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Habitat Preferences and Diving Behavior of White Marlin (Tetrapturus albidus) Released from the Recreational Rod-and-Reel and Commercial Pelagic Longline Fisheries in the Western North Atlantic Ocean: Implications for Habitat-Based Stock Assessment Models

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HABITAT PREFERENCES AND DIVING BEHAVIOR OF WHITE MARLIN (*Tetrapturus albidus*) RELEASED FROM THE RECREATIONAL ROD-AND-REEL AND COMMERCIAL PELAGIC LONGLINE FISHERIES IN THE WESTERN NORTH ATLANTIC OCEAN: IMPLICATIONS FOR HABITAT-BASED STOCK ASSESSMENT MODELS

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SUMMARY

To improve billfish assessments, researchers have applied habitat-based models that incorporate behavioral and oceanographic parameters to standardize historical catch-per-unit-effort time-series data, accounting for significant gear changes over time. However, there has been little behavioral data from Atlantic billfishes to support these models. We provide information on habitat preferences of white marlin released from recreational and commercial fisheries in the western North Atlantic. White marlin were tagged with pop-up satellite archival tags (PSATs) from recreational rod and reel (n=22) and commercial pelagic longline (n=2) fisheries between May-November 2002. Our data indicate that each surviving white marlin spent the majority of time at depths of 10m or less, with all fish displaying repetitive short duration diving behavior (less than 30 minutes) to depths of 60-100m. These dives were presumably related to foraging activities. Furthermore, the depths of many of the repetitive dives were within the range of deep-set pelagic longline gear. Longline sets targeting bigeye tuna may actually increase white marlin by-catch by placing baits at depths where this species may be highly motivated to feed. Until billfish feeding motivation is better understood, it may be premature to apply habitat-based stock assessment models to billfishes in the Atlantic Ocean.

RÉSUMÉ

Afin d'améliorer les évaluations sur les istiophoridés, les scientifiques ont appliqué des modèles basés sur l'habitat qui incorporent des paramètres comportementaux et océanographiques afin de standardiser les données des séries temporelles de prise par unité d'effort historique, en tenant compte des changements considérables d'engins survenus dans le temps. Toutefois, nous disposons de peu de données sur le comportement des istiophoridés de l'Atlantique pour appuyer ces modèles. Nous fournissons des informations sur les préférences en matière d'habitat du makaire blanc remis à l'eau par les pêcheries sportives et commerciales dans l'Atlantique nord-ouest. Entre mai et novembre 2002, les pêcheries sportives à la canne et moulinet (n=22) et les pêcheries palangrières pélagiques commerciales (n=2) ont apposé des marques-archives pop-up reliées par satellite à des makaires blancs. Nos données indiquent que chaque makaire blanc qui a survécu a passé la majorité du temps à des profondeurs de 10 m ou moins, chaque poisson effectuant de courtes plongées répétées (d'une durée inférieure à 30 minutes) à des profondeurs de 60-100 m. Ces plongées étaient vraisemblablement liées à des activités de recherche de nourriture. En outre, les profondeurs de nombreuses plongées répétitives se situaient dans la gamme des palangres pélagiques mouillées en profondeur. Les opérations à la palangre ciblant le thon obèse pourraient de fait augmenter les prises accessoires de makaires blancs en calant les appâts à des profondeurs où cette espèce peut être fortement motivée à s'alimenter. Tant que la motivation trophique des istiophoridés n'est pas mieux appréhendée, il sera trop tôt pour appliquer aux istiophoridés de l'Atlantique des modèles d'évaluation de stocks basés sur l'habitat.

