

Vertical habitat use of Atlantic blue marlin *Makaira nigricans*: interaction with pelagic longline gear

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ABSTRACT: We characterized Atlantic blue marlin *Makaira nigricans* temperature–depth vertical habitat utilization from data collected using 51 electronic pop-up satellite archival tags (PSATs) attached to fish released by recreational and commercial fishers. Most source data were in the form of 3 or 6 h, temperature- and depth-frequency histograms transmitted by the tags to the ARGOS satellite system. However, high resolution time series of temperatures, depths (30 or 60 s resolution), and light intensity were obtained from 6 tags that were physically recovered. The distributions of times at depth were significantly different between day and night. During daylight hours, the fish were typically below the near-surface layer, often at 40 to >100 m, sometimes remaining below the near-surface layer at depth throughout the daylight hours, but often returning briefly to the surface. At night, the fish spent most of their time at or very close to the surface. This pattern of behavior also meant that the distributions of time at temperature were significantly different between day and night, with the fish occupying warmer strata during darkness. We evaluated the fractions of time spent by each fish within each degree of water temperature relative to the temperature of the surface mixed layer to assess assumptions used to model population abundance trends from pelagic longline catch per unit effort (CPUE) data. Frequency distributions were determined for periods of darkness, daylight and, where possible, twilight. Results were highly variable within the time series for individual fish and among individuals. Assumptions about habitat usage in previous CPUE analyses are clearly inappropriate and may lead to serious errors that can propagate through the fisheries management system.

KEY WORDS: Blue marlin · Habitat · Behavior · Thermocline · Spatial variation · Longlines

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INTRODUCTION

The physiological adaptations of tropical pelagic fishes place fundamental constraints on the physical bounds of their habitats (Brill 1992). These otherwise invisible boundaries are shaped by each species' preferences for and/or tolerances of environmental conditions. In the open ocean, temperature and dissolved oxygen are thought to be dominant features that influence acceptable habitat (Fonteneau 1997, Eby & Crowder 2002, Stanley & Wilson 2004, Prince & Goodyear 2006). Because these features vary by season and depth, the

physical habitat can be viewed as an irregular, time-varying volume with physical dimensions of latitude, longitude, and depth, which are mediated by environmental preferences and physiological tolerances. Quantitative information about this habitat, and the species distribution within it, is important for both understanding the ecology of the species and its interaction with fishing gear (Brill & Lutcavage 2001, Luo et al. 2006). This need is especially vital for species such as overfished Atlantic blue marlin *Makaira nigricans*, which are primarily taken as bycatch in pelagic longline fisheries directed at other species (Serafy et al. 2005).

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It is clear from observed catch patterns that hook depth influences species selectivity of longline sets (Yang & Gong 1987, Boggs 1992, Hanamoto 1987, Nakano et al. 1997). Over the years, fishing depths have increased as tuna longline fishing fleets have shifted from targeting shallower species to the deeper-dwelling bigeye tuna *Thunnus obesus* (Jones et al. 1998, Restrepo et al. 2003, Serafy et al. 2005). These changes have complicated estimation of population trends from catch and effort data. Understanding the ramifications of such changes is crucial to the assessment of fish stock status, because the error and uncertainties resulting from poor estimates propagate through every aspect of the fishery management process (Serafy et al. 2005, Rice et al. 2007). The amount of time marlin spend at depth may be an important factor in the evaluation and prediction of their vulnerability to pelagic longline gear (Goodyear 2003).

Hinton & Nakano (1996) introduced a model that incorporates fish habitat information to estimate population abundance trends from longline catch–effort data by computing levels of ‘effective effort’ within the vertical habitat of the fish. This metric is intended to weight effort by adjusting longline effort by the proportions of time fish and hooks spend at the same depths. The proportions of time marlin spend at depth are predicted from the deviations between the temperatures at depth from the temperature of the surface mixed layer. This process, termed habitat standardization, offers a potential means to directly account for changes in fishing patterns that have occurred in the longline fishery through time (Takeuchi 2001, Yokawa & Uozumi 2001, Yokawa et al. 2001). However, it relies entirely on detailed knowledge of gear behavior (i.e. hook depths) and marlin habitat, 2 areas of research that have recently received attention (Goodyear 2003, Serafy et al. 2005). The methodology has since been enhanced by incorporating the concept into a more formal statistical framework (Maunder et al. 2006). Bigelow & Maunder (2007) concluded that an understanding of gear dynamics and environmental influences are important for analyzing catch per unit effort (CPUE) data correctly. The basic lack of information about actual marlin habitat use and hook depths of longline gear persists. Pop-up satellite archival tags (PSATs) are a recent technological innovation that allows fisheries independent retrieval of the temperatures and depths frequented by tagged animals. These data permit mapping habitat use in these dimensions (Luo et al. 2006). Here we present an evaluation of blue marlin vertical habitat use by temperature and depth from 51 blue marlin monitored with PSATs with particular concern for the requirements of models that predict or estimate population trends based on species distribution patterns.

MATERIALS AND METHODS

PSATs are attached to the fish externally and log the temperature, pressure (depth), and light intensity after the fish is released. Individuals can be monitored for up to several months or longer. The tags detach after a programmed interval and transmit summaries of the data through the ARGOS satellite system to a land station and then ultimately to the user via the Internet. This study used Wildlife Computers PAT model 2 and 3 tags. These tags allow the user to program pop-up date, sampling interval, criteria for premature release, bin demarcations for sampling temperature and depth, as well as transmission and memory priorities. We programmed these tags to sample depth, temperature, and light once every 30 or 60 s. Depth and temperature records were compiled into histogram tables at 6 h intervals for most deployments, while a few of the early deployments summarized data at 3 h intervals. Temperature bins for most tags started with $\leq 12^{\circ}\text{C}$, then each successive 2°C interval up to 32°C , and ending with $>32^{\circ}\text{C}$. Depth bins for most tags included ≤ 1 m, followed by successive intervals of 25 m, until reaching 250 m, then all depths >250 m. Minimum and maximum temperatures and depths encountered during each binning period were also recorded. The tags used in this study were programmed for deployment durations ranging from 7 to 90 d. A pressure-activated mechanical detachment device was used to sever the 400 pound test monofilament tether at a depth of about 1500 m (well before the rated 2000 m crush depth of the tag). This feature was intended to prevent data loss in the event of fish mortality (i.e. sinking). In addition, these tags were programmed to release if the vertical movement was ≤ 5 m for 24 h. This mechanism maintains data recovery for PSATs from dead marlin that did not sink below 1500 m. Release locations were estimated from global positioning systems on board the tagging vessels, while pop-up locations were estimated directly from ARGOS transmissions received from each tag. Although PSATs transmit until their batteries are exhausted, all measurements taken during the deployment are retained in the tag’s non-volatile memory. This feature allows access to the complete archived dataset should the tag be physically recovered.

