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Habitat Utilization and Dive Characterization of Blue Marlin (Makaira nigricans) and White Marlin (Kajikia albida) in the Western Atlantic Ocean

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Habitat Utilization and Dive Characterization of Blue Marlin (*Makaira nigricans)* and White Marlin (*Kajikia albida*) in the Western Atlantic Ocean

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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Approved, by the committee July 2010

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DEDICATION

This thesis is dedicated to the memory of my grandfather, Everett Leroy Livingston (1915-2003), who always shared his passion for fishes and people with me.

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ABSTRACT

Blue marlin *Makaira nigricans* and white marlin *Kajikia albida* (formerly *Tetrapturus albidus*) are overfished in the Atlantic Ocean, with the vast majority of fishing mortality resulting from the pelagic longline fishery that targets tunas (*Thunnus spp.*) and swordfish *Xiphias gladius*. Time series of catch-per-unit-effort (CPUE) data have been fundamental to assessments of blue marlin and white marlin stocks, but these time series have been affected by a shift over time in pelagic longline fishing practices from shallow to deeper sets. One method for adjusting CPUE data for changes in fishing practices is a habitat-based standardization that modifies fishing effort in proportion to the vertical distribution of the species of interest and the fishing gear. For these models to be successfully applied to population assessments, the vertical habitat utilized by blue marlin and white marlin must be known. Pop-up satellite archival tags (PSATs) provide a means of collecting high resolution vertical movement and distribution data for billfishes.

In my study, 62 blue marlin and 40 white marlin were caught in recreational fisheries off the U.S. mid-Atlantic, Yucatan Peninsula, northern Caribbean, Venezuela, and Brazil, tagged with Microwave Telemetry, Inc. PTT-100 HR PSATs, and released. Data were recovered from PSATs attached to 57 surviving blue marlin and 36 surviving white marlin. PSATs successfully transmitted 18-100% of the data they recorded (mean 72%). The minimum 10-day displacements of both species averaged 242 km (range 9 to 942 km) and varied significantly between tagging locations, but not between species. Blue marlin spent a significantly higher (62%) amount of time in the upper 10 m of water than white marlin (56%). Both species spent greater than 95% of the time in water that was within 8° C of the sea surface temperature. Only 3.1% of white marlin demonstrated diel differences in the maximum depth of dives, while 29% of blue marlin dove into deeper waters during the day. Variables identified as explaining the most variation in dives were total dive duration, bottom time, ascent time, number of wiggles, wiggle depth, interdive interval, skew of ascent and descent, % time ascending, and % time descending. Using these variables, two dive types were identified through cluster analysis: simple dives representing traditional "U" and "V" shapes, and complex dives with multiple descents, plateaus, and wiggles. There were significant differences in dive variables among locations, individuals, diel periods, and dive types. There was significant overlap in range, habitat use, and vertical movement patterns, and therefore no strong evidence of niche partitioning between blue marlin and white marlin. My analyses can be used to further define the physical and physiological factors limiting marlins' vertical movements and therefore improve stock assessments based on longline CPUE data by correcting for changes in fishing practices.

Habitat Utilization and Dive Characterization of Blue Marlin (*Makaira nigricans)* and White Marlin (*Kajikia albida*) in the Western Atlantic Ocean

INTRODUCTION

Billfishes are large pelagic fishes that are caught in commercial and recreational fisheries throughout tropical and temperate oceans of the world. Within the Atlantic Ocean, billfish populations have decreased dramatically over the past 50 years. During this time period the species targeting practices of commercial longline fisheries have changed, adding complexity to assessments based on CPUE, and that are also challenged by a paucity of historic data. Knowledge about the vertical habitat use of billfish can aid in making more accurate assessments of stock status. Pop-up satellite archival tags (PSATs) collect data revealing information about the habitat utilization of large pelagic fishes. Here, PSATs are applied to blue marlin (*Makaira nigricans* Lacepede 1802) and white marlin (*Kajikia albida* (formerly *Tetrapturus albidus*) (Poey 1860)) in the western Atlantic Ocean to gain insight to the movements, habitat utilization, and diving behaviors of these fishes.