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RESUMEN

Para mejorar las evaluaciones de marlines, los investigadores han aplicado modelos basados en el hábitat que incorporan parámetros de conducta y oceanográficos para estandarizar los datos de las series temporales de la captura por unidad de esfuerzo histórica, incluyendo los importantes cambios que se han producido en las artes con el tiempo. Sin embargo, se contó con pocos datos de conducta de los marlines atlánticos para dichos modelos. Proporcionamos información sobre preferencias de hábitat de la aguja blanca liberada en las pesquerías comerciales y de recreo del Atlántico noroccidental. Se marcó la aguja blanca con marcas archivo satélite "pop-up" (PSAT) de las pesquerías de recreo con caña y carrete (n=22) y de las pesquerías comerciales de palangre pelágico (n=2) entre mayo y noviembre de 2002. Nuestros datos indican que cada uno de los marlines supervivientes pasó la mayor parte del tiempo en profundidades de 10 m o menos, y que todos los especimenes mostraron una conducta repetitiva de inmersiones de corta duración (menos de 30 minutos) a profundidades de 60-100 m. Estas inmersiones están probablemente relacionadas con las actividades de búsqueda de alimento. Además, las profundidades de muchas de estas inmersiones repetitivas se hallaban en la zona de alcance del arte de palangre pelágico de aguas profundas. Los lances de palangre dirigidos al patudo pueden incrementar la captura fortuita de aguja blanca si se coloca el cebo a profundidades en la que esta especie pueda estar muy motivada para alimentarse. Hasta que no se comprenda mejor la motivación trófica de los marlines, podría ser prematuro aplicar a los marlines en el Atlántico modelos de evaluación del stock basados en el hábitat.

KEYWORDS

Behavior, Habitat, Vulnerability, Longlining, Pelagic Fisheries, Sportfishing, Tagging, Fishery Management

1 Introduction

Billfish are a common bycatch of pelagic longline gear deployed for target species such as tunas and swordfish. Within the Atlantic Ocean, stocks of several target and bycatch species of pelagic longline gear are considered to be overfished; for example, white marlin (*Tetrapturus albidus*) biomass may be as low as 12% of that necessary for maximum sustainable yield (ICCAT, 2002). In recent years there has been considerable debate during assessments of Atlantic billfish on how to account for historical changes in fishing practices of particular pelagic longline fleets whose catch-per-unit-effort (CPUE) time-series are used in the assessments. The trend in the Japanese fleet to move from shallow to deeper longline sets (Yokawa and Uozumi, 2001) undoubtedly has affected catch rates of target and bycatch species. Hinton and Nakano (1996) proposed a "habitat-based" model to standardize catch rates incorporating physiological parameters (depth and temperature preferences), oceanographic features, and longline fishing depth. However, application of this model to Atlantic billfishes is problematic because this model is based on data from Pacific istiophorids. There is currently is a lack of knowledge of depth and temperature preferences of istiophorid species in the Atlantic Ocean.

The development of pop-up satellite archival tag (PSAT) technology has made a significant contribution to our understanding of the movements, behavior and post-release survival of highly migratory marine fishes including bluefin tuna, swordfish, blue marlin, striped marlin, and white sharks (Block et al., 2001; Sedberry and Loefer, 2001; Boustany et al., 2002; Graves et al., 2002a; Domeier and Dewar, in press; Kerstetter et al., in press). In the present study we provide preliminary results from recent work attaching PSAT tags to 24 white marlin caught on recreational and commercial fishing gears in the western North Atlantic Ocean during 2002. By deploying PSATs that archived and reported sequential point measurements of depth and temperature over short time intervals we were able to reconstruct the actual tracks of tagged fish. We analyze these tracks for insight into the habitat preferences of white marlin and assess the applicability of these results to recent attempts at developing a habitat-based stock assessment model for istiophorid billfishes in the Atlantic.

2 Materials and Methods

The Microwave Telemetry PTT-100 model PSAT tag was used in this study. This model is programmed to record point measurements of temperature, light, and pressure (depth) in time intervals pre-set by the manufacturer. Tags programmed to release after five days (n=5) recorded measurements every two minutes, while tags programmed to release after ten days (n=19) recorded every four minutes. Data transmission by released tags to orbiting satellites of the Argos system lasted 7-10 days for both 5-day and 10-day tags.

Twenty-four PSATs were attached to white marlin from May-November 2002 in the recreational rod-and-reel fishery (n=22) and the commercial pelagic longline fishery (n=2). Fight times for recreationally-caught fish were typical of the fishery (4-30 min) with the exception of one animal that was on the line for 83 min. White marlin were fought until relatively calm, brought alongside of the vessel, and tags were implanted in the musculature below the dorsal fin but above the body cavity. Fish caught by longline gear were leadered to the side of the vessel and tags were implanted in the dorsal musculature. The rigging and attachment of tags followed Graves et al. (2002a) and Kerstetter et al. (2003).

Time-at-depth and time-at-temperature data were examined for each individual as a continuous track (data points in two or four minute intervals over the entire track duration) and as summarized in 10m and 1 C interval histograms. Potential diel differences in diving behavior were visually examined for each individual. Day and night designations were determined by sunrise/sunset information in concert with light level data.