All PSATs were rigged in a manner similar to those described by Block et al. (1998), Graves et al. (2002), and Prince & Goodyear (2006). Billfish handling and tagging procedures and associated devices were as recommended by Prince et al. (2002). The tags were placed about 4 to 5 cm ventral to the dorsal midline, adjacent to the first several dorsal spines. An effort was made to insert the anchor through the dorsal midline, pterygiophores, and connective tissue to a depth just

short of exiting the opposite side of the fish. We deployed 79 PSATs on blue marlin from recreational fishing and commercial longline fishing vessels during the period 2002 to 2004 (Fig. 1). Because of tag failures (i.e. non-transmitting tags) and death of 4 fish, our analyses are based on data from 51 tagged fish (Appendix 1). Of these, 6 tags were physically recovered, which allowed extraction of high-resolution archived data recorded at 30 or 60 s intervals during deployment.

We examined temperature and depth distribution patterns using data pooled from each fish by hours of darkness and daylight using linear methods to interpolate the data to bins of 1°C and 10 m for temperature and depth, respectively. For some analyses, we also used the high resolution data downloaded from physically recovered tags to characterize behaviors during periods of twilight. In addition to describing basic vertical habitat use patterns, we attempted to identify some aspect of blue marlin behavior that would allow prediction of blue marlin vertical habitat utilization for use in modeling population abundance trends using longline CPUE. The predominant methods currently in use are based on estimates of the proportion of time spent within successively deeper layers based on temperature relative to that of the surface mixed layer (e.g. Hinton & Nakano 1996, Takeuchi 2001, Yokawa & Uozumi 2001, Yokawa et al. 2001). ICCAT (2004) also

recommended that CPUE simulations intended to test alternative standardization methods should adopt this approach, and that day–night fishing patterns and species distributions also be included. In order to preserve the stochastic nature of animal behavior, we partitioned observations for each fish by its daily activity patterns to be commensurate with the duration of a longline set.

For the ARGOS-transmitted data, we compiled the proportions spent within successively deeper layers of temperature relative to the temperature of the surface mixed layer (termed Delta T) by each 6 h period that could be clearly identified as daytime or nighttime. For each time period, there are 3 types of summarized data transmitted via ARGOS satellites: (1) the proportion of time the fish spent within 12 user-defined depth bins (i.e. 25 m bin resolution in this study); (2) the proportion of time the fish spent within 12 user-defined temperature bins (i.e. 2°C bin resolution in this study); and (3) minimum and maximum temperatures at depth minima and maxima visited by the fish, and at 6 additional depths between those points (PDT). We extracted the temperatures from the PDT data where the depth is ≤ 1 m, and calculated the average surface temperature (T_0) for each day. When there were no surface temperature observations (i.e. when fish did not surface for a day), we used temperatures from the

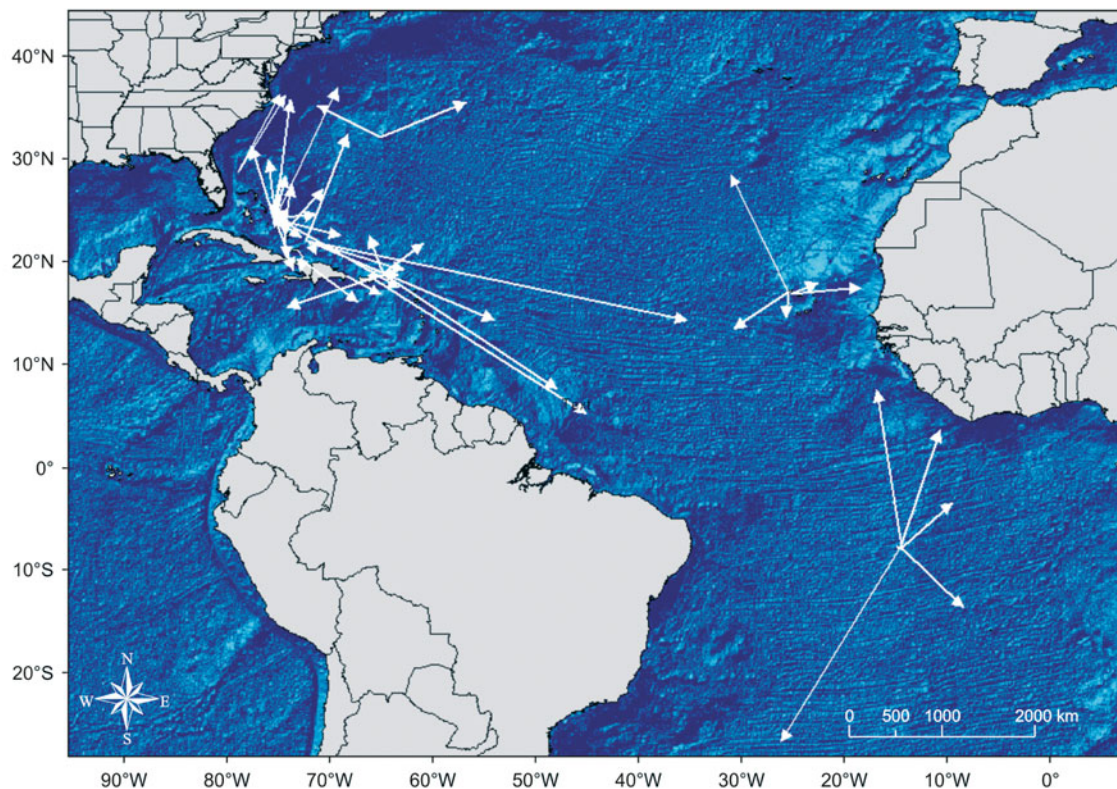


Fig. 1. *Makaira nigricans*. Tag release and pop-off locations of pop-up satellite archival tags (PSATs) applied to blue marlin. Arrows at the end of displacement vectors indicate pop-up locations

previous and subsequent days to linearly interpolate the surface temperature. Temperatures are illustrated at depth when the fish is shallower using a 3 d running average of all measurements at depth from the tag. Next, for each depth bin we generated 360 temperatures (GMT, 6 h, 1 temperature min^{-1}) from a random normal distribution, based on the range of temperatures from the PDT. Then, for each depth bin, we used the probability density function derived from the high-resolution data to randomly generate the number of temperature values for each depth bin. A new temperature histogram was tabulated for the generated temperatures, and it was compared to the temperature histogram (T) of the data. The differences in numbers for each temperature bin were corrected by randomly eliminating the temperature values in positive bins, and randomly adding temperature values in negative bins. Finally, Delta Ts were calculated by subtracting the generated temperatures (GT) from T_0 , and the proportions of time spent at decreasing Delta T were tabulated at 1°C bin resolution.

Inspection of the high-resolution data from recovered tags revealed that most of the time spent in the surface mixed layer (Delta T bin = 0) was actually spent at the ocean surface (arbitrarily defined here as ≤ 5 m). Time spent in this stratum was treated as a separate bin. The time periods for day, night, and twilight were determined from the light level data recorded by the tag. Daylight and darkness were easily separated. The change in light level at dusk and dawn was used to bound twilight based on the midpoint of the transition in light intensity. Specifically, we quantified twilight as the 2 h period about dusk or dawn. Daily dawn/dusk data were pooled by day. The daily day-night-twilight patterns of time spent at the ocean surface and Delta T were then determined by pooling the archived, high-resolution observations for the appropriate periods. The mean Delta T values were determined for each of the resulting distributions, and the

Delta T-time distributions for each day-night (and twilight) compilation were sorted by increasing depth. The data were then tabulated for several percentiles of the observed frequency distributions.

