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ARTICLE

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Abstract
　　Pop-up satellite archival tags ($n = 31$) were deployed on Yellowfin Tuna *Thunnus albacares* in the Gulf of Mexico for periods ranging from 14 to 95 d. Differences in diel vertical behavior were assessed by comparing time spent at temperature relative to the surface temperature (ΔT). Pooled samples revealed that 31% of darkness hours, 20% of twilight hours, and 12% of daylight hours were spent in the uniform-temperature surface layer (i.e., $\Delta T = 0$). Total time spent above 100 m was less during daylight (90.0%) than during darkness (99.8%), suggesting greater exploration of deeper depths during daylight hours. Maximum depth visited ranged from 208 to 984 m, and minimum temperature visited ranged from 5.4°C to 11.8°C. Only a small proportion of total time was spent at temperatures colder than 8°C below the surface temperature. Horizontal excursions for the majority of individuals were less than 100 km from the point of release; however, three individuals moved distances of 411–1,124 km, suggesting that this species has the capability to move relatively long distances within the Gulf of Mexico. The ΔT values are provided in tabular format and serve as direct input variables for use in habitat standardization models.

The Yellowfin Tuna *Thunnus albacares* is a highly migratory pelagic fish that is distributed worldwide in most tropical and subtropical areas. Economically, this species represents the number-one tropical tuna harvested by U.S. commercial fishermen in the Atlantic Ocean (NMFS 2013). The International Commission for the Conservation of Atlantic Tunas (ICCAT) is mandated to manage the single Atlantic-wide Yellowfin Tuna stock. This includes a responsibility to gather catch and effort data, conduct stock assessments, determine stock abundance, and invoke management practices that conserve the stock. Uncertainties do occur in the stock assessment process, particularly in instances where catch data are deficient or where gear interactions are poorly understood. Incorporating relevant biological data into the stock assessment process can reduce these uncertainties because catch itself is influenced by individual species' behavior and habitat preferences. For example, a correlation between the temporal and spatial behavior of tunas and their vulnerability to longline and surface fishing gears has been demonstrated (Boggs 1992; Bigelow and Maunder 2007).

Integration of vertical habitat preference and hook depth with catch and effort statistics is useful for reducing uncertainties associated with estimating relative abundance (Maunder et al. 2006). Key factors influencing habitat use by Yellowfin Tuna include environmental conditions, physiological traits, and foraging behavior (Brill and Lutcavage 2001). Hinton and Nakano (1996) introduced a model incorporating behavioral constraints into the standardization of catch and effort statistics. Major input variables for the model include the proportions of time spent within each degree of water temperature relative to the surface temperature (ΔT); ΔT is a major environmental factor governing the vertical habitat preference (i.e., depth distribution) of tunas and tuna-like species (Hinton and Nakano 1996; Brill and Lutcavage 2001; Goodyear et al. 2008; Hoolihan et al. 2011b).

One mechanism that allows monitoring of horizontal and vertical movements of marine species is electronic tagging (Sibert and Nielsen 2001; Nielsen et al. 2009). Previous electronic tagging studies have indicated that Yellowfin Tuna prefer to spend most of their time above the thermocline in the uniform-temperature surface layer (Block et al. 1997; Brill et al. 1999a; Schaefer et al. 2007; Weng et al. 2009). Pop-up satellite archival tags (PSATs) offer certain advantages over other types of electronic tags. The PSATs can be deployed for comparatively long periods (months) extending well beyond the time it typically takes the fish to recover and resume normal behavior after capture (Hoolihan et al. 2011a). The PSATs also have the advantage of being less dependent on fisheries than other tagging technologies, which require recapture (Arnold and Dewar 2001); PSATs need not be physically retrieved for data recovery. Instead, the PSAT detaches from the fish on a pre-programmed date and then transfers the stored data via the Argos satellite system (Block et al. 1998). The objective of this study was to deploy PSATs on Yellowfin Tuna in the Gulf of Mexico (GOM) to (1) investigate horizontal and vertical movement behavior and (2) compile detailed habitat use information that can be applied to spatiotemporal distributions and relative abundance estimations using habitat standardization modeling.

METHODS

We examined data that were collected from PSATs deployed on Yellowfin Tuna ($n = 31$) in the northern GOM during 2008–2011 (models MK10-PAT and Mini-PAT; Wildlife Computers, Redmond, Washington). Specimens were captured in the proximity of petroleum production platforms by using recreational fishing gear, and a 71- × 127-cm Frabill landing net (Plano Molding Company, Plano, Illinois) was then used to lift the fish onboard for tagging. Net and fish were placed together on a "bean bag" chair; a wet cloth was used to subdue the fish by covering the eyes, and a hose running salt water was placed in the mouth for gill aeration. The PSAT tethers consisted of a medical-grade nylon anchor with toggles attached to approximately 18 cm of 181.4-kg (400-lb) monofilament. Anchors were inserted in an anterolateral direction between the pterygiophores of the first or second dorsal fin. Tags were programmed to collect depth (pressure), ambient temperature, and light level data at 10- or 15-s intervals. The PSATs were programmed for deployment periods of 90, 150, or 180 d (Table 1). Our analysis included Argos-transmitted summary data from either 1-h or 4-h time blocks programmed into the PSATs. Each time block included (1) the proportion of time spent within each depth bin (25-m resolution); (2) the proportion of time spent within each temperature bin (2°C bin resolution); and (3) PSAT depth–temperature (PDT) profile messages. For cases in which PSATs were physically recovered ($n = 7$), the full archived data recorded at 10- or 15-s intervals were accessible.

