Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop-up archival satellite tags

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ABSTRACT

Researchers have applied numerous techniques to improve billfish stock assessments, including habitat-based models that incorporate behavioral and oceanographic parameters to standardize historical catch-per-unit-effort time-series data. These methods have allowed researchers to account for significant changes in the depths of pelagic longline (PLL) gear deployments over time. This study presents habitat-use data recovered from high-resolution 5- and 10-day pop-up satellite archival tags (PSATs) attached to 47 surviving white marlin released from commercial and recreational fishing gears offshore of the U.S. East Coast, the northern Caribbean, and Venezuela between 2002 and 2004. Data recovered from transmitting tags indicated that white marlin spent nearly half of their time associated with warm, near-surface waters (<10 m). All fish displayed frequent short duration (mean: 39.8 min) vertical excursions from surface waters to depths averaging 51 m. Qualitative and multivariate classifications of data from completely transmitted movements of surviving white marlin revealed two major types of descents: one pattern was characterized by deep 'V'-shaped excursions of relatively short duration (mean: 23.4 min) while the other featured descents that were more broadly 'U'-shaped and confined to a specific depth range for an extended period of time (mean: 75.8 min). Based on the frequency, persistence, and patterns of these vertical movements, white marlin appear to direct a considerable proportion of foraging effort well below surface waters, a behavior that may account for relatively high catch rates of white marlin on some deep-set PLL deployments.

INTRODUCTION

Stocks of Atlantic blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) are overfished, with harvests exceeding replacement yield (International Commission for the Conservation of Atlantic Tunas (ICCAT), 2001). These species are taken in directed recreational and artisanal fisheries and occur as incidental bycatch on commercial pelagic longline (PLL) gear targeting swordfish (*Xiphias gladias*) and tunas (*Thunnus* spp.). Although marlin bycatch comprises a small fraction of the total catch of the PLL fishery, this gear accounts for the majority of billfish fishing mortality in the Atlantic Ocean (ICCAT, 2001). With the onset of the PLL fishery, Atlantic blue marlin and white marlin stocks decreased dramatically in the 1960s and remain at low levels while fishing effort has increased substantially (ICCAT, 2001). Recent assessments conducted by the Standing Committee for Research and Statistics (SCRS) of the ICCAT suggest that the biomass of Atlantic blue marlin may be as low as 40% of that necessary for maximum sustainable yield (MSY) and white marlin biomass may be <12% of that required for MSY (ICCAT, 2001, 2003).

The continued exploitation of billfishes by commercial and recreational fisheries necessitates a more accurate understanding of the status of istiophorid stocks (Uozumi, 2003). Population assessments of Atlantic blue marlin and white marlin have historic-

ally applied a Schaefer non-equilibrium production model (Prager, 1995; ICCAT, 2001; Restrepo *et al.*, 2003) that uses standardized catch-per-unit-effort (CPUE) and landings data from five commercial fisheries and two recreational rod-and-reel fisheries (Goodyear, 2003; Uozumi, 2003). Changes in CPUE presumably reflect changes in the relative abundances of blue marlin and white marlin stocks (Goodyear, 2003). However, the CPUE data used in these assessments may be affected by historical changes in fishing practices; PLL gear deployments shifted from shallow sets targeting yellowfin tuna (*Thunnus albacares*) to deeper sets targeting swordfish and bigeye tuna (*Thunnus obesus*) in the 1970s (Hinton and Nakano, 1996; Yokawa and Uozumi, 2001). The degree to which these changes have altered the abundance of target and bycatch species is presently unknown.

Numerous methods have been proposed to standardize CPUE data for historical changes in fishing practices during population assessments of billfishes and tunas (Bigelow *et al.*, 2003; Hinton and Maunder, 2004). Most of the time series used in the assessments have been standardized to remove the effects of spatial changes in the fishery, the target species, and gear-use parameters; however, production models using these data do not always perform well (Babcock and McAllister, 2003). Hinton and Nakano (1996) proposed a 'habitat-based standardization' (HBS) approach that models effective longline effort as a function of the vertical distribution of longline gear and target and bycatch species, such as billfishes, in the water column. This model incorporates data on oceanographic features, fishing depths of longline hooks, and billfish physiologic and ecologic parameters (depth and temperature distributions). Applications of this model using behavioral data also assume that feeding motivation is proportional to the time spent at depth or temperature, and thus is constant over time, all depths, locations, and temperatures (Graves *et al.*, 2003). HBS models have been used to create standardized CPUE indices of relative abundance for several pelagic species in the Pacific Ocean (Hinton *et al.*, 2001; Hinton and Maunder, 2004). To perform well, all standardization techniques require that appropriate explanatory variables (e.g. billfish habitat preferences) are known without error, or that the error can be quantified (Hinton and Maunder, 2004).

Recent understanding of istiophorid depth and temperature utilization is limited, with little habitat-use data from Atlantic species to support the rigorous testing and application of HBS methods in this ocean. Studies in the Pacific Ocean using acoustic and pop-up satellite tags (PSATs) have shown that istiophorids spend the majority of their time in the upper 10 m of the water column in temperatures ranging from 25 to 27°C (blue marlin: Holland *et al.*, 1990; Block *et al.*, 1992a; striped marlin *Tetrapturus audax*: Brill *et al.*, 1993; black marlin *Makaira indica*: Pepperell and Davis, 1999). In the Atlantic Ocean, two studies using acoustic telemetry tracked white marlin (Skomal and Chase, 2002) and Atlantic sailfish (*Istiophorus platypterus*: Jolley and Irby, 1979) to assess recovery from exhaustion and evaluate post-release survival, respectively, but provided little information regarding the habitat use of study animals. Preliminary data from PSAT tagging studies conducted on Atlantic blue marlin generally suggest that this species associates with warm surface waters (Graves *et al.*, 2002; Kerstetter *et al.*, 2003).

The current study presents habitat-use data from 47 surviving white marlin caught on commercial and recreational fishing gear offshore of the U.S. East Coast, the northern Caribbean, and Venezuela between 2002 and 2004. The model of PSAT deployed in this study archived and reported sequential point measurements of pressure (depth), temperature, and light levels over short time intervals (5 or 10 days), allowing the reconstruction of actual tracks of tagged fish. These tracks were analyzed for short-term habitat utilization and diving behavior of white marlin.

MATERIALS AND METHODS

The Microwave Telemetry, Inc. (Columbia, MD, USA) PTT-100 HR model PSAT tag was used in this study. This model of tag recorded and archived sequential point measurements of temperature, light, and pressure (depth), and was able to withstand pressure equivalent to a depth of 3000 m. Pressure sensors recorded data in 5.4-m intervals and were accurate to within ±2.5 m; temperature sensors were accurate to ±0.2°C (P. Howey, Microwave Telemetry, Columbia, MD, personal communication). The temperature sensor of this tag model overcame thermal inertia because of changes in temperature with depth within a single recording interval (2 or 4 min). Tags programmed to release after 5 days ($N = 4$) recorded measurements about every 2 min (mean: 1.6 min), while tags programmed to release after 10 days recorded measurements about every 2 min ($N = 14$, mean: 1.6 min) or 4 min ($N = 29$, mean: 3.2 min). Additionally, 5- and 10-day tag models transmitted archived and real-time surface temperature, pressure, and light level readings to orbiting satellites of the Argos system for 7–10 days following release from

Table 1. Locations and dates of PSAT deployments on white marlin during 2002–04, with mean SST during tagging operations at each location.

Location	Tagging dates	Gear	Tag duration (day)	Number of deployed	Mean SST (°C)
U.S. East Coast	2002: August–September	R + R	10	7	26.1
	2003: July–September	R + R, PLL	10	4	26.6
	2004: August	PLL	10	9	26.1
Northern Caribbean	2002: May	R + R	5	4	27.5
	2003: June	R + R	10	3	28.2
	2004: January–February	PLL	10	1	28.1
La Guaira, Venezuela	2002: November	R + R	10	6	27.0
	2003: September–October	R + R	10	13	29.0

Gear types are recreational rod-and-reel (R + R) or PLL.
PSAT, pop-up satellite archival tag; SST, sea surface temperature; PLL, pelagic longline.

study animals. Archived data were transmitted from tag to satellite serially in clusters of nine consecutive data points.

