



Vertical habitat use of sailfish (*Istiophorus platypterus*) in the Atlantic and eastern Pacific, derived from pop-up satellite archival tag data

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ABSTRACT

Vertical habitat use of sailfish (*Istiophorus platypterus*) was evaluated using pop-up satellite archival tag data from the eastern tropical Atlantic, western North Atlantic, and eastern tropical Pacific. Data included Argos transmitted depth, temperature, and light level frequency histograms binned at 1–8-h intervals, and four recovered pop-up satellite archival tags that provided high resolution archival data recorded at 30-s intervals. We tabulated the proportions of time spent within each degree of water temperature relative to the surface temperature (Delta T) and proportions of time at temperature, as these are major input variables for habitat standardization models used in stock assessment procedures. Frequency distributions were calculated for daylight, darkness, and twilight for each of the three regions and for all regions combined. Vertical habitat envelopes indicated greater use of deeper strata in the western North Atlantic, compared to the hypoxia-based habitat compressed regions of the eastern Atlantic and Pacific. However, there were no significant differences in Delta T distributions when comparing the three regions, affirming this metric for its application in habitat standardization models.

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INTRODUCTION

Physiological attributes, foraging behavior, and environmental conditions are predominant traits influencing how billfish (Istiophoridae) utilize vertical habitat (Brill and Lutcavage, 2001; Prince and Goodyear, 2006; Prince *et al.*, 2010). Electronic tagging has been instrumental in understanding these traits (Arnold and Dewar, 2001), with the earliest studies using acoustic telemetry to monitor billfish for short (hours–days) periods (Jolley and Irby, 1979; Holts and Bedford, 1990; Block *et al.*, 1992). However, until the introduction of pop-up satellite archival tags (PSATs), there was minimal perception of the long-term (weeks–months) vertical behavior of billfish (Prince and Goodyear, 2006; Hoolihan and Luo, 2007).

PSAT technology established an effective fisheries-independent method to monitor depth (pressure), temperature, and ambient light levels over these extended periods (Block *et al.*, 1998; Arnold and Dewar, 2001) and has become an important tool for understanding how movement and habitat use by istiophorids are influenced by oceanographic conditions (Prince and Goodyear, 2006; Hoolihan and Luo, 2007; Goodyear *et al.*, 2008). In turn, behavioral adaptations resulting from physiological responses to oceanographic conditions are likely to affect vulnerability to some types of fishing gear (Prince *et al.*, 2010).

Many istiophorid stocks are considered overfished, mostly as a consequence of incidental and bycatch mortality from fisheries targeting swordfish (*Xiphias gladius*) and tunas (Serafy *et al.*, 2005). From a commercial point of view, istiophorids are generally valued less than target species and, consequently, information on billfish catches are frequently data-poor (Pilling *et al.*, 2008), a situation that has often compromised the stock assessment process (Prince and Brown, 1991). By including relevant biological data into the

billfish stock assessment process, the uncertainties associated with fishing gear interactions may be reduced (Goodyear *et al.*, 2008).

One approach for accomplishing this task is to parameterize catch rate models with PSAT behavioral data that characterizes habitat use and, therefore, vulnerability to various fishing gears (Brill and Lutcavage, 2001). For instance, the vulnerability of tunas and istiophorids to longline and surface fishing gears is correlated to both spatial and temporal characteristics of their vertical habitat distributions (Boggs, 1992; Nakano *et al.*, 1997; Bigelow and Maunder, 2007), which are influenced by distributions of prey species and oceanographic conditions (Prince and Goodyear, 2006; Prince *et al.*, 2010).

Studies have indicated that istiophorid billfish spend most of their time in the warmer shallow mixed layer above the thermocline (Gunn *et al.*, 2003; Goodyear *et al.*, 2008), with sailfish usually exhibiting a greater affinity for near-surface depths over continental shelves compared to other istiophorids (Prince and Goodyear, 2006; Hoolihan and Luo, 2007). Cardiac temperature thresholds are a major factor restricting the vertical habitat of istiophorids. The change in water temperature relative to the surface temperature (Delta T), rather than any particular temperature, limits their use of the water column (Brill and Lutcavage, 2001; Goodyear *et al.*, 2008). Istiophorids have physiological adaptations (e.g., brain heaters, enhanced photoreceptors) that allow brief ventures into deeper strata having lower temperatures and visibility, although depth distributions for time spent within the available water column are not well defined (Block, 1986; Fritsches *et al.*, 2003). Understanding depth distributions is useful for predicting vulnerability to fishing gears and improving estimates of relative abundance derived from catch rate indices (Bigelow and Maunder, 2007). The change in water temperature at-depth, relative to the surface temperature (Delta T), is a key environmental factor influencing the depth distribution, or vertical habitat preference, of istiophorids (Brill and Lutcavage, 2001; Goodyear *et al.*, 2008).

Hinton and Nakano (1996) introduced a habitat standardization model using Delta T values from blue marlin (*Makaira nigricans*) to predict the proportions of time spent at various depth strata, the purpose being to differentiate between the variation in abundance and availability estimates derived from longline catch rate indices. Information on vertical habitat preference (i.e., Delta T) and hook depth are crucial data input components for such habitat-based models (Ward and Myers, 2006). Only a few PSAT studies have described sailfish vertical habitat use (Prince and Goodyear,

2006; Hoolihan and Luo, 2007; Prince *et al.*, 2010) and these lacked the Delta T metric and detailed data needed for habitat standardization models (Hinton and Nakano, 1996; Bigelow *et al.*, 2002).

The objectives of the present study were to analyze temperature and depth data provided from 63 PSAT-monitored sailfish for the purpose of describing detailed vertical habitat use and to present the data in a compatible form (Delta T percentiles) necessary for estimating the spatial and temporal distributions and relative abundance of sailfish when using habitat standardization models.

METHODS

Our analyses included data from 63 PSATs deployed on sailfish during 2003–2006 in the eastern tropical Atlantic (ETA), western North Atlantic (WNA), and eastern tropical Pacific (ETP, Fig. 1). Release and pop-up locations were estimated from vessel global positioning systems and Argos transmissions, respectively (Table 1). We used Wildlife Computers (Redmond, WA, USA) PAT models 2, 3, 4, and Mk10 PSATs programmed to sample depth (pressure), ambient temperature, and light level (Table 1). The study animals were captured with recreational rod and reel gear. After being brought alongside the vessel, PSATs rigged with monofilament tethers and medical grade nylon anchors were attached by inserting the anchor into the dorsal musculature. The protocol used for fish handling, tag anchor placement, and resuscitation procedures followed those described by Prince and Goodyear (2006).