Using methods described by Luo et al. (2006), the distribution patterns of pooled data by hours of darkness, twilight, and daylight were interpolated using linear methods to 1°C temperature bins and 1-m depth bins. Luo et al. (2006) concluded that there is a very low rate of error associated with this method of simulation. These bin periods were determined by comparing the time of sunrise and sunset at release and pop-up locations. A daylight bin was defined when the entire bin duration fell between 1 h after sunrise and 1 h before sunset. A darkness bin was defined when the entire bin duration fell between 1 h after sunset and 1 h before sunrise. All bins that did not fit into one of these two categories were classified as crepuscular (i.e., twilight). This was done to ensure that the daylight and darkness categories were not compromised by bins falling into the crepuscular periods. The PDT data for a depth of 1 m or less were used to calculate average daily surface temperature (T_0). When surface temperatures were lacking, previous and subsequent day records were used to linearly interpolate values. Generated temperatures (GTs) per hour ($n = 720$) were estimated for each depth bin using a random normal distribution based on the PDT temperature range. The GT histogram was then compared to the temperature (T) data histogram.

TABLE 1. Summary of tagging information for 31 Yellowfin Tuna that were monitored with pop-up satellite archival tags (PSATs; Wildlife Computers) in the Gulf of Mexico (PAT = pop-up archival transmitting tag; DAL = days at liberty).

No.	Tag number	PSAT version	FL (cm)	Release date	Pop-up date	DAL/days programmed	Release location	Location of first transmission	Displacement (km)
1	06A1109	MK-10	98	Aug 6, 2008	Aug 22, 2008	16/90	28°39'N, 89°45'W	28°35'N, 88°90'W	54
2	08A0560	MK-10	125	Aug 6, 2008	Nov 4, 2008	90/90	28°39'N, 89°45'W	29°11'N, 88°19'W	146
3	08A0561[ab]	MK-10	105	Aug 6, 2008	Sep 7, 2008	32/90	28°39'N, 89°45'W	28°62'N, 89°47'W	26
4	06A1118[a]	MK-10	108	Aug 6, 2008	Aug 29, 2008	23/90	28°39'N, 89°45'W	28°16'N, 89°11'W	43
5	06A1126	MK-10	110	Aug 6, 2008	Sep 2, 2008	27/90	28°39'N, 89°45'W	27°9'N, 89°52'W	144
6	08A0559[bc]	MK-10	100	Aug 7, 2008	Aug 14, 2008	7/90	29°6'N, 88°9'W	28°2'N, 89°17'W	157
7	08A0562[bc]	MK-10	105	Aug 7, 2008	Sep 14, 2008	38/90	29°6'N, 88°9'W	28°65'N, 88°89'W	91
8	08A0570[a]	MK-10	110	Aug 7, 2008	Sep 6, 2008	30/90	29°6'N, 88°9'W	28°36'N, 89°48'W	156
9	08A0563[ac]	MK-10	87	May 11, 2009	May 16, 2009	5/90	28°39'N, 89°45'W	28°55'N, 89°28'W	24
10	06A1110	MK-10	109	Jul 23, 2009	Oct 25, 2009	94/180	28°74'N, 88°83'W	27°57'N, 91°41'W	285
11	06A1129	MK-10	120	Jul 23, 2009	Sep 23, 2009	62/180	28°74'N, 88°83'W	28°59'N, 89°97'W	113
12	06A1111	MK-10	116	Jul 25, 2009	Aug 13, 2009	19/180	28°86'N, 88°5'W	29°32'N, 87°85'W	56
13	06A1112[c]	MK-10	116	Jul 25, 2009	Jul 29, 2009	4/180	28°86'N, 88°5'W	29°35'N, 86°88'W	126
14	08A0565	MK-10	146	Jul 25, 2009	Aug 8, 2009	14/180	28°86'N, 88°5'W	29°23'N, 87°79'W	48
15	08A0568[ac]	MK-10	115	Jul 25, 2009	Jul 31, 2009	6/180	28°86'N, 88°5'W	28°77'N, 88°6'W	9
16	09P0215	Mini-PAT	147	Nov 28, 2009	Mar 3, 2010	95/150	28°74'N, 88°83'W	27°33'N, 88°94'W	0
17	09P0217	Mini-PAT	122	Nov 29, 2009	Dec 19, 2009	20/150	28°83'N, 88°49'W	27°9'N, 89°66'W	224
18	09P0225	Mini-PAT	133	Nov 30, 2009	Dec 26, 2009	26/150	28°74'N, 88°83'W	27°38'N, 88°55'W	154
19	09P0226	Mini-PAT	158	Nov 30, 2009	Dec 31, 2009	31/150	28°74'N, 88°83'W	28°91'N, 88°37'W	48
20	06A0354[bc]	MK-10	112	Aug 6, 2010	Sep 15, 2010	40/90	28°26'N, 89°2'W	28°39'N, 89°42'W	70
21	06A1119	MK-10	115	Aug 6, 2010	Sep 25, 2010	50/90	28°29'N, 89°2'W	28°49'N, 88°59'W	39
22	08A0566	MK-10	106	Aug 6, 2010	Nov 4, 2010	90/90	28°23'N, 89°23'W	27°34'N, 94°59'W	557
23	08A0570	MK-10	116	Aug 6, 2010	Nov 4, 2010	90/90	28°26'N, 89°2'W	18°42'N, 85°55'W	1,128
24	09P0223[a]	Mini-PAT	114	Aug 7, 2010	Sep 23, 2010	47/180	28°27'N, 89°2'W	28°50'N, 88°44'W	52
25	09P0227	Mini-PAT	113	Aug 7, 2010	Oct 31, 2010	85/180	28°26'N, 89°2'W	25°00'N, 86°16'W	411
26	09P0216	Mini-PAT	132	May 8, 2011	May 26, 2011	18/180	28°26'N, 89°34'W	28°13'N, 89°36'W	41
27	09P0218	Mini-PAT	119	May 8, 2011	May 26, 2011	18/180	28°26'N, 89°34'W	28°29'N, 89°58'W	65
28	09P0219[a]	Mini-PAT	110	May 8, 2011	Jul 3, 2011	56/180	28°26'N, 89°34'W	28°49'N, 88°58'W	78
29	09P0222	Mini-PAT	112	May 8, 2011	Jun 8, 2011	31/180	28°27'N, 89°34'W	28°22'N, 89°54'W	54
30	09P0233	Mini-PAT	118	May 8, 2011	May 23, 2011	15/180	28°26'N, 89°27'W	28°10'N, 89°6'W	70
31	09P0296	Mini-PAT	135	May 8, 2011	Jun 29, 2011	52/180	28°27'N, 89°34'W	28°29'N, 88°51'W	54

[a] The PSAT and archival data were recovered.
[b] Predation event.
[c] Excluded from analyses.