Forty-seven PSATs were attached to surviving white marlin released from commercial PLL and recreational rod-and-reel fisheries from May 2002 to August 2004 in the waters offshore of the U.S. East Coast (EC), the northern Caribbean (NC), and Venezuela (VZ; Table 1). Fish released from commercial PLL gear were caught with either squid (*Illex* sp.) or Atlantic mackerel (*Scomber scomber*) baited on size 16/0 non-offset circle hooks or size 7/0–9/0 offset straight-shank ('J') hooks. White marlin released from recreational fishing gear were caught on dead ballyhoo (*Hemiramphus brasiliensis*) rigged on size 7/0–9/0 circle hooks or size 7/0 straight-shank ('J') hooks. Fish were brought to the side of tagging vessels in a manner consistent with common practices in commercial PLL and recreational rod-and-reel fisheries and tags were implanted in the musculature below the dorsal fin but above the body cavity. Forty-six tags (97.9%) remained attached to study animals for the full 5- or 10-day period, reported to the satellites of the Argos system, and returned data consistent with survival of tagged animals over the duration of tag deployment.

Data analysis

Net movement was estimated as a minimum straight line distance traveled between the co-ordinates of initial tagging and the co-ordinates of the first reliable satellite contact with the detached tag (inferred to be the location of tag pop-up) using Argos location codes 1, 2, or 3 (position uncertainty ⩽ 1.5 km) for the first or second day of transmission (MATLAB, version 6.5, Mathworks Inc., Natick, MA, USA). In cases where tags did not report more precise location codes, an average of all location code 0 readings for

the first day of transmission was used for the location of tag pop-up.

Point measurements of depth and temperature were summarized in 10 m and 1°C interval histograms. Overall time-at-depth and time-at-temperature distributions included data pooled from all 47 surviving white marlin. Time-at-depth and time-at-temperature histograms were also generated for each tagging location by pooling the distributions of all fish tagged at a location. Potential diel differences in behavior were assessed for all individuals pooled at each location via Kolmogorov–Smirnov tests comparing the day and night distributions of depth and temperature count data (Brill *et al.*, 1999). Day and night periods were defined from light-level data recovered from tags and were referenced against times of local sunrise and sunset. Few crepuscular periods were completely recovered from transmitting tags, thus these data were excluded from diel analyses.

Daily patterns of vertical movement were characterized for each individual. A cursory visual examination of time-at-depth tracks revealed two general classes of vertical movements, arbitrarily called V-shaped and U-shaped dives (Fig. 1). V-shaped dives were characterized as deep descents of relatively short duration (6–83 min) during which white marlin generally spent <10 min at the maximum depth. U-shaped dives showed behavior confined to a specific depth range (±30 m) for an extended period of time (13–1140 min). Time spent on the surface following each vertical movement was defined as the interdive interval. Following the method of Brill *et al.* (1993), the relative change of water temperature with depth was assessed as the difference between sea surface temperature (SST) and the minimum temperature reached on every completely transmitted V-shaped and U-shaped descent. The entire 5- or 10-day track of

Figure 1. Representation of daily dive patterns of a sample day from white marlin NC02-02, tagged offshore of Punta Cana, Dominican Republic in May 2002. V-shaped dives were defined as deep descents of relatively short duration (6–83 min) during which white marlin generally spent <10 min at the maximum depth. U-shaped dives showed behavior confined to a specific depth range for an extended period of time. Interdive intervals are defined as the amount of time spent at the surface following a dive. The full 5-day track of white marlin NC02-02 is illustrated in Fig. 5e.
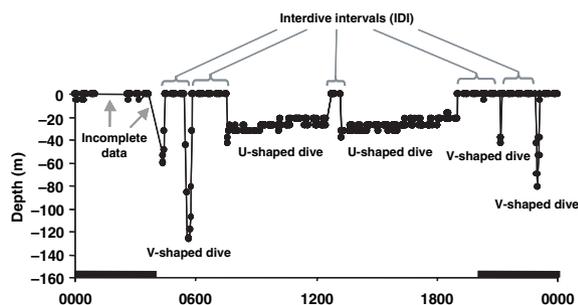
each animal was surveyed for dives with all data; excursions with missing packets of data were excluded from all analyses. The sample 24-h period represented in Fig. 1 featured three complete V-shaped dives, two complete U-shaped dives, and five complete interdive intervals. Not all archived data were successfully obtained from transmitting tags. Data reporting/transmission by PSATs can be affected by several variables, including battery strength, structural integrity of tags, and sea conditions (Kerstetter *et al.*, 2004). Our data set includes the complete (100%) data streams of three tags that were recovered after transmission ceased.

Five dive variables including total dive duration, maximum depth, depth divided by the dive duration (Schreer and Testa, 1995), the change of temperature with depth, and interdive interval were recorded for all completely transmitted dives undertaken by every surviving white marlin. To verify that our initial visual-based categorization of dive types was sufficient, we followed the methods of Lesage *et al.* (1999) by applying multivariate statistical techniques to objectively classify dive types. Specifically, the five dive variables were introduced into a principal components analysis (PCA; PROC FACTOR, SAS version 9.0, SAS Institute, Cary, NC, USA) to eliminate multi-collinearity and reduce their number to a smaller set of orthogonal factors for use as input variables in cluster analyses to objectively assess the number of dive types present. Variables were log-transformed and standardized to a mean of 0 and a variance of 1 because PCA is highly influenced by discordant scales (Hair *et al.*, 1998). After transformation and standardiza-

tion, none of the dive variables was normally distributed ($P < 0.05$, Kolmogorov–Smirnov test); however, departure from normality may only slightly reduce the observed correlation in PCA (Hair *et al.*, 1998). A VARIMAX rotation was applied to the factors resulting from the PCA to simplify interpretation. Collinear variables load on the same composite factor during PCA, and VARIMAX rotation emphasizes the correlation of variables within a factor by maximizing the loadings of variables that correlate strongly with it while simultaneously reducing the loadings of variables with lesser correlation (Lesage *et al.*, 1999). The result was a series of four orthogonal factors derived from dive duration, maximum depth, the change of temperature with depth, and interdive interval.

Dives were subsequently classified using a combination of hierarchical and non-hierarchical *K*-means clustering procedures. The orthogonal factors and scores resulting from the PCA were introduced to a hierarchical complete-linkage clustering procedure (PROC CLUSTER) to identify the appropriate number of clusters (dive types) and compute representative seed points for *K*-means clustering. Hierarchical complete-linkage clustering is an agglomerative method based on the maximum distance between objects in two clusters (Hair *et al.*, 1998). Observations with low estimated *k*-th nearest neighbor densities (10%) were removed from the analysis because complete-linkage cluster analysis can be heavily distorted by outliers. The appropriate number of clusters (e.g. dive types) was determined by examining the change in the agglomerative coefficient, which represents the squared Euclidean distance between the two clusters being combined, for increasing numbers of clusters from 2 to 10 (Hair *et al.*, 1998). Larger values of the agglomerative coefficient result from the joining of two highly different clusters. The cluster centroids identified by the hierarchical complete-linkage cluster analysis were subsequently used as initial seeds in a non-hierarchical *K*-means clustering procedure (PROC FASTCLUS) to further fine-tune the groups formed. This procedure assigns observations to the cluster with the centroid with the closest Euclidean distance, and new centroids are calculated following each iteration until the changes in the centroids decrease to near zero (Hair *et al.*, 1998).

