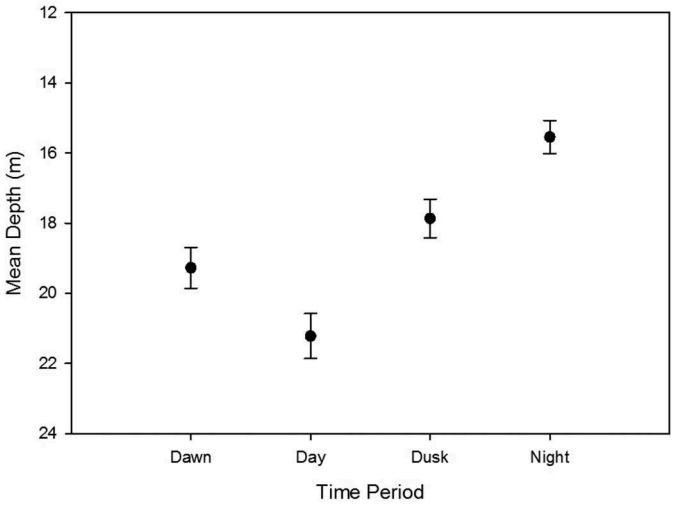



FIGURE 4. Mean depth occupied by juvenile Atlantic Bluefin Tuna ($n$ = 16) during four time periods: dawn, day, dusk, and night. Each point represents the model-predicted mean depth (±SE) occupied during a given time period. Fish were tagged with pop-up satellite archival tags and released offshore of Massachusetts in August and September 2012.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 3. Parameter estimates for the model describing the proportion of time spent below the thermocline by juvenile Atlantic Bluefin Tuna.

| Factor | Estimate | $t$ | $P$ |
|---|---|---|---|
| Intercept | –2.13 | –2.91 | <0.01 |
| Thermocline depth | –0.04 | –2.09 | 0.05 |
| Time period × lunar illumination | | | |
| Day | 0 | | |
| Night | 2.02 | 2.81 | <0.01 |

suggested that the mean occupied depth increased with increasing lunar illumination ($\gamma = 0.19$, $t = 1.88$, $P = 0.06$).

### Proportion of Time Spent below the Thermocline

The proportion of time in which juvenile ABT used waters below the thermocline was significantly affected by thermocline depth. As thermocline depth increased, the proportion of time spent below the thermocline decreased ($\alpha = –0.04$, $t = –2.09$, $P = 0.05$; Table 3). Additionally, the time period × lunar illumination interaction significantly affected the proportion of time spent below the thermocline. Regardless of lunar illumination, the proportion of time juvenile ABT spent below the thermocline was greater during the day than at night (Figure 5). Additionally, there was little effect of lunar illumination on the proportion of time spent below the thermocline during the day, but as lunar illumination increased, the proportion of time spent below the thermocline at night increased relative to the proportion spent there during the day ($\rho_{night} \times \gamma = 2.02$, $t = –2.81$, $P < 0.01$; Figure 5).

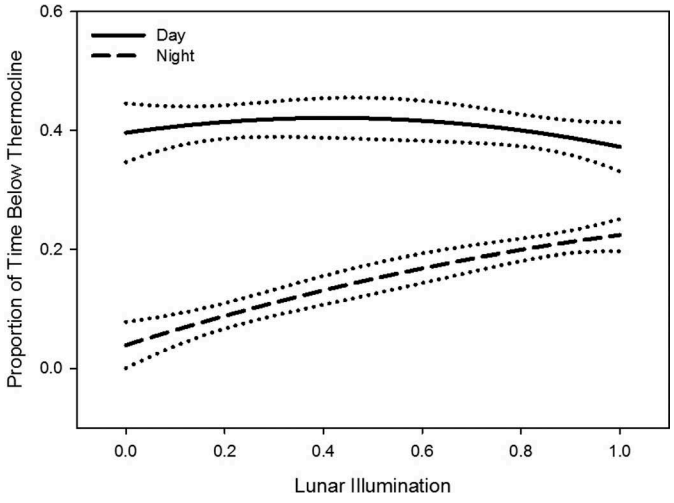



FIGURE 5. Proportion of time for which juvenile Atlantic Bluefin Tuna (ABT; $n = 16$) occupied waters below the thermocline in relation to increasing lunar illumination. The fish were tagged with pop-up satellite archival tags and released offshore of Massachusetts in August and September 2012. Day is represented with a solid line, and night is represented with a dashed line. The curves presented here are fitted to predictions from the model describing the proportion of time spent below the thermocline. Dotted lines represent the 95% confidence interval surrounding the model-predicted mean response.