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Differences in numbers were corrected by removing values in positive bins and adding them randomly to the negative bins. Values of ΔT were then calculated by subtracting the GT values from the T_0 values, and we tabulated the proportion of time spent at decreasing temperatures with a 1°C bin resolution. Proportions of records within successively deeper layers of temperature relative to the surface temperature (ΔT) were assembled, and the mean ΔT values were calculated for each distribution (Hoolihan et al. 2012b).

WC-DAP and WC-GPE2 software (Wildlife Computers) were used for the initial processing of light-level geolocation data, followed by a sea surface temperature-corrected Kalman filter (Nielsen et al. 2006; Lam et al. 2008). A custom bathymetry filter was then used to relocate any points that were on land or in shallow water based on 2- × 2-min grid ETOPO2 bathymetry data (National Geophysical Data Center 2006) and the daily maximum depth from the tag. For each point where maximum daily depth was greater than the bathymetric depth, we selected all grid cells along the longitude where bathymetric depth was greater than the daily maximum depth within ± 1°C of the previous day's latitude, and we then assigned a final location to a single cell that was randomly selected from that group (Hoolihan and Luo 2007).

Horizontal movements were analyzed for spatial variation using the kernel density estimators described by Worton (1995). Estimated values were cumulated based on highest to lowest areas of density whereby the 25% kernel area contour is reflective of the highest observed densities and the 95% contours represent up to 95% density areas (Hammerschlag et al. 2012). Values were plotted using Interactive Data Language software (www.ittvis.com).

RESULTS

We deployed PSATs on 31 Yellowfin Tuna in the GOM to monitor vertical and horizontal habitat use. Of these, six PSATs were excluded from our analyses because the fish either died or the PSAT remained attached for less than 10 d (Hoolihan et al. 2011a). The remaining 25 fish included in our analyses ranged in size from 98 to 158 cm FL, with estimated weights ranging from 22.6 to 70.0 kg. Days at liberty (DAL) ranged from 14 to 95 (mean = 45.2 DAL), while linear displacement between the release and pop-up locations ranged from 0 to 1,128 km (mean = 146.0; Table 1).

Vertical Behavior

Differences in diel vertical behavior of Yellowfin Tuna were compared by pooling individual histogram sets derived from periods of daylight ($n = 1,190$), twilight ($n = 768$), and darkness ($n = 939$) and were illustrated by using the range and proportions of time spent at ΔT for each period (Figure 1). The derived percentiles of mean ΔT for the pooled samples revealed that around 12% of daylight hours, 20% of twilight hours, and 31%

of darkness hours were spent in the uniform-temperature surface layer (i.e., $\Delta T = 0$; Table 2). The distributions for the percentiles of mean ΔT did exhibit variability.

The distributions for time (%) spent at depth during the daytime and nighttime were significantly different ($\chi^2 = 35.4$, df = 15, $P < 0.001$), showing that more time was spent nearer to the surface during darkness (Figure 2a). For example, 52.4% of time was recorded in the upper 20 m of the water column at night compared with just 20.9% during daylight hours. The distributions of time at temperature were significantly different as well ($\chi^2 = 35.8$, df = 20, $P < 0.05$), corresponding to the differences in the time-at-depth distributions (Figure 2b). Total time spent above 100 m was less (90.0%) during daylight than during darkness (99.8%), suggesting more exploration of deeper depths during the daylight hours (Figure 2a).

Preference of Yellowfin Tuna for the uniform-temperature surface layer was obvious from the ΔT time-at-temperature distributions (Table 2), although it did not preclude short-duration dives into deeper, colder strata. The maximum depths visited by individuals from this group ranged from 208 to 984 m, and minimum temperatures visited ranged from 5.4°C to 11.8°C. Vertical movements to depths below the thermocline were generally brief and occurred infrequently relative to vertical movements within the uniform-temperature surface layer. We questioned whether the longer monitoring periods in our study would provide a more detailed account of actual Yellowfin Tuna habitat use in comparison with earlier short-term studies (Holland et al. 1990; Brill et al. 1999a). If true, we surmised that encountering evidence of deeper dives and lower minimum temperatures should increase with the length of deployment. To confirm this, we compared novel maximum daily depths and minimum temperatures with DAL (Figures 3, 4). The novel maximum daily depth (D_{max}) increased, extending into deeper strata over time (i.e., DAL; $D_{max} = 113.55 \cdot DAL^{0.376}$; $r = 0.708$, $F = 85.2$, df = 86, $P < 0.0001$; Figure 3). There was also a trend toward colder novel minimum daily temperatures over time ($D_{max} = 19.96 \cdot DAL^{-0.209}$; $r = -0.678$, $F = 73.3$, df = 87, $P < 0.0001$), reflecting the trend observed for increasing daily maximum depths (Figure 4). However, both the novel maximum daily depths and minimum temperatures were highly variable over time (Figures 3, 4).