Biology

Billfishes of the family Istiophoridae are large pelagic apex predators which inhabit tropical and subtropical epipelagic waters worldwide (Nakamura, 1985). The circumtropically distributed sailfish (*Istiophorus platypterus* Shaw and Nodder, 1792) and blue marlin are found in both the Atlantic and the Indo-Pacific Oceans; whereas black marlin (*Istiompax indica* (formerly *Makaira indica*) Cuvier, 1832), striped marlin (*K. audax* (formerly *T. audax*) (Phillipi 1887)), and shortbill spearfish (*T. angustirostris* Tanaka 1915) are distributed in the Indo-Pacific Ocean. White marlin, Atlantic longbill spearfish (*T. pfluegeri* Robins and de Sylva 1963), Mediterranean spearfish (*T. belone* Rafinesque 1810), and roundscale spearfish (*T. georgii* Lowe 1840) are limited to the Atlantic Ocean. Blue and white marlins are found from 45° S to 45° N (Nakamura 1985), inhabiting higher latitudes during warm seasons. Nakamura (1985) suggested that ecological interactions between blue marlin and white marlin could lead to inverse fluctuations in local abundances.

Both blue marlin and white marlin have sufficient mixing to preclude the formation of significant genetic stock structure within the Atlantic Ocean, although stock structure has been noted between ocean populations for several species of billfish (Graves and McDowell 2003). Atlantic and Indo-Pacific blue marlin showed significant differences in allele frequencies in four classes of molecular markers (Finnerty and Block 1992, Graves and McDowell 2003, Buonaccorsi *et al.* 2001). Analysis of MtDNA haplotype and microsatellite loci variation suggests that following isolation of the Atlantic and Indo-Pacific populations, some gene flow has occurred from the Indo-Pacific to Atlantic populations. Likewise, white marlin do not show spatial structuring of genetic variation throughout their range in the Atlantic Ocean (Graves and McDowell 2003) and both are both currently managed as single stocks.

Because of their extensive mobility, blue marlin and white marlin encounter great variation in physical and biological oceanographic conditions such as light level, temperature, oxygen, and prey abundance. The billfishes have modifications that allow them to function as highly efficient visual predators at a wide range of temperatures and light levels. The superior rectus muscle is modified to provide heat to the eye and brain, while the temperature of the rest of the body fluctuates with that of the surrounding water (Block 1986). Portions of the superior rectus, which surrounds the orbit, are modified to produce heat while others maintain the function of moving the eye. Portions that produce heat lack contractile proteins and have increased numbers of mitochondria, allowing for heat production via the hydrolosis of ATP (Block 1986). A retia mirabilae provides for a countercurrent heat exchanger that maintains the heat produced in the tissues of the eye and brain, and minimizes loss to other parts of the body or surrounding water. This adaptation for maintenance of higher temperature in the eye and brain increases the temporal resolution of the eye as measured by the flicker fusion frequency, increasing the marlin's ability to detect and pursue fast moving prey (Fritsches *et al.* 2003).

Even during the day in well lit pelagic waters, light can be limiting at depth. At depths of 300 meters in clear oceanic waters, only 0.003% of surface light is available (Clark and Denton 1962). As visual predators, marlin have adaptations for high optical sensitivity, potentially the highest optical sensitivity of the teleosts (Fritsches *et al.* 2003). Marlin have large eyes and the cone photoreceptors are enlarged, allowing them to trap more light. A high convergence of photoreceptors to ganglion cells increases sensitivity, and allows for higher visual acuity in low light conditions (Fritsches *et al.* 2003). These same convergences have arisen independently in some mesopelagic fishes, such as the lantern fish *Lampancytus macdonaldi*, that spend considerable time in deeper water with low light levels (Warrant 2004).

Visual acuity is highest directly in front of and above the animal because of the high densities of photoreceptors in the ventro-temporal portion of the retina.

Marlin retinas contain three visual pigments in their cone cells, suggesting color vision in waters with broad spectrum light. The cone cells are only found on the ventral surface of the retina, an adaptation for utilizing the broad spectrum light coming from above (Fritsches *et al.* 2003) while optimizing retinal space in other regions for increased sensitivity.

Marlin diet studies show that they consume much of their prey at the surface. The main prey species found in marlin stomachs are epipelagic fishes and squids (Brock 1984, Garcia de las Salmones *et al.* 1989, Junior *et al.* 2004, Satoh 2004, Shimose *et al.* 2006, Shimose *et al.* 2010). A few studies have reported prey items that typically inhabit deeper water (Strasburg 1970, Nakamura 1985, Harvey 1989); however, most diet studies use opportunistic sampling of marlin generally caught at the surface, so prey items that typically inhabit deeper waters may be underrepresented.