We also compiled the maximum depths and minimum temperatures explored by our tagged fish by days at large to obtain statistics related to the deepest and coldest strata used by blue marlin. This included regressions of the number of days at large when each fish included a deeper or colder stratum in its daily vertical excursions.

RESULTS

There was a significant difference in the distributions of depths occupied by our study specimens between day and night ($\chi^2 = 45.7$; 25 df; $p < 0.01$; Fig. 2a). During hours of darkness the fish were higher in the water column, spending about 50% of their time in the surface 10 m and 86% in the upper 30 m. In contrast, during the daytime, less than 20% of time was spent above 10 m and only about 46% in the upper 30 m. In addition, the fish studied spent less than 2% of their time at or below 100 m at night, compared to about 17% during the day. The distribution of time at temperature was also significantly different between day and night ($\chi^2 = 55.1$; 20 df; $p < 0.01$), reflecting the observed differences in the day-night depth distribution (Fig. 2b). The nighttime modal temperature was 29°C, while the daytime mode was a degree lower at 28°C. More interestingly, our blue marlin spent about 5% of their time within or below 25°C at night, increasing to 46% during the day.

We examined diel differences in the vertical behavior of blue marlin using 996 sets of nocturnal (Table 1, Fig. 3a) and 898 sets of diurnal Delta T distributions (Table 1, Fig. 3b). Blue marlin clearly spent more time below the surface mixed layer (Delta T = 0) during the

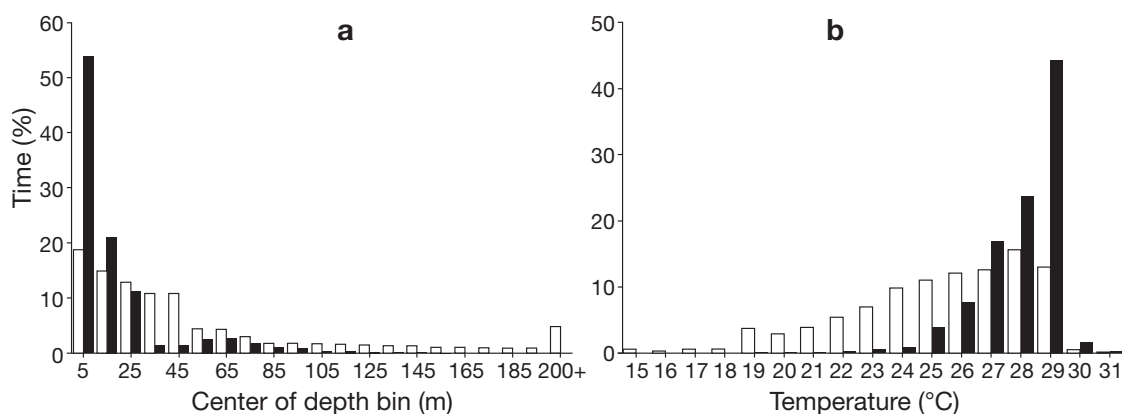


Fig. 2. *Makaira nigricans*. Fraction of time during daytime (white bars) and night-time (black bars) spent in (a) each successively deeper 10 m depth bin, and (b) each 1°C temperature bin, derived from PSAT data from ARGOS transmissions

Table 1. *Makaira nigricans*. Fractions of time spent by blue marlin at temperature relative to the temperature of the surface mixed layer (Delta T) during hours of darkness and daylight based on ARGOS-transmitted data from PSAT tags. -: no data

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	
Darkness												
0	1.000	1.000	1.000	1.000	1.000	0.947	0.694	0.265	0.041	0.532	0.028	0.849
-1	-	-	-	-	-	0.049	0.251	0.514	0.473	0.050	0.338	0.079
-2	-	-	-	-	-	0.004	0.047	0.216	0.463	0.026	0.213	0.033
-3	-	-	-	-	-	-	0.006	0.006	0.024	0.064	0.140	0.018
-4	-	-	-	-	-	-	0.002	-	-	0.101	0.120	0.008
-5	-	-	-	-	-	-	-	-	-	0.163	0.079	0.005
-6	-	-	-	-	-	-	-	-	-	0.056	0.065	0.003
-7	-	-	-	-	-	-	-	-	-	0.006	0.019	0.002
-8	-	-	-	-	-	-	-	-	-	0.002	-	0.001
-9	-	-	-	-	-	-	-	-	-	-	-	0.001
-10	-	-	-	-	-	-	-	-	-	-	-	0.000
-11	-	-	-	-	-	-	-	-	-	-	-	0.000
-12	-	-	-	-	-	-	-	-	-	-	-	0.000
Daylight												
0	1.000	1.000	1.000	1.000	0.960	0.372	0.455	0.335	0.000	0.210	0.017	0.583
-1	-	-	-	-	0.024	0.516	0.075	0.132	0.000	0.201	0.005	0.144
-2	-	-	-	-	0.016	0.098	0.025	0.018	0.000	0.016	0.001	0.069
-3	-	-	-	-	-	0.015	0.030	0.042	0.049	0.004	0.000	0.043
-4	-	-	-	-	-	-	0.154	0.043	0.368	0.028	0.005	0.031
-5	-	-	-	-	-	-	0.151	0.037	0.301	0.013	0.032	0.026
-6	-	-	-	-	-	-	0.041	0.031	0.184	0.016	0.114	0.022
-7	-	-	-	-	-	-	0.044	0.021	0.041	0.012	0.202	0.022
-8	-	-	-	-	-	-	0.021	0.046	0.000	0.028	0.214	0.019
-9	-	-	-	-	-	-	0.004	0.071	0.000	0.025	0.398	0.020
-10	-	-	-	-	-	-	-	0.170	0.003	0.223	0.013	0.012
-11	-	-	-	-	-	-	-	0.053	0.008	0.031	-	0.003
-12	-	-	-	-	-	-	-	0.002	0.027	0.087	-	0.003
-13	-	-	-	-	-	-	-	-	0.010	0.101	-	0.001
-14	-	-	-	-	-	-	-	-	0.007	0.006	-	0.001
-15	-	-	-	-	-	-	-	-	0.001	-	-	0.000

daytime than in darkness. Overall, 85 % of their nighttime hours and 58 % of their daytime hours were spent within the surface mixed layer (Table 1). However, inspection of these data revealed high variability in the individual distributions. For example, the percentage of time at depths occupied by the Delta T distribution with median mean depths indicated about 95 % of time was spent in the surface mixed layer at night compared to only 37 % during the day. The high-resolution data from recovered tags yielded 404 daily estimates of time spent at Delta T for conditions of nighttime and twilight, and 403 daily estimates for daytime conditions (Fig. 3c–e). These data indicated a trend of increasing use of cooler layers during the daytime, compared to night, with an intermediate behavior during periods of twilight. These results are entirely consistent with our analyses of the ARGOS summary datasets that were only available in the bins compiled by the tags' onboard software prior to transmission.