## DISCUSSION

The observation that juvenile ABT occupy greater mean depths during dawn and day than at night has not been noted in previous studies of juvenile ABT habitat use (Brill et al. 2002; Galuardi and Lutcavage 2012). This behavior may be related to the feeding ecology of ABT. The retinal cell density in the eyes of tunas indicates that their best visual axis is above and in front of the fish's direction of travel (Tamura and Wilsby 1963; Kawamura et al. 1981; Somiya et al. 2000), thus allowing ABT to detect the silhouettes of prey against downwelling light. As the sun rises, this strategy may provide a means of locating prey that have moved closer to the surface at night, thereby increasing foraging efficiency of juvenile ABT. They may employ a similar strategy during the day by using downwelling sunlight to detect silhouetted prey swimming higher in the water column.

The time period × lunar illumination interaction had a significant effect on the proportion of time spent below the thermocline by juvenile ABT. As lunar illumination increased, the proportion of time spent below the thermocline increased at night relative to day. Juvenile ABT likely spend more time below the thermocline during periods of greater lunar illumination so as to detect the silhouettes of prey and to increase their feeding efficiency as described above. Our results suggested that the mean depth occupied by juvenile ABT also increased with increasing lunar illumination, although the effect was not significant. Further investigation of this relationship is necessary, as lunar illumination has been shown to impact habitat use by other tunas, such as the Bigeye Tuna (Lam et al. 2014) and Southern Bluefin Tuna (Bestley et al. 2009).

We demonstrated that thermocline depth was a significant factor determining both the mean depth occupied by juvenile ABT and the proportion of time they spent below the thermocline. Depth–temperature profiles from the PSATs indicated that the thermocline in waters offshore of Massachusetts between late August and early September 2012 was approximately 15 m. Thermocline depth increased to about 60 m by late October, coincident with increases in the mean depth occupied by juvenile ABT and decreases in the proportion of time spent below the thermocline. Similar to the ABT observed by Brill et al. (2002) and Galuardi and Lutcavage (2012), the fish in this study made periodic excursions to depth but spent the vast majority of their time above the thermocline. Such behavior is also similar to that of juvenile Pacific Bluefin Tuna, which are primarily found above the thermocline but make periodic excursions to depth (Kitagawa et al. 2007a). Although juvenile ABT may exploit waters below the thermocline for feeding and behavioral thermoregulation, the amount of time juvenile

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

ABT can exploit these deep, cool waters is likely limited by their physiology. Altantic Bluefin Tuna are known to exhibit regional endothermy, maintaining their red muscle tissue and viscera above ambient temperature (Carey and Lawson 1973); however, the heart is not maintained above ambient temperature. Therefore, the cardiac function of ABT may limit the amount of time they can spend in cold water. Cardiac data are not available for ABT, but the heart rate of juvenile Pacific Bluefin Tuna was shown to decrease with decreasing temperature (Clark et al. 2013), indicating impaired cardiac function at low temperatures.

The relationships between thermocline depth and the mean depth occupied by juvenile ABT and the proportion of time spent below the thermocline may reflect a strategy for optimizing the fish's foraging efficiency while allowing them to remain within their physiological tolerance. As thermocline depth increases, juvenile ABT may be able to occupy deeper waters for a longer period of time because they are not moving through the thermocline but instead remain in the relatively warm, well-mixed layer of the water column, which allows them to forage more efficiently.