PSAT sampling intervals were programmed for 30 or 60 s; however, for Argos transmission efficiency the data were summarized and compiled into larger temporal blocks ranging from 1 to 8 h (Arnold and Dewar, 2001). Bin profiles for depth and temperature varied between the earlier PAT models 2 and 3 (12 bins), and the newer Mk 10 (14 bins, Table 2). The Argos transmitted summary data for each temporal block consisted of: (i) the proportion of time spent within each temperature bin (2°C bin resolution); (ii) the proportion of time spent within each depth bin (25 m resolution); and (iii) PAT Depth-Temperature (PDT) profile messages: the minimum and maximum temperatures for eight depth intervals that include the minimum and maximum depths and six additional points between those depths. Linear methods, as described by Goodyear *et al.* (2008), were used to interpolate the distribution patterns of pooled data by hours of darkness, twilight, and daylight to 1°C temperature bins and 10 m depth bins.

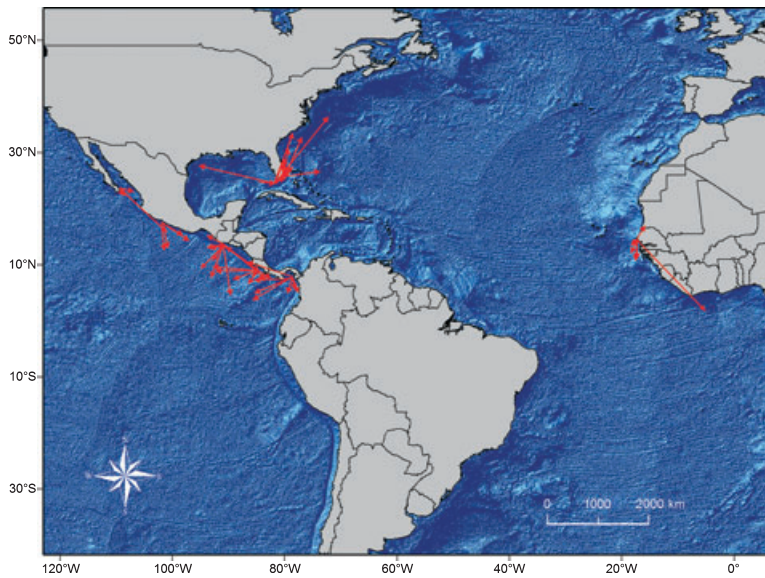


Figure 1. Linear displacements from point of release to point of first Argos transmission for 63 pop-up satellite archival tags deployed during 2003–2006 on sailfish in the Atlantic and eastern Pacific.

We assembled the proportions of records within successively deeper layers of temperature, relative to the surface temperature (termed Delta T), by each bin hour for periods of darkness, twilight, and daylight. Mean Delta T values were calculated for each distribution. Average daily surface temperature (T_0) was calculated by extracting the temperatures from PDT data where depth was ≤ 1 m. When surface temperatures were lacking, previous and subsequent day records were used to linearly interpolate values. Next, temperature estimates were generated (720 per hour) for each depth bin using a random normal distribution based on the PDT temperature range. A histogram of the generated temperatures was then compared to the histogram from the temperature (T) data. Any differences in numbers for each bin were corrected by randomly removing values in positive bins or adding values to negative bins (Luo *et al.*, 2006). Delta Ts were then assembled by subtracting the generated temperature values from T_0 values and tabulating the proportion of time spent at decreasing temperatures using 1°C bin resolution.

When generating the Delta T distributions, the high resolution archival data from four recovered PSATs were pooled with the Argos transmitted summary data. The archival data consisted of the actual depth, temperature, and light measurements recorded at 30 or 60 s intervals. Inclusion of the archival data helped to differentiate the twilight period, hereafter defined as the 2-h period centered at the transition in light intensity between dusk and dawn.

The mean Delta T distributions were calculated and ranked by increasing depth for periods of darkness,

twilight, and daylight. Regional groups (WNA, ETA, and ETP) were treated separately, and also pooled together for comparison. Several percentiles were then tabulated for each of the observed frequency distributions. For graphical presentation, vertical habitat envelopes depicting percent time spent at Delta T and depth were generated for each of the regions (Luo *et al.*, 2006). Minimum temperatures and maximum depth for each day at liberty were compiled to demonstrate the deepest and coldest strata encountered by our sailfish. Regressions were carried out on the days at liberty when sailfish encountered deeper or colder strata during their daily vertical movements.

Lastly, light attenuation coefficients were estimated for the four recovered PSATs. Light level was measured as irradiance at a wavelength of 550 nm. The sensor measures from 5×10^{-12} to $5 \times 10^{-2} \text{ W cm}^{-2}$ in logarithmic units. Light attenuation coefficients (k_t) were estimated for each time step (t) based on the light level and depth data according to:

$$k_t = (\ln(LL_t) - \ln(LL_{t+1})) \times 0.05(\ln(10)) / (D_{t+1} - D_t) \quad (1)$$

where $\ln(LL_t)$ and $\ln(LL_{t+1})$ are the logarithmic light units in db at time t and $t + 1$, as recorded by Wildlife Computer's PSATs; and, where D_t and D_{t+1} are the depth at time t and $t + 1$. We estimated k_t for all time steps where the absolute value of $(D_{t+1} - D_t) > 5$ m, then calculated the depth profile of light attenuation coefficient (k_D) for each recovered PSAT by averaging all k_t at each depth bin (D). Finally, we used k_D to calculate the light level for each depth (L_D) relative to the surface:

Table 1. *Istiophorus platypterus*. Summary details for setup, release, and pop-up/recovery from 63 pop-up satellite archival tags deployed on sailfish. Number of days data received denotes a minimum one message received per calendar day from transmitted data or recovered archival data.