To investigate whether the characteristics of each dive type varied among locations, the orthogonal dive variables were analyzed using multivariate analyses of variance (MANOVA). As the number of dives recovered from each tag varied by more than an order of magnitude, we considered the mean values of the

four measured dive variables for each fish (rather than the underlying data) as independent observations for V-shaped and U-shaped dives to avoid temporal autocorrelation within individuals. Individual white marlin represented independent replicates at a location; thus the response variables for this analysis were the mean values of dive duration, dive depth, the relative change of temperature with depth, and interdive interval, and the factors were location, fish, and their interaction term. Tests were conducted separately for V-shaped and U-shaped behaviors. None of the response variables was normally distributed ($P < 0.05$, modified Kolmogorov–Smirnov test); however, MANOVA is robust to both violations of normality and homogeneity of variance for larger sample sizes (Paukert and Wittig, 2002). Post hoc comparisons were performed using Tukey's test.

The thermal environment surrounding individual white marlin was recreated by using the fish as autonomous samplers of the water column (Boehlert et al., 2001; Block et al., 2003). Twenty-four hour periods were selected from six white marlin that had high percentages of successfully transmitted data and demonstrated representative vertical movements for respective geographic tagging regions. Within a given 24-h period, archived temperature and depth data were separated into 48 30-min blocks, and temperature–depth profiles were created for the first 6 and last 6 h of a 24-h period. Temperature readings between data points were interpolated from these profiles at 5 m and 0.1°C resolution. Interpolated temperatures and depth tracks were superimposed using the archived depth and temperature data recorded during the vertical movements of these individual fish (MATLAB version 6.5).

RESULTS

Overall, 46 of 47 tags (97.9%) remained attached to study animals for the full programmed 5- or 10-day duration. One 5-day tag released prematurely from a surviving white marlin after 2.5 days, presumably because of poor attachment. This individual exhibited behavior similar to other surviving white marlin while the tag was attached, and the data from this fish were included in habitat analyses for the purposes of this study. Visual surveys of each subject's track suggested that the vertical movement behaviors of surviving white marlin in this study did not appear to demonstrate evidence of stress associated with capture, handling, tagging, and release during their first day following their release, thus the data for all days were included for each surviving fish. In contrast, three

additional moribund individuals not included in this study showed almost exclusively surface-oriented behavior prior to death, suggesting stress associated with capture (discussed in Kerstetter et al., 2004; Horodysky and Graves, 2005). An average of 63% (range: 3–95) of the total archived data points were recovered from each tag. An additional nine white marlin that died while carrying PSATs are discussed elsewhere (Horodysky and Graves, 2005; Kerstetter and Graves, 2006).

Movements

Analysis of minimum straight line distances revealed that tagged white marlin dispersed 16–632 nautical miles (nmi) from the point of release. Fish tagged with 5-day tags moved an average of 0.3 nmi h^{-1} (7.8 nmi day^{-1} average; range: 4.6–12.0 nmi) while those tagged with 10-day tags moved an average of 0.4 nmi h^{-1} (14.9 nmi day^{-1} average; range: 1.6–63.2 nmi). Offshore of the U.S. East Coast, surviving white marlin tagged with 10-day tags dispersed 24–632 nmi (2.4–63.2 nmi day^{-1}) from the point of release (Fig. 2a). Data recovered from tags deployed offshore of northern Caribbean locations indicate that those white marlin traveled a minimum of 23–422 nmi (4.6–42.2 nmi day^{-1}) from the point of release (Fig. 2b). White marlin carrying 10-day tags offshore of Venezuela displaced 16–131 nmi (1.6–13.1 nmi day^{-1}) minimum straight line distance over the 10-day period (Fig. 2c).

Depth and temperature

White marlin demonstrated a strong association with warm surface waters, spending over 48% (±2.8) of their time in the upper 10 m of the water column (Fig. 3a), although this near-surface association varied slightly among locations and substantially among individuals at a location (Fig. 3b–d). There were no significant diel differences in temperature or depth distributions at any of the locations sampled in this study ($P > 0.20$). The marlin tagged offshore of the U.S. East Coast (Fig. 3b) spent the largest amount of time in the upper 10 m of the water column (56 ± 4.8%), while those tagged offshore of northern Caribbean locations and Venezuela spent considerably less time associated with the upper 10 m of the water column (Fig. 3c: 39.3 ± 4.6% and Fig. 3d: 42 ± 3.1%, respectively). Generally, white marlin spent less time in the 10–20 m stratum (range: 1.3–17.9%) than between 20–30 m (range: 2.1–33.9%) in the northern Caribbean and Venezuela, but this difference was less pronounced offshore of the U.S. East Coast. White marlin spent 40% (±2.7) of their time at depths

Figure 2. Minimum straight line displacements of white marlin tagged offshore the three sampling locations in this study: (a) U.S. East Coast 2002–04 (*N* = 20), (b) northern Caribbean 2002–04 (*N* = 8), and (c) Venezuela 2002–03 (*N* = 19). Black dots denote tagging locations, and text labels denote first point of contact with transmitting tag after release from the fish. For each location, text labels are presented as 'location code year – fish number'. Note that fish did not move between the three locations in this study during the 5- to 10-day tag attachments.


White Marlin 2002–2004 (*N* = 47)
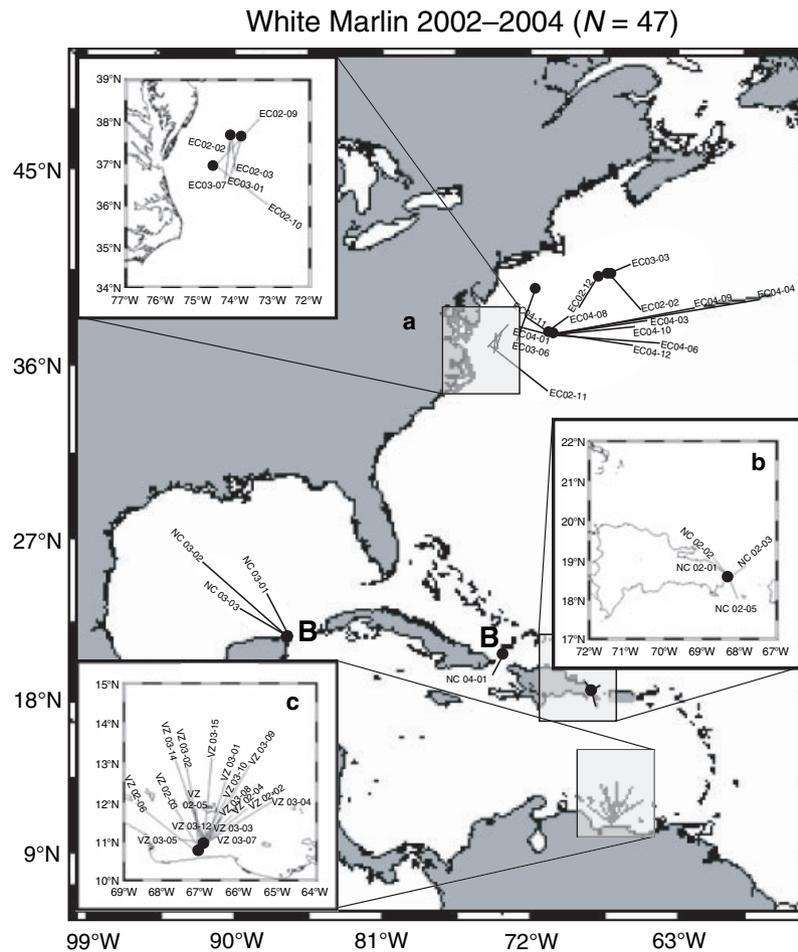
ranging from 20 to 80 m, but only 4% (±1.1) at depths >80 m.

Pooled temperature data demonstrated that white marlin spent 86.5% (±11.4) of their time in water temperatures ranging from 24 to 29°C (Fig. 4a), which encompasses the range of SSTs encountered during tagging operations (Table 1: 24.0–29.7°C). Time-at-temperature distributions varied by location, with modal temperatures generally increasing southward. White marlin tagged offshore of the U.S. East Coast (Fig. 4b) spent over 77% (±16.9) of their time between 24 and 28°C (mode: 26°C, 36.5%), while fish tagged in northern Caribbean locations (Fig. 4c: 83.3 ± 19.7%, mode: 27°C, 27.0%) and Venezuela (Fig. 4d: 80.9 ± 12.8%, mode: 27°C, 25.4%) spent slightly more time at these temperatures.