Daily diving behavior was characterized for each individual. A cursory examination of time at depth plots revealed two classes of diving behavior which we arbitrarily called Type 1 and Type 2 dives. Type 1 dives were typically deep and of relatively short duration. This class of dives was characterized as a round-trip excursion to a maximum depth and was preceded and followed by time at the surface. Type 2 dives were typically confined to a specific depth range for an extended period of time. Figure 1 provides examples of the two daily dive patterns. Inter-dive interval was defined as the time spent on the surface between dive events. Dives only encompassing one data point at depth (not at the surface) were excluded from the subsequent behavior analyses.

3 Results

Twenty-four tags were deployed between May and November 2002 in several locations in the western North Atlantic Ocean (**Table 1**). Twenty-three tags (95.8%) reported to the satellites of the Argos system, and roughly 80% of the data points were recovered for each tag. Based on analyses of depth, temperature and light level data, it was inferred that 17 individuals survived the tagging period. The following analyses only consider the data from the 17 white marlin that survived for the five or ten day tagging period.

White marlin spent the largest proportion of their time in the upper 10m of the water column and within three degrees of ambient sea surface temperature. Time-at-depth and time-at-temperature data varied between locations (Fig 2). The marlin tagged off of Georges Bank spent the largest amount of time (80 percent) in the upper 10m while those tagged offshore of the Mid-Atlantic, Dominican Republic, and Venezuela spent less than 60 percent of their time in the upper 10m. All fish spent the vast majority of their time between 24-27 C, which encompasses the range of sea surface temperatures during tagging operations.

All white marlin made frequent, short duration dives, many of which went below 100m. Distinct day/night patterns were evident during the track duration of nine individuals. It should be noted that contrasting patterns (deeper at night, shallower during the day and vice versa) were observed within and among individuals, and that a particular diel dive pattern rarely persisted throughout the entire track for any individual. One exception to this observation was white marlin DR2 (Fig 3a), which moved throughout the water column during the day and directed the majority of its efforts between 20-60m during night for the entire five day tracking period. One white marlin appeared to change its diving behavior as it moved from cooler coastal waters off Virginia into the warmer, oceanic waters of the Gulf Stream (VA4, Fig 3b).

Patterns of daily dive behavior indicate that all white marlin exhibited Type 1 and Type 2 dive behaviors. Mean duration and depth of dives, mean temperature ranges between the starting and terminal points of dives, and interdive intervals were variable within and among individuals (**Table 2**). The mean duration of Type 1 dives was 26.2 min (S.D. 22.0) to an average depth of 57.6m. Mean Type 1 dive durations were shortest in Georges Bank (mean 12.8 min) and increased southward. The mean range of temperatures encountered on Type 1 dives was 3.3 C (S.D. 2.6). Between Type 1, white marlin returned to the surface for interdive intervals averaging 53.4 min (S.D. 71.7). Interdive intervals decreased from Georges Bank southward to the Dominican Republic, then increased in Venezuela (where dives were deepest). Type 2 dives occurred when white marlin confined their behavior to specific dive ranges for relatively long time intervals (mean 45.3 min S.D. 85.2). Type 2 dive behavior was variable with respect to dive duration.

4 Discussion

The model of PSAT used in the present study measures physical parameters (light, temperature and pressure) at relatively high frequency (2 or 4 min intervals) and transmits the data in a serial fashion. Archival and transmission of the raw, serial data was possible because the tags were programmed to release after relatively short deployments of five or ten days. Most other models of PSATs are designed to collect data for longer periods of time, and the information must be summarized to allow for efficient transmission to the Argos satellites. The serial data archived by other tag models are available only if the tag is later recovered, a relatively rare event. The reception of data in a serial (unsummarized) format in the present study has revealed behaviors not readily apparent with traditional summarized (binned) data.

