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ARTICLE

Sailfish Habitat Utilization and Vertical Movements in the Southern Gulf of Mexico and Florida Straits

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Abstract

Pop-up satellite archival tags (PSATs) were deployed on 19 sailfish *Istiophorus platypterus* captured in the southern Gulf of Mexico and Florida Straits between 2005 and 2007 on commercial pelagic longline gear ($n = 18$) and recreational rod-and-reel gear ($n = 1$). The data from three tags indicated mortality events and were excluded from subsequent analyses. All PSATs were programmed to collect pressure (depth), temperature, and light-level data for 10 d at approximately 90-s intervals. These transmitted point data subsequently allowed the reconstruction of vertical movement patterns. The remaining 16 PSAT data sets indicate that sailfish are primarily associated with the upper surface waters within the top 20 m (75.7% of total time during the day versus 46.7% at night) but undertake numerous short-duration vertical movements below the local mixed layer to depths of 50–150 m, presumably to feed. Analyses of 2,279 individual vertical movements among all 16 tagged sailfish indicated two distinct types (short-duration "V" and longer-duration "U" movements) similar to those reported for white marlin *Kajikia albida*. Sailfish also exhibited movement type differences between diel periods (having higher proportions of V movements in daytime), suggesting directed foraging at depth. Although short-duration movement to depths by these tagged fish contribute a small percentage of the total time at depth, these depths overlap with the monitored shallow-set pelagic longline gear depths actively targeting swordfish by the vessel in the local fishery. These results suggest that time-at-depth histograms alone may be insufficient to capture feeding motivations at depth and, therefore, true interaction potentials between individual sailfish and pelagic longline gear.

The sailfish *Istiophorus platypterus* is a large, cosmopolitan teleost found worldwide in tropical and subtropical waters, generally with higher concentrations near continental shelf areas (Nakamura 1985). Conventional tagging data have shown broad movements of sailfish within the western Atlantic Ocean (Ortiz et al. 2003), although no trans-Atlantic or trans-Equatorial movements have been documented (Orbesen et al. 2009). The latest assessment of the western Atlantic sailfish stock suggests that the stock is overfished and that this overfishing is primarily the result of international pelagic longline fleets targeting swordfish and tunas (SCRS 2009).

In Florida, sailfish support a large, mostly catch-and-release recreational fishery based primarily in the coastal shelf region between Key West and Jupiter (Jolley 1977). The Florida Straits have been closed to the U.S. pelagic longline fishery since 2001, primarily to protect local concentrations of juvenile swordfish *Xiphias gladius*. However, vessels continuing to use pelagic longline gear to the west and north of this closed area

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occasionally encounter high rates of sailfish bycatch while targeting large swordfish and yellowfin tuna *Thunnus albacares*. Several studies using electronic tag technologies have shown that sailfish are capable of daily horizontal movements (e.g., Hoolihan and Luo 2007; Orbesen et al. 2008) on the scale of tens of kilometers. These ranges of distances would provide connectivity for sailfish between the portions of the Florida Straits that are open and closed to the pelagic longline fishery, a continuing source of domestic fisheries conflict in south Florida waters.

Evaluating vertical habitat use by large pelagic fishes has historically presented challenges owing to a combination of their individual size, movement speed, and depth ranges. Previous work generally focused on the manual tracking of animals with acoustic tag technology for short periods of time with dedicated chase vessels (e.g., Jolley and Irby 1979). However, the development of pop-up satellite archival tag (PSAT) technology has enabled researchers to record environmental data on animals for much longer periods and at much more detailed resolution while eliminating the need for direct monitoring of the animal or fisheries-dependent returns of the tag. Electronic monitoring technology, such as small temperature and depth recorders (TDRs), has enabled a concurrent increase in our understanding of fishing gear behavior, including movements and effective fishing depths. The combined use of these technologies to describe both vertical short-duration movements and overall habitat utilization can provide insights into the vulnerability of bycatch species to various fishing gears, and allow for more-informed management measures. The present study used the point data from 16 PSATs with 90-s sampling period resolution for 10-d deployment durations attached to sailfish to describe the short-duration behavior and vertical habitat utilization of this species in the southern Gulf of Mexico and Florida Straits.

METHODS

Sailfish tagging occurred in two locations within the southern Gulf of Mexico: location 1, approximately 90 km south-southwest of Key West, Florida, in an area traditionally fished by the U.S. coastal pelagic longline fleet; and location 2, offshore of the island of Isla Mujeres, Mexico, the site of a large recreational fishery for sailfish (Figure 1). Tagging operations off Key West occurred aboard the U.S. commercial pelagic longline fishing vessel FV *Kristin Lee* during May 2006 and June 2007. The target species for all three trips was nominally swordfish, and (as is standard in the fishery) all sets were made overnight, gear deployment occurring at dusk and retrieval at dawn. The gear configuration was similar to that used throughout this local fishery and consisted of 18.3-m (10-fathom) leaders and 18.3-m (10-fathom) buoy float line lengths during each set in five-hook

