



Vertical and horizontal habitat use by white marlin *Kajikia albida* (Poey, 1860) in the western North Atlantic Ocean

John P. Hoolihan^{1*}, Jiangang Luo², Derke Snodgrass³, Eric S. Orbesen³, Ann M. Barse⁴, and Eric D. Prince³

¹Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School for Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

²Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

³Sustainable Fisheries Division, U.S. Dept of Commerce NOAA-NMFS Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149, USA

⁴Department of Biological Sciences, Salisbury University, 1101 Camden Avenue, Salisbury, MD 21801, USA

*Corresponding author: tel: +1 305 365 4116; fax: +1 305 361 4219; e-mail: john.hoolihan@noaa.gov

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Pop-up satellite archival tags were deployed on 40 white marlin *Kajikia albida* (synonym: *Tetrapturus albidus*) off the coasts of Maryland and North Carolina (United States), and the island nation of Aruba in the Caribbean. Useful data were available for analysing vertical and horizontal habitat use from 28 individuals. Time at liberty ranged from 10 to 181 d (mean 115, SD 53.3). Seasonal southerly fall migration routes were documented for fish released off the northeastern United States, while those released off Aruba remained in the Caribbean basin. Horizontal movements ranged from 228 to 8084 km ($19 - 100 \text{ km d}^{-1}$) based on light-level geolocation estimates using a sea surface temperature and bathymetry-corrected Kalman filter. Analyses included an evaluation of vertical movements using ΔT , the time spent at temperature relative to the uniform temperature surface layer. Movements included exploration of depths as great as 387 m and ambient temperatures as low as 7.8°C. However, the greatest proportion of time was spent in the upper 20 m of the water column for both day (50.8%) and night (81.6%), and time spent in water colder than 7°C below the uniform temperature surface layer was negligible. Overall, this group showed less variability in vertical movement, and less tolerance to colder temperatures compared with similar studies for blue marlin *Makaira nigricans* and sailfish *Istiophorus platypterus*. Values for ΔT are presented in tabular format to allow direct input into habitat standardization models used to estimate vertical distribution and population abundance. The large spatial dispersion and disparate tracks illustrated in the present study serve to underscore the complexity of white marlin behaviour and habitat use, and further emphasize the many challenges facing the management and conservation of this overexploited species.

Keywords: Δt , habitat preference, migration routes, pop-up satellite archival tag, *Tetrapturus albidus*.

Introduction

Billfish (Istiophoridae) are challenged by exploitation throughout their ranges, sometimes as a result of direct targeting, but most often as a bycatch of fishing efforts targeting tunas and swordfish *Xiphias gladius* (Serafy *et al.*, 2005). White marlin *Kajikia albida* (synonym: *Tetrapturus albidus*) are a highly vagile predatory species endemic to the Atlantic Ocean and primarily inhabit tropical and subtropical areas, but do venture into temperate areas during warm seasons (Mather *et al.*, 1972; Nakamura, 1985; Arocha and Bárrios, 2009). Stock assessment indicators have shown severe

overfishing and a marked reduction in the population size of white marlin since 1990 (Anon., 2012), suggesting that better information on the biology, life history, and habitat use is necessary to improve the management and conservation of these fish.

The current perception of long-range horizontal movements for white marlin is based predominantly on conventional tagging studies that detail release/recapture locations, but lacks further information that would explain movements or behaviour during periods at liberty (Scott *et al.*, 1990; Ortiz *et al.*, 2003; Orbesen *et al.*, 2008). One method to remedy this deficiency is by monitoring

their behaviour using electronic tags. Pop-up satellite archival tags (PSATs) record detailed information on depth, ambient water temperature, and light levels used for estimating geolocation (Arnold and Dewar, 2001). PSATs can be deployed for relatively long periods and transmit data via the Argos satellite system; consequently, fish recapture is not necessary (Hoolihan and Luo, 2007; Goodyear et al., 2008; Hoolihan et al., 2011b).

Oceanographic conditions, foraging behaviour, and physiological constraints influence how billfish interact with their surrounding environment (Brill and Lutcavage, 2001; Goodyear et al., 2008; Prince et al., 2010; Hoolihan et al., 2011b). While capable of exploring depths to hundreds of meters, electronic tagging data have shown billfish spend most of their time in the warmer uniform temperature surface layer (Gunn et al., 2003; Goodyear et al., 2008; Hoolihan et al., 2011b).

Studies have indicated that spatial and temporal use of vertical habitat by billfish and tunas are correlated with their vulnerability to longline and surface fishing gears (Boggs, 1992; Nakano et al., 1997; Bigelow and Maunder, 2007). Hinton and Nakano (1996) introduced a model for standardizing fishing effort by integrating the ecological and behavioural constraints (e.g. vertical habitat use) placed on a particular species. By including PSAT behavioural data as parameters, predictions of vulnerability can be estimated using catch rate models (Brill and Lutcavage, 2001). The Hinton and Nakano (1996) habitat standardization model uses ΔT (i.e. the change in water temperature at depth relative to the uniform temperature surface layer) to predict the proportions of time spent within a range of depth strata, to differentiate between the variation in abundance and estimates of availability derived from longline catch rate indices.

The most recent white marlin assessment concluded that the stock was overfished, with a relative biomass level at 0.50 of that needed to achieve maximum sustainable yield (Anon., 2014). There is clearly a need to expand and improve the knowledge base pertaining to the biology, life history, and distribution of white marlin. The objectives of this study were to monitor white marlin with PSATs to determine the characteristics of their vertical and horizontal movements, and to develop ΔT distributions that are applicable to habitat-based standardization models.