The 17 white marlin surviving the five or ten day tagging period exhibited some similarities in overall use of the water column. All fish were predominantly surface-oriented, with most spending 40-60 percent of their time in the upper 10m. An exception to the latter is the fish tagged in the waters of Georges Bank, which spent almost 80% of its time in the upper 10m. While comparative behavioral data are not available for white marlin, prior acoustic and PSAT studies of striped marlin indicate that this closely-related species spends over 30% of its time in the top 10m (Holts and Bedford, 1990; Brill et al., 1993). Similarly, PSAT investigations of blue marlin released from recreational rod-and-reel (Graves et al., 2002) and pelagic longline (Kerstetter et al., in press) fisheries indicate that this species likewise spends the majority of its time near the surface, a behavior that is strikingly different from the diel pattern observed by Sedberry and Loefer (2002) for Atlantic swordfish. It is important to note that even though general similarities in behavior (dive frequency, dive depth, diel periodicity) were found among the 17 individual white marlin, considerable variation was exhibited within an individual on different days or among different individuals. Comparable levels of within and among individual variation have been noted for billfish in previous acoustic and PSAT studies (Holland et al., 1990; Holts and Bedford, 1990; Block et al., 1992; Pepperell and Davis, 1999; Graves et al., 2002a; Domeier and Dewar, in press; Kerstetter et al., in press).

Almost all of the white marlin tagged exhibited several Type I (short, deep) dives on a daily basis followed by periods of time spent in surface waters. The temperature differences encountered on these dives were typically 3-4 C at most locations, although rare excursions resulted in water temperature differences as great as 13.5 C. White marlin, like blue marlin, feature specialized muscle tissue beneath the brain that generates and maintains warmer-than-ambient temperatures in the eye/brain (Block, 1986); however, they lack the ability to maintain body muscle temperatures above ambient water levels (Brill and Lutcavage, 2001). While white marlin appear to be well adapted for searching at depth, they seem to not be adapted for staying in cooler, deeper waters for extended periods of time. Likewise, diving behavior of blue, striped, and black marlin (Holland et al., 1990; Holts and Bedford, 1990; Brill et al., 1993; Pepperell and Davis, 1999) suggest limited abilities to stay at depth for extended amounts of time; these species appear to constrained to a maximum temperature difference of 8 C. Brill et al. (1999) and Brill and Lutcavage (2001) suggest that temperature-induced reductions in cardiac function are responsible for limiting the depth distributions of yellowfin tuna and the istiophorid billfishes. Like tunas, billfishes may need to warm their core temperature and restore cardiac function in warmer surface waters after forays into cooler waters. Our data supports this hypothesis as evidenced by the fact that dives to depth were typically followed with extended periods of time at the surface. Dives were of shortest duration, and temperature ranges and interdive intervals were greatest in Georges Bank, where the coolest water and presumably largest thermal gradients were encountered (**Table 2**). Dive duration increased southward to Venezuela, and interdive intervals decreased southward to the Dominican Republic, suggesting that movement through warmer waters required less time at the surface between dives. Mean dive durations were longest and mean dive depths deepest in Venezuela, which may indicate why interdive intervals increased in this southernmost location sampled.

We propose that Type 1 dives represent excursions of white marlin through the water column in search of prey. In many instances, relatively rapid Type 1 dive descents were paired with Type 2 (much longer duration) ascents. Given that the presence of prey in the pelagic realm is thought to be episodic and clustered in nature and that Type 2 behavior occurs with varying breadth and intensity, this “directed” pattern may be reflective of marlin locating schooling prey and exploiting that resource for extended amounts of time. That white marlin appear to direct their efforts in confined ranges of depth during the ascent from a search dive may indicate that dives to depth (i.e., Type 1 search dives) afford these billfish an opportunity to silhouette concentrations of prey against the sky/surface. Type 2 dives were observed most often during daylight hours and on nights with brighter moon phases, a behavior consistent with the silhouetting hypothesis. While data from this PSAT model cannot record feeding events, the duration, patterns, and periodicity of white marlin diving behavior suggests frequent, short-duration feeding dives and occasional prolonged foraging efforts at depths in excess of 50m.

Recent assessments of billfishes have considered habitat-based models that standardize catch rates in proportion to time at depth or temperature, an adjustment that accounts for historical differences in the depths of longline gear deployments. A fundamental assumption of the catch rate standardizations is that feeding motivation is constant over time as well as all depths and temperatures. Our results suggest that assumption is not well founded (Fig 4).