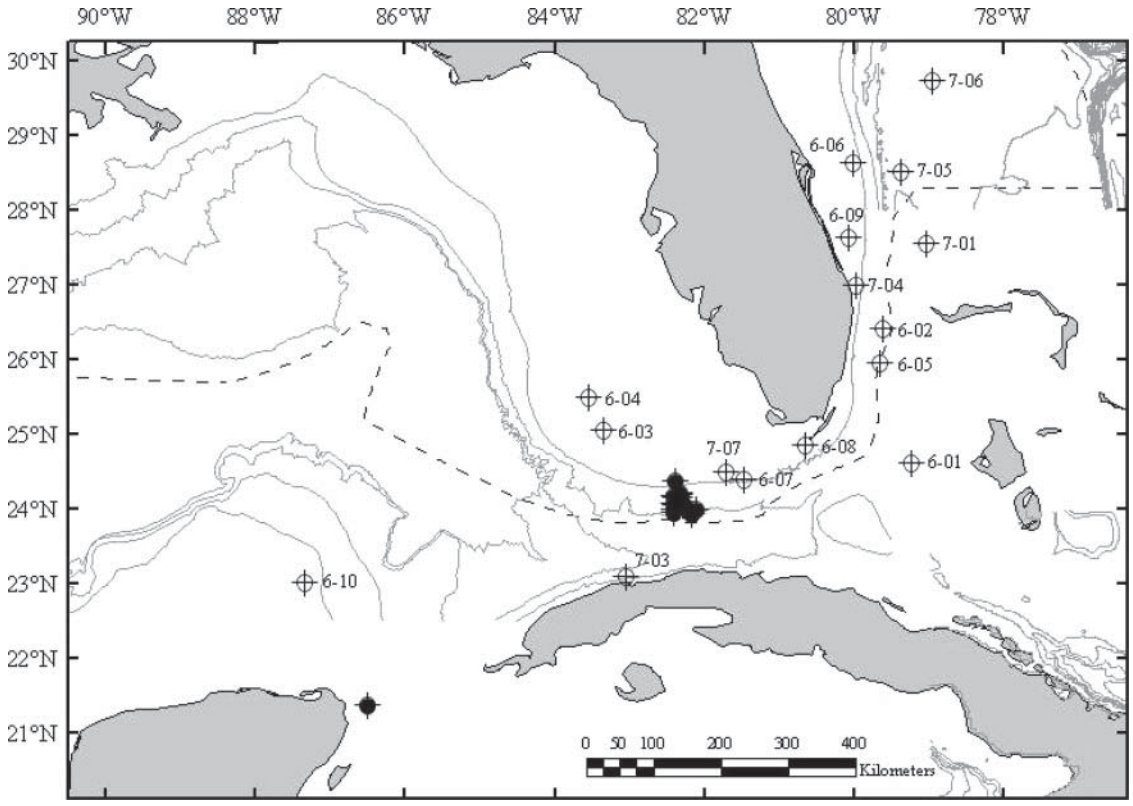


FIGURE 1. Southern Gulf of Mexico and Florida Straits study area in which deployments of pop-up satellite archival tags on sailfish were made. Filled dots indicate tagging locations, while open dots indicate the locations of first satellite transmission. Depth contours are shown for 200, 1,000, 2,000, and 3,000 m.

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baskets (hooks between floats). Per current U.S. fisheries regulations, all sailfish were caught on either non-offset size 16/0 or 10° offset size 18/0 circle hooks using squid *Illex* spp. or Atlantic mackerel *Scomber scombrus* bait. The tag deployment for the Isla Mujeres sailfish occurred aboard the sportfishing vessel *Sea-D* during May 2006 while trolling a ballyhoo baited with a non-offset size 7/0 circle hook.

We used the Microwave Telemetry (Columbia, Maryland) Model PTT-100 HR satellite tag in all tag deployments during this study. Tags were rigged with approximately 16 cm of 136-kg (300-lb) test strength Momoi brand (Momoi Fishing, Ako City, Japan) fluorocarbon monofilament attached to a large hydroscopic nylon intramuscular tag head with aluminum crimps per Graves et al. (2002). On all tags but the Isla Mujeres deployment, a 68-kg (150-lb) test strength Sampo brand (Sampo, Barneveld, New York) ball bearing swivel was incorporated midway along the tether to reduce twisting torque at the attachment location caused by drag forces on the tag. Tags sampled temperature, pressure (depth), and irradiance (light level) at 93-s intervals. This tag model also included emergency release software that automatically detached the tag if the pressure sensor indicated depths approaching the crush limit of the tag casing (ca. 2,000 m). All tags were preprogrammed to release from the fish after 10 d at large.

Data were transmitted through the Argos satellite system while the tags floated at the surface following detachment from the animal. Tags used in this study transmitted archived data in "packets," each encompassing several minutes of consecutive data points. However, each packet was transmitted in a discontinuous overall pattern such that gaps exist between packets within the transmitted record. This tag model also contained proprietary "SiV" programming, which directs the tag to only transmit data when an Argos satellite is expected to be above the horizon. This programming extends the onboard battery power and allows for additional Argos transmissions, thereby increasing the total transmitted data.

To delineate the maximum effective fishing depths for the configuration of pelagic longline gear used by the commercial vessel, small TDRs (Model LTD-1100; Lotek Wireless, St. John's, Newfoundland) were attached to the lower end of the middle branch lines (hook three in the five-hook baskets) during gear deployments (see additional details on placement in Kerstetter and Graves 2006a). This model of TDR records pressure (as pounds per square inch [PSI]) and temperature at 14-s intervals. The pressure data from the TDRs were standardized from PSI to depth (m) with latitude and seawater density corrections using Harris (2000). Data from these TDRs were also used to confirm local mixed-layer depths (MLDs).

Sailfish tagging.—Prior to deployment, all PSATs were allowed to cycle through the full internal activation process. The captain of the pelagic longline vessel identified incoming sailfish on the line, and individuals were initially evaluated as live or dead based on movement (or lack thereof) alongside the vessel. The sailfish tagged from the recreational vessel was identified to species prior to becoming hooked on one of the surface baits.

Live fish were manually brought alongside the vessel rail and held briefly by the leader until calm. The PSAT tagging procedures used were identical to the ones described in Kerstetter and Graves (2006b), although a shorter applicator tip (8 cm) was employed to compensate for the much more laterally compressed sailfish body form. The nylon anchor attached to the PSAT tether was carefully inserted about 5–10 cm below the midpoint of the first dorsal fin to a depth of about 4–6 cm. This location on the fish provides an opportunity for the nylon tag head to pass through the dorsal pterygiophores without approaching the coelemic cavity (see Prince et al. 2002). A conventional National Oceanic and Atmospheric Administration Fisheries Service Cooperative Tagging Center streamer tag was also attached posterior of the PSAT on all fish tagged from the pelagic longline vessel.

Sailfish were released as soon as possible after tagging by cutting the leader near the hook unless the hook was readily accessible for manual removal. For the single recreationally caught fish, total time from capture to release was less than 10 min. No animals were resuscitated by either vessel platform after tagging. Prior to release, the hooking location (following the terminology of Yamaguchi 1989) and overall physical condition of the animal were noted, and fish lengths and weights were estimated. All other pertinent data—including the time of day, vessel location, and sea surface water temperature—were recorded immediately after tagging.

Data analysis.—The net movement of tagged sailfish was estimated as the minimum straight-line distance (MSLD) traveled between the initial tagging location and the location of the first reliable satellite contact with the detached tag (inferred as the location of tag pop-up) using Argos location codes 1, 2, or 3 (position uncertainty, $\leq$1.5 km; CLS 2011) for the first or second day of transmission. "Great Circle" distances between these points were calculated with program inverse (version 2.0; NGS 1975; modified by M. Ortiz, National Marine Fisheries Service Southeast Fisheries Science Center, Miami, Florida).

For analysis of diel differences, data were separated into day and nighttime periods. Sunrise and sunset times for approximated positions were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil). Because individual daily positions could not be matched with cloud cover data, no attempts were made to standardize light levels for local atmospheric conditions. Crepuscular periods were identified and excluded for diel analyses by removing the 30-min period before and after estimated times of local sunrise and sunset (corroborated with light-level data). Using only day and night period data, histograms were generated at 10-m (depth) and 1°C (temperature) intervals for each individual sailfish and compared using paired *t*-tests. Finally, depth differences between sequential ca. 90-s period point data were used to examine the range and speed of vertical movements. Due to the "packet" transmission of the archived tag data, the final data

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sets occasionally had discontinuous intervals, usually less than 1 h in length. All discontinuous intervals within each tag record were identified and excluded from the individual dive analyses.