Mortality by predation was suspected for at least four Yellowfin Tuna in our study (Table 1) based on their altered vertical habitat use (i.e., depth and temperature readings). For example, PSAT data from fish 3 (Table 1) indicated a radical change in behavior after about 20 DAL (Figure 5). Maximum depths increased greatly, but ambient water temperature readings were much warmer than expected for the depths attained. Rather, they were more consistent with internal abdominal temperature, suggesting predation (e.g., shark) and ingestion of the PSAT. Depth and temperature data suggested that this PSAT (Figure 5) was regurgitated after about 30 DAL, allowing it to float to the surface and transmit.

TABLE 2. Proportions of time spent at each temperature relative to the surface temperature (ΔT) during darkness, twilight, and daylight for 25 Yellowfin Tuna that were monitored with pop-up satellite archival tags (PSATs). Proportions were derived from combined data (archival data recovered from MK-10 PSATs; mini-PAT series data; and archival data simulated from transmitted MK-10 PSATs). Dashes indicate zero probability. Data were sorted in order of decreasing ΔT (left column); proportions of time spent at the various temperatures were then calculated for a range of percentiles. As an example, for 75% of the data points during darkness, 10.6% were at surface temperature ($\Delta T = 0$, top row) and 30.6% were at 2°C below surface temperature ($\Delta T = -2$, third row).

| | | | | | Percentile of mean ΔT | | | | | | | |
ΔT	0.010	0.025	0.050	0.100	0.250	0.500	0.750	0.900	0.950	0.975	0.990	Mean
Darkness (n = 939)												
0	0.981	0.683	0.405	0.230	0.110	0.064	0.106	0.187	0.206	0.217	0.223	0.310
−1	0.011	0.268	0.463	0.433	0.300	0.202	0.164	0.161	0.158	0.158	0.157	0.225
−2	0.009	0.041	0.107	0.254	0.394	0.381	0.306	0.270	0.261	0.256	0.254	0.230
−3	—	0.004	0.015	0.050	0.110	0.193	0.190	0.171	0.167	0.164	0.163	0.112
−4	—	0.004	0.005	0.019	0.049	0.076	0.092	0.085	0.084	0.082	0.082	0.052
−5	—	—	0.004	0.009	0.018	0.039	0.056	0.051	0.050	0.049	0.049	0.030
−6	—	—	0.002	0.004	0.014	0.027	0.041	0.036	0.035	0.035	0.034	0.021
−7	—	—	—	0.001	0.003	0.011	0.027	0.023	0.022	0.022	0.022	0.012
−8	—	—	—	—	0.001	0.005	0.010	0.009	0.009	0.009	0.009	0.005
−9	—	—	—	—	—	0.002	0.006	0.005	0.005	0.005	0.005	0.002
−10	—	—	—	—	—	0.001	0.002	0.002	0.002	0.002	0.002	0.001
−11	—	—	—	—	—	—	0.001	0.001	0.001	0.001	0.001	—
−12	—	—	—	—	—	—	—	—	—	—	—	—
−13	—	—	—	—	—	—	—	—	—	—	—	—
−14	—	—	—	—	—	—	—	—	—	—	—	—
−15	—	—	—	—	—	—	—	—	—	—	—	—
Twilight (n = 768)												
0	0.475	0.295	0.195	0.117	0.060	0.034	0.149	0.218	0.232	0.245	0.249	0.206
−1	0.392	0.523	0.455	0.323	0.215	0.140	0.125	0.129	0.129	0.129	0.129	0.244
−2	0.110	0.149	0.276	0.448	0.456	0.365	0.272	0.244	0.236	0.233	0.230	0.274
−3	0.022	0.024	0.046	0.065	0.143	0.190	0.153	0.142	0.139	0.137	0.136	0.109
−4	0.001	0.007	0.015	0.026	0.064	0.098	0.083	0.078	0.078	0.076	0.076	0.055
−5	—	0.003	0.009	0.014	0.027	0.054	0.048	0.044	0.044	0.043	0.042	0.030
−6	—	0.001	0.002	0.006	0.021	0.050	0.044	0.039	0.038	0.037	0.037	0.025
−7	—	—	0.001	0.001	0.007	0.030	0.033	0.028	0.028	0.027	0.027	0.016
−8	—	—	—	—	0.005	0.019	0.029	0.024	0.024	0.023	0.023	0.013
−9	—	—	—	—	0.001	0.010	0.020	0.017	0.016	0.016	0.016	0.009
−10	—	—	—	—	—	0.006	0.017	0.014	0.014	0.013	0.013	0.007
−11	—	—	—	—	—	0.002	0.012	0.010	0.009	0.009	0.009	0.005
−12	—	—	—	—	—	0.001	0.007	0.006	0.005	0.005	0.005	0.003
−13	—	—	—	—	—	0.001	0.006	0.005	0.005	0.004	0.004	0.002
−14	—	—	—	—	—	—	0.003	0.003	0.002	0.002	0.002	0.001
−15	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 2. Continued.