While white marlin spend the majority of their time in the upper 10m, we question the assertion that their feeding motivation is greatest in surface waters. Some motivation for surface association may instead lie in increasing core temperature and restoring cardiac function between frequent foraging dives (Brill et al., 1999) rather than for feeding alone. Based on the nature and persistence of daily dive patterns observed in our data, it is probable that a considerable proportion of white marlin foraging occurs at depth. In addition to epipelagic prey such as halfbeaks, flying fishes, filefish, and dolphinfishes, white marlin have also been observed with various scombrids, squid (*Loligo* and *Illex* sp.), Atlantic moonfish (*Vomer setapinnis*), butterfish (*Peprilus* sp.), cutlassfish (Trichuridae) (Nakamura, 1985; Davies and Bortone, 1976), and even benthic rays (J. Graves, pers. obs) in their stomach contents, indicating that white marlin actively forage beyond surface waters.

If white marlin dive to depth to silhouette prey against the surface, their vulnerability to longline gear is high at those times when dives exceed the minimum fishing depths of longline hooks. A comparison of the full ten day track versus the summary data for white marlin CM2 (Fig 4) illustrates that the time-at-depth histogram may not accurately reflect the vulnerability of this marlin to longline gear if its motivation to feed was high at depth or in the ascent from depth. Further obscured in the time-at depth histogram is that the vulnerability of this animal to longline gear varied across days and between day and night periods. It would have been subjected to capture by the gear on all nine nights, but only on six of the ten daytime periods. Admittedly, different fish show differing patterns with respect to diel diving behavior (some dive deeper at night, some deeper during the day, and some with no difference) and the nature, duration, and extent of Type 1 and Type 2 diving behavior. However, analyses based on tracks of these animals rather than on summaries of their respective activities may yield far more insight into their possible feeding motivations and vulnerability to pelagic longline gear. Graves et al. (2002b) suggest that standardization of catch rates on the basis of time-at-depth data, but devoid of considerations of feeding motivations, will lead to biased estimates of abundance.

The PSAT data from this study indicate that white marlin undertake frequent short-duration dives, excursions that are likely related to foraging. These dives occur well within the range of measured depths of pelagic longline gear. Therefore, deep longline gear targeting bigeye tuna could actually result in the increased bycatch of billfishes by placing baits within, rather than beyond, the feeding depths of some billfish species. Results from the PSAT deployments on white marlin further demonstrate that summary data do not fully capture the extent and nature of activity at depth while track data may indicate repetitive foraging far deeper than that considered by previous modeling efforts. Clearly, more research is in order. One potential means of addressing this question may be to combine paired shallow and deep longline sets in close proximity and compare catch rates at various depths to stomach contents of the resulting billfish catch and prey abundance data in the region sampled. Until further data clarify the species-specific relationships between depth and feeding behavior, we believe that it remains premature to apply habitat-based stock assessment models to billfishes in the Atlantic Ocean.

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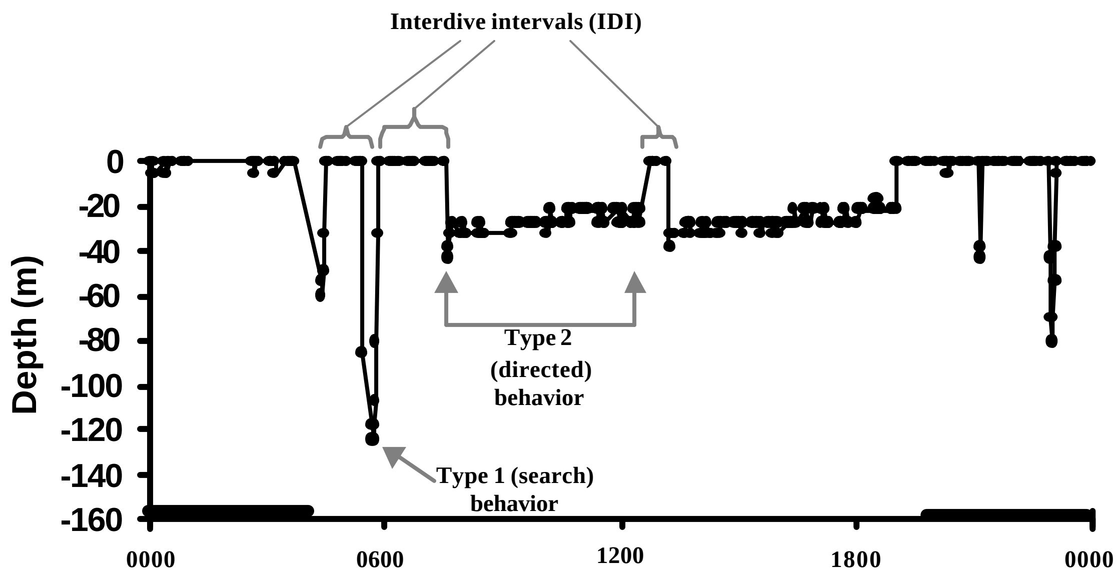
Table 1. Locations of PSAT deployments on white marlin during 2002.