Material and methods

PSATs (Model Mk10, Wildlife Computers, Redmond, WA, USA) were deployed on 40 white marlin in the western North Atlantic during 2007–2012. Fish were captured using recreational fishing gear off the eastern coast of the United States near Ocean City, Maryland and Manteo, North Carolina; and, off the Caribbean island of Aruba. Based on local knowledge, deployments were carried out within a few weeks of anticipated fall migrations to help elucidate seasonal movements. PSAT tethers were constructed with ~ 18 cm of 300 lb monofilament attached to a medical grade nylon anchor with toggles. Anchors were inserted into the dorsal musculature ~ 4 –5 cm below the dorsal midline. Fish handling, tag anchor placement, and resuscitation procedures followed the protocols described by Prince and Goodyear (2006). Size (weight) was estimated by visual assessment.

PSATs were programmed for deployment periods ranging from 120 to 180 d, while sampling depth (pressure), ambient temperature, and light levels at 10 s intervals (Table 1). Summary data generated from pre-programmed 2 or 3 h temporal blocks were transmitted via Argos satellites. Each block included: (i) the proportion of time spent within each assigned 25 m depth bin; (ii) the

proportion of time spent within each assigned 2°C temperature bin; and (iii) PSAT depth–temperature (PDT) profile messages. In cases where a PSAT was physically recovered ($n = 1$), the full archived data recorded at 10 s intervals were accessible.

Linear methods were used to interpolate the distribution patterns of pooled data by hours of darkness and daylight into 1°C temperature bins and 1 m depth bins (Luo et al., 2006). A daylight bin was defined when the entire bin duration fell within 1 h after sunrise and 1 h before sunset. A darkness bin was defined when the entire bin duration fell within 1 h after sunset and 1 h before sunrise. All bins that did not fit these two categories were classified as crepuscular (i.e. twilight). This was done to eliminate contamination of daylight and darkness categories from bins extending into crepuscular periods. Average daily surface temperatures (T_0) were calculated using PDT data of ≤ 1 m. If surface temperatures were unavailable for a given day, values were linearly interpolated using previous and subsequent day records. For each depth bin, generated temperatures (GTs) per hour ($n = 720$) were estimated using a random normal distribution based on the PDT temperature range. The GT histogram was then compared with the temperature (T) data histogram. Differences in numbers for each bin were corrected by randomly removing values from positive bins or adding values to negative bins (Luo et al., 2006). The ΔT values were compiled by subtracting the GT values from T_0 values, then tabulated to display the proportion of time spent at decreasing temperatures (1°C bin resolution). Proportions of records within successively deeper layers of temperature relative to the surface temperature ($\Delta T = 0$) were assembled, and the mean ΔT values were calculated for each distribution (Hoolihan et al., 2011b). The Chi-squared goodness-of-fit test was used to compare the observed frequency distributions of mean time spent at temperature for periods of darkness, twilight, and daylight.

Light-level geolocation data were processed using the WC-DAP and WC-GPE2 software (Wildlife Computers), and a sea surface temperature-corrected Kalman filter (Nielsen et al., 2006; Lam et al., 2008). A custom bathymetry filter was then applied to relocate any points that were on land or in shallow water, based on 2×2 min grid ETOPO2 bathymetry data (Anon., 2006) and the daily maximum depth from the tag. For points where maximum daily depth exceeded the bathymetric depth, all grid cells were selected along the longitude where bathymetric depth was greater than the daily maximum depth within $\pm 1^\circ\text{C}$ of the previous day's latitude. A final location was then assigned to a single cell selected randomly from that group (Hoolihan and Luo, 2007).

Results

A total of 40 PSATs were deployed on white marlin in the western North Atlantic during 2007–2012. Twelve white marlin were excluded from further analyses because of apparent mortality within 24 h of release ($n = 2$); or, a PSAT failed to report ($n = 5$); or, a PSAT prematurely released < 10 d post-deployment ($n = 5$, Table 1). Previous analyses of billfish PSAT data have indicated behavioural abnormalities for ~ 10 d following deployment (Hoolihan et al., 2011a). Hence, our decision to exclude from further analyses those PSATs that were at liberty for < 10 d. The remaining 28 white marlin account for 2561 representative days of useable data available from 3197 total days at liberty (DAL, Table 1). Individual DAL ranged from 10 to 181 (mean 115, SD 53.3, Table 1). Size (weight) ranged from 13.6 to 38.6 kg (mean 21.2, SD 5.1, Table 1). Great-circle distance measured between

Table 1. Summary tagging information for 40 PSAT-monitored white marlin *K. albidus*.