The detailed archival data from recovered PSATs provide a complete uninterrupted history of temperature, depth, and light levels experienced by blue mar-

lin during the entire length of monitoring, from initial release through first transmission to the ARGOS satellite system. Inspection of the depths explored (Fig. 4) revealed that characterization of habitat in terms of proportions of time spent at depth and temperature is inadequate to describe how these fish actually use the available water column. Fig. 4 was constructed with data retrieved from a single recovered tag. Each panel represents the activity pattern during a single day of different weeks over a 39 d monitoring period. Fig. 4a,b shows the daily activity pattern of early- and mid-time series. A decidedly surface orientation at night and deeper use of the water column during the daytime, including the deepest observed dive to 340 m (Fig. 4a). During this period, the fish spent considerable time below the surface mixed layer during daylight hours. After descending at the beginning of the day, this individual remained deep in the water column without returning to the surface until late in the day (Fig. 4a). The time trace depicted in Fig. 4b is 1 wk later, when the fish was wandering more widely in the water column with frequent returns to the surface.

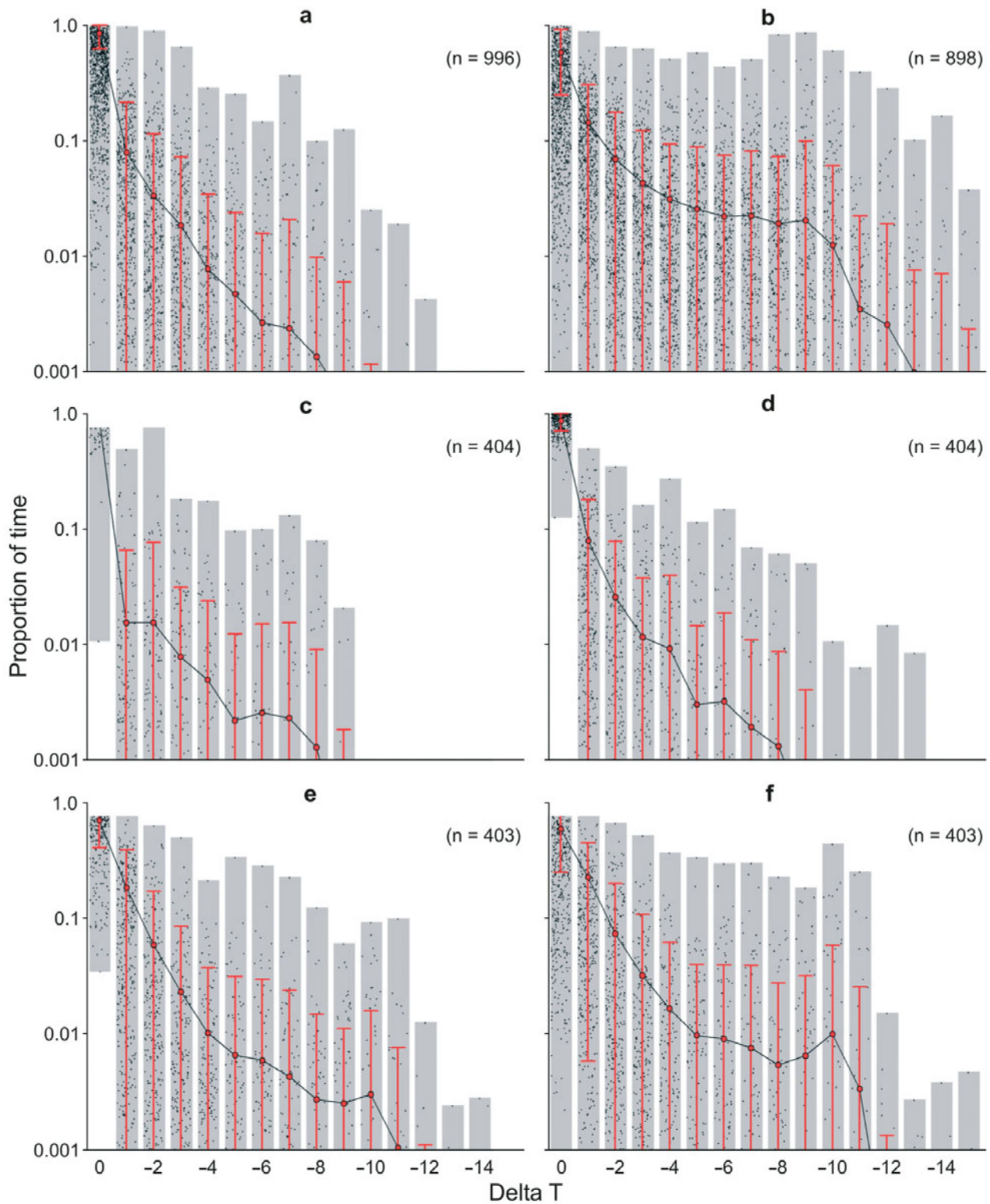


Fig. 3. *Makaira nigricans*. Proportions of time spent by Delta T (temperature of the surface mixed layer) (a) during hours of darkness estimated from the ARGOS data, (b) during daytime hours estimated from the ARGOS data, (c) during hours of darkness estimated from archived data, (d) during twilight hours estimated from archived data, (e) during daytime hours estimated from archived data, and (f) during daytime hours estimated from archived data, but excluding time spent at the surface. Shaded bars signify the range of observations (depicted by small gray dots). Red circles and associated error bars denote means and 95% confidence intervals