Considerable daily variation was evident in the temperature/depth data of most individual white marlin over the course of the tracking period (Fig. 5a–f). White marlin EC02-12 (Fig. 5a), tagged offshore of George's Bank, encountered some of the coldest waters of any white marlin in this study and rarely ventured deeper than 60 m during vertical excursions. The track of white marlin EC02-09, which displaced 260 nmi southeast of the tagging location, shows a similar shallow diving pattern until the ninth day of tag deployment, when temperature readings were elevated despite a threefold increase in depth (Fig. 5b). Combined, the depth, temperature, and net displacement data strongly suggest that this fish changed its diving behavior as it moved from cooler coastal waters off Virginia into the warmer, oceanic waters of the Gulf Stream.

Figure 3. Time-at-depth histograms for the white marlin tagged in this study: (a) all surviving white marlin pooled ($N = 47$), (b) U.S. East Coast ($N = 20$), (c) northern Caribbean ($N = 8$), and (d) Venezuela ($N = 19$). Error bars are ±1 SE.
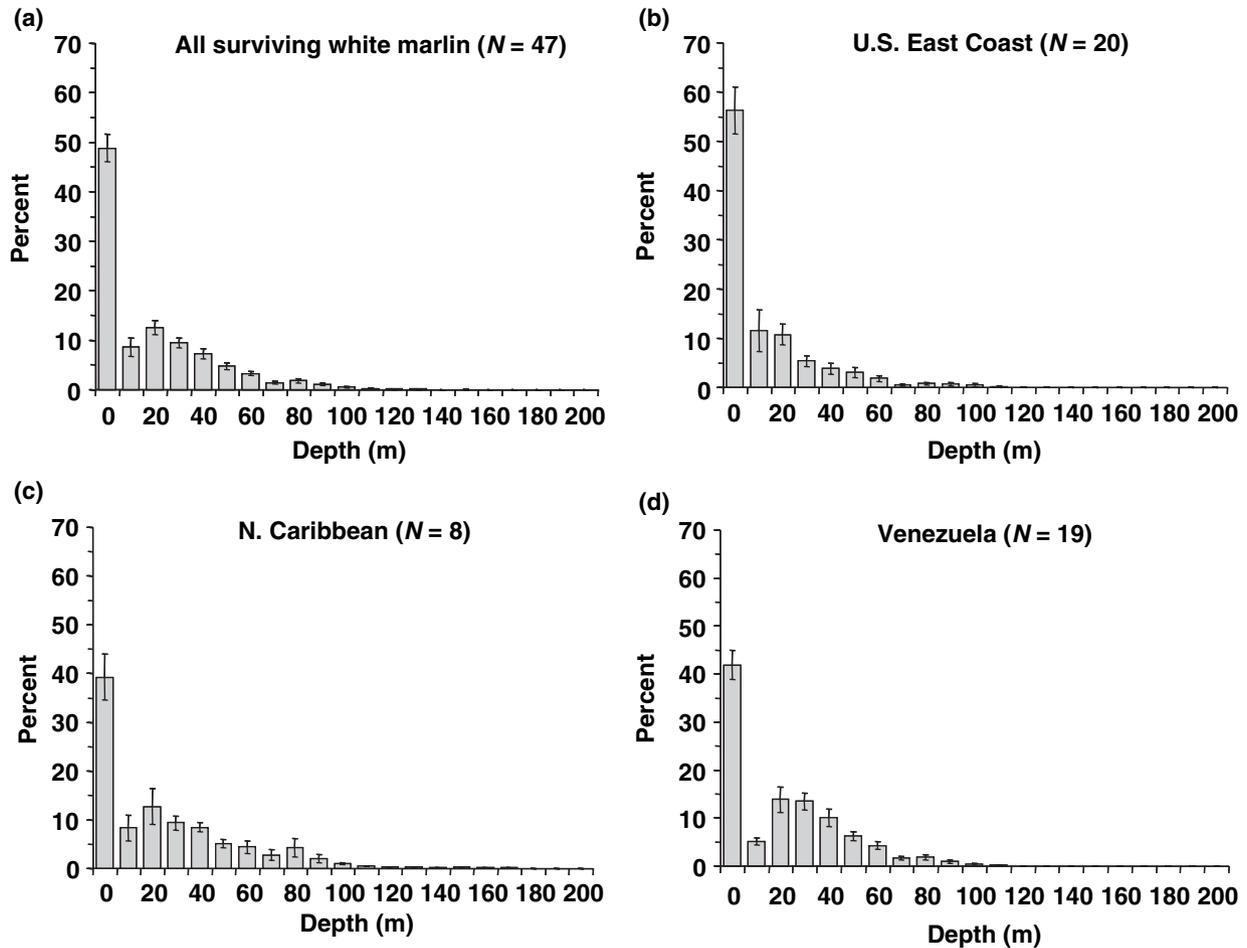

All white marlin in this study made frequent, short duration descents, many of which exceeded 100 m in depth. The maximum depths attained by tagged white marlin varied with location (U.S. East Coast: 161 m, northern Caribbean: 210 m, Venezuela: 199 m). Visual examination of time-at-depth tracks revealed that white marlin undertake two general types of vertical movements: short duration V-shaped descents and more broadly U-shaped dives, which showed behavior confined to a specific depth range for an extended period of time. Cluster analyses indicate a rapid decrease in the agglomerative coefficient after the formation of two clusters, suggesting that the classification of two dive types was appropriate (Fig. 6).

Significant differences were observed among locations and individuals for some, but not all, of the dive characteristics of V-shaped and U-shaped dives (Table 2). Mean duration ($P = 0.0003$) and depth

($P < 0.027$) of V-shaped dives varied significantly with location. V-shaped dives were shortest and shallowest offshore of the U.S. East Coast and longest and deepest offshore of northern Caribbean locations (Table 3). The mean duration of V-shaped dives also varied significantly among individual fish ($P < 0.0001$); however, the interaction effect was significant ($P = 0.01$), compromising interpretation. Tukey's *post hoc* comparison suggests that significant differences between dive depths only exist between the U.S. East Coast and the northern Caribbean ($P < 0.05$). For U-shaped dives, durations differed significantly across fish ($P < 0.0001$), but not among locations. The relative change of temperature with depth experienced by white marlin in this study was not significantly different among locations or between fish at a location for either V-shaped or U-shaped dives. Interdive intervals differed significantly between individual white marlin for both V-shaped