|					Percentile of mean ΔT							
ΔT	0.010	0.025	0.050	0.100	0.250	0.500	0.750	0.900	0.950	0.975	0.990	Mean
					Daylight (n = 1,190)							
0	0.414	0.226	0.142	0.092	0.046	0.027	0.021	0.079	0.091	0.097	0.101	0.121
−1	0.508	0.626	0.445	0.306	0.193	0.129	0.095	0.096	0.098	0.097	0.097	0.244
−2	0.062	0.107	0.332	0.432	0.393	0.309	0.240	0.211	0.205	0.202	0.200	0.245
−3	0.015	0.035	0.061	0.123	0.224	0.212	0.175	0.158	0.154	0.153	0.152	0.133
−4	0.001	0.002	0.006	0.021	0.067	0.105	0.090	0.087	0.086	0.087	0.086	0.058
−5	—	0.002	0.005	0.010	0.026	0.061	0.055	0.055	0.055	0.055	0.055	0.034
−6	—	0.001	0.004	0.010	0.024	0.050	0.052	0.052	0.052	0.052	0.052	0.032
−7	—	—	0.003	0.004	0.011	0.034	0.045	0.045	0.045	0.045	0.045	0.025
−8	—	—	0.002	0.002	0.009	0.033	0.053	0.051	0.050	0.050	0.050	0.027
−9	—	—	—	0.001	0.003	0.017	0.045	0.044	0.044	0.043	0.043	0.022
−10	—	—	—	—	0.002	0.011	0.037	0.037	0.038	0.038	0.038	0.018
−11	—	—	—	—	0.001	0.005	0.029	0.028	0.027	0.027	0.027	0.013
−12	—	—	—	—	—	0.003	0.024	0.022	0.021	0.021	0.021	0.010
−13	—	—	—	—	—	0.002	0.021	0.019	0.018	0.018	0.018	0.009
−14	—	—	—	—	—	0.001	0.019	0.017	0.016	0.016	0.016	0.008
−15	—	—	—	—	—	—	—	—	—	—	—	—
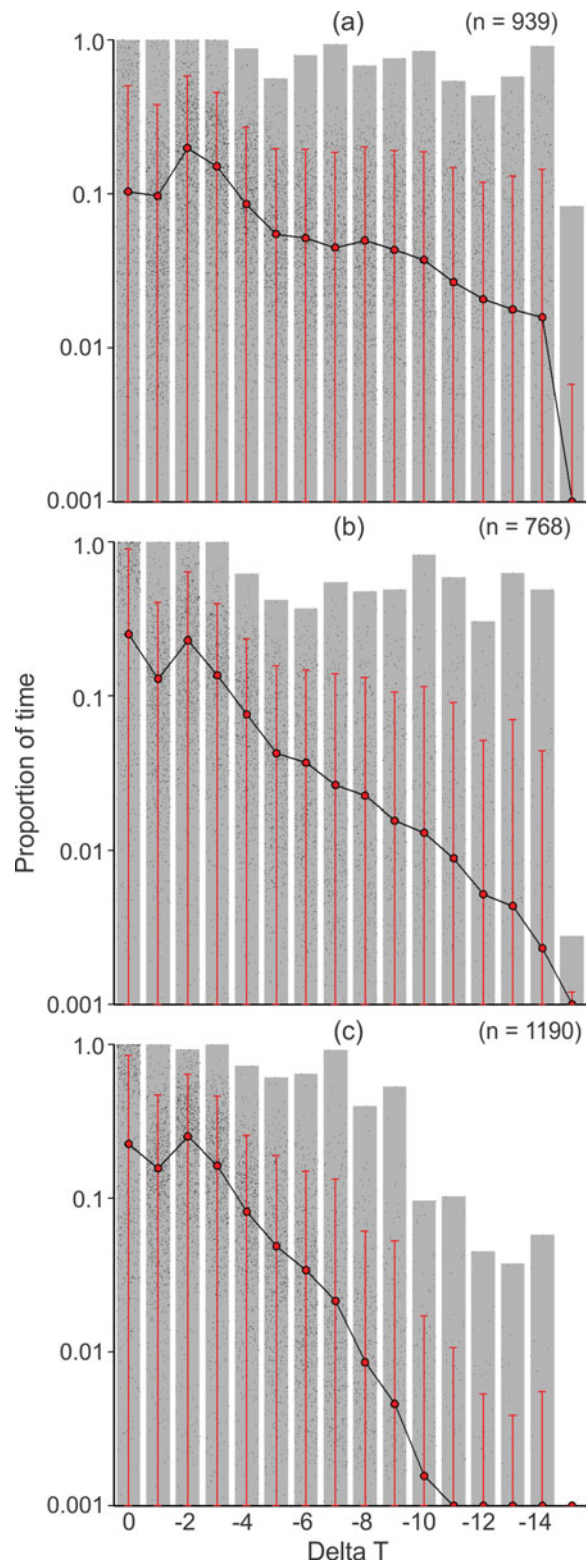
FIGURE 1. Proportions of time (log scale) spent at temperature relative to the surface temperature (ΔT) during **(a)** daylight, **(b)** twilight, and **(c)** darkness, as estimated by using combined Argos-transmitted and archival data from 25 Yellowfin Tuna that were monitored with pop-up satellite archival tags. Shaded bars denote the range of observations (shown by small gray dots). Red circles denote means ($\pm 95\%$ confidence interval).

Horizontal Behavior

The kernel density estimated from horizontal tracking data indicated that the highest densities of movement were confined to a relatively small area around the release locations (Figure 6). Three individuals (fish 23, 24, and 26; Table 1) undertook more lengthy excursions. Fish 23 moved 557 km to the western GOM; fish 24 moved 1,124 km in a southerly direction into the Caribbean; and fish 26 moved southeasterly 411 km into the area of the Loop Current. All three fish exhibited higher periods at liberty (85–90 DAL). However, time was not the sole factor regulating long-distance movement, as many other tagged fish had comparable DAL periods and remained in relative proximity to their release locations (Table 1; Figure 6).

DISCUSSION

Habitat preference and vertical movement behavior of Yellowfin Tuna are influenced by a variety of factors, including physiological capabilities, oceanographic features, environmental conditions, and prey species behavior (Dizon and Brill 1979; Block et al. 1997; Brill and Lutcavage 2001). Yellowfin Tuna in the GOM remained primarily within the uniform-temperature surface layer. This was similar to the findings of Weng et al. (2009) for six PSAT-monitored Yellowfin Tuna in the GOM and to the results of earlier ultrasonic tracking studies near Hawaii, California, French Polynesia, and the Comoros Islands (Carey and Olson 1982; Holland et al. 1990; Cayré and Marsac 1993; Block et al. 1997; Josse et al. 1998; Brill et al. 1999a). A notable difference between PSAT and ultrasonic tracking studies is that extremes in the maximum depth and minimum temperature used are more likely to be detected over the longer deployment periods associated with PSAT use (Figures 3, 4). Yellowfin Tuna were present in deeper, colder depths below the thermocline, albeit with less frequency and for shorter periods in comparison with vertical movement activities above the thermocline (Schaefer et al. 2011). Our study recorded Yellowfin Tuna as deep as 984 m, with ambient temperatures as low as 5.4°C. Studies based on implanted archival tagging of Yellowfin Tuna in the eastern Pacific Ocean revealed that the fish are capable of diving to at least 1,600 m (Schaefer et al. 2014). Presumably, the main purpose of deep diving is associated with foraging activity, which also allows them to prey upon deep-dwelling species. Deep diving can also be an advantage when used tactically to elude predators, such as sharks and billfishes.