Habitat use by potential prey is likely to change with environmental factors (e.g., thermocline depth and lunar illumination), and juvenile ABT likely react to changes in prey depth. Incidental observations of stomach contents from juvenile ABT indicated that some fish had recently fed on sand lances *Ammodytes* spp., while others fed primarily on Atlantic Herring *Clupea harengus* (B. J. Marcek, personal observation). Juvenile ABT may alter their habitat use to maximize their co-occurrence with prey species such as sand lances and Atlantic Herring (Eggleston and Bochenek 1990; Chase 2002; Schick and Lutcavage 2009; Logan et al. 2011, 2015); such behaviors have been observed in other large pelagic fishes like the Bigeye Tuna, Yellowfin Tuna (Grubbs and Holland 2003), and Swordfish *Xiphias gladius* (Carey 1990). Atlantic Herring, which are commonly found from Cape Cod to Greenland (Bigelow and Schroeder 2002), occupy depths of 0 to 200 m (Whitehead 1985) and prefer temperatures between 8°C and 12°C (Stickney 1969). Sand lances are widely distributed from inshore waters to offshore banks (Bigelow and Schroeder 2002) from Cape Hatteras to Greenland (Nizinski et al. 1990) and are abundant from New Jersey to the Gulf of Maine (Bigelow and Schroeder 2002). Sand lances are most commonly found at temperatures ranging from –2°C to 11°C (Scott 1968) and move inshore during summer, particularly at northern latitudes (Reay 1970). Differences in the distributions of sand lances and Atlantic Herring and their co-occurrence with juvenile ABT may cause those prey fishes to have differential predation susceptibility. Sand lances and Atlantic Herring are often found at temperatures that occur below the thermocline during summer; this may induce more frequent vertical feeding excursions by juvenile ABT, potentially leading to increased mean occupied depths and more time spent below the thermocline.

Most of our study fish displayed vertical movement patterns similar to those described in previous studies of juvenile ABT (Brill et al. 2002; Galuardi and Lutcavage 2012): they spent the majority of their time in warm, shallow waters while making periodic excursions to depths well below the thermocline. Additionally, most of the fish in this study displayed diel differences in habitat use, as their vertical excursions took place primarily during daylight.

Our results show that environmental factors, such as thermocline depth, lunar illumination, and time period, can have significant effects on habitat use by juvenile ABT. However, because of the small sample size included in these analyses ($n$ = 16) and the small spatial and temporal scales covered, additional data will help to elucidate some of the spatial and temporal dynamics of ABT habitat use that were beyond the scope of this project. Furthermore, a temporally intensive assessment of pelagic prey distribution and abundance, conducted simultaneously with a tagging study of juvenile ABT, would allow investigation of prey abundance effects on juvenile ABT habitat use. A better understanding of how the distribution of juvenile ABT is affected by environmental factors and prey abundance will improve spatial and temporal estimates of catchability in the recreational fishery and will result in more accurate estimates of juvenile ABT abundance.

Finally, we note that the beta regression technique allowed the use of proportion data to describe habitat utilization—something that was not possible with conventional linear modeling techniques without transforming the data to values outside the bounded range of [0, 1]. Beta regression could be incorporated into many habitat use studies in addition to studies that employ PSATs. For instance, implantable archival tags could yield similar data and could allow investigation of seasonal components. Beta regression models could also be applied to data from studies using passive acoustic arrays to monitor the use of a prescribed habitat or a marine protected area. Despite the fact that beta regression is new to fisheries research, it clearly can be a useful tool for analyzing habitat use from temporally intensive data.

## ACKNOWLEDGMENTS

This project was supported by the Guy Harvey Ocean Foundation and the National Science Foundation GK-12 Program (0840804). We thank the captains and crews of the Big Fish II, Big Fish III, For2na, Ocean Runner, Matador, Salty Dogs, Know Name, Game On, Sea Habit, Gina Marie, Oyster Catcher, McSeas, and Aries 55 for their participation in the study. We are also grateful to R. Brill for providing comments on an earlier version of this paper. This paper is Contribution 3538 of the Virginia Institute of Marine Science, College of William and Mary.

## REFERENCES

Bertrand, A., E. Josse, P. Bach, P. Gros, and L. Dagorn. 2002. Hydrological and trophic characteristics of tuna habitat: consequences on tuna

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

distribution and longline catchability. Canadian Journal of Fisheries and Aquatic Sciences 59:1002–1013.

Bestley, S., J. S. Gunn, and M. A. Hindell. 2009. Plasticity in vertical behavior of migrating juvenile Southern Bluefin Tuna (*Thunnus maccoyii*) in relation to oceanography of the south Indian Ocean. Fisheries Oceanography 18:237–254.