Figure 4. Time-at-temperature histograms for the white marlin tagged in this study: (a) all surviving white marlin pooled ($N = 47$), (b) U.S. East Coast ($N = 20$), (c) northern Caribbean ($N = 8$), and (d) Venezuela ($N = 19$). Error bars are ±1 SE.
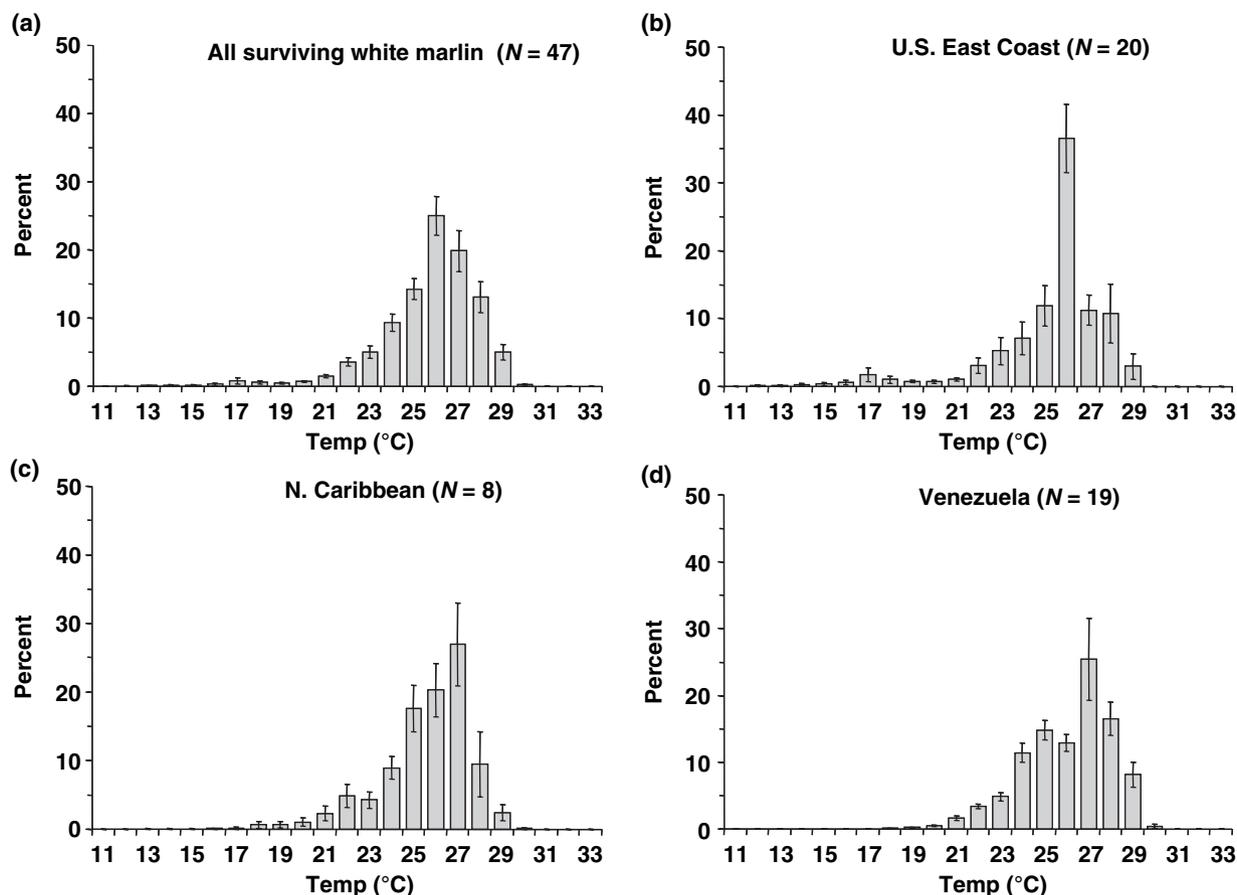
(P < 0.001) and U-shaped (P = 0.0013) dives, but did not differ among the three locations sampled.
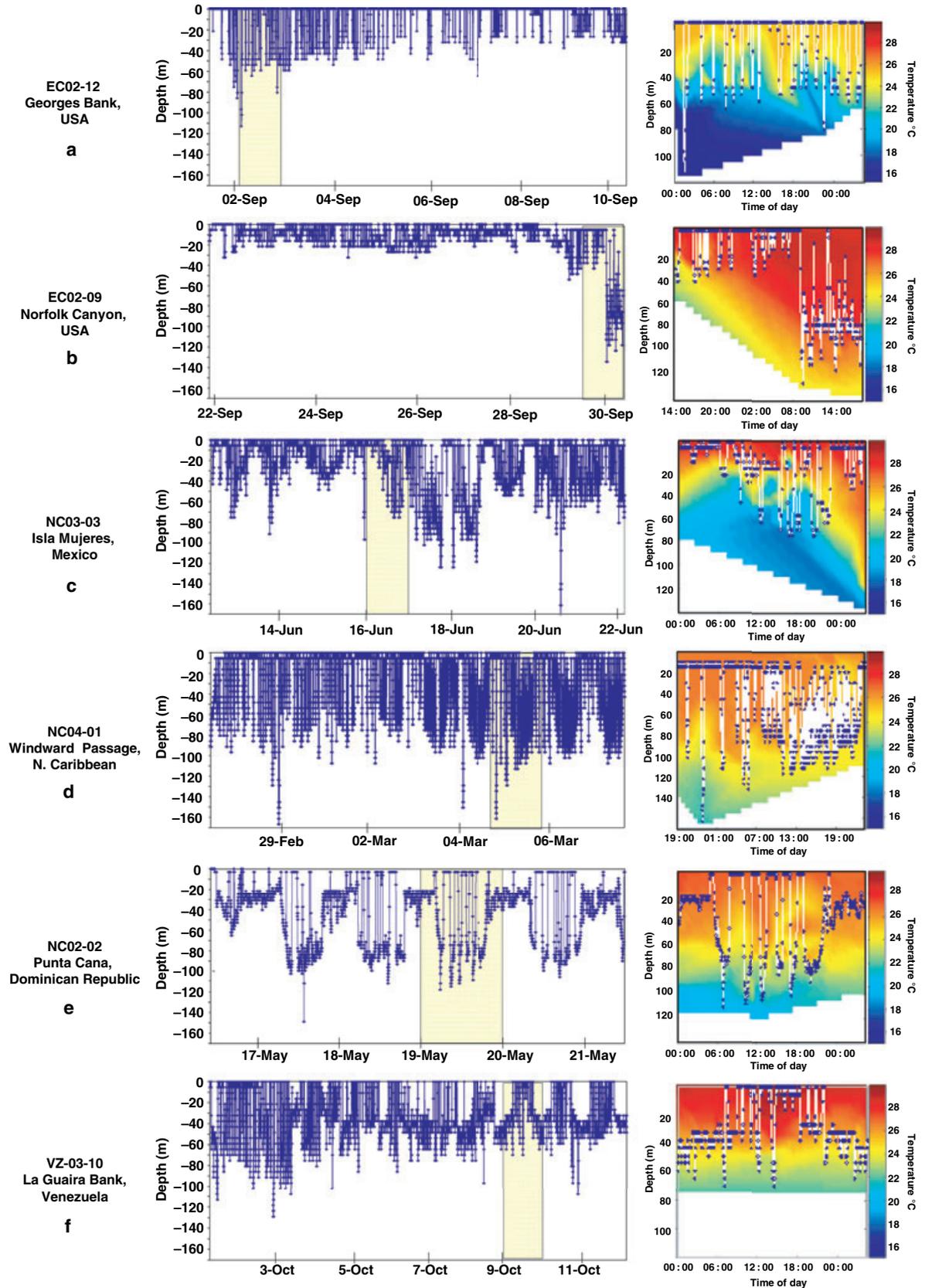
White marlin vertical movements appear to be regulated by the relative change of water temperature with depth, rather than a preference for a specific depth. An analysis of the relative change of water temperature with depth during both V-shaped and U-shaped dives revealed that about 90% of white marlin vertical movements occurred within the upper 8°C of the water column regardless of location (Fig. 7).

DISCUSSION

Directions and magnitudes of white marlin displacement patterns were generally consistent with results from prior istiophorid tagging studies, though variation was evident among individual white marlin and between locations. Swimming speeds of acoustically tracked istiophorids agree favorably with the net displacements calculated from short duration recaptures of billfishes tagged with conventional tags (Brill et al.,

1993). White marlin in this study moved between 0.07 and 2.6 nmi h^{-1}, encompassing the 0.73 nmi h^{-1} and 0.95 nmi h^{-1} average speeds reported by Graves et al. (2002) and Kerstetter et al. (2003), respectively, for Atlantic blue marlin. These results are also comparable with the average speeds reported for striped marlin (1.18 nmi h^{-1}, Holts and Bedford, 1990), black marlin (1.35–1.98 nmi h^{-1}, Pepperell and Davis, 1999), and Pacific blue marlin (1–2 nmi h^{-1}, Holland et al., 1990; 0.29–4.37 nmi, Block et al., 1992b). Differences between mean hourly displacements of white marlin in this study may have been due to natural patterns of movement associated with seasonal migrations of this species.