No.	PTT ID	Weight estimate (kg)	Release date	Pop-up date	Days attached/days programmed to pop-up	Release location (ddmm)	Location of first transmission	Linear displacement (km)
1	68017	18.1	08 September 2007	29 December 2007	112/120	36°57'N 074°27'W	20°41'N 069°00'W	1887
2	52219	20.4	04 September 2007	na	na/150	36°04'N 074°47'W	na	na
3	52229	18.1	04 September 2007	26 September 2007	22/150	36°04'N 074°47'W	38°27'N 063°31'W	1034
4	49863	22.7	05 September 2007	23 December 2007	109/120	36°07'N 074°45'W	31°28'N 078°40'W	630
5	49864	20.4	05 September 2007	11 December 2007	97/150	36°06'N 074°47'W	20°23'N 070°49'W	1789
6	49865	27.2	05 September 2007	na	na/160	36°04'N 074°48'W	na	na
7	49866	15.9	06 September 2007	29 December 2007	114/150	36°09'N 074°53'W	07°58'N 056°30'W	3630
8	49867	24.9	08 September 2007	5 February 2008	150/150	36°58'N 074°25'W	07°38'N 055°45'W	3754
9	49868	20.4	08 September 2007	20 December 2007	103/150	36°49'N 074°27'W	12°15'N 054°43'W	3351
10	49869	13.6	13 September 2007	22 January 2008	131/150	37°43'N 073°57'W	07°49'N 040°04'W	4769
11	49870	27.2	13 September 2007	31 December 2007	109/150	37°44'N 073°57'W	18°51'N 063°48'W	2320
12	49871	13.6	08 September 2007	29 November 2007	82/170	36°51'N 074°10'W	25°06'N 077°42'W	1352
13	49990	20.4	13 September 2007	10 February 2008	150/150	37°45'N 073°57'W	10°22'N 059°07'W	3377
14	49901 ^a	20.4	13 September 2007	14 September 2007	1/150	37°49'N 073°54'W	37°49'N 073°57'W	1
15	52118	20.0	13 September 2007	19 September 2007	6/150	37°45'N 073°57'W	37°01'N 072°35'W	145
16	52213	20.0	13 September 2007	28 September 2007	15/150	37°47'N 073°57'W	33°47'N 072°41'W	459
17	52217	15.9	08 September 2007	1 December 2007	84/160	36°49'N 074°27'W	18°53'N 067°57'W	2094
18	110629	22.7	05 September 2011	02 October 2011	28/180	35°54'N 074°46'W	39°18'N 068°23'W	736
19	110630	22.7	05 September 2011	15 September 2011	10/180	35°55'N 074°46'W	37°25'N 074°26'W	171
20	110632	18.1	05 September 2011	3 March 2012	180/180	35°57'N 074°50'W	25°29'N 075°05'W	1166
21	110633	27.2	05 September 2011	9 February 2012	157/180	35°57'N 074°30'W	28°14'N 079°33'W	981
22	110634	24.9	05 September 2011	24 February 2012	172/180	35°58'N 074°51'W	11°11'N 077°57'W	2776
23	110635 ^b	24.9	05 September 2011	3 January 2012	120/180	36°02'N 074°52'W	19°04'N 065°55'W	2080
September 24	110636	22.7	05 September 2011	17 January 2012	134/180	36°02'N 074°52'W	12°14'N 078°15'W	2670
25	110637	20.4	05 September 2011	24 January 2012	141/180	36°02'N 074°52'W	13°12'N 062°05'W	2837
26	110638	18.1	05 September 2011	8 September 2011	3/180	36°02'N 074°52'W	35°57'N 074°38'W	26
27	110639	22.7	05 September 2011	21 September 2011	16/180	36°03'N 074°51'W	33°39'N 074°17'W	274
September 28	110640	20.4	14 September 2011	16 September 2011	2/180	12°20'N 069°45'W	12°29'N 070°13'W	52
29	110641	22.7	14 September 2011	Na	na/180	12°20'N 069°45'W	na	na
30	110642	22.7	14 September 2011	11 January 2012	119/180	12°19'N 069°44'W	12°48'N 066°23'W	373
31	110643	20.4	19 September 2011	25 January 2012	128/180	12°25'N 069°52'W	13°20'N 065°36'W	489
32	110644	20.4	19 September 2011	21 September 2011	2/180	12°19'N 069°40'W	12°20'N 070°05'W	50
33	110645	22.7	20 September 2011	23 September 2011	3/180	12°18'N 069°40'W	12°55'N 070°41'W	115
34	110646	18.1	21 September 2011	12 March 2012	173/180	12°18'N 069°40'W	16°42'N 071°03'W	511
35	110647	24.9	14 October 2011	na	na/180	12°30'N 069°44'W	na	na
36	110648	20.4	16 October 2012	na	na/180	12°15'N 069°41'W	na	na
37	110649	38.6	17 October 2012	14 April 2013	180/180	12°21'N 069°47'W	17°00'N 074°47'W	770
38	110650	22.7	18 October 2012	16 April 2013	181/180	12°17'N 069°34'W	15°57'N 077°00'W	939
39	122118	13.6	18 October 2012	15 April 2013	180/180	12°09'N 069°45'W	16°17'N 075°36'W	780
40	122120 ^a	13.6	19 October 2012	20 October 2012	1/180	12°20'N 069°45'W	12°13'N 070°13'W	1

Shaded individuals were excluded from analyses.

na, not available.

^aDied.^bRecovered PSAT.