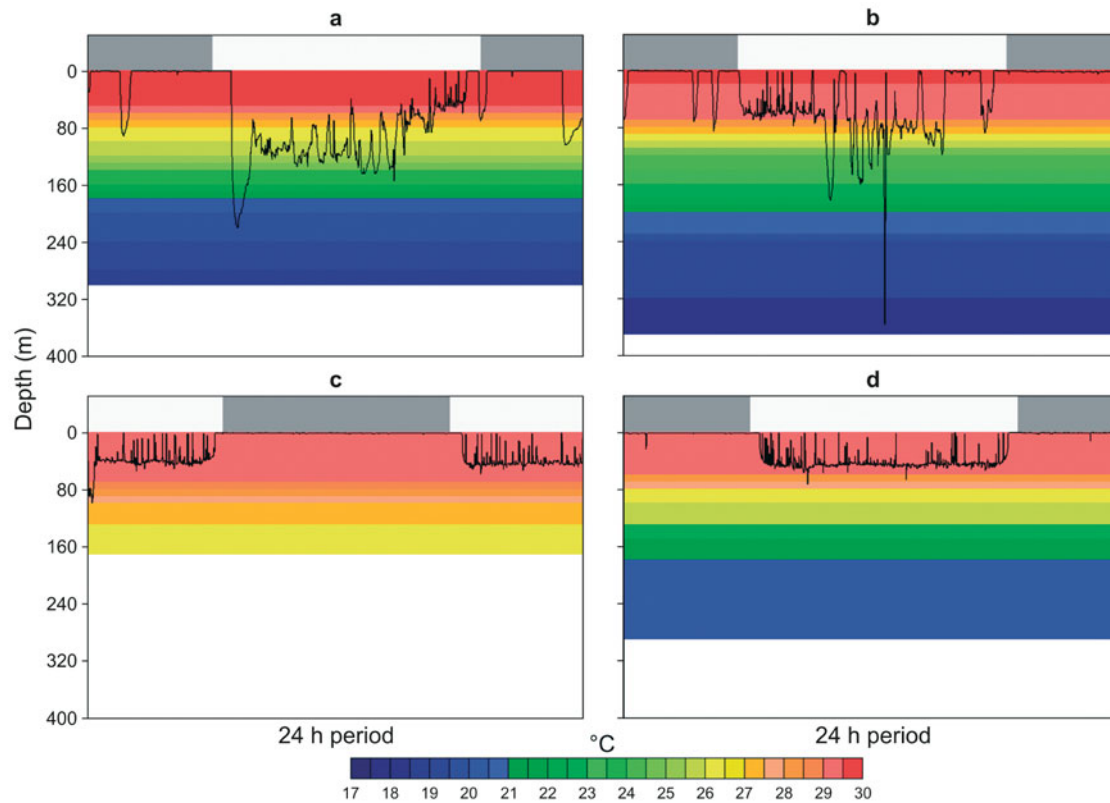


Fig. 4. *Makaira nigricans*. Excerpt from a time series (12 October to 20 November 2003) of temperature and depth measurements by PSAT 27825 applied to a blue marlin and later recovered. The shaded/white area above the 0 depth value on the y-axis denotes darkness/daylight periods, respectively. Excerpts were taken from (a) the first part of the time series on 17 October, showing typical daytime diving activity during the first part of the track, (b) the early part of the time series on 24 October, showing the deepest dive (340 m) during the track, (c) the latter part of the time series on 17 November, showing quiescent (dormant) activity during nocturnal periods towards the end of the track, and (d) near the end of the time series on 19 November, showing restrictive daytime diving activity during the later part of the track

Later in the time series, this marlin became much more surface oriented, but still showed clear day–night shifts in depths occupied (Fig. 4c,d). Nighttime depths were mostly restricted to the very near surface layer, and daytime depths were almost entirely restricted to the surface mixed layer, with only infrequent exploration of deeper, cooler water (Fig. 4c,d). The time–depth habitat use by another monitored individual trended in the opposite direction from initially shallow to later deeper habitat occupancy.

Results also illustrate that a disproportionate fraction of the time spent in the surface mixed layer was at the surface itself, particularly at night. Hooks on pelagic longlines are generally at the surface for only very brief periods during set and retrieval operations. Consequently, this region should receive special treatment. We partitioned the frequency distributions of time into the proportion of time in the surface 5 m and the remainder into proportions at Delta T (Table 2). The proportions of time at the surface varied by time of day, with means of 91% during the night, 52% during twilight, and 22% during the daytime (Table 2).

Remarkably, the percentage of time at depth occupied by the Delta T distribution with median mean depths indicates that nearly all (>99%) of the time spent in the surface mixed layer at night was at the surface (Table 2). In contrast, about half of the time during twilight was at the surface and a much smaller proportion during the day (Table 2). Excluding the time at the surface from the computation of times at Delta T for the detailed data shifts the proportions at higher Delta T upward (cf. Fig. 3e,f).

In order to assess the effect of the deepest recorded dives on vertical habitat use, we examined maximum depths and minimum temperatures explored by our tagged fish by days at large and time of day (Figs. 5 & 6). Marlin occupied deeper strata (maximum observed depth, D_{\max}) in their daily movements with increasing days at large, $T(D_{\max} = 116.3 T^{0.266}$; $r^2 = 0.262$; $F = 76.5$; $p < 0.001$; 216 df), but the overall pattern reflects high daily variability (Fig. 5). A few of the monitored fish confined their vertical excursions to less than 100 m during the time monitored, while another ventured below 800 m, for an average maximum depth of 319 m

Table 2. *Makaira nigricans*. Fractions of time spent by blue marlin in the upper 5 m and at temperature relative to the temperature of the surface mixed layer (Delta T) during hours of darkness, twilight and daylight based on data retrieved from recovered PSAT tags. –: no data

Depth or 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
Darkness												
>5 m	1.000	1.000	1.000	1.000	0.998	0.991	0.914	0.358	0.525	0.641	0.584	0.911
0	–	–	–	–	0.002	0.003	0.045	0.362	0.053	0.038	0.070	0.037
–1	–	–	–	–	–	0.006	0.024	0.241	0.082	0.029	0.020	0.015
–2	–	–	–	–	–	0.001	0.016	0.038	0.148	0.022	0.021	0.015
–3	–	–	–	–	–	–	0.001	0.001	0.141	0.025	0.029	0.008
–4	–	–	–	–	–	–	–	–	0.029	0.042	0.043	0.005
–5	–	–	–	–	–	–	–	–	0.022	0.031	0.041	0.002
–6	–	–	–	–	–	–	–	–	–	0.067	0.044	0.003
–7	–	–	–	–	–	–	–	–	–	0.076	0.068	0.002
–8	–	–	–	–	–	–	–	–	–	0.029	0.079	0.001
Twilight												
>5 m	1.000	0.958	0.898	0.710	0.552	0.446	0.339	0.674	0.523	0.456	0.581	0.520
0	–	0.042	0.065	0.290	0.423	0.477	0.423	0.013	0.119	0.174	0.023	0.344
–1	–	–	0.020	–	0.004	0.073	0.238	0.044	0.179	0.066	0.017	0.079
–2	–	–	0.016	–	0.004	0.004	–	0.074	0.013	0.004	0.019	0.026
–3	–	–	–	–	0.004	–	–	0.111	0.019	0.100	0.025	0.012
–4	–	–	–	–	0.004	–	–	0.084	0.038	0.021	0.081	0.009
–5	–	–	–	–	0.008	–	–	–	0.040	0.042	0.058	0.003
–6	–	–	–	–	–	–	–	–	0.071	0.112	0.113	0.003
–7	–	–	–	–	–	–	–	–	–	0.025	0.029	0.002
–8	–	–	–	–	–	–	–	–	–	–	0.054	0.001
Daylight												
>5 m	0.998	0.990	0.979	0.741	0.022	0.134	0.501	0.176	0.263	0.029	0.051	0.222
0	0.002	0.010	0.008	0.172	0.977	0.562	0.053	0.617	0.394	0.054	0.102	0.478
–1	–	–	0.007	0.072	0.002	0.245	0.033	0.012	0.015	0.051	0.021	0.183
–2	–	–	0.006	0.012	0.000	0.049	0.170	0.011	0.015	0.227	0.052	0.058
–3	–	–	–	0.003	0.000	0.011	0.159	0.016	0.030	0.495	0.226	0.023
–4	–	–	–	–	–	–	0.078	0.016	0.029	0.145	0.127	0.010
–5	–	–	–	–	–	–	0.005	0.015	0.041	–	0.134	0.007
–6	–	–	–	–	–	–	–	0.019	0.082	–	0.280	0.006
–7	–	–	–	–	–	–	–	0.015	0.091	–	0.007	0.004
–8	–	–	–	–	–	–	–	0.014	0.006	–	–	0.003
–9	–	–	–	–	–	–	–	0.029	0.018	–	–	0.003
–10	–	–	–	–	–	–	–	0.023	0.010	–	–	0.003
–11	–	–	–	–	–	–	–	0.027	0.005	–	–	0.001
–12	–	–	–	–	–	–	–	0.012	0.000	–	–	0.000
–13	–	–	–	–	–	–	–	–	0.001	–	–	0.000
–14	–	–	–	–	–	–	–	–	0.001	–	–	0.000

(Fig. 6). There was also a significant trend for our marlin to have visited cooler strata (minimum observed temperature, C_{\min}) in their daily movements with increasing days at large ($C_{\min} = 24.5 T^{-0.103}$; $r^2 = 0.421$; $F = 157.0$; 217 df) but the overall pattern also reflects high daily variability (Fig. 6). The mean of the lowest temperatures explored was 17°C, with a range of just less than 10°C to just over 24°C.