Constraints on cardiac function are the primary reason why Yellowfin Tuna do not spend more time below the warmer uniform-temperature surface layer (Brill and Lutcavage 2001). Heart temperature in tunas and billfishes is directly affected by changes in water temperature because the heart is on the water side of their vascular countercurrent heat exchangers (Brill et al. 1999b; Galli et al. 2009). This fact supports prior evidence that most tropical tunas and billfishes generally seek out the warmest water available and is further supported by empirical data showing that Yellowfin Tuna, Blue Marlins *Makaira nigricans*, White Marlins *Kajikia albida*, and Sailfish *Istiophorus*
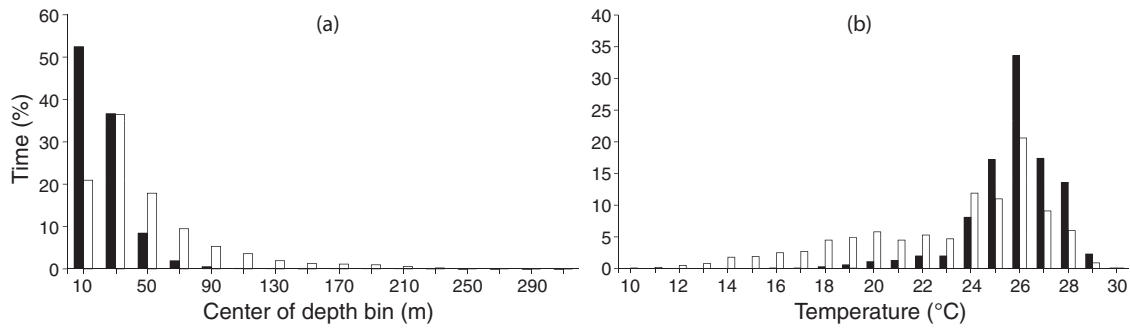
FIGURE 2.   Pooled percentage of time spent at **(a)** depth and **(b)** temperature for periods of darkness (black-shaded bars) and daylight (open bars) for 25 Yellowfin Tuna that were monitored with pop-up satellite archival tags. Interpolated 1-m depth bins were grouped (20-m bins) in this figure to conserve space.

platypterus usually spend only a small fraction of total time at temperature in waters colder than $-8 \Delta T$ (Goodyear et al. 2008; Hoolihan et al. 2011b, 2012a).

Because tunas and billfishes are sight feeders, their foraging activities should be more prevalent during daylight hours. The presumption that most descents below the thermocline are associated with foraging activity is supported by comparing the percentiles of mean ΔT for darkness and daylight hours for Yellowfin Tuna in the present study (Table 2). The percentiles plainly indicate an increased use of deeper, colder depths during daylight hours and more surface-oriented behavior during darkness, suggesting an opportunity to take advantage of warmer temperatures when foraging opportunities are low. Previous studies have also reported greater deep-diving behavior during daylight hours for Yellowfin Tuna as well as billfishes, which share similar physiological traits (Holland et al. 1990; Block et al. 1997; Brill et al. 1999a; Schaefer et al. 2007, 2011, 2014; Goodyear et al. 2008; Weng et al. 2009; Hoolihan et al. 2011b, 2012a).

While ambient temperature is clearly a major factor limiting vertical movements of Yellowfin Tuna, other factors also affect their use of vertical habitat. Brill (1996) pointed out several high-performance physiological traits of Yellowfin Tuna, including rapid rates of somatic growth, gonadal growth, digestion, and recovery from exhaustive exercise. Each of these energy demands requires oxygen delivery rates in excess of those needed for routine metabolic functions as well as the sustained propulsion that is mandatory for obligate ram ventilators, such as tunas and billfishes (Brill 1996). Therefore, these species must adhere to environmental conditions (e.g., depths) that provide adequate levels of dissolved oxygen to maintain these functions. Known areas with hypoxic conditions are associated with limited vertical habitat use by tunas and tuna-like species (Prince and Goodyear 2006; Prince et al. 2010; Stramma et al. 2012). Although hypoxic conditions of varying severity do form periodically along the continental shelf near the Mississippi River's outflow into the northern GOM (Rabalais et al. 1996), there were no apparent indications that this phenomenon impacted the behavior of Yellowfin Tuna in the present study.

Unfortunately, only 4 of the 31 deployed PSATs remained attached for the entire pre-programmed period (Table 2), and those four PSATs were programmed for 90 d. We concluded that at least four of the premature releases in our study (Table 2) were the result of predation (presumably sharks). Predation followed by predator ingestion of the PSAT was assumed when depth increased greatly for extended periods, counter to the vertical behavior we normally witnessed in Yellowfin Tuna. Concomitant to these depth changes, temperature readings were elevated above the values expected for a given depth; these temperatures were relatively constant, suggesting that the PSAT was ingested and therefore recorded the predator's internal body temperature. In addition, light level measurements were negligible, suggesting that the PSAT was shielded from light after being ingested. When the PSAT reverted to recording temperature values that were plausible for the concurrent depth values and started transmitting data via the Argos system, the PSAT was presumed to have been regurgitated. Predatory behavior resulting in PSAT ingestion has been reported in previous studies (Kerstetter et al. 2004; Béguer-Pon et al. 2012; Lacroix 2014). Predation may have been responsible for the loss of other Yellowfin Tuna in our study, particularly when PSATs were at large for only a few days (Table 1).