No.	PTT* ID	PAT version	Release date	Sampling interval (s)	Summary data bin (h)	Days at liberty/days programmed	Displacement (km)	Release area	Release location (ddmm)	Location of first transmission	No. days data received†
1	67990	Mk10	8-Aug-06	30	3	46/120	268	Mexico	23°40'N, 109°24'W	23°01'N, 106°52'W	47
2	67991	Mk10	9-Aug-06	30	3	109/120	1238	Mexico	23°35'N, 109°23'W	15°46'N, 100°59'W	19
3	67992	Mk10	9-Aug-06	30	3	63/90	182	Mexico	23°36'N, 109°28'W	22°19'N, 108°23'W	42
4	68017	Mk10	10-Aug-06	30	3	57/150	153	Mexico	23°30'N, 109°24'W	22°18'N, 108°40'W	61
5	66699	Mk10	28-Jun-06	30	3	114/120	382	Senegal	14°04'N, 17°10'W	10°40'N, 17°32'W	84
6	66700	Mk10	26-Jun-06	30	3	90/90	86	Senegal	14°03'N, 17°10'W	13°27'N, 17°40'W	79
7	66703	Mk10	2-Jul-06	30	3	90/90	298	Senegal	14°27'N, 17°14'W	12°00'N, 18°20'W	72
8	66704	Mk10	2-Jul-06	30	3	116/120	52	Senegal	14°26'N, 17°16'W	13°59'N, 17°11'W	91
9	66705	Mk10	2-Jul-06	30	3	90/90	380	Senegal	14°26'N, 17°16'W	11°01'N, 17°16'W	84
10	66707	Mk10	2-Jul-06	30	3	21/90	20	Senegal	14°26'N, 17°14'W	14°24'N, 17°03'W	22
11	66708	Mk10	3-Jul-06	30	3	145/120	163	Senegal	14°27'N, 17°14'W	13°26'N, 18°19'W	90
12	57176	4	25-Apr-05	30	8	118/120	1057	Florida, US	24°25'N, 81°55'W	33°26'N, 78°32'W	107
13	57177	4	8-May-05	30	8	119/120	448	Florida, US	24°29'N, 81°32'W	27°27'N, 78°30'W	119
14	57178	4	28-Apr-05	30	8	119/120	417	Florida, US	24°25'N, 81°53'W	27°50'N, 80°10'W	113
15	57179	4	11-May-05	30	8	135/120	241	Florida, US	24°29'N, 81°32'W	26°06'N, 79°57'W	135 [‡]
16	57180	4	3-May-05	30	8	120/120	1406	Florida, US	24°27'N, 81°41'W	27°38'N, 95°16'W	114
17	57181	4	8-May-05	30	8	118/120	228	Florida, US	24°27'N, 81°45'W	25°47'N, 79°58'W	105
18	57182	4	8-May-05	30	8	120/120	1611	Florida, US	24°26'N, 81°48'W	36°19'N, 72°12'W	112
19	57183	4	8-May-05	30	8	6/120	4	Florida, US	24°27'N, 81°45'W	24°28'N, 81°43'W	8
20	57184	4	10-May-05	30	8	120/120	291	Florida, US	24°47'N, 84°33'W	24°27'N, 81°42'W	121 [‡]
21	57188	4	3-May-05	30	8	5/120	395	Florida, US	25°20'N, 80°08'W	28°52'N, 79°58'W	20
22	57189	4	3-May-05	30	8	6/120	879	Florida, US	25°21'N, 80°07'W	32°43'N, 76°55'W	7
23	39337	Mk10	6-Dec-05	30	1	7/7	377	Florida, US	24°58'N, 80°31'W	28°20'N, 80°12'W	8
24	49033	Mk10	6-Dec-05	30	1	7/7	35	Florida, US	24°55'N, 80°34'W	25°04'N, 80°16'W	8
25	40615	Mk10	19-Jan-06	30	4	28/90	656	Florida, US	24°55'N, 80°34'W	30°42'N, 79°19'W	27
26	57196	4	4-Jul-05	30	4	60/60	125	Senegal	14°30'N, 17°21'W	13°23'N, 17°25'W	60*
27	57197	4	4-Jul-05	30	4	5/120	61	Senegal	14°30'N, 17°21'W	13°58'N, 17°12'W	8
28	57199	4	5-Jul-05	30	4	46/45	41	Senegal	14°35'N, 17°24'W	14°13'N, 17°18'W	47
29	57201	4	7-Jul-05	30	4	95/90	1946	Senegal	14°25'N, 17°19'W	01°45'N, 05°06'W	73
30	49776	4	26-Jun-04	30	8	43/45	307	Panama	07°33'N, 78°34'W	04°58'N, 77°35'W	46
31	49779	4	26-Jun-04	30	8	59/60	312	Panama	07°31'N, 78°38'W	04°52'N, 79°32'W	26
32	49780	4	26-Jun-04	30	8	65/90	812	Panama	07°41'N, 78°35'W	04°56'N, 85°23'W	47
33	49782	4	26-Jun-04	30	8	45/45	236	Panama	07°36'N, 78°38'W	05°33'N, 78°07'W	46
34	52260	4	28-Jun-04	30	8	53/60	941	Panama	07°47'N, 78°33'W	10°27'N, 86°40'W	51

Table 1. (Continued)

No.	PTT* ID	PAT version	Release date	Sampling interval (s)	Summary data bin (h)	Days at liberty/days programmed	Displacement (km)	Release area	Release location (ddmm)	Location of first transmission	No. days data received [†]
35	52261	4	28-Jun-04	30	8	88/90	892	Panama	07°43'N, 78°45'W	03°40'N, 85°41'W	40
36	52262	4	27-Jun-04	30	8	5/45	82	Panama	07°30'N, 78°27'W	07°32'N, 79°12'W	7
37	52263	4	27-Jun-04	30	8	56/90	765	Panama	07°30'N, 78°28'W	07°11'N, 85°22'W	56
38	52265	4	27-Jun-04	30	8	26/120	101	Panama	07°31'N, 78°29'W	06°38'N, 78°18'W	26
39	41548	3	15-Jan-04	30	8	19/91	445	Mexico	17°22'N, 101°38'W	15°13'N, 98°08'W	20
40	41549	3	15-Jan-04	30	8	25/61	534	Mexico	17°37'N, 101°43'W	12°54'N, 100°48'W	25
41	46094	3	16-Jan-04	30	8	30/92	553	Mexico	17°28'N, 101°58'W	12°32'N, 101°26'W	33
42	46097	3	17-Jan-04	30	8	22/62	642	Mexico	17°31'N, 101°57'W	14°15'N, 97°01'W	24
43	42721	3	23-Jan-04	30	8	52/61	140	Florida, US	25°41'N, 80°05'W	26°56'N, 79°59'W	22
44	39334	3	3-Apr-03	60	3	8/7	172	Florida, US	25°44'N, 80°17'W	26°43'N, 78°57'W	8
45	39335	3	3-Mar-03	60	3	8/7	220	Florida, US	25°49'N, 80°04'W	27°48'N, 79°57'W	8
46	40606	3	30-Apr-03	60	3	62/60	658	Florida, US	25°42'N, 80°10'W	26°36'N, 73°40'W	63
47	25340	2	17-Nov-03	30	8	61/61	329	Guatemala	13°37'N, 90°51'W	13°02'N, 93°49'W	42
48	25344	2	18-Nov-03	30	2	29/59	361	Guatemala	13°22'N, 90°55'W	10°43'N, 92°50'W	29
49	1900	3	17-Nov-03	30	8	48/90	1060	Guatemala	13°37'N, 90°51'W	07°30'N, 83°25'W	49 [‡]
50	41512	3	17-Nov-03	30	8	53/92	365	Guatemala	13°38'N, 90°51'W	15°10'N, 93°50'W	55
51	41532	3	17-Nov-03	30	8	54/92	280	Guatemala	13°39'N, 90°51'W	12°46'N, 93°16'W	55
52	41533	3	17-Nov-03	60	8	90/92	713	Guatemala	13°39'N, 90°50'W	07°40'N, 93°09'W	71
53	41541	3	18-Nov-03	30	8	72/121	868	Guatemala	13°21'N, 90°55'W	08°45'N, 84°29'W	75
54	41545	3	18-Nov-03	30	8	22/94	633	Guatemala	13°21'N, 90°55'W	09°18'N, 94°59'W	23
55	42583	4	18-Nov-03	30	8	106/121	123	Guatemala	13°22'N, 90°55'W	13°10'N, 92°01'W	47
56	41542	3	18-Nov-03	30	8	118/124	998	Guatemala	13°22'N, 90°55'W	04°30'N, 89°38'W	62
57	23077	2	10-Mar-03	60	3	30/30	168	Costa Rica	09°00'N, 84°46'W	07°55'N, 85°49'W	31
58	23022a	2	10-Mar-03	60	3	21/24	246	Costa Rica	08°58'N, 84°46'W	07°04'N, 83°38'W	30
59	22870	2	10-Mar-03	60	3	40/40	827	Costa Rica	08°58'N, 84°46'W	08°49'N, 92°17'W	40
60	22873	2	11-Mar-03	60	3	59/59	884	Costa Rica	08°52'N, 84°46'W	09°34'N, 92°46'W	56
61	23022b	2	11-Mar-03	60	3	29/29	300	Costa Rica	08°58'N, 84°46'W	07°34'N, 82°27'W	29
62	25379	2	11-Mar-03	60	3	29/29	514	Costa Rica	08°58'N, 84°46'W	07°23'N, 89°09'W	30
63	23442	2	12-Mar-03	60	3	29/28	327	Costa Rica	08°57'N, 84°45'W	06°31'N, 86°26'W	28