DISCUSSION

Overall, our observations indicate substantial variability in habitat use by temperature and depth, and in terms of time spent at temperature relative to the surface mixed layer. This variability occurred within and among individual blue marlin. The Delta T fractions for

the different percentiles in Tables 1 & 2 highlight the stochastic nature of the behavior with respect to Delta T. The distributions are not only highly variable, but even when sorted by mean Delta T, there is no smooth progression of increasing use of cooler Delta T with the increase in the mean. For example, the fish contributing to observations at the 90th and 95th percentiles of the distributions (sorted by mean) ventured into relatively colder/deeper water than those at the 97.5th and 99th percentiles. These observations support the view that the behavior of blue marlin with respect to depth is more complex than can be captured by a model of Delta T alone.

We suspect that time spent at the surface may not be primarily associated with feeding behavior, but takes place when the fish are in a quiescent mode, particularly during nocturnal periods. Blue marlin appear to

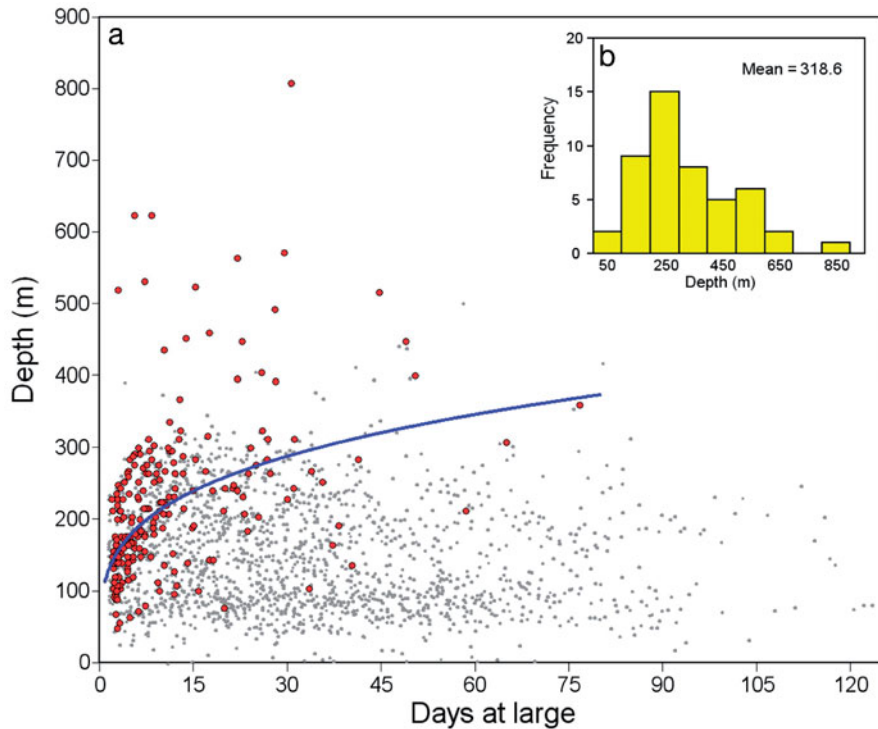


Fig. 5. *Makaira nigricans*. Maximum depths to which each tagged fish dove during its time at large. (a) Deepest dive in each 6 h record. Larger red dots signify first records of each fish at the observed depth, and the blue line is the exponential fit to the first occurrence data. (b) Deepest dives observed for each fish

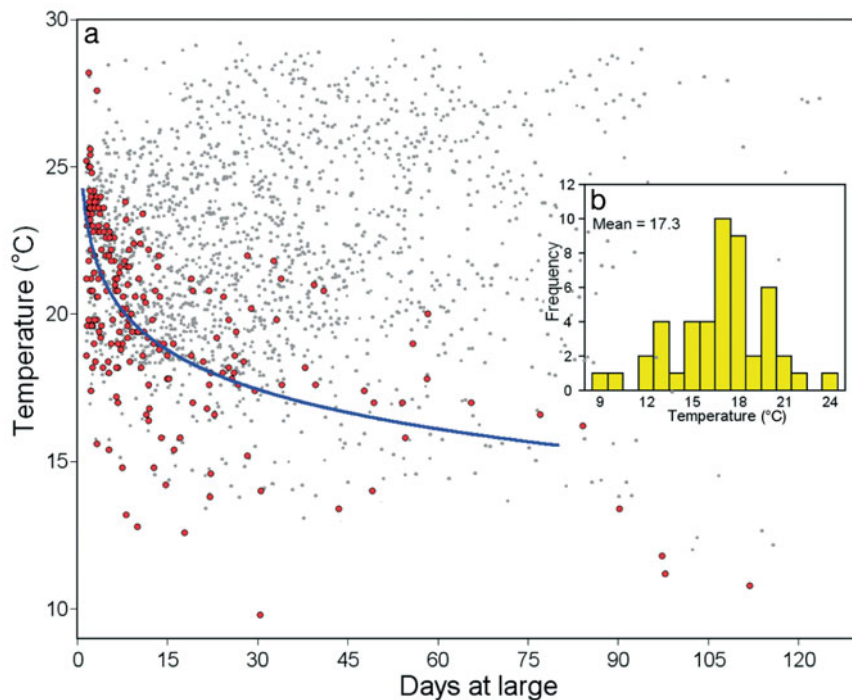


Fig. 6. *Makaira nigricans*. Minimum temperatures experienced by each tagged fish during its time at large. (a) Coolest temperature for each fish in each 6 h record. Larger red dots signify first records of each fish at the observed temperature, and the blue line is the exponential fit to the first occurrence data. (b) Coolest temperature observed for each fish

be daylight sight feeders that regularly penetrate into the water column to feed or possibly view prey above. The temperatures and depths explored are likely a function of the distribution of the forage species (Dagorn et al. 2000) more so than a response to the Delta T experienced by the marlin. Furthermore, the forage depth distribution reflects its species composition and relationship to oceanographic features, such as the thermocline, which probably represents a physiological 'boundary' for many forage species (from both directions). There is a strong association between Delta T and the temperature distribution within and above the thermocline. These factors would lead to strong, spatially local correlations between Delta T and habitat use that are unlikely to be highly predictive across the entire vertical spatial distribution of blue marlin. Certainly, the individual fish depicted in Fig. 4 exhibited fundamentally different behaviors during the period monitored.