The results of this study demonstrate that white marlin are associated with the epipelagic zone and spend the largest amount of time (mean: 48%) in the upper 10 m of the water column. Previous acoustic and PSAT studies have shown that other istiophorids likewise are associated with near-surface waters. For example, blue marlin tagged offshore of Hawaii and

EC02-12
Georges Bank,
USA

a

EC02-09
Norfolk Canyon,
USA

b

NC03-03
Isla Mujeres,
Mexico

c

NC04-01
Windward Passage,
N. Caribbean

d

NC02-02
Punta Cana,
Dominican Republic

e

VZ-03-10
La Guaira Bank,
Venezuela

f

Figure 6. Plot of the agglomerative coefficient calculated from a complete-linkage hierarchical cluster analysis conducted on the white marlin dive data to assess the appropriate number of dives. Results are based on 2598 dives after a 10% trimming of outliers. Greater values of the agglomerative coefficient indicate the joining of two very different clusters. The rapid decrease in the agglomerative coefficient after the formation of two clusters suggested that two dive types were appropriate.
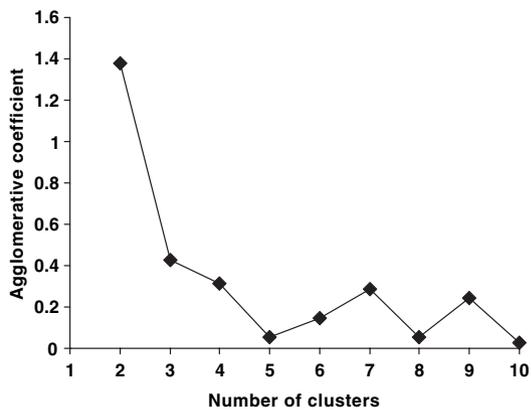
Bermuda spent between 50% and 80% of their time in the upper 10 m of the water column, respectively (Holland *et al.*, 1990; Block *et al.*, 1992a; Graves *et al.*, 2002), and striped marlin offshore of Hawaii spent nearly 30% of their time in the upper 10 m of the water column (Brill *et al.*, 1993). The depth distributions of white marlin are similar, but not identical, to those of Hawaiian striped marlin and Atlantic blue marlin. White marlin in this study spent less time between 10 and 20 m than at depths of 20–80 m. Kerstetter *et al.* (2003) reported that Atlantic blue marlin tagged with 30-day tags also spent little time at depths from 3 to 25 m, but considerably more time below 25 m depth. Similarly, striped marlin tagged offshore of Hawaii associated with depths between 51 and 90 m for a comparable amount (40%) of time (Brill *et al.*, 1993). Collectively, these results demonstrate that istiophorids spend appreciable time at depth.

The short duration of 60–100 m vertical movements undertaken by white marlin are similar to

patterns of descents to variable depths observed in Pacific istiophorids (Block *et al.*, 1992a; Brill *et al.*, 1993; Pepperell and Davis, 1999; Graves *et al.*, 2003; Kerstetter *et al.*, 2003). Maximum depths of white marlin dives at each location in this study (149–210 m) fell within the range reported for other tagged istiophorids (100–270 m: Block *et al.*, 1992a; Brill *et al.*, 1993; Pepperell and Davis, 1999; Kerstetter *et al.*, 2003). However, these results should be viewed with some caution because sampling intervals in this study were limited to roughly every 1.6 or 3.2 min. As evidenced by the change in depth of 170 m in 3 min by white marlin VZ02-01, deep dives may occur rapidly, and all maximum dive depths may not have been successfully captured with the sampling intervals used in this study. However, by definition, the most rapid and deepest dives of a species represent extreme events, and successful recording of such episodes reveals little about routine animal behavior (Hays *et al.*, 2004). It is possible that rather than reflecting 'real' behaviors, such rare rapid/deep readings may instead be the result of physical contact of the pressure sensor of the PSAT tag with either the tagged fish's body or the body of a conspecific or prey item. Anomalous depth readings have occasionally been recorded by PSAT tags during tag handling and manipulation, and during the tagging process (P. Howey, Microwave Telemetry, Inc., Columbia, MD, personal communication). Accordingly, additional data recorded by tags, such as temperature and light level, should be used to corroborate these behaviors.

Depth distributions of white marlin and other istiophorids are likely more influenced by water temperature than by an absolute depth preference (Brill and Lutcavage, 2001). The results of this study demonstrate a strong association of white marlin with warm waters within a few degrees of SSTs. White marlin spent over 85% of their time in waters ranging from 24 to 29°C, similar to the range of temperatures frequented by Atlantic blue marlin (26–31°C, Graves *et al.*, 2002; Kerstetter *et al.*, 2003). Temperature distributions of Pacific blue marlin and black marlin are also comparable (Holland *et al.*,

Figure 5. Representative dive profiles of six white marlin illustrating the use of each fish as its own bathythermograph. Full 5- and 10-day time series of vertical movements are presented at the left. Shaded regions correspond to insets at right. Insets are 24-h tracks superimposed on the thermal structure of the surrounding water column reconstructed from temperature data recorded by each pop-up satellite archival tag (PSAT). White marlin EC02-12 (a) and EC02-10 (b) were tagged offshore of the U.S. East Coast. Fish NC03-02 (c), NC04-01 (d), and NC02-02 (e) were tagged in the northern Caribbean, and VZ03-10 (f) was tagged offshore of La Guaira Bank, Venezuela.

Dive type	Response	Factor	d.f.	F	P-value
V-shaped	Duration	Location	2	10.19	0.0003
		Fish	1	21.02	<0.0001
		Location × Fish	2	5.22	0.0101
	Depth	Location	2	3.99	0.027
		Fish	1	1.56	0.22
		Location × Fish	2	2.29	0.1158
	Temperature	Location	2	0.11	0.8917
		Fish	1	0.01	0.9087
		Location × Fish	2	1.97	0.1538
	Interdive interval	Location	2	0.23	0.7960
		Fish	1	28.46	<0.0001
		Location × Fish	2	2.13	0.1330
U-shaped	Duration	Location	2	0.88	0.4253
		Fish	1	25.71	<0.0001
		Location × Fish	2	1.55	0.2260
	Depth	Location	2	2.67	0.0836
		Fish	1	1.09	0.3045
		Location × Fish	2	1.48	0.2424
	Temperature	Location	2	0.14	0.8663
		Fish	1	0.20	0.6606
		Location × Fish	2	1.12	0.3389
	Interdive interval	Location	2	1.89	0.1655
		Fish	1	12.20	0.0013
		Location × Fish	2	1.22	0.3065

Table 2. Results of multivariate analyses of variance performed on the mean dive characteristics of V-shaped and U-shaped dives.

Individual white marlin was treated as independent replicates at a location. Response variables in the analyses were mean values of dive duration, dive depth, the relative change of temperature with depth, and interdive interval. Factors in the analyses were location (three levels), individual fish, and an interaction term. Tests were conducted separately for V-shaped and U-shaped behaviors.

**Table 3.** Summary of dive statistics by location for both U-shaped and V-shaped dives.

Location	Dive behavior	Number of fish	Mean dive duration (min)	Mean dive depth (m)	Temperature range (°C)	Interdive interval (min)
U.S. East Coast	V-shaped	20	19.2 ± 4.9	36.8 ± 4.9	3.2 ± 0.7	39.1 ± 13.3
	U-shaped		89.9 ± 33.7	39.8 ± 6.7	3.2 ± 0.7	31.6 ± 15.9
Northern Caribbean	V-shaped	8	22.3 ± 6.5	57.3 ± 10.2	3.3 ± 1.4	23.8 ± 12.6
	U-shaped		52.1 ± 31.5	76.5 ± 8.9	1.6 ± 0.7	20.0 ± 12.6
Venezuela	V-shaped	19	25.6 ± 3.4	52.8 ± 5.9	3.7 ± 0.5	35.1 ± 11.8
	U-shaped		89.0 ± 17.4	53.5 ± 6.0	4.2 ± 0.5	23.7 ± 6.5
Overall	V-shaped	47	23.4 ± 2.6	48.9 ± 3.9	3.5 ± 0.4	24.7 ± 7.7
	U-shaped		75.8 ± 17.3	56.2 ± 4.7	2.8 ± 0.4	25.0 ± 7.8

V-shaped dives were characterized as deep descents of relatively short duration (6–83 min) during which white marlin generally spent <10 min at the maximum depth. U-shaped dives showed behavior confined to a specific depth range (±30 m) for an extended period of time (13–1140 min). The time spent on the surface between vertical movements was defined as the interdive interval. All data are presented as mean ± 1 SE.