Bigelow, A. F., W. C. Schroeder, B. B. Collette, G. Klein-MacPhee, and H. B. Bigelow. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

Block, B. A., H. Dewar, S. B. Blackwell, T. D. Williams, E. D. Prince, C. J. Farwell, A. Boustany, S. L. Teo, A. Seitz, A. Walli, and D. Fudge. 2001. Migratory movements, depth preferences, and thermal biology of Atlantic Bluefin Tuna. Science 293:1310–1314.

Block, B. A., I. D. Jonsen, S. J. Jorgensen, A. J. Winship, S. A. Shaffer, S. J. Bograd, E. L. Hazen, D. G. Foley, G. A. Breed, A.-L. Harrison, J. E. Ganong, A. Swithenbank, M. Castleton, H. Dewar, B. R. Mate, G. L. Shillinger, K. M. Schaefer, S. R. Benson, M. J. Weise, R. W. Henry, and D. P. Costa. 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90.

Block, B. A., K. E. Keen, B. Castillo, H. Dewar, E. V. Freund, D. J. Marcinek, R. W. Brill, and C. Farwell. 1997. Environmental preferences of Yellowfin Tuna (*Thunnus albacares*) at the northern extent of its range. Marine Biology 130:119–132.

Brill, R. W. 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. Fisheries Oceanography 3:204–216.

Brill, R. W., K. A. Bigelow, M. K. Musyl, K. A. Fritsches, and E. J. Warrant. 2005. Bigeye Tuna (*Thunnus obesus*) behavior and physiology and their relevance to stock assessments and fishery biology. Collective Volume of Scientific Papers ICCAT 57:142–161.

Brill, R., M. Lutcavage, G. Metzger, P. Bushnell, M. Arendt, J. Lucy, C. Watson, and D. Foley. 2002. Horizontal and vertical movements of juvenile Bluefin Tuna (*Thunnus thynnus)*, in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry. U.S. National Marine Fisheries Service Fishery Bulletin 100:155–167.

Carey, F. G. 1990. Further acoustic telemetry observations of Swordfish. Marine Recreational Fisheries 13:103–122.

Carey, F. G., and K. D. Lawson. 1973. Temperature regulation in free-swimming Bluefin Tuna. Comparative Biochemistry and Physiology A 44:375–392.

Chase, B. C. 2002. Differences in diet of Atlantic Bluefin Tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. U.S. National Marine Fisheries Service Fishery Bulletin 100:168–180.

Clark, T. D., C. J. Farwell, C. J. L. E. Rodriguez, W. T. Brandt, and B. A. Block. 2013. Heart rate responses to temperature in free-swimming Pacific Bluefin Tuna (*Thunnus orientalis*). Journal of Experimental Biology 216:3208–3214.

Cosgrove, R., I. Arregui, H. Arrizabalaga, N. Goni, and M. Sheridan. 2014. New insights to behaviour of North Atlantic Albacore Tuna (*Thunnus alalunga*) observed with pop-up satellite archival tags. Fisheries Research 150:89–99.

Dickey, D. A. 2010. Ideas and examples in generalized linear models. SAS Global Forum 2010. SAS Institute, Cary, North Carolina.

Druon, J. N., J. M. Fromentin, A. R. Hanke, H. Arrizabalaga, D. Damalas, V. Tičina, G. Quílez-Badia, K. Ramirez, I. Arregui, G. Tserpes, and P. Reglero. 2016. Habitat suitability of the Atlantic Bluefin Tuna by size class: an ecological niche approach. Progress in Oceanography 142:30–46.

Eggleston, D. B., and E. A. Bochenek. 1990. Stomach contents and parasite infestation of school Bluefin Tuna *Thunnus thynnus* collected from the Middle Atlantic Bight, Virginia. U.S. National Marine Fisheries Service Fishery Bulletin 88:389–395.

Galli, G. L. J., H. A. Shiels, and R. W. Brill. 2009. Temperature sensitivity of cardiac function in pelagic fishes with different vertical mobilities: Yellowfin Tuna (*Thunnus albacares*), Bigeye Tuna (*Thunnus obesus*), Mahimahi (*Coryphaena hippurus*), and Swordfish (*Xiphias gladius*). Physiological and Biochemical Zoology 82:280–290.