Sea surface temperature (SST) was calculated as the average temperature for all depths 0–5 m to reduce fine-scale variability between measured data. Relationships between vertical habitat utilization and thermal structure of the water column used two calculated values for each photoperiod: SST and the mixed-layer depth temperature (MLDT = SST – 0.5°C as per Levitus 1982). Paired *t*-tests between diel periods were used to assess habitat utilization above and below respective SST and MLDT values for each 24-h period of the deployment.

The structure of the transmitted data from the PSATs allows for a re-creation of the thermal environment surrounding individual sailfish by using the fish as autonomous samplers of the water column (Boehlert et al. 2001; Block et al. 2003; Horodysky et al. 2007). Forty-eight hour periods were selected from three sailfish that had their tags physically recovered (hence, 100% data recovery) and demonstrated representative short-duration vertical movements to depth. Within a given 48-h period, archived temperature and depth data were used to create 96 temperature–depth profiles for each 30-min block of time. Temperature readings between data points were interpolated from these profiles at 5 m and 0.1°C resolution (MATLAB R2006a, version 7.2.0.232). To provide a visual description of local subsurface temperature and short-duration movements, interpolated temperatures and depth tracks were then superimposed using the archived depth and temperature data recorded during the vertical movements of these individual fish per the methods of Horodysky et al. (2007).

The structure of the PSAT data also allowed the reconstruction of individual vertical movements to depth. As all movements began and ended in shallow depths, these movements are referred to hereafter as "dives." The characteristics of these individual dive events were assessed through a variety of analyses. Data from onboard vessel electronics, deployed TDRs (for the pelagic longline vessel sets), and reconstructed vertical profiles from the tag data sets all indicated an MLD of approximately 10 m in the waters of the southern Gulf of Mexico. A vertical movement was therefore considered a single dive if it (1) began at a depth less than 10 m, (2) incurred a maximum depth greater than 10 m, and (3) returned to a depth less than 10 m. Any vertical movement not meeting these three criteria or that was missing any data from within the movement itself was considered an "incomplete" dive event and excluded from subsequent analyses. Individual dives were then analyzed for maximum depth, minimum temperature, SST at beginning of dive, overall duration of dive, and the "interdive interval" (the period between the end of one dive event and the start of the next). Most dive events demonstrated a period of rapid movement to depth, followed by a relatively stable period at this depth before returning to near-surface waters. Any period of time at depth within an individual dive was termed "bottom time" and calculated as the period within the dive when the vertical movement rate was less than 5 m/min. All vertical movements and movement parameters were assessed through a manual review of each tag data set. Any extreme dive events were confirmed by corroboration with concurrent temperature data.

Once a movement was classified as a dive event, subsequent tests were conducted comparing mean maximum depth and duration between diel periods among tagged individuals. Relationships between mean dive depth and duration for pooled data were also explored through regression analyses as well as between diel periods. Significance was assessed at the $\alpha = 0.05$ level.

Dive characterization.—All 16 sailfish appeared to exhibit the two different types of dives described by Horodysky et al. (2007) for white marlin *Kajikia albida*. So-called "V-shaped" dives involved rapid descents with relatively small amount of time at depth or bottom time ($\leq$10 min), and a rapid ascent to a shallower depth. Conversely, the "U-shaped" dives had similar rapid descents but a relatively longer time at depth (16–245 min) before the rapid ascent to shallower depths. Since the primary difference between the dive types is amount of time spent at the lower depths of the dive, dive type can be determined as a function of bottom time. To confirm dive classification by bottom time, multivariate statistical techniques were applied to six different dive characteristics manually recorded for each completely transmitted dive of each surviving sailfish to determine if there were indeed two different dive types present, and what minimum and maximum bottom times best characterized a dive type. The six dive characteristic variables (dive duration, maximum depth, change in temperature, depth divided by dive duration, interdive interval, and bottom time) were entered into the quantitative techniques described by Lesage et al. (1999) and Horodysky et al. (2007).

Dive characteristics were standardized (PROC STANDARD, SAS version 9.2; SAS Institute, Cary, North Carolina), and a principal components analysis (PCA) was used to both eliminate collinearity and produce a smaller set of orthogonal factors to input into cluster analysis (Horodysky et al. 2007). Four orthogonal factors were derived from the PCA (dive duration, maximum depth, change in temperature, and interdive interval) and were entered into a hierarchical complete-linkage cluster procedure to ascertain the appropriate number of clusters and dive types, and to determine seed points for nonhierarchical *K*-means clustering (Horodysky et al. 2007). Hierarchical complete-linkage clustering is an agglomerative method which classifies clusters by the maximum distance between one cluster and the next (Hair et al. 1998). The number of dive types sufficient to capture the variability between dives was determined by examining the agglomerative coefficient, the squared Euclidean distance between two clusters being combined, from 2 up to 10 clusters (Horodysky et al. 2007). The cluster centroids that resulted from the complete-linkage clustering are next entered into a nonhierarchical *K*-means clustering that further fine-tuned the formed clusters. Observations were assigned to the cluster with the centroids with the closest Euclidean distance, and new

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TABLE 1. Summary of satellite archival tagging deployments for sailfish in the southern Gulf of Mexico. The ACESS score refers to a physical condition index based on a 10-point scale (10 being the highest score; see Kerstetter et al. 2002 for further details); MSLD = minimum straight-line distance traveled. The three mortalities described within text are not included.