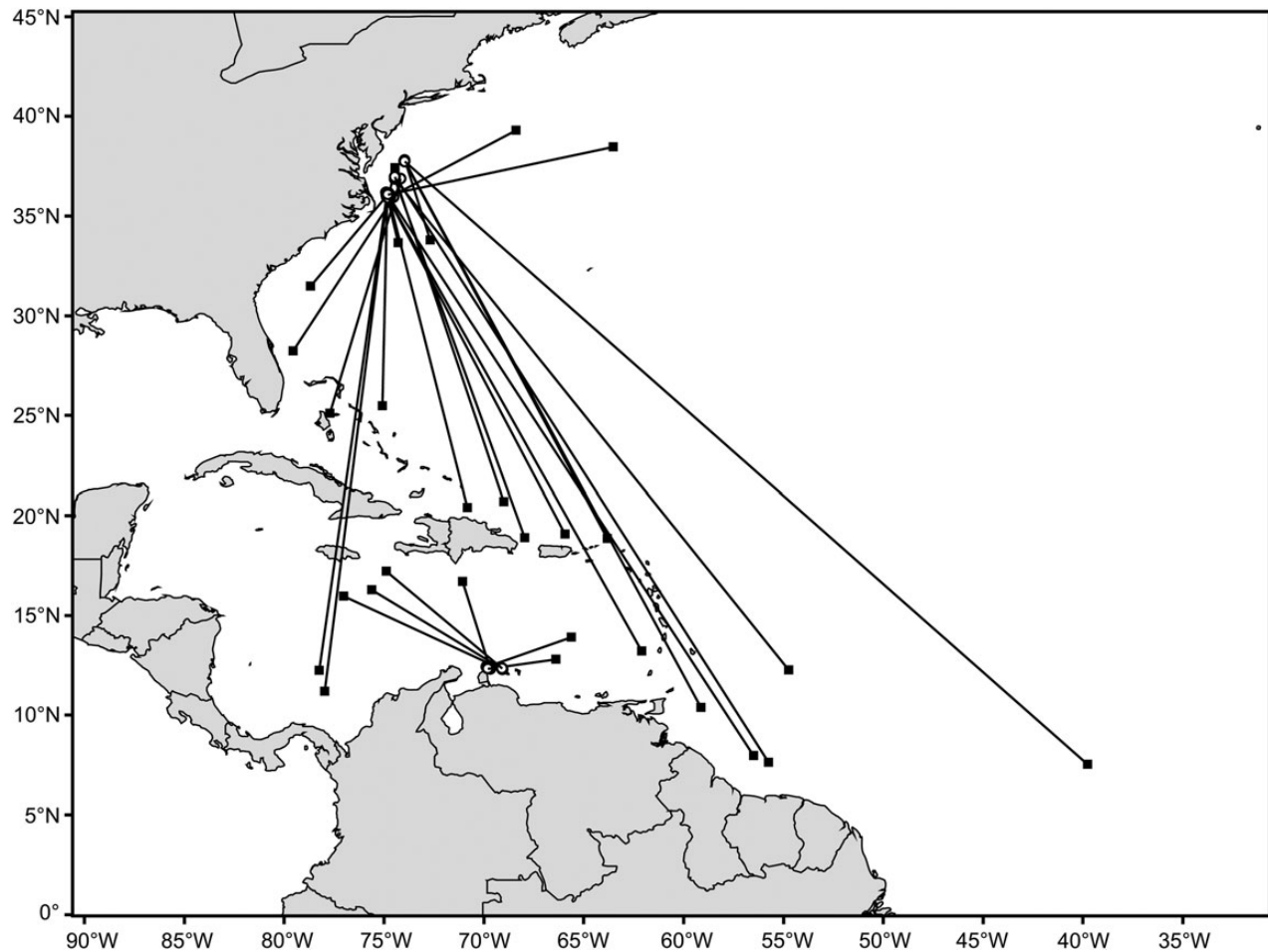


Figure 1. Displacement vectors for white marlin ($n = 28$) deployed with PSATs during the period 2007–2012. Circles and squares represent deployment and pop-up locations, respectively.

locations of release and PSAT pop-up ranged from 171 to 4769 km (mean 1730, SD 1246 Figure 1 and Table 1).

Vertical habitat use

PSAT-monitored white marlin explored depths ranging from 0 to 387 m, and ambient water temperatures ranging from 7.8 to 30.0°C. Overall, the greatest proportion of time was spent in the upper 20 m of water column during both day (50.8%) and night (81.6%, Figure 2a). Also, the greatest proportion of time was spent in 26°C water for both day (23.9%) and night (35.6%, Figure 2b).

Diel differences of vertical movement were assessed by evaluating the proportions of time spent at temperature, relative to that of the uniform temperature surface layer (ΔT). Samples were pooled to compile histogram sets for periods of darkness ($n = 2484$), twilight ($n = 1502$), and daylight ($n = 1988$, Table 2). The tabulated distributions of ΔT (Table 2) provide values that are directly applicable to the habitat standardization models described by Hinton and Nakano (1996) and Bigelow *et al.* (2002). The mean ΔT percentiles revealed that 98.6% of darkness, 95.4% of twilight, and 87.1% of daylight hours were spent in the uniform temperature surface layer ($\Delta T = 0$, Table 2). Figure 3 displays the range and means of observations for the proportions of time spent at ΔT for darkness (Figure 3a), twilight (Figure 3b), and daylight (Figure 3c). Chi-squared goodness-of-fit between the observed mean distribution frequencies for time spent at

temperature (Table 2) showed a significant difference for darkness vs. daylight ($\chi^2 = 11.890$; $p = 0.002$) and twilight vs. daylight ($\chi^2 = 6.312$; $p = 0.042$), but no significant difference for darkness vs. twilight.

We speculated whether the length of deployment would affect the characterization of habitat use by our PSAT-monitored fish. This was tested by plotting the daily observed maximum depths (D_{max}), based on the presumption that exploration of deeper strata was more likely as DAL increased. The D_{max} of our pooled samples showed an increasing trend to explore deeper strata over time T ($D_{max} = 77.70 T^{0.226}$; $r^2 = 0.572$; $F = 43.4$; $p < 0.00001$; 90 d.f.), although the overall pattern showed high daily variability (Figure 4a).

Horizontal habitat use

White marlin released off Maryland and North Carolina embarked on a seasonal southerly migration within a few weeks of release (Figure 1). Geolocation estimates of the most probable tracks incorporating the sea surface temperature and bathymetry-corrected Kalman filter revealed widespread movement, reaching as far south as the northeastern coast of South America (Figure 5). The most probable estimated tracks ranged from 228 to 8094 km (mean 4258, SD 2131), while the rates of movement ranged from 19 to 100 km d^{-1} (mean 40, SD 19). There was a notable difference between the horizontal movements of the 2007 and 2011 white