Galuardi, B., and M. Lutcavage. 2012. Dispersal routes and habitat utilization of juvenile Atlantic Bluefin Tuna, *Thunnus thynnus*, tracked with mini PSAT and archival tags. PLoS (Public Library of Science) One [online serial] 7(5):e37829.

Graves, J. E., A. Z. Horodysky, and R. J. Latour. 2009. Use of pop-up satellite archival tag technology to study postrelease survival of and habitat use by estuarine and coastal fishes: an application to Striped Bass (*Morone saxatilis*). U.S. National Marine Fisheries Service Fishery Bulletin 107:373–383.

Grubbs, R. D., and K. N. Holland. 2003. Yellowfin and Bigeye tuna in Hawai'i: dietary overlap, prey diversity and the trophic cost of associating with natural and man-made structures. Pages 13–16 *in* Back to basics in pelagic fisheries research: proceedings of the 54th annual international tuna conference. Inter-American Tropical Tuna Commission, San Diego, California.

Hastie, T., R. Tibshirani, and J. Friedman. 2009. The elements of statistical learning, 2nd edition. Springer, New York.

Horodysky, A. Z., D. W. Kerstetter, R. J. Latour, and J. E. Graves. 2007. Habitat utilization and vertical movements of White Marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop-up archival satellite tags. Fisheries Oceanography 16:240–256.

ICCAT (International Commission for the Conservation of Atlantic Tunas). 2014. Report of the 2014 Atlantic Bluefin Tuna stock assessment session. ICCAT, Madrid.

Kawamura, G., W. Nishimura, S. Ueda, and T. Nishi. 1981. Vision in tunas and marlins. Memoirs of the Kagoshima University Research Center for the South Pacific 1:3–47.

Kitagawa, T., A. M. Boustany, C. J. Farwell, T. D. Williams, M. R. Castleton, and B. A. Block. 2007b. Horizontal and vertical movements of juvenile Bluefin Tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean. Fisheries Oceanography 16:409–421.

Kitagawa, T., S. Kimura, H. Nakata, and H. Yamada. 2007a. Why do young Pacific Bluefin Tuna repeatedly dive to depths through the thermocline? Fisheries Science 73:98–106.

Lam, C. H., B. Galuardi, and M. E. Lutcavage. 2014. Movements and oceanographic associations of Bigeye Tuna (*Thunnus obesus*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 71:1529–1543.

Littell, R. C., J. Pendergast, and R. Natarajan. 2000. Modelling covariance structure in the analysis of repeated measures data. Statistics in Medicine 19:1793–1819.

Logan, J. M., W. J. Golet, and M. E. Lutcavage. 2015. Diet and condition of Atlantic Bluefin Tuna (*Thunnus thynnus*) in the Gulf of Maine, 2004–2008. Environmental Biology of Fishes 98:1411–1430.

Logan, J. M., E. Rodríguez-Marín, N. Goñi, S. Barreiro, H. Arrizabalaga, W. Golet, and M. Lutcavage. 2011. Diet of young Atlantic Bluefin Tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. Marine Biology 158:73–85.

Logan, M. 2010. Biostatistical design and analysis using R: a practical guide. Wiley, West Sussex, UK.

Lutcavage, M. E., R. W. Brill, G. B. Skomal, B. C. Chase, J. L. Goldstein, and J. Tutein. 2000. Tracking adult North Atlantic Bluefin Tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. Marine Biology 137:347–358.

Marcek, B. J., and J. E. Graves. 2014. An estimate of postrelease mortality of school-size Bluefin Tuna in the U.S. recreational troll fishery. North American Journal of Fisheries Management 34:602–608.

Marchal, E., and A. Lebourges. 1996. Acoustic evidence for unusual diel behavior of a mesopelagic fish (*Vinciguerria nimbaria*) exploited by tuna. ICES Journal of Marine Science 53:443–447.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Musyl, M. K., R. W. Brill, D. S. Curran, N. M. Fragoso, L. M. McNaughton, A. Nielsen, B. S. Kikkawa, and C. D. Moyes. 2011. Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. U.S. National Marine Fisheries Service Fishery Bulletin 109:341–368.