Sailfish	Date deployed	Hooking location	Hook size	Hook removed	ACESS score	Estimated length (cm)	Reporting (%)	MSLD (km)
6-01	3 May 2006	Corner	16/0	Yes	9	137	59	448.0
6-02	4 May 2006	Lower jaw	18/0	Yes	9	183	82	375.5
6-03	4 May 2006	Fouled	16/0	No	8	168	63	150.1
6-04	4 May 2006	Isthmus	18/0	Yes	10	183	55	188.6
6-05	4 May 2006	Corner	16/0	No	10	168	68	332.4
6-06	5 May 2006	Eye socket	16/0	No	9	152	75	554.9
6-07	5 May 2006	Fouled	16/0	Yes	8	152	65[a]	97.3
6-08	5 May 2006	Lower jaw	18/0	Yes	8	168	40	193.5
6-09	6 May 2006	Corner	18/0	Yes	8	152	68	447.0
6-10 (IM)[b]	31 May 2006	Corner	7/0	Yes	10	137[c]	49	217.1
7-01	6 Jun 2007	Corner	16/0	No	9	122	75	522.9
7-03	6 Jun 2007	Corner	16/0	No	6	122	87	125.0
7-04	6 Jun 2007	Corner	16/0	No	10	122	74	406.2
7-05	6 Jun 2007	Corner	16/0	No	10	137	86	564.0
7-06	9 Jun 2007	Corner	16/0	No	5	107	88	717.3
7-07	9 Jun 2007	Corner	16/0	No	6	122	88	67.4

[a]Original reporting percentage; tags were later returned, allowing a 100% data recovery rate.
[b]Animal tagged off the recreational vessel in Isla Mujeres, Mexico.
[c]Not estimated.

centroids were calculated after each iteration until the changes in centroids become small or zero (Horodysky et al. 2007). Dive classification was confirmed by discriminant function analyses, using the two nearest neighbors to identify which cluster (dive type) to be assigned (Lesage et al. 1999). Percentages of misclassified dives, or error rates, were calculated by cross-validation.

A matrix of minimum bottom time values (1, 5, 10, and 15 min) for U-shaped dives was compared with a maximum bottom time values for V-shaped dives to investigate which combination of minimum and maximum bottom time best represented dive type. The resultant dive types were then entered into the quantitative methods described previously to determine which minimum and maximum values were agreed upon by both dive type via bottom time and objectively by multivariate statistical techniques. The set of minimum and maximum values that covered the broadest scope of dives and had the lowest percentages of misclassified dives was used to determine dive type.

RESULTS

Tagging Events

Eighteen PSATs were deployed on sailfish caught on pelagic longline gear targeting swordfish in the southern Gulf of Mexico between November 2005 and July 2007. Overall bycatch of istiophorid billfishes comprised less than 3% by number of the total catch on the three observed trips. One PSAT was deployed on a sailfish caught from a sportfishing vessel off Mexico in May 2006.

Three sailfish caught on pelagic longline gear died shortly after release, and the data from these fish were excluded from subsequent analyses (see Kerstetter and Graves 2008). A summary of tagging information and the physical condition of the surviving tagged animals is presented in Table 1. For all 16 PSATs, an average of 70.3% (range = 40–88%) of the archived data were successfully recovered through the Argos system. Four archival data sets (2006: $n = 1$; 2007: $n = 3$) were recovered after the tags washed up onto Atlantic beaches and were returned to the authors. All (100%) of the archived data were recovered from these four returned tags and included in subsequent analyses.

Horizontal Movement

Individual sailfish moved away from the tagging location various distances and and in various directions (mean distance = 337.9 km; range = 97.3–564.0 km). There was no relationship between MSLD traveled and estimated individual size. Three of the fish tagged within the U.S. Exclusive Economic Zone (EEZ) crossed into foreign EEZ waters, including the Bahamas ($n = 2$) and Cuba ($n = 1$), while the fish tagged in Mexican waters remained within the Mexico EEZ (Figure 1).

Depth and Temperature

There were no significant diel differences in either the time-at-temperature or time-at-depth distributions between the 2 years of this study, and data were subsequently pooled to include fish from both years. Sailfish demonstrated a very strong

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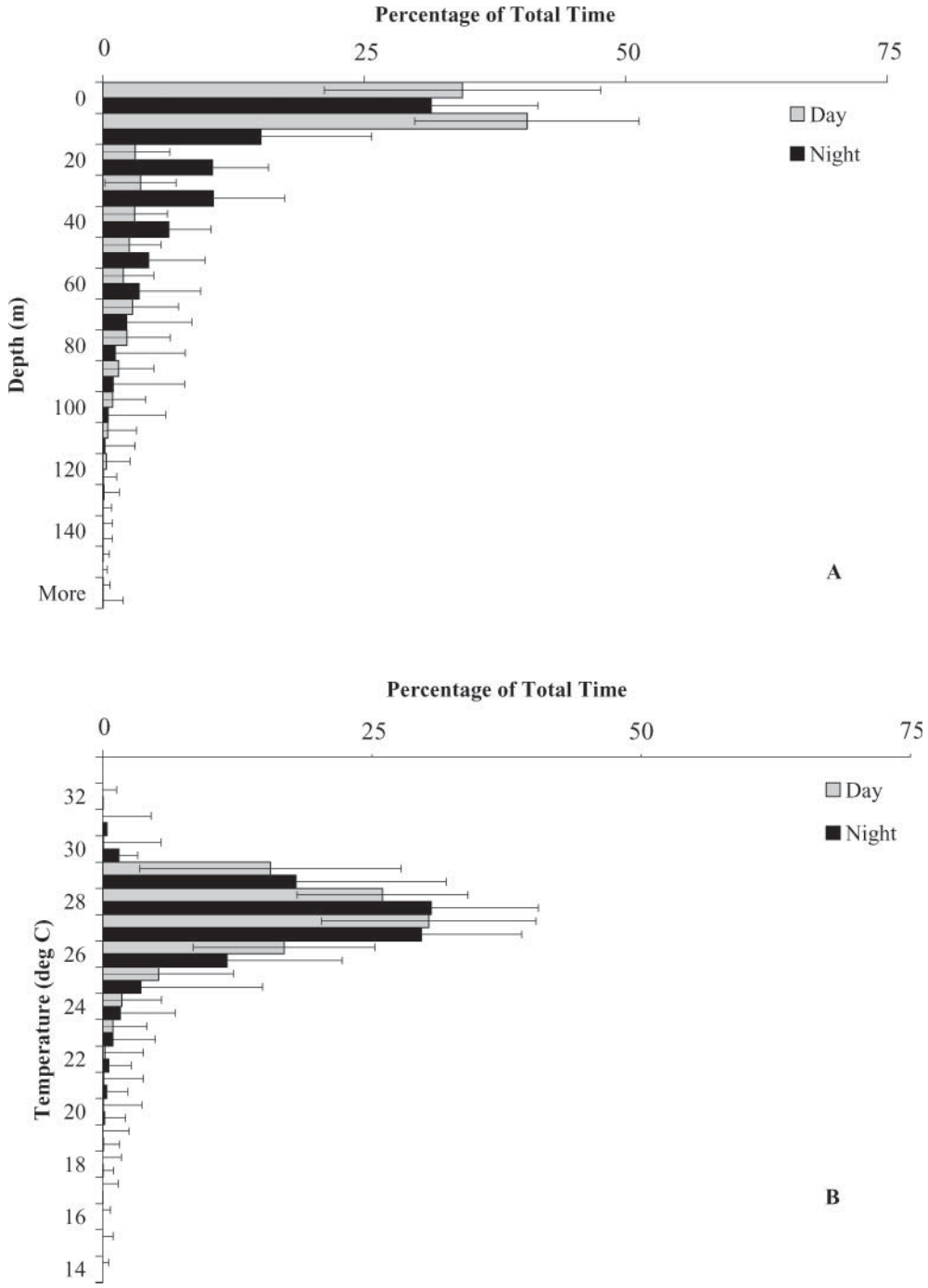