*PTT, platform transmitter terminal.

[†]Number of calendar days represented by Argos transmission, not necessarily an entire dataset for any particular 24 h period.

[‡]Recovery of intact PSAT. For these cases, detailed data were available for all days at liberty.

Table 2. Histograms setup limits for depth and temperature for PAT 2, 3, 4 (12 bins), and Mk 10 (14 bins) tag models deployed on sailfish.

PAT 2, 3, and 4		Mk 10	
Depth (m)	Temp (°C)	Depth (m)	Temp (°C)
-1	12	25	6
25	14	50	8
50	16	75	10
75	18	100	12
100	20	125	14
125	22	150	16
150	24	175	18
175	26	200	20
200	28	300	22
225	30	400	24
250	32	500	26
1000	60	600	28
		700	30
		>700	>30

$$L_D = L_{D-1} e^{-k_D \times \Delta D} \quad (2)$$

where we set surface light level (L_0) to 100% and depth interval (ΔD) to 1 m.

RESULTS

A total of 63 sailfish monitored with PSATs in the ETA, WNA, and ETP regions were evaluated for the proportion of time spent at temperature relative to the surface temperature (Delta T). Diel differences in vertical behavior were compared using 1595 sets of histograms derived for the period of darkness, 1110 sets for twilight, and 1920 sets for daylight. No significant differences were detected between regional groups when comparing the mean Delta T distributions for darkness, twilight, and daylight (Kolmogorov–Smirnov test). For this reason, we pooled the Delta T distributions from all 63 individuals as a single group (Table 3). Nevertheless, individual Delta T distributions for the ETA, WNA, and ETP are provided as Supporting Information tables (Appendices S1–S3). Each table contains Delta T values that can be directly applied to habitat standardization models (Hinton and Nakano, 1996; Bigelow *et al.*, 2002). The percentiles of mean Delta T for the pooled group indicated that about 93% of darkness, 86% of twilight, and 82% of daylight hours were spent near the surface (i.e., Delta T = 0; Table 3). Variability among the distributions for the percentiles of mean Delta T is evident in Table 3. For example, the percentage of time at depths occupied by the Delta T distribution with median

mean depths (i.e., 0.500) showed 96, 83, and 81% of time was spent at the surface for darkness, twilight, and daylight hours, respectively (Table 3). The range and means of observations associated with the proportions of time spent at Delta T are illustrated for periods of darkness (Fig. 2a), twilight (Fig. 2b), and daylight (Fig. 2c). Examination of the detailed archival data from recovered tags revealed that the actual use of available vertical habitat by sailfish is more complex than suggested by the proportions of time spent at-depth and temperature alone. As an example, the daily activity of sailfish PTT 57179 (Fig. 3) shows vertical activities mostly limited to <100 m depth, and characterized by frequent short-duration dives followed by a return to the surface. The occurrence of frequent short-duration dives is an important consideration, as they are likely to increase the rate of interaction with pelagic longline hooks.

Although sailfish in this study exhibited an obvious preference for areas near the surface, diving to deeper and colder depths occurred. Because of their low occurrence, deep dive events were more likely to be detected as days at liberty increased. To demonstrate this, we analyzed the maximum depths and minimum temperatures by days at liberty to determine the effect of deepest recorded dives on vertical habitat use (Figs 4 and 5). Evidence of exploration to deeper strata (maximum recorded depth, D_{\max}) during the daily movements of PSAT-monitored sailfish increased with days at liberty, T ($D_{\max} = 42.29T^{0.283}$; $r^2 = 0.329$; $F = 1322.7$; $P < 0.001$; 271 df), although the overall pattern showed high daily variability (Fig. 4). One sailfish (PTT 57179) ventured as deep as 340 m off the eastern coast of Florida (Table 1, Fig. 4). There was a corresponding increase in the minimum observed temperature, C_{\min} , with increasing days at liberty ($C_{\min} = 24.06T^{-0.131}$; $r^2 = 0.407$; $F = 205.2$; 299 df), but again with high daily variability (Fig. 5).

Means for the proportions of time spent at Delta T, separated by region, are provided in Table 4. The ETA group spent the greatest proportion of time at surface temperature, followed by the ETP and WNA groups. Mean temperature at-depth for the three groups indicate stronger thermoclines in the ETA and ETP, compared to the WNA (Table 4). Time spent at Delta T and depth, which is illustrated in the vertical habitat envelopes (Fig. 6), clearly shows the WNA group spending more time exploring deeper strata.

We recovered two PSATs from the WNA, and one each from the ETP and ETA. The depth profiles of light attenuation coefficients (k_D) are shown in Fig. 7a. In general, the largest k_D occurs at the surface

Table 3. Proportions of time spent by sailfish *Istiophorus platypterus* at temperature relative to the surface temperature (Delta T) during darkness, twilight, and daylight, based on combined Argos-transmitted and archival PSAT data. Dashes indicate zero probability. Data were sorted in order of decreasing Delta T (left column), then proportions of time spent at various temperatures were calculated for a range of percentiles. As an example, for 75% of the data points during darkness (top row), 85.3% were at surface temperature and 2.0% were at 2° below surface temperature.