Newlands, N. K., M. E. Lutcavage, and T. J. Pitcher. 2004. Analysis of foraging movements of Atlantic Bluefin Tuna (*Thunnus thynnus*): individuals switch between two modes of search behaviour. Population Ecology 46:39–53.

Nizinski, M. S., B. B. Collette, and B. B. Washington. 1990. Separation of two species of sand lances, *Ammodytes americanus* and *A. dubius*, in the western North Atlantic. U.S. National Marine Fisheries Service Fishery Bulletin 88:241–255.

Reay, P. J. 1970. Synopsis of the biological data on North Atlantic sand eels of the genus *Ammodytes* (*A. tobianus, A. dubius, A. americanus*, and *A. marinus*). FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis 82.

Schabenberger, O. 2005. Introducing the GLIMMIX procedure for generalized linear mixed models. SAS Institute, SUGI 30 Proceedings Paper 196-130, Cary, North Carolina.

Schick, R. S., J. Goldstein, and M. E. Lutcavage. 2004. Bluefin Tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–1996). Fisheries Oceanography 13:225–238.

Schick, R. S., and M. E. Lutcavage. 2009. Inclusion of prey data improves prediction of Bluefin Tuna (*Thunnus thynnus*) distribution. Fisheries Oceanography 18:77–81.

Scott, J. S. 1968. Morphometrics, distribution, growth, and maturity of offshore sand lance (*Ammodytes dubius*) on the Nova Scotia banks. Journal of the Fisheries Research Board of Canada 25:1775–1785.

Somiya, H., S. Takei, and I. Mitani. 2000. Guanine and its retinal distribution in the tapetum of the Bigeye Tuna, *Thunnus obesus*. Ichthyological Research 47:367–372.

Stickney, A. P. 1969. Orientation of juvenile Atlantic Herring (*Clupea harengus* L.) to temperature and salinity. Pages 323–342 *in* Proceedings of the FAO conference on fish behavior in relation to fishing techniques and tactics. FAO (Food and Agriculture Organization of the United Nations) Fisheries Report 62.

Stokesbury, M. J., S. L. Teo, A. Seitz, R. K. O'Dor, and B. A. Block. 2004. Movement of Atlantic Bluefin Tuna (*Thunnus thynnus*) as determined by satellite tagging experiments off New England. Canadian Journal of Fisheries and Aquatic Sciences 61:1976–1987.

Swearingen, C. J., M. S. Melguizo Castro, and Z. Bursac. 2012. Inflated beta regression: zero, one, and everything in between. SAS Institute, SAS Global Forum 2012, Paper 325-2012, Cary, North Carolina.

Tamura, T., and W. J. Wilsby. 1963. The visual sense of pelagic fishes especially the visual axis and accommodation. Bulletin of Marine Science of the Gulf and Caribbean 13:433–448.

Teo, S. L. H., A. Boustany, H. Dewar, M. J. W. Stokesbury, K. C. Weng, S. Beemer, A. C. Seitz, C. J. Farwell, E. D. Prince, and B. A. Block. 2007. Annual migrations, diving behavior, and thermal biology of Atlantic Bluefin Tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. Marine Biology 151:1–18.

Vonesh, E. F. 2012. Generalized linear and nonlinear models for correlated data: theory and applications using SAS. SAS Institute, Cary, North Carolina.

Walli, A., S. L. H. Teo, A. Boustany, C. J. Farwell, T. Williams, H. Dewar, E. Prince, and B. A. Block. 2009. Seasonal movements, aggregations, and diving behavior of Atlantic Bluefin Tuna (*Thunnus thynnus*) revealed with archival tags. PLoS (Public Library of Science) ONE [online serial] 4(7): e6151.

Whitehead, P. J. P. 1985. King Herring: his place amongst the clupeoids. Canadian Journal of Fisheries and Aquatic Sciences 42 (Supplement 1):3–20.

Wilson, S. G., M. E. Lutcavage, R. W. Brill, M. P. Genovese, A. B. Cooper, and A. W. Everly. 2005. Movements of Bluefin Tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. Marine Biology 146:409–423.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use