Our blue marlin often made deep, short-duration dives that took them into relatively cold environments (Fig. 5). The mode was at 200 to 300 m, but a dive below 800 m was observed. These correspond to a mode of minimum temperatures ranging from 17 to 18°C, and a minimum observed temperature below 10°C (Fig. 6). Clearly, blue marlin can penetrate these depths and temperatures as conditions require, if only briefly. Such excursions may be related to feeding or predator avoidance and are no doubt facilitated by a brain heater organ that permits ocular and physical function at low temperatures and low light conditions (Block 1986, Block & Finnerty 1994, Fritsches et al. 2003, 2005). In any event, the view that this species' vertical habitat does not extend to depths targeted by deep-set pelagic longlines (i.e. >200 m) is false. Previous studies of blue marlin monitored via acoustic telemetry (Block et al. 1992a,b) were conducted over much shorter time periods (hours to days) than reported here (weeks and months). Resulting

depth and temperature preferences from those studies predictably indicated a more limited use of the water column. We predict that even deeper and colder excursions will be revealed as longer and longer tag deployments become technologically possible.

From our results, we feel the mean behaviors over all Delta T are not locally predictive for either an individual animal or its spatial location. Fishers tend to set gear in proximity to local oceanographic features, such as current rips or temperature boundaries (Hoey & Moore 1999, Watson et al. 2005). Consequently, the observed mean behavior with respect to Delta T may bear little relation to actual behavior patterns where longlines are commonly deployed. Similarly, oceanographic features at set locations probably deviate importantly from mean oceanographic conditions in the $5^\circ \times 5^\circ$ latitude-longitude cells used to associate longline sets with physical measures of their habitat (Goodyear 2003). Further, longline sets tend to span day–night boundaries, and consequently the proportions in each must vary with latitude and season. The strong day–night differences in species distributions within habitat documented herein suggest that CPUE analyses to estimate population abundance trends based on habitat assumptions must integrate day–night behaviors. These factors include longline effort and the depth-, temperature-, and/or Delta T-predictors of vertical habitat space. Depending on the availability of detailed effort data, this task may or may not be feasible for the analysis of historical CPUE trends using habitat-based methods, regardless of whether the species distributions estimated here are appropriate.

For reasons of economy, our study focused on areas where blue marlin were highly available to recreational and longline fishers. The blue marlin included in this study were selected based on the availability of platforms to perform the tagging operations, and may not be representative (random) of animal behavior within the Atlantic-wide population. Our current temperature utilization data are similar to the findings of Goodyear (2003), who contrasted World Ocean Atlas predictions of average sea surface temperatures (Conkright et al. 1998) with longline sets that caught blue marlin. However, Goodyear (2003) found that the highest proportion of positive sets occurred where average surface temperatures were 27°C , about 1°C below the peak daytime temperature observed in the present study. Also, the lower (cooler) tail of the distribution estimated by Goodyear (2003) included temperatures not observed in the present study. Part of the difference between the 2 findings is likely the result of Goodyear's application of monthly averages, which do not reflect micro-scale features of ocean circulation. However, it is also likely that our data concerning tem-

peratures and depths used by blue marlin are biased to some extent by the local adaptation of the fish we tagged. Therefore, it seems likely that blue marlin nearer to the northern/southern limits of their range may have temperature and depth habitat profiles that differ importantly from those seen in our study.

Absolute temperature, Delta T, actual depth (light concentration), and prey and predator distributions and abundances are all likely to be important features of blue marlin habitat. Our data support the notion that blue marlin vertical habitat is a complex multivariable continuum consisting of a near-surface 'core' area where they spend most of their time, particularly at night, and an elastic temperature–depth space defined by physiological tolerances and predator–prey distributions. The mixed surface layer is also the warmest part of the local habitat, which may have some metabolic significance (Brill 1996). All of our fish periodically descended into cooler water below the surface, typically during daylight hours. We believe most of this activity was associated with feeding behavior, possibly to exploit resources near, within, or below the thermocline, or to provide a better view of potential prey above. However, our fish sometimes remained at depth for the entire day, possibly suggesting successful foraging at depth, a view further supported by diet observations (Goodyear et al. 2003). For example, deep water prey items such as the mesopelagic snake mackerels, Gempylidae, or pomfrets *Brama* spp. have occasionally been identified in the diet of blue marlin (Erdman 1962, Baker 1966, Strasburg 1970, Rivas 1975, Brock 1984, Harvey 1989). Although some deep water prey undertake diurnal vertical migrations at night, marlin appear to be primarily daytime sight feeders. We found that the same fish would make frequent trips to the surface during the daylight hours. We speculate that this change of behaviors may be associated with differing spatial distributions of prey species, and that blue marlin can make use of a larger vertical habitat than that actually frequented on most days.

For whatever reasons, our fish explored depths to more than 800 m and encountered absolute temperatures of less than 10°C and Delta Ts of -15°C . Certainly, their physiological and anatomical adaptations permit short-term excursions into otherwise inhospitable temperatures and low light conditions in response to visual and olfactory cues. This may actually enhance predation success of less adapted prey species downward through the thermocline. These colder deeper strata may be disproportionately important components of blue marlin habitat, particularly in regions where dissolved oxygen does not limit the depth of acceptable habitat, as reported for the western North Atlantic Ocean (Prince & Goodyear 2006).

Our PSAT analysis presents the most comprehensive description to date of actual vertical habitat use for Atlantic blue marlin, as it relates to water temperature and depth. Vertical movements extending from the surface to greater than 800 m are reflected in the wide spectrum of food items consumed by blue marlin (Rivas 1975). The size range of organisms eaten by adults is relatively large, ranging from 2 cm sargassumfish *Histrio histrio* (E. D. Prince pers. obs.) to 20 kg white marlin *Tetrapturus albidus* (D. Snodgrass pers. obs.) and 29 kg bigeye tuna (Strasburg 1969). As such, our results offer invaluable information relevant to ecosystem-based management, an increasingly mandated approach to conserve fisheries (Kitchell et al. 2006). Specifically, this information may contribute to improving modeling approaches that address vulnerability and encounter probabilities of blue marlin with pelagic longline fishing gears.

In the context of habitat standardizations of abundance trends from CPUE data, several issues need additional study. The day–night timing of gear deployment and retrieval varies with target species, and it is likely that the diel pattern of gear depth distributions and fish feeding behavior would translate to important differences in blue marlin vulnerability to different fishing practices. Having said this, there appear to be few places in the vertical tropical pelagic environment in which longline gear deployments can avoid interactions with blue marlin. In addition, the physical composition of fishing equipment has changed with time and target species, such that the historical trends in fished times at depth are uncertain at best. Boggs (1992) observed that striped marlin *Tetrapturus audax* had a much greater propensity to take longline baits that were moving during deployment or retrieval rather than while settled. Such observations indicate that, by itself, hook time at depth is a crude index of vulnerability; fish can likely perceive a given bait from olfactory and visual cues from 10s if not 100s of meters away and home in on it within seconds. Life of an apex predator in the patchy food-poor environment of the open ocean must depend on more than random encounters. To this end, as new versions of PSAT technology advance to a wider selection of environmental sensors, increased memory, greater battery life, and improved anchoring mechanisms, our understanding of vertical habitat use of this species can be expected to improve.