Delta T	Percentile of mean Delta T											Mean
	0.010	0.025	0.050	0.100	0.250	0.500	0.750	0.900	0.950	0.975	0.990	
<i>Darkness</i> (N = 1595)												
0	1.000	1.000	1.000	1.000	0.997	0.963	0.853	0.859	0.861	0.855	0.842	0.930
-1	–	–	–	–	0.002	0.024	0.106	0.097	0.093	0.095	0.100	0.047
-2	–	–	–	–	–	0.006	0.020	0.021	0.021	0.024	0.030	0.011
-3	–	–	–	–	–	0.003	0.010	0.011	0.011	0.012	0.015	0.006
-4	–	–	–	–	–	0.002	0.004	0.005	0.006	0.006	0.006	0.003
-5	–	–	–	–	–	0.001	0.003	0.003	0.003	0.003	0.003	0.002
-6	–	–	–	–	–	0.001	0.002	0.002	0.002	0.002	0.002	0.001
-7	–	–	–	–	–	0.001	0.002	0.002	0.002	0.001	0.001	0.001
-8	–	–	–	–	–	–	–	–	–	–	–	0.000
-9	–	–	–	–	–	–	–	–	–	–	–	0.000
-10	–	–	–	–	–	–	–	–	–	–	–	0.000
-11	–	–	–	–	–	–	–	–	–	–	–	0.000
-12	–	–	–	–	–	–	–	–	–	–	–	0.000
-13	–	–	–	–	–	–	–	–	–	–	–	0.000
-14	–	–	–	–	–	–	–	–	–	–	–	0.000
<i>Twilight</i> (N = 1110)												
0	1.000	1.000	1.000	0.999	0.959	0.834	0.736	0.739	0.736	0.734	0.733	0.861
-1	–	–	–	0.001	0.024	0.112	0.147	0.139	0.137	0.137	0.136	0.076
-2	–	–	–	–	0.007	0.022	0.037	0.039	0.040	0.040	0.040	0.021
-3	–	–	–	–	0.003	0.009	0.023	0.026	0.028	0.028	0.028	0.013
-4	–	–	–	–	0.001	0.006	0.013	0.015	0.016	0.017	0.017	0.008
-5	–	–	–	–	0.001	0.003	0.008	0.009	0.010	0.010	0.010	0.005
-6	–	–	–	–	0.001	0.003	0.007	0.007	0.007	0.007	0.007	0.004
-7	–	–	–	–	0.002	0.002	0.006	0.005	0.006	0.006	0.006	0.003
-8	–	–	–	–	0.002	0.003	0.007	0.006	0.006	0.006	0.007	0.003
-9	–	–	–	–	0.001	0.002	0.006	0.005	0.005	0.005	0.006	0.003
-10	–	–	–	–	–	0.001	0.005	0.005	0.004	0.005	0.005	0.002
-11	–	–	–	–	–	–	0.002	0.002	0.002	0.002	0.002	0.001
-12	–	–	–	–	–	–	0.002	0.001	0.001	0.001	0.002	0.001
-13	–	–	–	–	–	–	0.001	0.001	0.001	0.001	0.001	0.000
-14	–	–	–	–	–	–	–	–	–	–	–	0.000
<i>Daylight</i> (N = 1920)												
0	1.000	1.000	1.000	0.999	0.951	0.814	0.679	0.641	0.635	0.630	0.626	0.816
-1	–	–	–	–	0.027	0.094	0.149	0.152	0.150	0.150	0.151	0.079
-2	–	–	–	–	0.008	0.031	0.062	0.069	0.069	0.069	0.069	0.034
-3	–	–	–	–	0.003	0.018	0.038	0.046	0.048	0.048	0.049	0.023
-4	–	–	–	–	0.003	0.014	0.022	0.028	0.031	0.032	0.033	0.015
-5	–	–	–	–	0.002	0.008	0.013	0.016	0.017	0.018	0.019	0.009
-6	–	–	–	–	0.002	0.006	0.010	0.012	0.013	0.014	0.014	0.007
-7	–	–	–	–	0.001	0.004	0.007	0.009	0.010	0.010	0.010	0.005
-8	–	–	–	–	0.001	0.004	0.006	0.008	0.008	0.009	0.009	0.004
-9	–	–	–	–	0.001	0.003	0.005	0.007	0.008	0.008	0.008	0.004
-10	–	–	–	–	–	0.002	0.003	0.005	0.005	0.006	0.006	0.002
-11	–	–	–	–	0.001	0.001	0.003	0.003	0.003	0.004	0.004	0.002
-12	–	–	–	–	–	0.001	0.001	0.002	0.002	0.002	0.002	0.001
-13	–	–	–	–	–	–	0.001	0.001	0.001	0.001	0.001	0.000
-14	–	–	–	–	–	–	–	–	–	–	–	0.000

Figure 2. *Istiophorus platypterus*. Proportions of time spent by Delta T (relative to the surface temperature, (a) during period of darkness, (b) during period of twilight, and (c) during period of daylight estimated from 63 PSAT-monitored sailfish. Shaded bars denote the range of observation (shown by small gray dots). Red circles and associated error bars denote means and 95% confidence intervals.

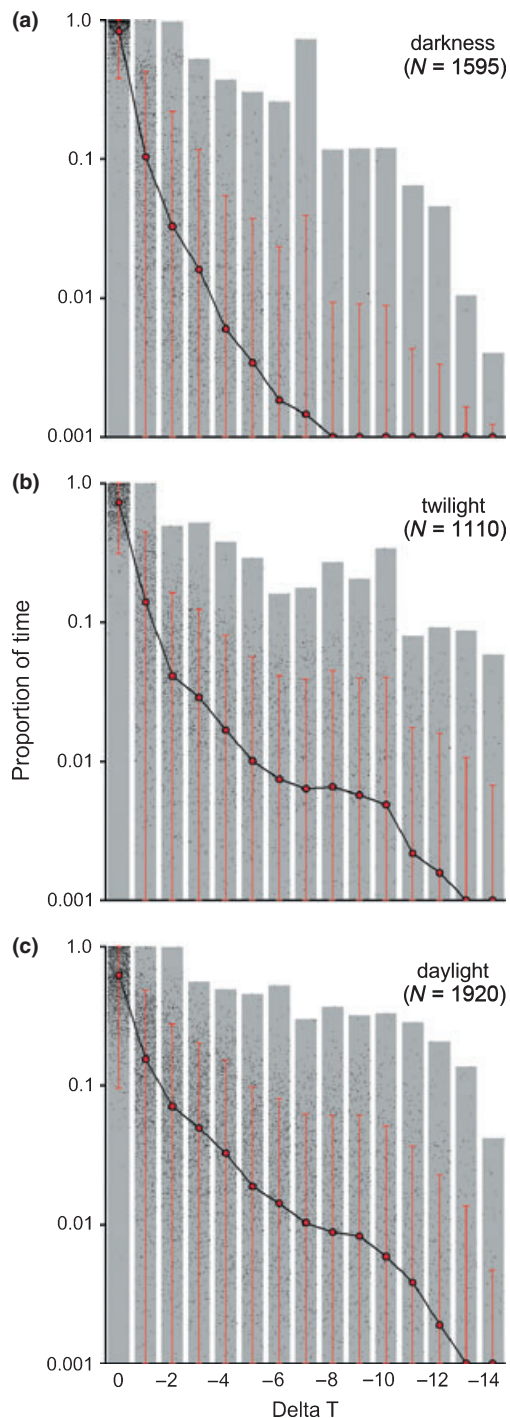
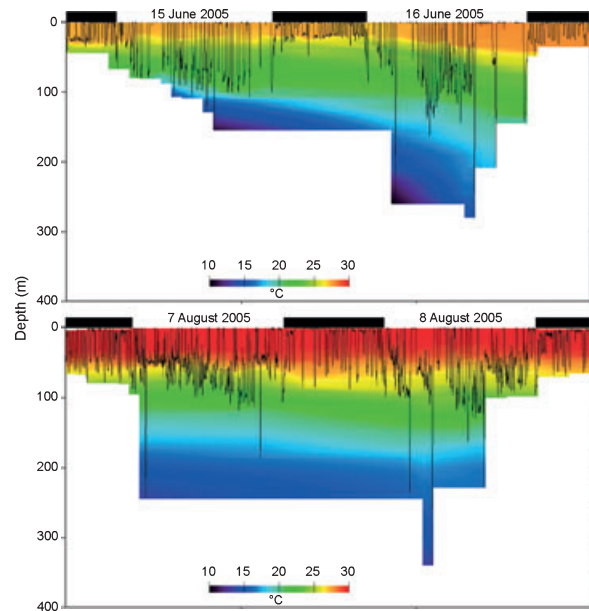