Location	Type of fishery	Dates of tagging	Deployment duration	Number deployed
Punta Cana, Dominican Republic	Recreational rod-and-reel	15-19 May	5-day	5
Mid-Atlantic Coast, USA	Recreational rod-and-reel	18-22 August, 5-21 September	10-day	11
Georges Bank, USA	Commercial longline	31 August	10-day	2
La Guaira Bank, Venezuela	Recreational rod-and-reel	23-25 November	10-day	6

Table 2. Summary of daily dive statistics by location.

Location	Dive behavior	Mean dive duration (min) +/- SD	Mean dive depth (m)	Temperature range (C)	Inter-dive interval (min)
Georges Bank	Type 1 (search)	12.8 +/- 69.9	42.7 +/- 14.7	4.0 +/- 2.0	90.4 +/- 102.5
	Type 2 (directed)	176.4 +/- 195.4	40.8 +/- 12.9	3.6+/- 1.5	171.6+/- 171.6
Mid-Atlantic	Type 1 (search)	26.6 +/- 29.3	41.0 +/- 26.4	3.2 +/- 3.4	55.3 +/- 70.6
	Type 2 (directed)	210.6 +/- 209.3	48.3 +/- 38.1	4.0 +/- 3.4	53.5 +/- 101.7
Dominican Republic	Type 1 (search)	27.5 +/- 15.6	41.7 +/- 19.9	2.1 +/- 1.2	32.8 +/- 55.6
	Type 2 (directed)	165.9 +/- 153.8	63.4 +/- 29.8	3.2 +/- 1.8	33.7 +/- 57.2
Venezuela	Type 1 (search)	42.8 +/- 58.9	73.3 +/- 24.7	3.3 +/- 2.0	47.3 +/- 64.1
	Type 2 (directed)	137.4 +/- 118.2	79.3 +/- 22.7	4.0 +/- 2.2	29.9 +/- 34.3
Grand mean	**Type 1 (search)**	**26.2 +/- 22.0**	**57.6 +/- 29.0**	**3.3 +/- 2.6**	**53.4 +/- 71.7**
	Type 2 (directed)	**183.1 +/- 181.8**	**58.5 +/- 35.3**	**3.7 +/- 2.8**	**45.3 +/- 85.2**