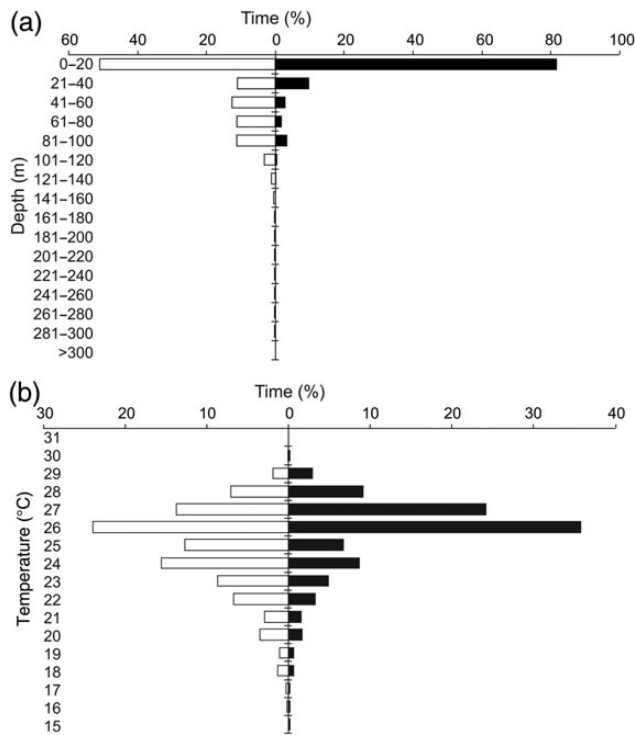


Figure 2. Pooled percentage of time spent at depth (a) and temperature (b) for periods of darkness (black bars) and daylight (white bars) for PSAT-monitored white marlin ($n = 28$). Interpolated 1 m depth bins were grouped (20 m bins) in this figure to conserve space.

marlin released off Maryland and North Carolina (Figure 5). Fish deployed in 2007 dispersed over a much larger area of the western North Atlantic, moving as much as 2000 km farther east than the 2011 group (Figure 5). Most of the 2007 tracks terminated just north of the Caribbean or along the northeastern coast of South America, without entering the Caribbean (Figure 5). In contrast, 2011 individuals moved in a more pronounced southerly direction (Figure 5). Although some 2011 tracks terminated just north of the Caribbean similar to the 2007 group, three individuals ventured into the Caribbean, one to the far eastern side and two just north of Panama (Figure 5 and Table 1).

All the individuals tagged off Aruba remained within the Caribbean basin (Table 1 and Figure 5). Movement patterns for these fish were somewhat similar for 2011 and 2012, with some individuals exploring the eastern Caribbean and others moving north towards the direction of Jamaica (Figure 5 and Table 1). None of the fish released off Aruba ventured into the western Caribbean (Figure 5).

Discussion

The useable data garnered from 28 of the 40 PSAT-monitored white marlin provided a new insight into their behaviour. Considering the spatial distribution, a pooled number of observations (2561 d of data), and lengths of deployment (3197 total DAL), our analyses present the most comprehensive description of vertical and horizontal habitat use currently available for white marlin. This information offers clear advantages for conservation management by its potential capacity to reduce the uncertainties associated with the stock assessment process.

A robust population assessment requires an understanding of the relationships between fish behaviour and the physical environment (Brill and Lutcavage, 2001). The tabulated distributions presented here for ΔT illustrate a detailed picture of vertical habitat use, in a metric that can be applied directly to habitat standardization models for the purpose of estimating vertical distribution and relative abundance (Hinton and Nakano, 1996; Bigelow *et al.*, 2002).

In general, billfish prefer the warmest water available, which is usually associated with the uniform temperature surface layer (Brill *et al.*, 1993; Goodyear *et al.*, 2008; Hoolihan *et al.*, 2011b). Brill *et al.* (1999) surmised that the vertical distribution of billfish is regulated more by the change in water temperature (i.e. ΔT), rather than any specific temperature, and concluded that the coldest water tolerated usually does not exceed $\sim 8^\circ\text{C}$ below the uniform temperature surface layer, due to constraints on cardiac muscle function. Our group of fish easily fell within these parameters, with negligible time spent at temperatures below $\Delta T - 7$ during periods of daylight, or below $\Delta T - 4$ during darkness (Table 2).

An affinity for the uniform temperature surface layer has also been described in ΔT studies for blue marlin *Makaira nigricans* and sailfish *Istiophorus platypterus* (Goodyear *et al.*, 2008; Hoolihan *et al.*, 2011b). Notably, the percentile distributions for ΔT from our study group exhibited less variability and fewer excursions into colder waters than those reported for blue marlin or sailfish (Goodyear *et al.*, 2008; Hoolihan *et al.*, 2011b), suggesting that white marlin cardiac muscle function may be less tolerant of colder temperatures. This was supported by the fact that our fish spent a greater proportion of their time in the uniform temperature surface layer, 98.6% during darkness, and 87.1% during daylight periods (Table 2). In comparison, blue marlin spent 84.9 and 58.3%, whereas sailfish spent of 93.0 and 81.6% of their time in the uniform temperature surface layer for periods of darkness and daylight, respectively (Goodyear *et al.*, 2008; Hoolihan *et al.*, 2011b).

While the fish in our study encountered a range of water temperatures ($7.8\text{--}30.0^\circ\text{C}$), their greatest proportions of time were spent at 26.0°C (23.9% of daylight and 35.6% of darkness periods; Figure 2). Billfish are adapted with brain and eye heater tissues that support function of these organs at colder temperatures; however, they lack vascular countercurrent heat exchangers that help to sustain swimming muscle temperatures above ambient water temperatures (Lindsey, 1968; Block, 1986; Brill and Lutcavage, 2001). As a consequence, cardiac muscle function is increasingly compromised as ambient temperature decreases, making the warmer uniform temperature surface layer more desirable.

In terms of time spent at depth, our fish spent 95.2% of their time in the upper 100 m of the water column during the daylight, and 50.8% in just the upper 20 m. Other PSAT studies for white marlin in the western North Atlantic have reported 48% of time spent in the upper 10 m of the water column (Horodysky *et al.*, 2007), and 53% of total time above 25 m (Prince *et al.*, 2005). Although the analyses of time spent at depth and temperature indicate a preference for the warmer and shallower depths of the uniform temperature surface layer, billfish do regularly undertake deep dives to colder strata, given that adequate levels of dissolved oxygen are available (Prince *et al.*, 2010). However, these dive events are comparatively short in duration, after which these fish retreat to the warmer water near the surface (Horodysky *et al.*, 2007; Hoolihan *et al.*, 2009). Presumably, these dive events are mostly foraging related, either seeking or in direct pursuit of prey.