Figure 3. *Istiophorus platypterus*. Time series excerpts from 15–16 June 2005 (upper panel) and 7–8 August 2005 (lower panel) showing depth and temperature measurements for sailfish PTT 57179 that was later recovered (see Table 1).



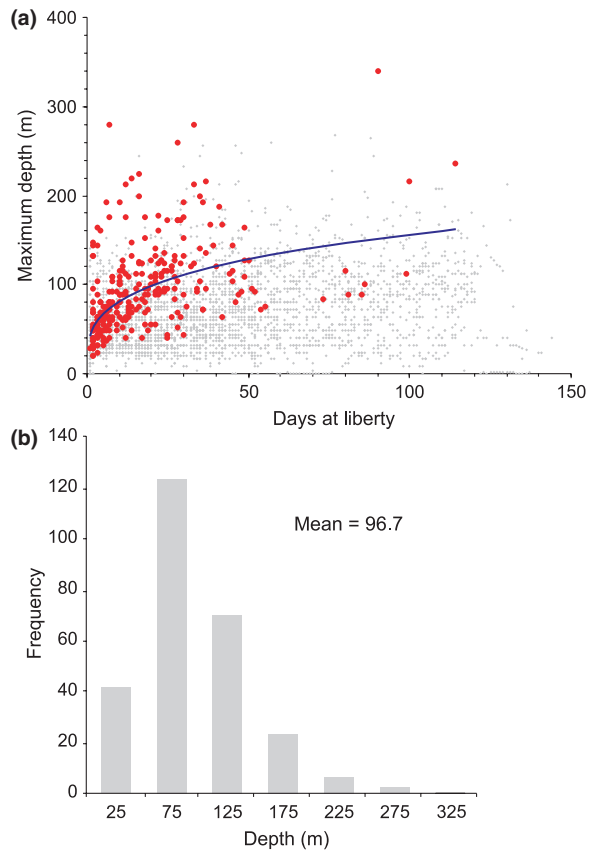
and decreases with depth. The average light attenuation coefficients for the top 50 m were 0.111, 0.124, 0.154, and 0.167 m^{-1} for the WNA1, WNA2, ETP, and ETA, respectively. The relative light level profiles are shown in Fig. 7b, where the depths of 0.01% surface light are 88, 74, 63, and 55 m for the WNA1, WNA2, ETP, and ETA, respectively. The cumulative depth frequency distribution (Fig. 7c) indicated that sailfish spent 95% of time above 92, 76, 46, and 32 m for the WNA1, WNA2, ETP, and ETA, respectively.

DISCUSSION

This study has presented an analysis of vertical movement for 63 PSAT-monitored sailfish derived from 2818 days of Argos summary data and 365 days of high resolution (30-s interval) archival data. In terms of the number of observations, length of duration, and geographical range, it offers the most comprehensive description of sailfish vertical habitat use reported to date. Furthermore, it presents the first tabulated distributions of Delta T values, a metric that can be applied directly to habitat standardization models (Hinton and Nakano, 1996; Bigelow *et al.*, 2002) to facilitate predictions for vertical distribution and relative abundance of sailfish.

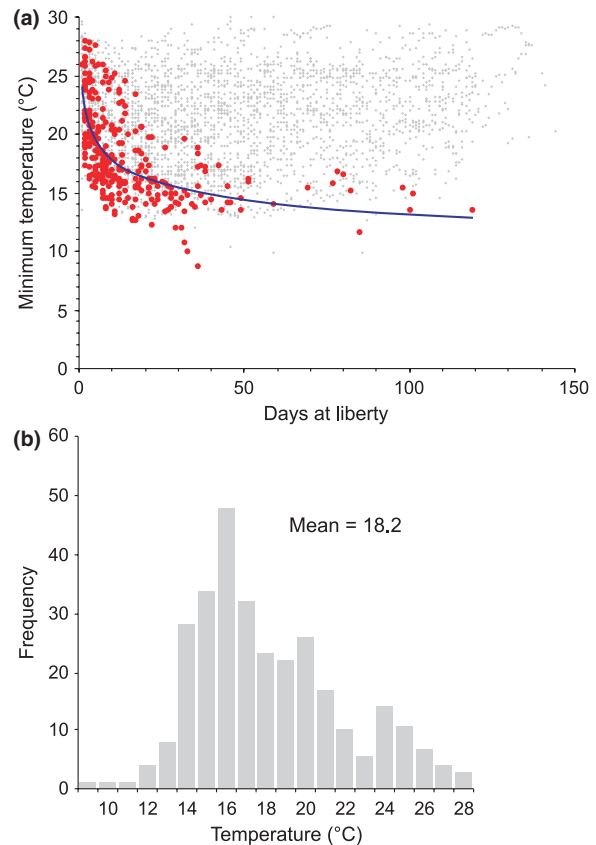
The time spent in various temperature strata indicate that sailfish have a generally greater prefer-

Figure 4. *Istiophorus platypterus*. Maximum depths reached by sailfish during time at liberty. (a) Deepest dives recorded during individual time bins (gray dots). Red dots denote first records of each fish at the observed depth. Blue line is the exponential fit to the first occurrence data. (b) Deepest dives observed for each fish.



ence for warmer near-surface depths than other istiophorids (ICCAT, 2002). For a large proportion of daylight hours (~82%), sailfish in the present study remained at surface temperature. This is similar to the 80% of daylight hours spent above 10 m reported for sailfish monitored with acoustic telemetry and PSATs in the Arabian Gulf (Hoolihan, 2005; Hoolihan and Luo, 2007). In comparison, blue marlin spent only around 46% of daylight hours in depths above 30 m (Prince and Goodyear, 2006), white marlin spent about 53% of total time above 25 m (Prince *et al.*, 2005), and striped marlin spent >50% of the time above 5 m (Sippel *et al.*, 2007). During darkness, sailfish spent a greater proportion of time near the surface (93.0%), which is consistent with behavior reported for other istiophorid species (Prince *et al.*, 2005; Prince and Goodyear, 2006; Sippel *et al.*, 2007). Because all istiophorids are visual

Figure 5. *Istiophorus platypterus*. Minimum temperatures experienced by each sailfish during time at liberty. (a) Lowest temperature recorded during individual time bins (gray dots). Red dots denote first records of each fish at the observed temperature. (b) Lowest temperatures observed for each fish.



feeders, they must limit foraging activities to periods with adequate visibility. Vertical excursions, which are often associated with istiophorid foraging activity, occur most often during daylight periods (Hoolihan *et al.*, 2009). Accordingly, spending as much time as possible in warmer surface temperatures during periods of decreased activity (darkness) may serve as an energy-saving opportunity.