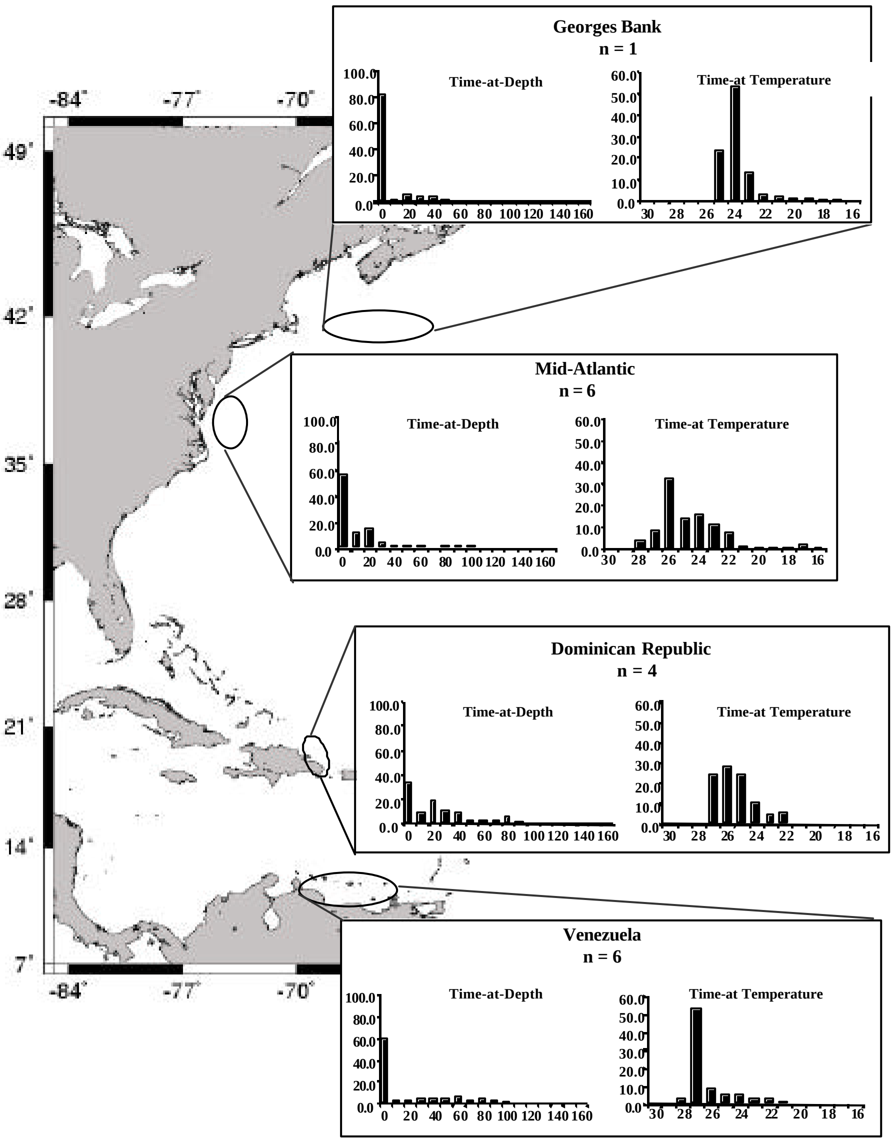


Figure 2. Time-at-depth and time-at-temperature histograms for white marlin tagged in 2002, pooled by location. Sample sizes for each location are given. Note: temperatures in degrees C and depth in meters.

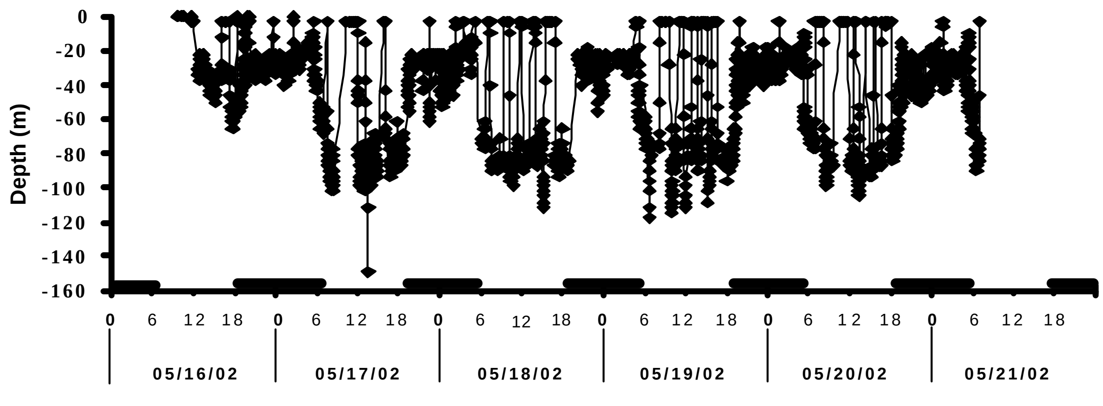


Figure 3a. Strong diel pattern of diving behavior of DR2, tagged offshore of the Dominican Republic in May 2002 with a 5-day MT PTT-100 tag. Black bars along the x-axis denote periods of darkness, derived from time-of-day and light level data archived by the tag.