Although temperature and dissolved oxygen are major influences governing billfish vertical habitat use, other less understood

Table 2. Proportions of time spent by white marlin ($n = 28$) at ΔT during periods of darkness, twilight, and daylight.

ΔT	Percentile of mean 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 ($n = 2484$)												
0	1.000	1.000	1.000	1.000	1.000	1.000	0.988	0.972	0.966	0.962	0.960	0.986
-1	-	-	-	-	-	-	0.010	0.021	0.026	0.029	0.030	0.011
-2	-	-	-	-	-	-	0.002	0.004	0.005	0.005	0.006	0.002
-3	-	-	-	-	-	-	-	0.002	0.002	0.003	0.003	0.001
-4	-	-	-	-	-	-	-	0.001	0.001	0.001	0.001	0.000
-5	-	-	-	-	-	-	-	-	-	-	-	0.000
-6	-	-	-	-	-	-	-	-	-	-	-	0.000
-7	-	-	-	-	-	-	-	-	-	-	-	0.000
-8	-	-	-	-	-	-	-	-	-	-	-	0.000
Twilight ($n = 1502$)												
0	1.000	1.000	1.000	1.000	1.000	0.978	0.936	0.906	0.895	0.890	0.887	0.954
-1	-	-	-	-	-	0.020	0.050	0.068	0.073	0.074	0.076	0.033
-2	-	-	-	-	-	0.002	0.010	0.016	0.020	0.022	0.023	0.008
-3	-	-	-	-	-	-	0.003	0.006	0.008	0.008	0.009	0.003
-4	-	-	-	-	-	-	0.001	0.002	0.003	0.003	0.003	0.001
-5	-	-	-	-	-	-	-	0.001	0.001	0.001	0.001	0.001
-6	-	-	-	-	-	-	-	-	-	-	-	0.000
-7	-	-	-	-	-	-	-	-	-	-	-	0.000
-8	-	-	-	-	-	-	-	-	-	-	-	0.000
Daylight ($n = 1988$)												
0	1.000	1.000	1.000	1.000	0.990	0.911	0.807	0.742	0.718	0.708	0.702	0.871
-1	-	-	-	-	0.008	0.075	0.136	0.156	0.160	0.160	0.160	0.078
-2	-	-	-	-	0.001	0.009	0.036	0.064	0.077	0.081	0.084	0.032
-3	-	-	-	-	-	0.003	0.012	0.022	0.027	0.031	0.032	0.012
-4	-	-	-	-	-	0.001	0.005	0.008	0.010	0.011	0.012	0.004
-5	-	-	-	-	-	0.001	0.003	0.005	0.005	0.005	0.005	0.002
-6	-	-	-	-	-	-	0.001	0.002	0.002	0.002	0.002	0.001
-7	-	-	-	-	-	-	0.001	0.001	0.001	0.001	0.001	0.001
-8	-	-	-	-	-	-	-	-	-	-	-	0.000

Proportions were derived from temperature sets (n) compiled using combined archival data and archival data simulated from transmitted data. Dashes indicate zero probability. Data were sorted in order of decreasing ΔT (left column), and 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), 98.8% were at surface temperature and 0.2% were at 2° below surface temperature.

or unknown factors may also play a role. Sailfish monitored using ultrasonic tracking and PSATs in the Arabian Gulf showed a preference for near surface depths, spending 85% of their time in the upper 10 m of the water column (Hoolihan, 2005). This occurred regardless of the fact that total depth averaged only ~ 30 m in the study area, with negligible difference in temperature or dissolved oxygen levels throughout the water column (Hoolihan, 2005). Billfish rely on sight to identify and catch prey and avoid predators, suggesting that the amount of available light is an important factor in habitat preference. The ability to see colour, along with adaptations that aid visibility in low light and cold ambient temperatures, contributes to the success of these activities (Block, 1986; Fritsches et al., 2000, 2003). A light attenuation analysis of sailfish PSAT data indicated that depths explored were related to the depth of light penetration (Hoolihan et al., 2011b). Remaining near the surface during periods of darkness and less activity allows billfish to take advantage of the warm uniform temperature surface layer and also places them in a position to take advantage of the maximum available ambient light, which may confer some advantage for visualizing and evading predators.

Similar comparisons of daily maximum depth for PSAT-monitored sailfish and yellowfin tuna *Thunnus albacares* indicated that longer deployments resulted in a more comprehensive portrayal of actual behaviour (Hoolihan et al., 2011b, 2014). Considering these studies and

the observed trend of increasing depths (D_{\max}) visited over time in the present study, we are confident that longer deployment periods do provide a more comprehensive portrayal of actual habitat use by white marlin.

The timing of our PSAT deployments off Maryland, North Carolina, and Aruba occurred during the same period of the year (Figure 1 and Table 1). Given the large distance between these locations suggests the possibility of stock substructure, white marlin have long been known to aggregate Maryland and North Carolina during the warmer months (July to September), and constitute an economically important recreational fishery established in the 1930s (Earle, 1940; Jesien et al., 2006). The annual influx of white marlin into this area is the result of a northward post-spawning foraging migration (DeSylva and Davis, 1963). Evidence of white marlin spawning activity in the western North Atlantic has been reported for the Caribbean Basin and Gulf of Mexico during April to June (Baglin, 1979; Prince et al., 2005; Arocha and Bárrrios, 2009).