Brill *et al.* (1993) concluded that istiophorids prefer the warmest water available and that the change in water temperature rather than a specific temperature is what governs vertical distribution, given that adequate dissolved oxygen is available. The similarity in distributions for the range and time spent at Delta T exhibited by sailfish in the ETA, ETP, and WNA support this conclusion. Further, Brill *et al.* (1993) concluded that the maximum Delta T visited is usually no more than ~8°C below the surface temperature, due to cardiac temperature thresholds that limit the

ability of istiophorids to endure cold extremes over extended periods (Brill *et al.*, 1999). Sailfish in the present study spent <1% of their time in strata colder than -8°C and exhibited less individual variability in overall vertical habitat use compared to the more stochastic and complex behavior described for blue marlin (Goodyear *et al.*, 2008). Both sailfish and blue marlin are primarily cold-blooded, but do possess brain and eye heater tissue that support functionality of these organs as ambient temperatures decrease (Block, 1986). In fact, one sailfish in the present study experienced temperatures as low as 8.7°C . However, sailfish are much smaller and more laterally compressed than blue marlin, limiting their capacity to retain body heat when exploring colder depths for extended periods. PSAT studies indicate that blue marlin routinely take greater advantage of deeper strata compared to

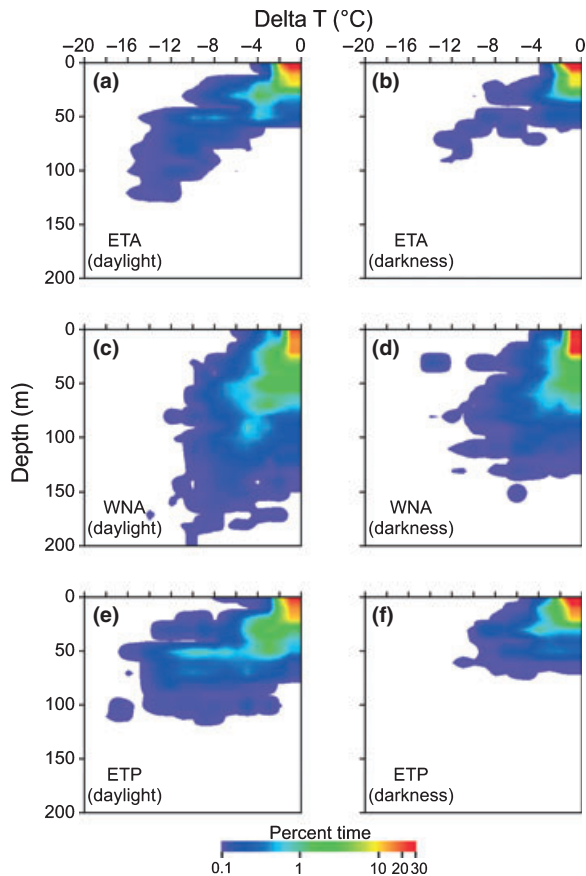
sailfish (Prince and Goodyear, 2006; Goodyear *et al.*, 2008). Further, the maximum depth of 804 m recorded by a PSAT for blue marlin (Goodyear *et al.*, 2008) is well beyond the 340 m recorded for sailfish in the present study. Consequently, in terms of Delta T, the greater body mass and ability to explore deeper and colder strata contributes to the more variable use of vertical habitat by blue marlin.

Oceanographic similarities between the ETA, WNA, and ETP include having water temperature and DO levels that are inversely proportional to depth (Prince and Goodyear, 2006; Prince *et al.*, 2010). However, the WNA lacks the vast oxygen minimum zones (OMZs) that distinguish the ETA and ETP (Helly and Levin, 2004; Stramma *et al.*, 2008). Consequently, the vertical profiles for temperature and DO vary between the regions (Prince and Goodyear, 2006;

Table 4. Number of records, means, and standard deviations for temperature at depth for 63 sailfish monitored with PSATs in the western North Atlantic (WNA), eastern tropical Atlantic (ETA), and eastern tropical Pacific, generated from Argos summary data.

Depth (m)	WNA (N = 18)		ETA (N = 11)		ETP (N = 34)	
	No. records	$^{\circ}\text{C}$ Mean (SD)	No. records	$^{\circ}\text{C}$ Mean (SD)	No. records	$^{\circ}\text{C}$ Mean (SD)
5	164819	27.8 (2.18)	121079	27.9 (0.88)	217577	28.5 (1.44)
15	129895	27.3 (2.09)	58737	28.0 (0.82)	228009	27.9 (1.63)
25	160467	27.8 (2.24)	248853	28.1 (0.99)	217539	28.4 (1.73)
35	47261	26.8 (2.38)	5216	26.3 (1.56)	48444	25.0 (3.72)
45	33927	27.2 (2.08)	3811	26.3 (1.52)	22135	26.5 (2.31)
55	61992	26.8 (2.10)	21949	25.8 (2.08)	36837	25.6 (2.86)
65	28540	25.6 (2.31)	699	21.2 (2.37)	10542	22.2 (3.52)
75	30336	26.0 (2.02)	3168	21.5 (2.20)	11165	23.4 (2.93)
85	12304	24.8 (1.98)	279	19.4 (2.56)	2639	19.9 (3.29)
95	7723	25.5 (1.51)	258	18.7 (1.37)	1078	21.4 (3.27)
105	8236	24.7 (1.79)	700	18.8 (1.55)	1588	21.4 (3.47)
115	4625	24.3 (1.91)	3	16.4 (0.48)	737	18.0 (2.92)
125	2538	24.1 (1.66)	94	17.4 (1.12)	240	16.1 (2.88)
135	1112	23.3 (1.85)	8	15.1 (0.24)	222	15.0 (2.58)
145	634	23.3 (1.60)	0	–	52	14.6 (2.65)
155	594	22.5 (2.07)	21	16.0 (1.52)	85	14.6 (2.11)
165	351	21.4 (2.21)	0	–	63	15.7 (4.08)
175	132	21.0 (2.23)	4	16.5 (2.52)	31	17.8 (3.36)
185	164	21.3 (2.42)	0	–	15	17.2 (3.07)
195	35	19.7 (2.35)	0	–	0	–
205	81	19.4 (2.84)	1	–	11	18.9 (5.15)
215	41	21.1 (2.60)	0	–	14	16.6 (1.33)
225	17	19.1 (2.24)	0	–	4	23.0 (0.31)
235	38	19.3 (2.92)	0	–	10	17.1 (2.88)
245	0	–	0	–	0	–
255	40	17.8 (1.57)	0	–	15	17.4 (5.23)
265	3	22.6 (0.33)	0	–	26	14.7 (4.41)
275	29	16.5 (0.28)	0	–	2	18.7 (4.24)
285	6	15.0 (0.50)	0	–	0	–

Figure 6. *Istiophorus platypterus*. Day and night vertical habitat envelopes derived from PSAT data of 63 sailfish monitored in the eastern tropical Atlantic (ETA), western North Atlantic (WNA), and eastern tropical Pacific (ETP). Plots depict percent time at Delta T and depth for (a) ETA daylight, (b) ETA darkness, (c) WNA daylight, (d) WNA darkness, (e) ETP daylight, and (f) ETP darkness.