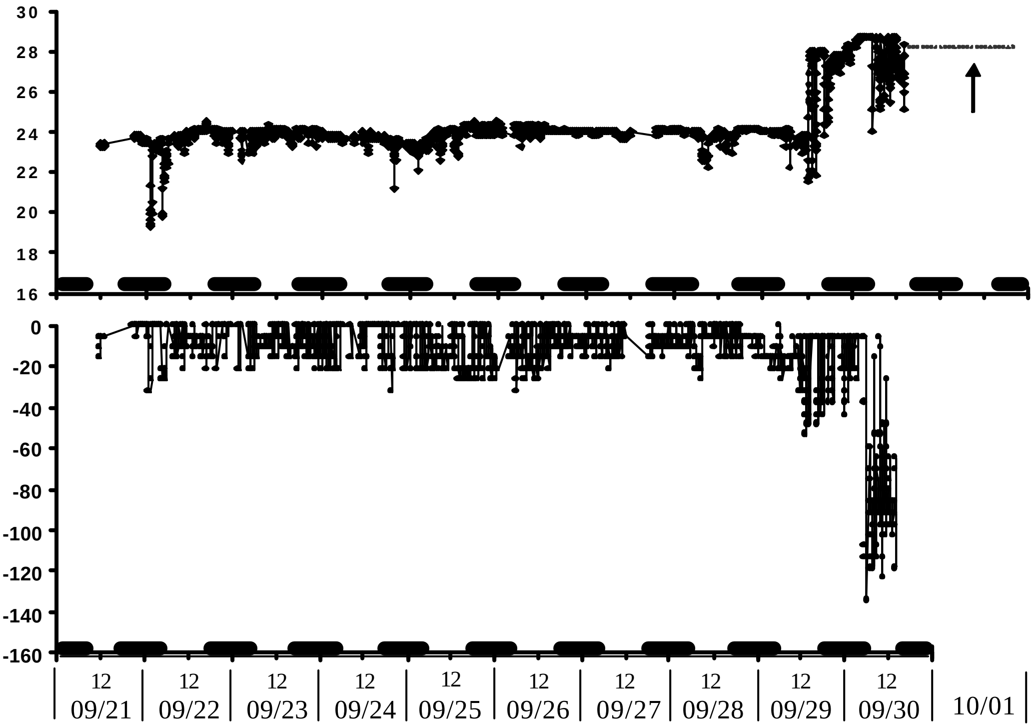


Figure 3b. Change in the dive behavior of VA 4, tagged in the waters of the Mid-Atlantic in September 2002 with a 10-day MT PTT-100 tag. Black bars along the x-axis denote periods of darkness, derived from time-of-day and light level data archived by the tag. The increase in dive depths concomitant with the increase in temperature readings and the general path of this animal (not presented) suggest that the change in diving behavior of this fish occurred as it entered the Gulf Stream on 29 September.

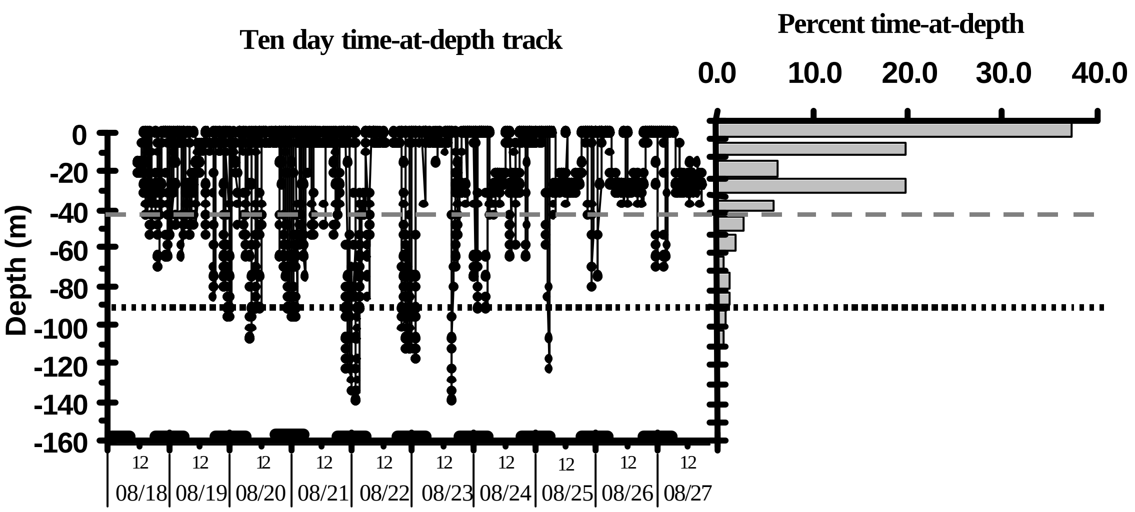


Figure 4. Overlay of the time-at-depth track and summarized histogram of depth preferences of CM2, tagged offshore of the Mid Atlantic in August 2002. The gray dashed line denotes the minimum and the black dotted line denotes the maximum depth of longline hooks observed in the Mid Atlantic during sets targeting swordfish (D. Kerstetter, pers. obs). This figure suggests that gear susceptibility models using summarized time-at-depth data may not accurately depict the diving behavior and, by analogy, the potential feeding preferences and gear susceptibility of white marlin.