All the fish tagged and released off Maryland and North Carolina during 2007 were captured and released within proximity to each other. The same was true for those tagged in 2011. After embarking on a seasonal fall migration, these individuals dispersed over a wide area of the western North Atlantic (Figure 1). This was not surprising, as mark-recapture data from conventional tagging studies have shown white marlin connectivity between the northeastern US

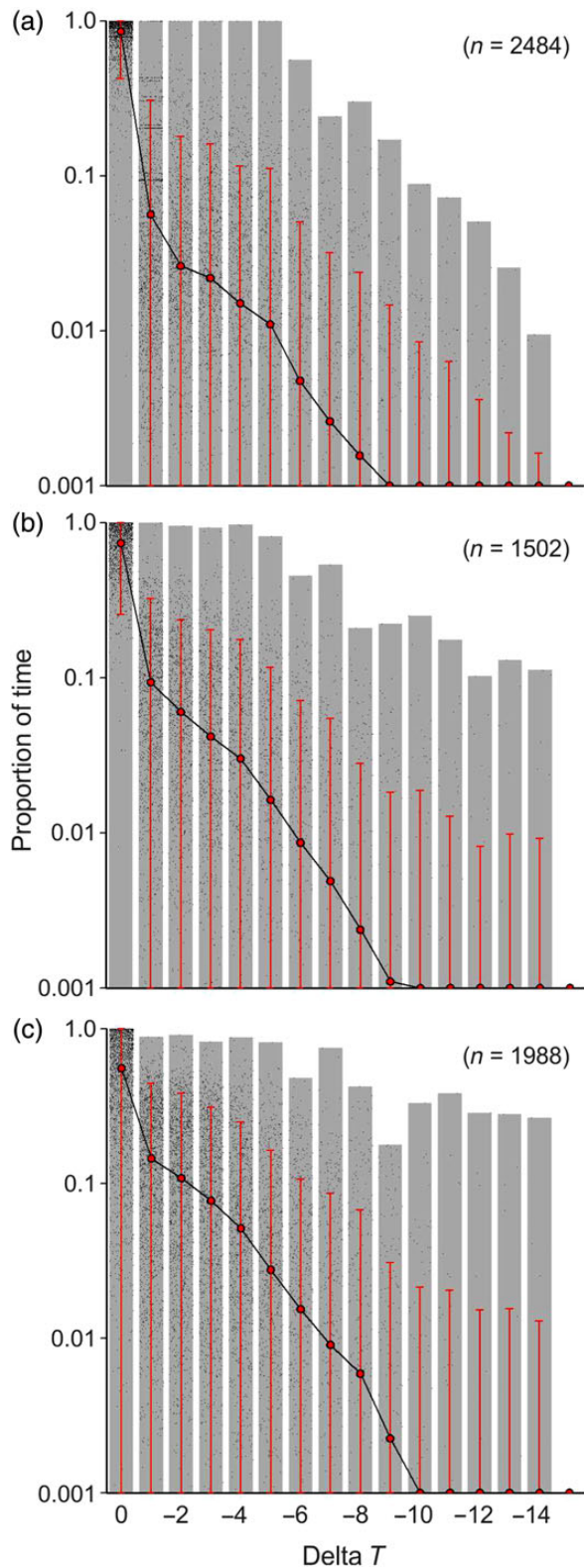


Figure 3. Proportions of time spent at ΔT (relative to the surface temperature) during (a) daylight, (b) twilight, and (c) darkness, estimated using combined Argos transmitted and archival data from 28 PSAT-monitored white marlin. Shaded bars denote the range of observations (shown by small grey dots), and n denotes the number of interpolated datasets. Red circles and associated error bars denote means and 95% confidence intervals.

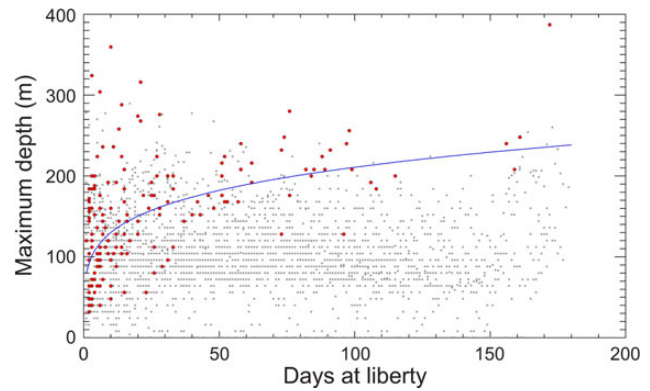


Figure 4. Maximum depths reached by white marlin ($n = 28$) during time at liberty. Deepest dives recorded during individual time bins (grey dots). Red dots denote first records of each fish at the observed depth. Blue line is the exponential fit to the first occurrence data.

coast, Caribbean Basin, Gulf of Mexico, northern coast of South America, as well as a few transatlantic crossings (Mather *et al.*, 1972; Orbesen *et al.*, 2008). One interesting realization was the high degree of variability exhibited by the horizontal track movements (Figure 5). Except for a few short-term deployments (<28 DAL), all individuals eventually ended up south of their release locations; however, the paths taken to reach their pop-up destinations varied considerably (Figure 5).

The stark difference in dispersal patterns between 2007 and 2011 for the fish released off Maryland and North Carolina may be an effect of variable environmental conditions (e.g. water temperature) influencing prey availability.