FIGURE 2. **(A)** Combined time-at-depth and **(B)** time-at-temperature histograms for 16 sailfish tagged with pop-up satellite archival tags for 10-d deployment durations in the southern Gulf of Mexico and Florida Straits, 2006 and 2007. Error bars indicate SEs around mean values.

association with warm surface waters (Figure 2A, B), spending approximately 34% (SD, 13.2) of their total time in the upper 10 m of the water column and 41% (SD, 10.7) within the 10–20-m stratum. Sailfish spent 12.4% (SD, 12.9) of their time at depths ranging from 20 to 50 m, and only 10.6% (SD, 26.7) at depths greater than 50 m. Broad standard errors reflect large within-individual (daily) variation in time at depth rather than differences among individuals. The absolute depth difference between sequential 90-s point measurements ("delta *D*") observed in three of the fish with 100% data recovery found a highly significant difference between day and night periods ($t = -4.58$, $P \ll 0.001$ using Satterthwaite test for unequal

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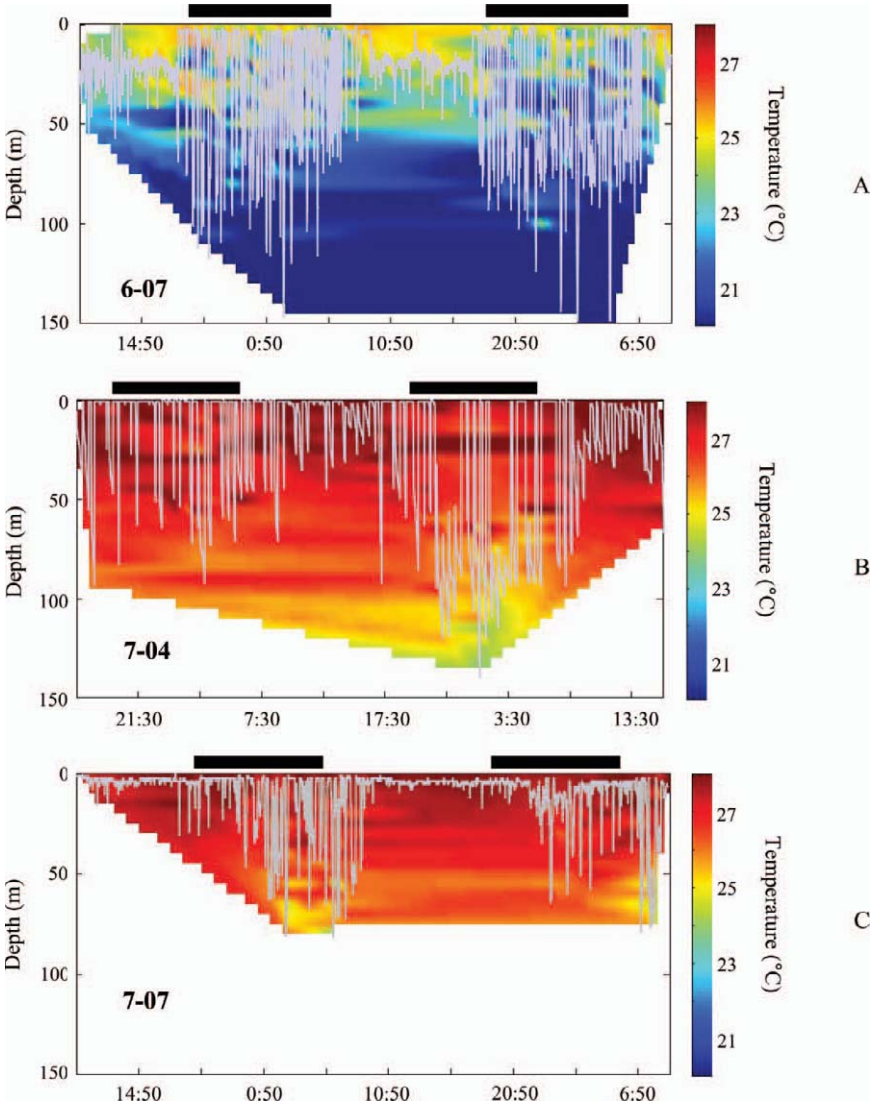


FIGURE 3. **(A)–(C)** Detailed 48-h pattern of vertical movements overlaid on re-created local temperature-at-depth profiles generated from archived tag data for three sailfish tagged with pop-up satellite archival tags for 10-d deployment durations in the southern Gulf of Mexico and Florida Straits, 2006 and 2007. Clear diel differences in dive periodicity are evident in (A) but not (B), and a moderate effect of diel period is displayed in (C). The black bars along the top of each panel represent the local periods of night generated from archived light-level data from the tags. Night periods varied slightly in length between fish owing to different deployment dates.

variances), with sailfish moving vertically much more frequently between depths at night.

Pooled temperature data demonstrated that sailfish spent 89.6% (SD, 45.4) of their time in water temperatures ranging from 25–29°C (Figure 2B), although archived SSTs occasionally reached over 30°C. Many individuals exhibited considerable daily variation in the temperature–depth data over the course of the 10-d tag deployment period (Figure 3, A–C), including deep short-duration movements below the MLDT. The absolute temperature difference within each dive event ("delta *T*") showed that 71.7% (SD, 29.7) occurred between 0°C and 2.0°C, 99.2% (SD, 6.4) occurring between 0°C and 8.0°C (Figure 4).

All of the fish in this study spent more time at depths below the MLD during daylight hours (significantly for 14 fish of the 16 total; $P < 0.05$; Table 2). Individual fish exhibited different patterns regarding total time spent below the MLD; however, of the four individuals showing a significant difference between day and night periods for time below the MLD, three were at those depths more at night and one during day. Pooling all individual sailfish, a regression analysis of time spent below the MLD and individual body size (as estimated LJFL) showed no significant effect (adjusted $r^2 = 0.116$, $F = 2.9$, $P = 0.1069$).