All of our Yellowfin Tuna were captured in close proximity to petroleum production structures (i.e., platforms). In addition to their intended purpose, these structures function as fish aggregating devices (FADs). Foraging Yellowfin Tuna and their prey are known to aggregate around FADs (Holland et al. 1990; Cayré 1991; Itano and Holland 2000). In turn, larger predators that target Yellowfin Tuna (e.g., sharks and Blue Marlins) take advantage of this situation. In fact, shark predation on Yellowfin Tuna that were hooked and being retrieved near the GOM petroleum production structures was a problem acknowledged by local fishermen.

None of the PSATs with 150- or 180-d deployments functioned for full term. Early or premature release can result for a variety of reasons, including breakage of the tether component, breakage of the corrosive link pin, failure of the anchor mechanism, failure of PSAT internal programming or hardware, and
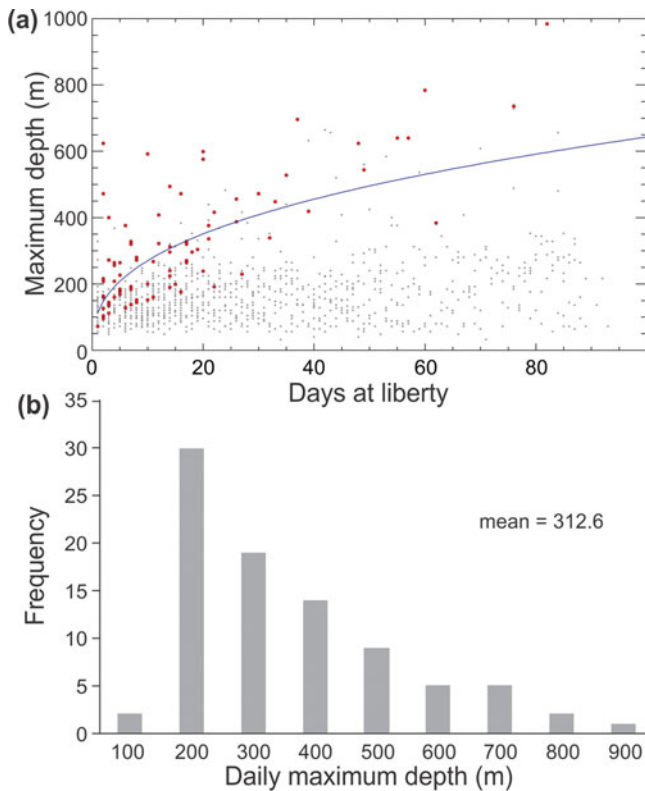
FIGURE 3. Maximum depth reached by Yellowfin Tuna during time at liberty: **(a)** deepest dives recorded during individual time bins (gray dots), first records of each fish at the observed depth (red dots), and exponential fit to the first occurrence data (blue line); and **(b)** frequency distribution of the deepest dives observed for each fish.

FIGURE 4. Minimum temperature experienced by Yellowfin Tuna during time at liberty: **(a)** lowest temperature recorded during individual time bins (gray dots), first records of each fish at the observed temperature (red dots), and exponential fit to the first occurrence data (blue line); and **(b)** frequency distribution of the lowest temperatures observed for each fish.

predation (Musyl et al. 2011). In many cases, it is difficult to pinpoint any single reason for PSAT failure. In some instances, events such as predation can be ascertained by scrutinizing the transmitted or stored archival data. Notification of pin breakage is provided by Argos transmission, although there is no way to determine the exact cause of the breakage. Possible reasons that may contribute to metal fatigue and pin breakage include (1) behaviors exhibited by Yellowfin Tuna during the pursuit of prey (i.e., rapid turning and jumping out of the water) and (2) misidentification of the PSAT as prey and subsequent attack on the PSAT by other Yellowfin Tuna during a feeding frenzy.

Except for three individuals (Table 2; Figure 5), the Yellowfin Tuna in our study did not undertake long-distance horizontal movements. Conventional tagging studies indicate that Yellowfin Tuna are capable of long-distance movements, even trans-Atlantic crossings beginning from the GOM (Ortiz 2001; Prince and Goodyear 2007). Detection of long-distance movements is more likely when tag deployment periods increase to the point of encompassing seasonal changes that induce population migrations. None of the PSATs in our study exceeded 95 DAL (Table 2); thus, the chances of revealing seasonal movements were lessened. Factors such as spawning activity, environmental conditions, and foraging opportunities may provide
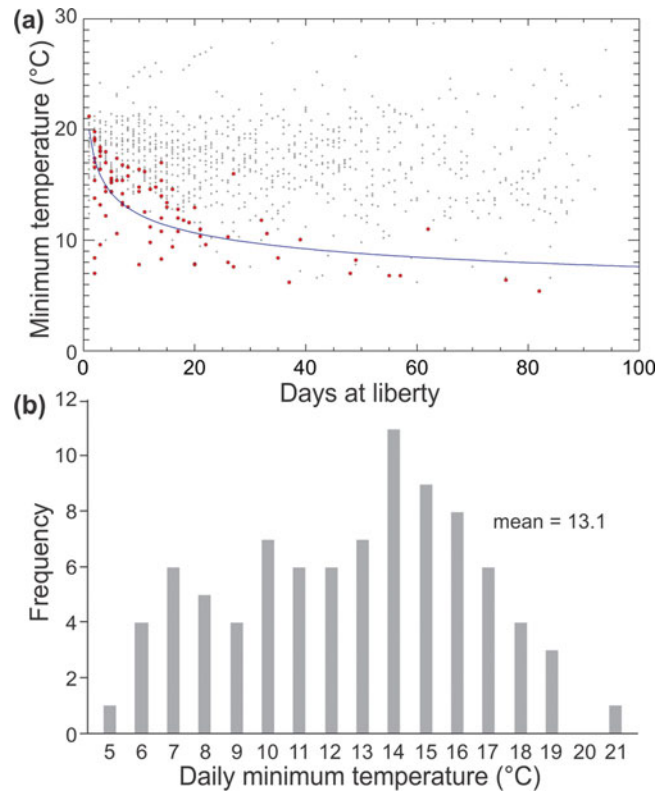
an incentive to remain in one locale for an extended period. The petroleum production platform FADs certainly contribute to more opportune foraging situations. The presence of nearly 4,000 such structures in the northern GOM (NOAA 2012) may entice Yellowfin Tuna to remain in a specific area for extended periods; this could explain why the Yellowfin Tuna in our study stayed within relative proximity to their release locations.