1990; Block *et al.*, 1992a; Gunn *et al.*, 2003). The striped marlin tracked by Brill *et al.* (1993) offshore of Hawaii spent about 80% of their time in waters between 25 and 27°C, while those tracked by Holts and Bedford (1990) offshore of California spent the majority of their time in cooler water (20 and 21°C) – a disparity presumably due to differences in surface and mixed-layer temperatures between

Figure 7. Frequency distribution of the relative change of water temperature with depth during white marlin dives, assessed as the difference between sea surface temperature (SST) and the minimum temperature reached on every completely transmitted V-shaped and U-shaped dive. Data are presented for white marlin tagged offshore of the (a) U.S. East Coast ($N = 20$), (b) northern Caribbean ($N = 8$), and (c) Venezuela ($N = 19$).
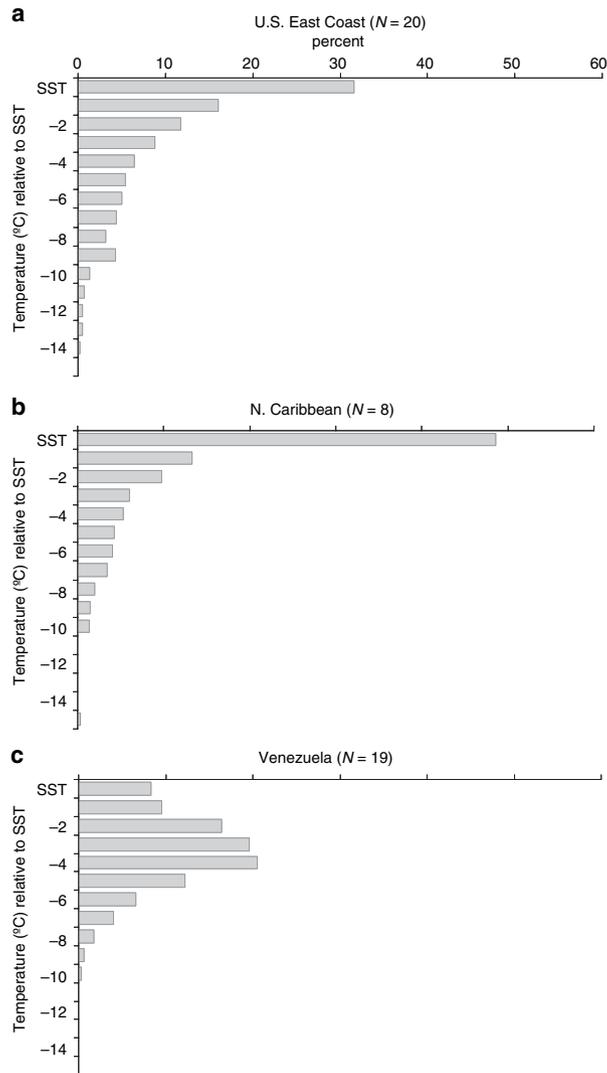
respective tagging locations (Brill *et al.*, 1993). A similar phenomenon may be driving the time-at-temperature distributions of white marlin at the three tagging locations in this study. Mean SST values during tagging operations at each of the four locations correspond strongly with modal temperatures selected by tagged white marlin, suggesting that this species may spend the majority of its time in the warmest waters available. White marlin tagged in the northern Caribbean and Venezuela experienced warmer surface temperatures and spent less time in the upper 10 m of the water column. In contrast, fish offshore of the U.S. East Coast experienced the

lowest SSTs and spent the longest amount of time in the upper 10 m of the water column. Generally, interdive intervals were longer and dives were shallower and of shorter duration in the cooler waters offshore of the U.S. East Coast.

Analyses of the diel depth preferences of tagged istiophorids have yielded contrasting results. Most istiophorid tagging studies have suggested a tendency toward deeper diving behavior during daylight hours (Holland *et al.*, 1990; Block *et al.*, 1992a; Pepperell and Davis, 1999; Kerstetter *et al.*, 2003), although some have demonstrated deeper dives at night (Holts and Bedford, 1990), while others have not revealed

any diel differences (Brill *et al.*, 1993; Gunn *et al.*, 2003). In the present study, diel trends were occasionally observed qualitatively in the tracks of individual fish, but this behavior rarely persisted for more than a few days of the track. Comparable levels of variation within and among individuals have been noted for other billfishes in previous acoustic and PSAT studies (Holland *et al.*, 1990; Holts and Bedford, 1990; Block *et al.*, 1992a; Pepperell and Davis, 1999; Graves *et al.*, 2002; Domeier *et al.*, 2003; Kerstetter *et al.*, 2003). Temperature and depth distributions of white marlin did not vary significantly with diel period for any of the locations sampled in this study.

Multivariate statistical techniques have proven useful to rapidly classify and process large volumes of behavioral data (such as dives) recorded by numerous logging devices (Schreer and Testa, 1995; Lesage *et al.*, 1999). In the present study, cluster analyses and manual classification schemes agreed on the existence of two dive types. V-shaped dives were characterized as deep descents of relatively short duration (6–83 min) during which white marlin generally spent <10 min at the maximum depth, while U-shaped dives showed behavior confined to specific depth ranges (±30 m) for extended periods of time (13–1140 min). Multivariate analyses of V-shaped and U-shaped behaviors undertaken by white marlin revealed that dive durations and interdive intervals were more significantly affected by the behavior of individual fish than by location in this study. Generally, V-shaped dives were of longest duration offshore of northern Caribbean locations and shortest offshore of the U.S. East Coast. Depths of these vertical movements were also shallowest offshore of the U.S. East Coast and deepest offshore of northern Caribbean locations. However, the significant interaction term compromises the interpretation of significance in the analysis of V-shaped dive durations, and caution is recommended in making inferences based on these data. It is very likely that this relationship is confounded by other variables not measured in this study, such as physical properties of the water column or biotic effects such as prey abundance. No other interaction terms were significant in this analysis. The change in temperature with depths encountered on both dive types did not differ among locations (3.5°C and 3.8°C respectively) or individuals at a location, suggesting that the physical and physiologic bounds of white marlin habitat and the manner in which these fish exploit this habitat were fairly consistent during the short-term tracks and across the geographic range sampled in this study.

Interdive intervals following V-shaped descents were greater offshore of the U.S. East Coast and Venezuela than the northern Caribbean.

Recent PSAT models cannot record feeding events; however, the frequency, duration, and periodicity of white marlin diving behavior suggest that vertical movements may reflect foraging patterns. Graves *et al.* (2003) reached similar conclusions regarding the purpose of short duration dives in Atlantic blue marlin. Based on the nature and persistence of daily dive patterns, it is probable that a considerable proportion of istiophorid foraging occurs at depth. These observations are supported by high CPUE values for white marlin and sailfish at calculated hook depths of 105–125 m in the Caribbean Sea (Gonzalez and Gaertner, 1990) and high CPUE values of blue marlin at hook depths of 130–170 m (Maksimov, 1970). Stomach contents of white marlin also suggest foraging at depth. In addition to epipelagic prey, stomach contents of white marlin have also included deeper dwelling prey, such as cutlassfish (Trichuridae; Davies and Bortone, 1976; Nakamura, 1985), lancetfish (*Alepisaurus* sp.), and even benthic rays (J. Graves, unpublished observation).