A total of 2,279 complete individual dive events were examined. To minimize autocorrelation effects between individual dives, a mean maximum dive depth and mean dive duration were

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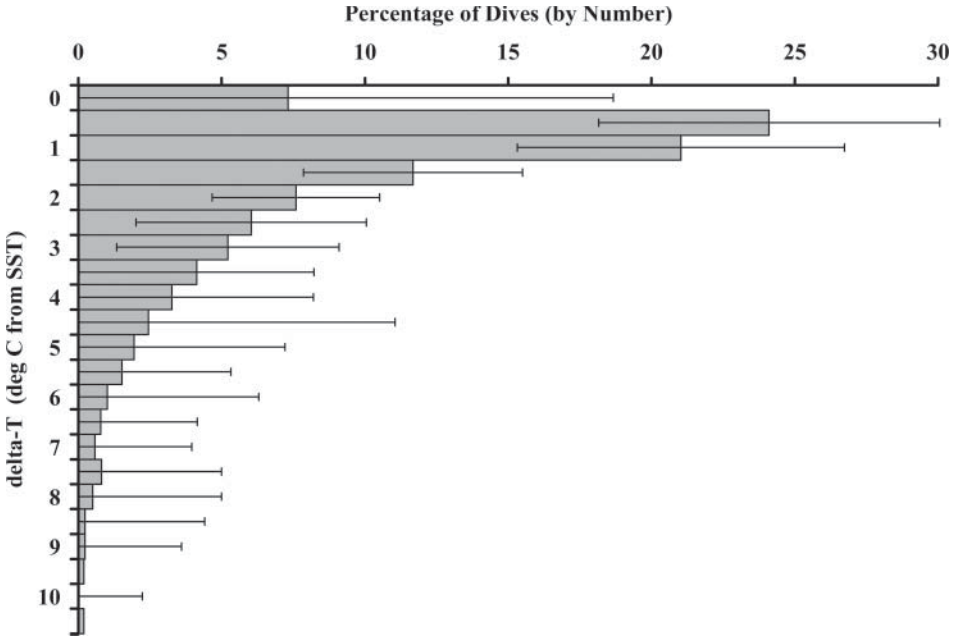


FIGURE 4. Percentages of dives versus differences between the local sea surface temperature (SST) and the minimum temperature encountered on a dive event by 1°C intervals for 16 sailfish tagged with pop-up satellite archival tags for 10-d deployment durations in the southern Gulf of Mexico and Florida Straits, 2006 and 2007.

calculated for day and night for each fish. Night dive events had a mean maximum depth of 38.6 m and mean dive duration of 19.4 min, while day dive events had a mean maximum depth of 45.0 m and a mean duration of 14.4 min. Relationships between mean dive depth and mean dive duration within each diel period were significant (night: adjusted $r^2 = 0.615$, $P < 0.001$; day: adjusted $r^2 = 0.746$, $P < 0.001$), although the regressions were not significantly different from each other (Fisher's z comparison: $z = -0.615$, $P > 0.25$; Cohen and Cohen 1983). Comparisons of dive depth and duration by diel period for all

TABLE 2. Comparisons between day and night periods for the percentage of time spent below the mixed-layer depth (MLD) and the percentage of time spent below the sea surface temperature depth (SSTD). Asterisks denote significant differences.

	Percent < SSTD			Percent < MLD		
Sailfish number	Mean day	Mean night	Significance	Mean day	Mean night	Significance
6-01	0.051	0.583	*	0.913	0.179	*
6-02	0.267	0.020		0.625	0.369	*
6-03	0.121	0.117		0.814	0.642	*
6-04	0.257	0.239		0.784	0.556	*
6-05	0.219	0.133		0.318	0.745	*
6-06	0.285	0.219		0.929	0.650	*
6-07	0.328	0.342		0.508	0.164	*
6-08	0.184	0.187		0.800	0.673	*
6-09	0.235	0.412		0.690	0.167	*
6-10 (IM)[a]	0.056	0.112		0.919	0.793	*
7-01	0.345	0.277		0.606	0.483	
7-03	0.211	0.296		0.675	0.200	*
7-04	0.035	0.061	*	0.766	0.473	*
7-05	0.082	0.278	*	0.900	0.493	*
7-06	0.400	0.097	*	0.319	0.293	
7-07	0.238	0.361		0.533	0.328	*
Mean	0.207	0.233		0.694	0.450	*

[a]Animal tagged off the recreational vessel in Isla Mujeres, Mexico.

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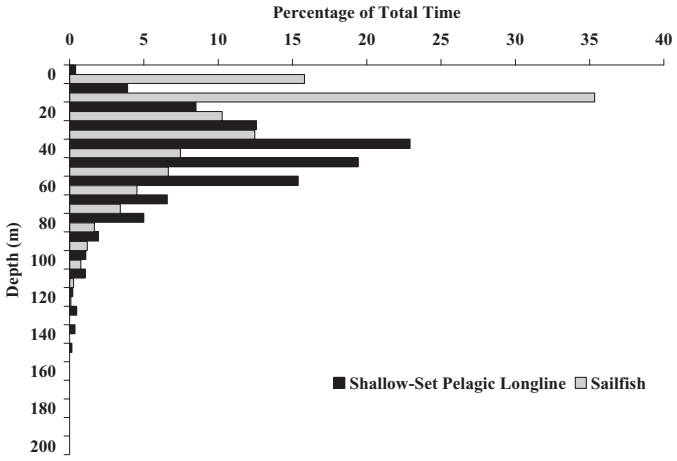


FIGURE 5. Combined time-at-depth histogram for hook depths and sailfish depth utilization during the same period as pop-up satellite tag deployments in the southern Gulf of Mexico, 2006. Pelagic longline gear hook depths are for the deepest (middle) hook within a five-hook basket of shallow-set pelagic longline gear representative of commercial gear deployments in the area. Depth distributions represent combined day and night periods. Error bars are omitted for clarity.

pooled individual dives also resulted in significant relationships (night: adjusted $r^2 = 0.615$, $P < 0.001$; day: adjusted $r^2 = 0.746$, $P < 0.001$), although the regressions for the day and night diel periods were not significantly different from each other (Fisher's z comparison: $z = -0.615$, $P > 0.25$).

Depths of Shallow-Set Pelagic Longline Gear

Thirty-one individual TDR deployments were conducted during four sets in 2006, all in hook position 3 of the five-hook baskets, the middle and presumably deepest hook position. The mean depth of the TDRs was 42.3 m (±SD 19.6), and the maximum depth recorded was 143.8 m. The time at depth distribution for the pooled TDR data set for the deepest hook position and the combined day and night time depth distribution of sailfish tagged in 2006 is presented in Figure 5 and shows a large percentage of overlapping depths (including the implied greater percentages for the pelagic longline gear at the two shallower hook positions). However, these apparently overlapping depth distributions do not reflect the actual movements of individual sailfish to greater depths, even if such movements are for relatively minor proportions of total time at depth. Examinations of the sequential data "tracks" for these sailfish (e.g., Figure 3A–C) showed frequent short-duration movements below the depths of the shallow-set pelagic longline gear.