Yellowfin Tuna remain economically important in countries throughout their range, where the bulk of catches are attributed to commercial and artisanal fleets using longline and purse-seine gears. A 2011 ICCAT assessment of Atlantic Yellowfin Tuna based on production and age-structured models estimated a 76% probability that the stock was either (1) overfished or (2) overfished and undergoing overfishing (ICCAT 2011). For stock assessment purposes, knowledge of hook depth and vertical habitat preference (i.e., distribution) of the catch (Hinton and Nakano 1996; Bigelow et al. 2006) are important considerations for reducing the uncertainties that are often associated with estimating fishing effort and relative abundance from longline catch rate indices. Longline hook depth has been shown to affect species selectivity of longline sets (Boggs 1992); however, there are difficulties in accurately estimating hook depth (Rice et al. 2007). Habitat-based standardization
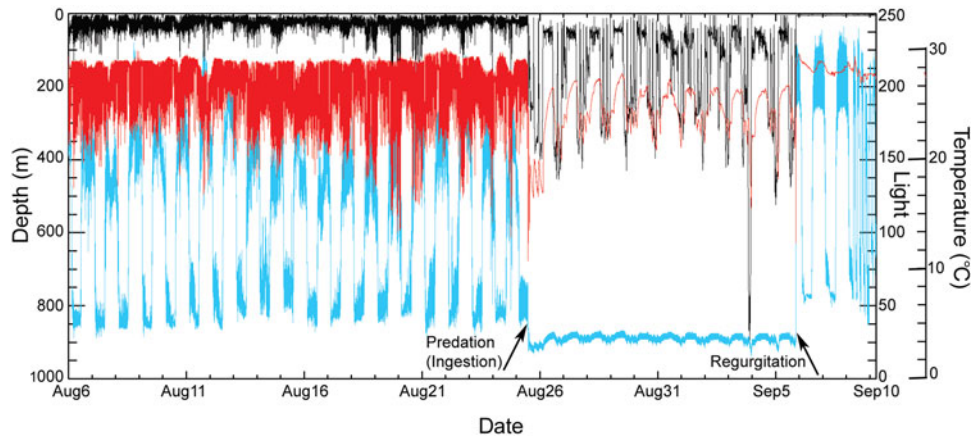
FIGURE 5.   Depth (black line), temperature (red line), and light level (blue line) profiles for a Yellowfin Tuna (pop-up satellite archival tag 08A0561; see Table 1), illustrating the change in vertical habitat use after a presumed shark predation event. Times of tag ingestion and subsequent regurgitation are indicated.

models were developed to improve the methodology for estimating relative abundance, and standardization of historical catch and effort data, through use of detailed information on actual hook depth and vertical distribution of catch (Hinton and Nakano 1996; Bigelow et al. 2002; Maunder et al. 2006). We have presented tabulated ΔT percentiles that can be used as direct input variables for entry into habitat-based standardization models, such as the one described by Hinton and Nakano (1996). As such, the results of the present study represent the most comprehensive description to date for actual vertical habitat use by Yellowfin Tuna in the Atlantic Ocean. However, this information was obtained from a localized area of the northern GOM. Variation in oceanographic features can affect fish behavior (Rooker et al. 2012), so vertical habitat use by Yellowfin Tuna in other areas of the Atlantic Ocean may differ from that identified in the present study.
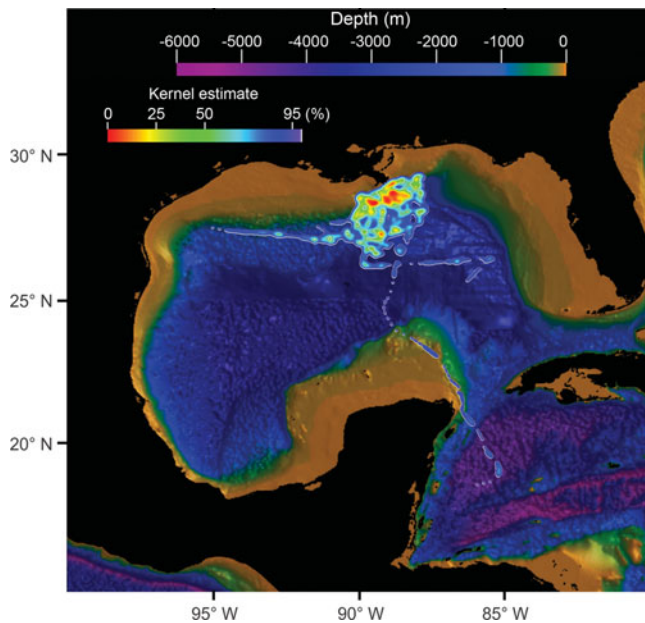
ACKNOWLEDGMENTS

FIGURE 6.   Kernel density estimates for horizontal habitat use by 25 Yellowfin Tuna that were monitored with pop-up satellite archival tags in the Gulf of Mexico.

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