V-shaped diving behavior may represent a searching or foraging pattern targeting prey at depth, a movement/travel function, or a combination of the two. By moving vertically throughout the water column rather than swimming continually at the surface, traveling animals reduce swimming drag (Williams and Kooyman, 1985) while increasing prey encounter rates without substantially increasing travel distance (Thompson *et al.*, 1991). The increased, but variable, duration of U-shaped behavior suggests that this pattern may be representative of marlin locating and exploiting aggregated prey for extended amounts of time. Similar conclusions about the functions of V-shaped and U-shaped dives have been reached for a number of marine animals (Le Boeuf *et al.*, 1988; Lesage *et al.*, 1999). It is unclear if white marlin and other istiophorids dive to depth to feed directly on deeper-dwelling prey, or to obtain olfactory or visual cues, such as transecting horizontally dispersing odor plumes or silhouetting concentrations of epipelagic prey above them against downwelling light. The silhouetting hypothesis is supported by the prevalence of U-shaped dives during daylight hours and on nights with brighter moon phases. Similar foraging strategies involving the silhouetting of prey have been described for a number of marine animals (McFarland and Munz, 1975; Davies *et al.*, 1999; Ponganis *et al.*, 2000; Fristrup and Harbinson, 2002).

Istiophorids possess several adaptations that may facilitate foraging at depth. Recent investigations into the vision of blue marlin demonstrate that the marlin eye is specifically adapted for sensitivity at low light levels during deep foraging dives (Fritsches *et al.*, 2003a). Additionally, the presence of three visual pigments and areas of high retinal cell densities in striped marlin indicates trichromatic color vision and greatest acuity in the visual field above and ahead of the animal (Fritsches *et al.*, 2003b), suggesting that marlin attack prey from behind or below. Visual pigments optimally matched to the near monochromatic light upwelling from depth were found on the upper part of the retina (Fritsches *et al.*, 2003b), allowing marlin to detect objects against the dim depths in the visual field below the animal. White marlin, like other istiophorids and swordfish, also feature a specialized thermogenic organ beneath the brain that generates and maintains elevated temperatures in the eye/brain (Block, 1986). A warmer than ambient retinal temperature maintains the temporal resolution of the eye and a high speed of vision during vertical movements into cooler waters (Fritsches *et al.*, 2005). This adaptation provides the large, fast, and sensitive eyes of these fishes up to an order of magnitude greater temporal resolution (thus, a better ability to detect rapid motion) than their cold-blooded prey at dimly lit, cooler depths of the ocean (Fritsches *et al.*, 2005).

While white marlin appear to be well adapted for searching at depth, they may not be adapted for staying in cooler, deeper waters for extended periods of time. Diving behaviors of blue, striped, and black marlin (Holland *et al.*, 1990; Holts and Bedford, 1990; Brill *et al.*, 1993; Pepperell and Davis, 1999) also suggest limited abilities to stay at depth for extended amounts of time; these species appear to spend the majority of their time in waters within 8°C of SST (Brill and Lutcavage, 2001). White marlin vertical movements also appear to be largely constrained by the relative change in temperature with depth. Both V-shaped and U-shaped dives were the shortest offshore of the U.S. East Coast, where the coldest SSTs were encountered, and dive duration increased southward with increasing SST. Over 90% of white marlin dives were in the range of temperatures between SST and 8°C below SST, although rare and very brief excursions resulted in water temperature differences as great as 13.5°C. While vertical movements of individual white marlin often varied greatly with respect to maximum depth, minimum water temperatures at the deepest points on dives usually remained within the range of 8°C. Brill *et al.* (1999)

and Brill and Lutcavage (2001) suggested that temperature-induced reductions in cardiac function are responsible for generally limiting the depth distributions of yellowfin tuna and, by extension, the istiophorid billfishes to a range of 8°C. White marlin return to the warm surface waters of the upper 10 m between vertical excursions (i.e. interdive intervals); thus some motivation for the high degree of near-surface association in this species may lie in increasing core temperature and restoring cardiac function between frequent foraging dives rather than for feeding alone. Additionally, the reduced amount of time spent between 10 and 20 m relative to waters shallower and deeper of this region may represent an artifact of the competing physiologic need to restore body temperature (thus, cardiac function) in the warmest waters available and the ecologic need to search for prey in cooler, deeper waters.

Habitat-based standardization methods used during recent stock assessments of pelagic fishes weight CPUE rates in proportion to the time species spend at depth or temperature to account for historical changes in the depths of longline gear deployments (Hinton and Nakano, 1996; Hinton *et al.*, 2001; Bigelow *et al.*, 2003). Initial application of HBS models used data from acoustic tracking studies of Pacific blue marlin and striped marlin (Holland *et al.*, 1990; Block *et al.*, 1992a; Brill *et al.*, 1993). Application of this model to Atlantic istiophorids may assume that the temperature and depth preferences, physiology, and behavior of various billfish species are constant across all locations, ages/sizes, and sexes, as well as between ocean basins (Goodyear, 2003). Preliminary data regarding the habitat utilization of Atlantic istiophorids has only recently become available, thus many of these assumptions remain untested. HBS models provide robust estimates of CPUE when explanatory variables are well-described (Maunder and Harley, 2003; Hinton and Maunder, 2004), but the incorporation of inaccurate or incomplete data into any CPUE standardizations can increase the probability of erroneous conclusions (Goodyear, 2003).

Time-at-depth distributions of istiophorids, including white marlin, suggest that they are predominantly surface oriented, thus standardization by time-at-depth data would predict greatest catchability of white marlin in near-surface waters. While higher billfish catches have been noted in shallow-set research on longline deployments (Yokawa and Saito, 2004), the historical shift to deeper fishing longlines has not always resulted in reduced billfish catch rates. In fact, recent billfish catch rates on Japanese deep-set longlines occasionally exceeded those on shallow-set

longlines (Yokawa and Uozumi, 2001). Dive patterns of white marlin in this study, along with limited investigations into istiophorid diet, vision, and thermal physiology, suggest that billfishes are well adapted for foraging at depth and may be associated with near-surface waters for purposes other than foraging (i.e. to increase cardiac temperature). Graves *et al.* (2003) concluded that standardization of CPUE using time-at-depth data, but devoid of considerations of feeding motivation, will lead to inaccurate estimates of abundance. For example, if billfish feeding motivation is greater at depth than in near-surface waters, then catchability may not be proportional to overall time-at-depth or time-at-temperature distributions demonstrating greatest association with near-surface waters. Finally, the location-specific differences in habitat use of white marlin in this study suggest that Atlantic-wide application of HBS methods during istiophorid population assessments may provide misleading results unless consideration is given to the possible effects of spatial differences in habitat utilization and fishing practices on catchability (Walters, 2003).

This study provides data on the short-term habitat use and vertical movements of white marlin in several locations along the western portion of their range; however, although PSAT tags appear fairly well-suited for providing basic habitat-use data for large mobile species, such as billfishes, their current utility is limited by an inability to record foraging events, and additional data on the physical properties of surrounding waters (e.g. productivity, conductivity). These limitations demonstrate the importance of incorporating various methods and data sets to provide the information needed to implement robust CPUE standardization methods. Further investigations into the vertical distribution of longline fishing gears and habitat use of Atlantic istiophorids, including longer duration PSAT deployments, are clearly needed to improve stock assessments for these species. Current knowledge of the habitat utilization of Atlantic istiophorids is limited to two species in only a few locations. Given the relatively small sample sizes and limited seasonal coverage per location in this study, the large geographic range of this species, and the likely temporal and spatial variation in habitat variables and prey abundance, the results of this study should be viewed as preliminary and descriptive. Increased data on billfish habitat use, physiology, and trophic ecology, in concert with recently developed length-based, age-structured statistical models (Klieber *et al.*, 2003), statistical HBS (Hinton *et al.*, 2001), and fully integrated habitat-based population dynamics models (Hinton, 2003), hold promise for improving

habitat standardization of CPUE indices for Atlantic billfishes (Uozumi, 2003).

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