Dive Characterization

Appropriate bottom time limits to determine dive type were considered by comparing differing minimum bottom time values for U-shaped dives and maximum bottom times for V-shaped dives for each minimum and maximum value (i.e., a V-shape maximum of 1 min would be compared for the entire series of U-shape minimums [1, 5, 10, and 15 min]). A maximum bottom time of 10 min for V-shaped dives and a minimum bottom time of 15 min for U-shaped dives yielded the highest percentage of total dives (91.5%) with the lowest percentage of misclassified dives (5.7%); 224 dives types remain undetermined with bottom times between 11 and 14 min. Cluster analysis showed that after the joining of two clusters the agglomerative coefficient dropped precipitously (agglomerative coefficient of 2.5 at two clusters, dropping to 0.6 at three clusters), implying that two dive classifications is sufficient.

Differences were observed between the dive characteristics of U-shaped versus V-shaped dives. U-shaped dives had deeper mean dive depths (53.5 ± 34.0 m), longer dive durations (28.0 ± 27.1 min), and a larger change in temperature (5.0 ± 12.5°C) than V-shaped dives (38.2 ± 26.2 m versus 10.2 ± 9.5 min, 2.2 ± 5.6°C). However, U-shaped dives and V-shaped dives had similar interdive intervals (24.4 ± 50.2 min and 24.8 ± 66.8 min, respectively).

DISCUSSION

The description of sailfish behavior is of interest not only to the various fishing constituencies but also to those seeking gear-based bycatch avoidance solutions and habitat-based standardization methods for stock assessment purposes. Using point-level data allowed for a clearer characterization of short-duration sailfish movements, as opposed to overall habitat utilization through summary histograms. The ability to recreate individual dives over a relatively longer period of time than previous acoustic studies also presented a better picture of sailfish behavior, including the potential for interactions of individuals with pelagic longline gear. Furthermore, the successful deployment of these PSATs with no premature releases on sailfish supports the observation that fishes smaller than large marlin and tunas can accommodate these tags for short-duration deployments (Kerstetter and Graves 2006b; Horodysky et al. 2007). The development of smaller PSAT models will clearly expand the size range, and thus species list, of similar tagging studies in the future.

Horizontal Displacement

The horizontal movements of sailfish in multiple directions away from the initial tagging locations for long distances were similar to the behavior reported by Graves et al. (2002) for blue marlin *Makaira nigricans*, Kerstetter and Graves (2006b) for white marlin, and Sippel et al. (2007) for striped marlin *K. audax*, as well as that seen for sailfish by Prince et al. (2006) and Hoolihan and Luo (2007). Only two of the 16 tagged sailfish had MSLDs of less than 100 km over the 10-d deployment period. The horizontal displacements observed in this study may be related to spawning, as they are consistent with the postspawning movements northward along the shelf edge described in Jolley and Irby (1979). The spawning period for sailfish in the southern Gulf of Mexico and Florida Straits is from late April through June (Voss 1953), and female sailfish caught in areas southwest of the Florida Keys during this time often have hydrated

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oocytes (A. Mercier, FV *Kristen Lee*, personal communication; G. O'Neill, FV *Carol Ann*, personal communications). Jolley (1977) used detailed analyses of recreational catch records to argue that sailfish indeed undertake a seasonal movement southward into the Florida Keys during the winter and spring, then moving northward through the summer. The movement of the majority of the tagged animals in this study northward along the Gulf of Mexico and Atlantic edges of the shelf supports the patterns observed by Jolley (1977) as well as available conventional tagging data (Orbesen et al. 2009).

Habitat Utilization

Maximum depths of sailfish in the 10-d deployments used during this study (36.3–463.9 m; mean = 141.0 m) fell within the general range reported for other tagged istiophorids (Block et al. 1992; Brill et al. 1993; Pepperell and Davis 1999; Kerstetter et al. 2003). However, these results should be viewed with some caution because sampling intervals in this study were limited to roughly every 90 s; the animal with the 36.3-m maximum depth was the fish with the poorest Argos reporting rate. As described for white marlin in Horodysky et al. (2007) and as seen in the present study with sailfish, deep dives may occur rapidly. It is therefore possible that all maximum dive depths may not have been successfully captured with the sampling interval used in this study. However, by definition, the most rapid and deepest dives of a species represent extreme events, and successful recording of such episodes reveals little about routine animal behavior (Hays et al. 2004).

Sailfish habitat utilization in the western North Atlantic has not been well studied. Two acoustically tagged sailfish off Florida showed a clear preference for surface waters (Jolley and Irby 1979), and prior work with sailfish habitat preferences in the Arabian Gulf (Hoolihan and Luo 2007) showed only rare utilization of depths greater than 50 m. The present study found a broad range of depths encountered by these tagged individuals, even if the majority of the time as a whole was spent within the upper 20 m. However, the range of possible depths for the sailfish tagged in the southern Gulf of Mexico far exceeded those for the animals in the Arabian Gulf (Hoolihan 2005). Other possible reasons for narrow depth preferences (e.g., oxycline depth per Prince and Goodyear 2006) similarly do not apply to the western North Atlantic in the same degree, permitting a broad range of depth utilization for pelagic fishes.

The results presented here demonstrate frequent, mostly short-duration movements to depth for sailfish that change in frequency and depth between day and night diel periods. The repeated, clear patterns of movements suggest that the majority of them are likely for feeding, although predator avoidance cannot be rejected. However, prior studies of sailfish diet composition suggest that individual sailfish forage at depth during both day and night periods. In an examination of 241 stomachs of sailfish caught during daylight hours off Florida, Voss (1953) reported finding that epipelagic fishes (i.e., families Scombridae, Hemiramphidae, and Belonidae) constituted the vast majority of prey items. However, sea robins (family Triglidae) and deepwater octopods *Grimpoteuthis* sp. were also present in the Voss (1953) study, and since these animals do not vertically migrate with the deep scattering layer, their presence also supports the view that sailfish are feeding at depth rather than opportunistically feeding on vertically migrating prey; the occurrence of *Grimpoteuthis* sp. in particular resulted in Voss (1953) concluding that "sailfish are not typical surface dwellers by habit." Jolley (1977) analyzed contents from stomachs of sailfish caught during daylight hours and found epipelagic fishes such as little tunny *Euthynnus alletteratus* and exocoetid flyingfishes. In contrast, Júnior et al. (2003) found mesopelagic fishes and cephalopods in sailfish stomachs collected from pelagic longline fisheries where the animals were caught during nighttime gear deployment periods. The observed pattern was of generally deeper, shorter-duration movements at night and shallower, longer ones during the day. Despite the difficulties in stomach content analyses (e.g., postcapture digestion), these prior diet studies nonetheless corroborate the vertical movement patterns observed in this study.