The white marlin released off Aruba remained inside the Caribbean basin and did not display the extremely long horizontal tracks that were observed from individuals released off Maryland and North Carolina (Figure 5), although many had deployment periods of similar length (Table 1). The Aruba fish, however, were not faced with having to escape the seasonal onset of decreasing water temperatures associated with the higher latitude conditions off the eastern coast of the United States. Although the Aruba fish remained in the Caribbean, none ventured into the western region. We are unsure of why this area was avoided, noting that two of the fish released off North Carolina in 2011 did indeed go into the western Caribbean with tracks terminating north of Panama (Figure 5). This area does characteristically feature an eddy structure that is often cooler than the eastern Caribbean, which may have been a factor. Also, the southeastern Caribbean features an area of substantial upwelling and increased productivity that attracts billfish and their prey (Rueda-Roa and Muller-Karger, 2013), which may have eliminated any incentive for the Aruba fish to leave the area and explore the western region.

The most recent (2012) estimate of relative biomass for the white marlin stock was about half of that required for maximum sustainable yield (Anon., 2014). The stock was determined to be overfished, although consideration for whether overfishing was continuing to occur was tenuous because of uncertainties surrounding the reporting of catches (Anon., 2014). One important factor causing uncertainty is the apparent mix of white marlin catch with the morphologically similar roundscale spearfish *Tetrapturus georgii* (Robins, 1972), resulting in a mixed species complex for stock assessment purposes (Anon., 2012). Separating catches and accurate reporting of catches and discards are key concerns for improving

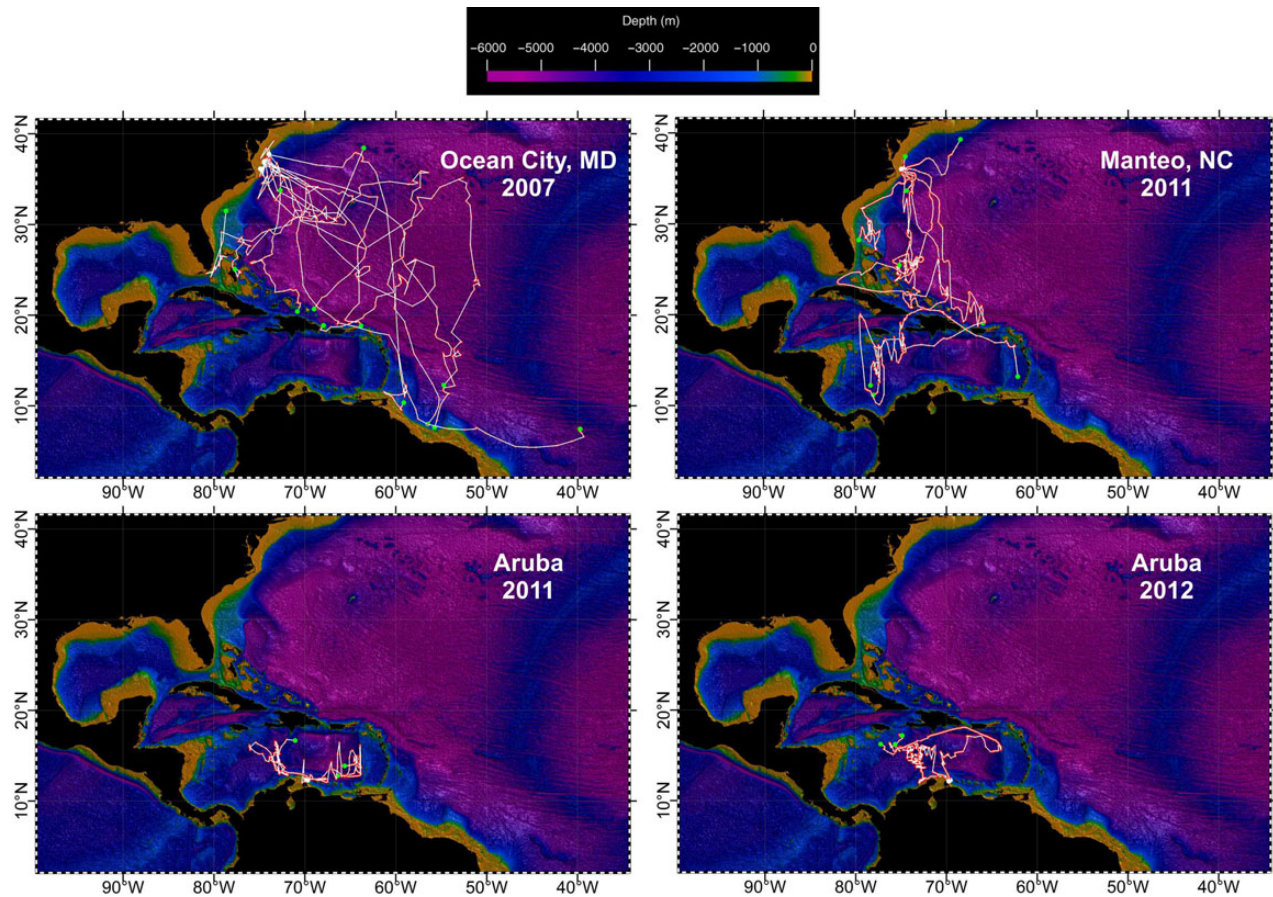


Figure 5. Estimated most probable horizontal tracks for 28 PSAT-monitored white marlin plotted by year and deployment location. Circles denote deployment locations (yellow), pop-up locations (green), and intermittent locations estimated from light-level data (red).

stock assessments for these species. Genetic analyses have helped to define the distribution of white marlin and roundscale spearfish in the western North and South Atlantic; however, information for the eastern Atlantic is very limited (Bernard *et al.*, 2014). Areas where white marlin/roundscale spearfish mixing ratios have been estimated indicate high spatial variability (Beerkircher *et al.*, 2009; Bernard *et al.*, 2013).

The large spatial dispersion and disparate tracks illustrated in the present study serve to underscore the complexity of white marlin behaviour and habitat use, and further emphasize the many challenges facing the management and conservation of these overexploited species. It is hoped the new information presented here on the horizontal and vertical behaviour of these species will help to address these challenges.

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