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Appendix 1. *Makaira nigricans*. Details for setup, release, and pop-up/recovery from 51 PSATs deployed on Atlantic blue marlin. PTT: platform transmitter terminal

No.	PTT ID	Date released	Sampling interval (s)	Estimated weight (kg)	Days-at-liberty/ days programmed	Displacement (km)	Release location	Location of first transmission	No. days data transmitted ^a
1	22870	9 Jun 02	60	68	36/36	924	28° 43' N, 78° 54' W	36° 16' N, 74° 46' W	36
2	23548	11 Jun 02	60	147	29/41	904	28° 46' N, 78° 47' W	36° 00' N, 74° 22' W	29
3	22872	14 Jun 02	60	57	26/44	653	23° 56' N, 74° 37' W	25° 00' N, 68° 16' W	26
4	25999	14 Jun 02	60	57	44/45	1386	23° 56' N, 74° 31' W	17° 24' N, 63° 15' W	44
5	24793	17 Jun 02	60	50	5/41	127	22° 51' N, 74° 23' W	24° 00' N, 74° 24' W	5
6	23077	21 Jun 02	60	40	23/37	143	23° 47' N, 74° 22' W	22° 30' N, 74° 19' W	23
7	22873	28 Jun 02	60	57	22/43	208	28° 55' N, 74° 24' W	24° 26' N, 75° 36' W	5
8	25874	30 Jun 02	60	57	26/41	282	22° 48' N, 74° 23' W	20° 15' N, 74° 10' W	2
9	26000	1 Jul 02	60	57	27/40	1230	21° 56' N, 74° 19' W	32° 19' N, 68° 13' W	7
10	23520	2 Jul 02	60	102	25/39	452	22° 48' N, 74° 21' W	26° 47' N, 73° 24' W	25
11	26005	6 Jul 02	60	57	13/35	135	22° 49' N, 74° 23' W	22° 42' N, 75° 41' W	9
12	26001	8 Jul 02	60	159	26/33	1468	22° 47' N, 74° 31' W	35° 31' N, 70° 09' W	26
13	26935	12 Oct 02	60	57	39/39	529	18° 43' N, 74° 22' W	21° 47' N, 60° 55' W	39
14	27825	12 Oct 02	60	57	39/39	1049	18° 42' N, 64° 49' W	15° 34' N, 74° 07' W	38 ^b
15	23205	13 Oct 02	60	57	38/38	2213	18° 43' N, 74° 22' W	07° 32' N, 69° 54' W	35
16	39334	14 Oct 02	60	36	37/37	423	18° 51' N, 64° 47' W	22° 26' N, 66° 11' W	16
17	23520	23 Apr 03	60	60	40/40	409	18° 29' N, 68° 23' W	16° 45' N, 65° 00' W	40
18	41523	4 Jun 03	30	80	95/95	407	24° 06' N, 75° 15' W	24° 33' N, 71° 17' W	92
19	41524	4 Jun 03	30	68	82/95	594	24° 06' N, 75° 17' W	19° 04' N, 73° 33' W	81 ^b
20	41518	5 Jun 03	30	45	63/63	840	24° 03' N, 75° 20' W	31° 12' N, 77° 36' W	63
21	41520	5 Jun 03	30	82	63/63	1530	24° 06' N, 75° 15' W	36° 52' N, 69° 13' W	63
24	23388	7 Jun 03	30	55	60/60	853	20° 15' N, 72° 28' W	16° 14' N, 66° 17' W	10
22	41521	7 Jun 03	30	68	61/61	367	24° 06' N, 75° 15' W	22° 15' N, 72° 46' W	44 ^b
23	41525	7 Jun 03	30	102	41/121	645	24° 07' N, 75° 16' W	29° 54' N, 75° 56' W	41
25	41526	7 Jun 03	30	82	84/121	1289	24° 07' N, 75° 18' W	35° 42' N, 73° 49' W	82
26	23389	8 Jun 03	30	55	61/61	892	20° 15' N, 72° 50' W	16° 02' N, 67° 15' W	61
27	23397	9 Jun 03	30	50	38/93	259	20° 18' N, 72° 37' W	18° 59' N, 69° 51' W	38
28	41522	9 Jun 03	30	50	10/59	159	24° 05' N, 75° 15' W	25° 05' N, 74° 08' W	10
29	41528	10 Jun 03	30	52	69/69	468	24° 07' N, 75° 17' W	28° 16' N, 74° 17' W	69 ^b
30	41516	11 Jun 03	30	45	57/57	401	24° 03' N, 75° 26' W	27° 15' N, 73° 47' W	56
31	41538	16 Jun 03	30	136	47/75	2092	21° 59' N, 72° 02' W	14° 17' N, 54° 02' W	47
32	41534	17 Jun 03	30	193	46/67	1014	22° 00' N, 72° 04' W	19° 08' N, 62° 47' W	46 ^b
33	41539	18 Jun 03	30	45	74/74	183	21° 59' N, 72° 04' W	20° 37' N, 71° 19' W	73
34	41531	19 Jun 03	30	68	91/92	4007	22° 00' N, 72° 04' W	14° 15' N, 35° 13' W	90
35	41530	26 Jun 03	30	55	7/63	182	22° 51' N, 74° 24' W	24° 30' N, 74° 16' W	7
36	41527	14 Jul 03	30	45	41/96	672	32° 03' N, 65° 01' W	35° 09' N, 71° 07' W	41
37	41537	24 Jul 03	30	160	45/45	870	32° 07' N, 64° 60' W	35° 26' N, 56° 26' W	45
38	41535	2 Sep 03	30	227	28/90	574	18° 34' N, 66° 13' W	14° 35' N, 64° 18' W	28
41	41540	3 Sep 03	30	57	7/94	109	18° 34' N, 66° 13' W	19° 04' N, 65° 22' W	7
39	42723	3 Sep 03	30	68	124/124	2639	18° 32' N, 66° 11' W	03° 25' N, 48° 51' W	93
40	42724	3 Sep 03	30	52	93/93	298	18° 32' N, 66° 11' W	18° 38' N, 63° 19' W	82 ^b
42	49774	5 May 04	30	113	47/62	1361	16° 55' N, 25° 20' W	28° 24' N, 30° 57' W	46
43	49773	9 May 04	30	82	21/30	283	16° 59' N, 25° 21' W	14° 26' N, 25° 34' W	18
44	49777	10 May 04	30	95	15/45	730	16° 57' N, 25° 23' W	13° 27' N, 30° 40' W	15
46	49775	12 May 04	30	145	70/90	748	16° 45' N, 25° 06' W	17° 25' N, 18° 16' W	54
45	49778	12 May 04	30	181	56/56	303	16° 45' N, 25° 06' W	17° 55' N, 22° 30' W	28
47	53733	14 Oct 04	30	363	4/100	35	07° 54' S, 14° 26' W	08° 06' S, 14° 34' W	4
48	53244	16 Oct 04	30	45	44/44	1663	07° 51' S, 14° 24' W	07° 24' N, 16° 43' W	44
49	53245	19 Oct 04	30	125	36/55	728	07° 54' S, 14° 14' W	03° 32' S, 09° 25' W	36
50	53736	7 Nov 04	30	90	90/90	2535	07° 49' S, 14° 20' W	26° 47' S, 26° 06' W	15
51	53734	17 Nov 04	30	205	38/89	1356	07° 49' S, 14° 20' W	03° 32' N, 10° 39' W	38

^aNumber of calendar days represented by ARGOS transmissions, not necessarily an entire dataset for any particular 24 h period
^bRecovery of intact PSAT. For these cases, detailed data were available for all days-at-liberty