Habitat utilization of large pelagic fishes has been previously characterized by depth, temperature, or both (e.g., Weng and Block 2004; Sippel et al. 2007; Kerstetter et al. 2008). Several studies have suggested that istiophorids in particular prefer a narrow temperature range, such as Graves et al. (2002) with Atlantic blue marlin, Gunn et al. (2003) with Coral Sea black marlin *M. indica*, and Hoolihan and Luo (2007) for sailfish in the Arabian Gulf. The sailfish in this study showed no temperature distribution differences between years 2006 and 2007, suggesting that these tagged fish may have been consistently utilizing a specific temperature range between ~25–29°C. The two sailfish tracked by Jolley and Irby (1979) off the Florida coast did not dive below the local thermocline, but the tracks were very short in duration. The comparatively shallow waters of the Arabian Gulf also limited the range of temperatures available to be encountered by the sailfish described there, although no such limitation exists in the southern Gulf of Mexico and Florida Straits.

The so-called "thermal inertia" hypothesis suggests that large-bodied fishes retain heat and more effectively forage in colder waters for short periods of time than smaller fishes, although it has not been extensively tested across pelagic taxa (see Neill et al. 1976 with skipjack tuna *Katsuwonus pelamis* and Schaefer and Fuller 2005 with skipjack and bigeye tuna *Thunnus obesus*). Nonetheless, all billfishes and swordfish possess a brain-eye "heater organ" (Block 1986) that maintains these structures at higher temperatures than the ambient water, presumably to enable higher foraging efficiency in cooler waters and lower light intensities (Block and Finnerty 1994; Fritsches et al. 2005). While Block (1986) reported that the heater organ of sailfish was not as robust as that of the larger billfish species such as blue marlin, it could still provide a competitive predatory advantage to sailfish foraging in slightly colder subsurface waters. Brill and Lutcavage (2001) hypothesized that there was an absolute value for temperature that governed the

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vertical behavior of pelagic teleosts, which they estimated to be an 8°C difference between SST and temperature at depth for individual movements. The individual dive event analyses for sailfish in this study showed that 99.2% occurred within an 8°C difference, data that are very consistent with the Brill and Lutcavage (2001) hypothesis.

The dive events in these 16 tagged sailfish showed similarities with the V- and U-shaped patterns described in Horodysky et al. (2007) for white marlin, and although there was a continuum of bottom times, further analyses of the "bottom time" factor confirmed that there are two main types of individual dive events. These results suggest that this species may also engage in similar types of "search" (U) and "directed" (V) behaviors. U-shaped dives had deeper mean dive depths and longer dive durations than V-shaped dives, suggesting an undirected search pattern. Many individual daytime dives had a stepwise pattern of increasingly shallow depths, further suggesting a possible "skylighting" behavior of silhouetting prey against the bright surface. However, the vertical and horizontal behavior of sailfish is likely mediated by many different factors, including prey density, local oceanographic conditions, and perhaps even spawning events and seasonal effects as previously discussed. The varying behavior between the southeastern Gulf of Mexico sailfish in the present study and those described in Hoolihan (2005) from the Arabian Gulf may simply reflect these differences and preclude a "one-size-fits-all" conclusion on the behaviors of sailfish as a species.

Application to Stock Assessments

The role for habitat standardization models of pelagic longline catch-per-unit-effort (CPUE) data for stock assessment purposes, such as that proposed by Hinton and Nakano (1996), remains an area of considerable disagreement. This type of model directly relates population abundance with the joint probability of the depths of individual fish with fishing gear depths. As suggested by Kraus and Rooker (2007), a good deal of the concern regarding the application of these models to the billfishes relates to the incomplete knowledge of both pelagic longline gear behavior and the behaviors of the individual istiophorid species (see also Venizelos et al. 2001; Goodyear et al. 2003; Yokawa et al. 2001). For example, Boggs (1992) found that pelagic longline catch rates in the central Pacific were affected by overall gear depth and the position of the depth relative to the local thermocline. More recent efforts by Bigelow et al. (2006) and Rice et al. (2007) to describe the depths of the pelagic longline gear have begun to clarify some of the differences between the predicted depths of Yoshihara (1954) and the actual depths actively fished by the gear. However, the differences between geographic locations and the effects of surface and subsurface currents may preclude a simple assumption of actual fishing depths from gear characteristics alone (see discussion in Bigelow et al. 2006). Further modeling efforts are needed prior to the assumption of particular depths for any given gear configuration.

Similarly, the increasing number of studies of habitat utilization by swordfish, tunas, and billfishes has begun to elaborate the complex relationships involved in pelagic longline gear interactions (e.g., deployment time, bait). The higher utilization percentages for shallower depths by sailfish over several studies has suggested that it might be possible to reduce bycatch of sailfish by configuring shallow-set pelagic longline gear to fish "below" the depths utilized by the species. Recent work in the Pacific Ocean with experimental deep-set longline gear (minimum depths $>$ 100 m) showed significant reductions in catch rates of blue marlin, striped marlin, and shortbill spearfish *Tetrapturus angustirostris*, although the catch of sailfish was not significantly different (Beverly et al. 2009). Such experimental sets have yet to be done in the Atlantic Ocean and so cannot be evaluated here for potential sailfish bycatch reduction.

The TDRs in this study only monitored the lowest hook position within the pelagic longline "basket;" however, all other hook positions would presumably be at shallower depths and therefore would similarly have a high potential for sailfish interactions. While the majority of time at depth for sailfish is above the depths actively fished by shallow-set pelagic longline gear, the demonstrated frequent movements to depth of sailfish through this depth distribution likely negate most potential for bycatch reduction for the shallow-set, swordfish-targeting pelagic longline fishery through changes in gear depth alone. These results suggest that time-at-depth histograms alone may be insufficient to capture feeding motivations at depth and, therefore, true interaction potentials between individual sailfish and pelagic longline gear. As suggested by Kraus and Rooker (2007) and others, the role of deeper depths during short-duration dives by istiophorid billfishes, presumably for foraging events, may result in an ironic situation in which the depths of least amount of aggregate time are the depths of highest feeding motivation, and hence the depths of highest interaction potential with the baited hooks of pelagic longline gear. Until time at depth and feeding motivations can be more clearly modeled, particularly with respect to photoperiod, it remains premature to apply habitat-based stock assessment models to sailfish.

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