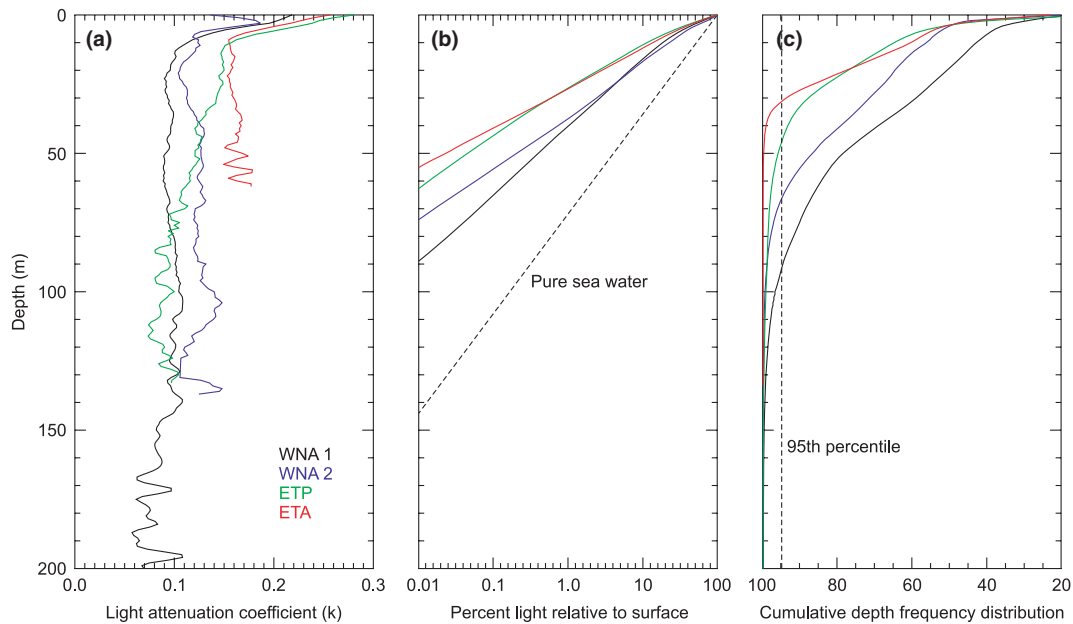
Prince *et al.*, 2010). Biology, oceanography, and climate all factor in the development and maintenance of the ETA and ETP OMZs, whose characteristic features include intense upwelling, a highly productive surface layer, shallow thermocline, and cold hypoxic environment beneath (Diaz, 2001; Stramma *et al.*, 2008). The OMZ thermoclines are often as shallow as ~25–50 m, below which DO levels are ≤ 3.5 mL L⁻¹. Yellowfin tuna (*Thunnus albacores*) and skipjack tuna (*Katsuwonus pelamis*), species that share similar physiology, gill structure, and mode of respiration (obligate ram ventilation) to istiophorids have been shown to experience physiological stress when DO decreases below 3.5 mL L⁻¹ (Gooding *et al.*, 1981; Bushnell and Brill, 1991; Idrisi *et al.*, 2003). Using this DO level as the lower threshold limit of useable habitat for sailfish

and blue marlin, PSAT studies indicated that time spent at depth and maximum dive behavior in the ETP and ETA were directly influenced by DO concentrations, whereas higher levels of DO present throughout the WNA water column allowed these species to actively explore deeper strata (Prince and Goodyear, 2006; Prince *et al.*, 2010). Although decreasing levels of DO at depth can certainly limit the vertical movement of istiophorids, our results indicate that Delta T is also an important factor. The vertical habitat envelopes for sailfish clearly show exploration of deeper strata in the WNA compared to the ETA and ETP. However, there were no significant differences detected between the Delta T distributions from the three regions. In other words, although higher DO levels may have allowed sailfish to explore deeper strata in the WNA, the range of their Delta T distribution remained the same as in the ETA and ETP groups. Presumably this is a response to the physiological temperature thresholds governing cardiac function (Brill *et al.*, 1999; Brill and Lutcavage, 2001).

The light attenuation coefficient for pure seawater at wavelength 550 nm is 0.064 (Mobley, 2010). The range of k at wavelength 550 nm estimated from this study (Fig. 7) was similar to the values reported by other studies (Siegel and Dickey, 1987; Zheng *et al.*, 2002). The light attenuation results suggested that the depths sailfish explored were related to the depth of light penetration. Since sailfish are visual feeders, it is possible that they seek out some optimal light level to maximize predation success. Patterson *et al.* (2008) reported that southern bluefin tuna (*Thunnus maccoyii*) were able to maintain a constant light level by adjusting depth. The shallower light penetration in the ETA and ETP was most likely related to the higher primary production in the upper ocean layer resulting from intense upwelling, which also limits to shallower depths the secondary production and the distribution of prey for sailfish. Therefore, the combined shallower characteristics of the hypoxic layer, light penetration, and prey distribution in the ETP and ETA may have contributed to the shallower distribution of the sailfish in these regions.

The similarity in Delta T behavior exhibited by sailfish groups from the ETA, WNA, and ETP, despite the difference in depth and temperature distributions, affirms the merit of this metric when applied to habitat standardization models. Given the results of our study, we would expect the Delta T distributions and vertical habitat envelopes to improve predictions for sailfish vertical distribution and relative abundance when using such models.

Figure 7. (a) Depth profile of light attenuation coefficient (k_D) at wavelength 550 nm estimated from four recovered PSATs deployed on sailfish in WNA (PTT 57179 and 57184), ETP (PTT 1900), and ETA (PTT 57196). (b) Depth profile of relative light intensity to the surface. Dashed line indicates the profile for pure seawater. (c) Cumulative depth frequency distributions for the four recovered PSATs. Dashed line indicates 95th percentile.



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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Table of Delta T distributions for PSAT-monitored sailfish in the eastern tropical Atlantic.

Appendix S2. Table of Delta T distributions for PSAT-monitored sailfish in the western North Atlantic.

Appendix S3. Table of Delta T distributions for PSA-monitored sailfish from the eastern tropical Pacific.

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