While light levels may limit the depths that visual predators such as marlin can effectively forage, water temperature may limit their swimming performance. Tunas and presumably also billfishes have limited ability to control the stroke volume of the heart, leaving heart rate as the main controller of cardiac output (Farrell *et al.* 1992, Brill and Bushnell 2001). A decrease in water temperature causes an immediate decrease in heart rate and therefore cardiac output (Brill *et al.* 1998). This decrease in cardiac output lowers the swimming performance of billfish and tuna, even with the countercurrent heat exchangers in the brains and body musculature, respectively. In support of the idea that the change in water temperature with depth limits tunas' and billfishes' vertical movements through effects on cardiac function, acoustic tracking studies of marlin and some tunas (Brill *et al.*1993, 1998, Holland *et al.*1990) have demonstrated that these pelagic predators spend greater than 90% of their time in water that is less than 8° C colder than the surface layer. Moreover, recent studies on isolated cardiac tissue (Galli *et al.* 2009) have shown that cardiac muscle function in pelagic fishes with extensive vertical movement patterns (e.g., bigeye tuna *Thunnus obesus* and swordfish *Xiphias gladius*) is less effected by acute reductions in temperature than cardiac muscle of fishes generally limited to epipelagic waters (e.g., yellowfin tuna *T. albacares* and dolphin fish *Coryphaena hippurus*).

Along with light and temperature, oxygen levels may limit the vertical movements of pelagic fishes, including marlins (Bernal *et al.* 2009). Because of the difficulty of field measurements and maintenance of billfish in captivity, oxygen requirements for marlin are not known (Post *et al.* 1997, Holland *et al.* 2001). The oxygen consumption of juvenile sailfish ranged from 3.00 - 33.01 mL O^2 g^{-1} h^{-1} (Idrisi *et al.* 2002), similar to that seen in other high performance pelagic fishes with high metabolic rates and oxygen requirements (Benetti 1992, Brill 1996), suggesting that ambient oxygen requirements are probably similar. Prince and Goodyear (2006) suggest that oxygen could limit the depth of blue marlin dives in the eastern tropical Pacific Ocean but not in the western North Atlantic Ocean. The eastern tropical Pacific Ocean and the eastern Atlantic Ocean are areas where upwelling introduces cold, nutrient rich, and oxygen poor deep water towards the surface. Below the shallow (25m) thermocline lies a hypoxic layer (<2mg L^{-1}) into which marlin rarely venture. The waters of the western Atlantic are influenced by subtropical gyres that maintain dissolved oxygen levels in excess of 4mg L^{-1} to depths of 300 m, levels at which dissolved oxygen would not be limiting (Prince and Goodyear 2006).

Acoustic and PSAT tagging studies have also demonstrated differences in diel patterns of vertical distributions for istiophorids billfishes. As visual predators, marlin would be expected to dive to greater depths during the day when light penetrates the furthest and remain near the surface at night when light is limiting. This trend was reported for blue marlin and black marlin (Holland *et al.* 1990, Block *et al.* 1992, Pepperell and Davis 1999, and Kerstetter *et al.* 2003), but with considerable variation among individual fish. No diel patterns in habitat utilization were observed for striped marlin, black marlin, or white marlin (Brill *et al.* 1993, Gunn *et al.* 2003, Horodysky *et al.* 2007).

Differences in dive behavior and habitat utilization have been attributed to physiological limitations and feeding strategies in a variety of pelagic organisms (Brill *et al.* 1993, Baechler *et al.* 2002, Hays *et al.* 2004, Prince and Goodyear 2006, Horodysky *et al.* 2007, Schaefer *et al.* 2009, Bernal *et al.* 2009). Physiological temperature limits could cause differences in dive behavior across spatial and temporal scales as water conditions change. However, the distribution of prey species, physical oceanographic conditions, and the foraging patterns of a given species may influence diving behaviors.

Although blue marlin and white marlin share many physiological traits that could influence or limit their habitat selection, there are differences between these species that could lead to differences in diving behaviors. Blue marlin attain larger sizes than white marlin. Blue marlin caught on commercial longline gear typically range from 200 to 275 cm (LJFL), while white marlin range from 130 to 210 cm. There is an even greater difference in maximum sizes, with blue marlin exceeding 375 cm and 580 kg, while the smaller white marlin attain maximum size of 280 cm and 82 kg. Blue marlin with masses over 136 kg are generally females (Nakamura 1985).

Fisheries and stock status

Blue marlin and white marlin are caught in the Atlantic Ocean as bycatch in international commercial pelagic longline and purse seine fisheries mainly targeting tropical tunas (genera *Thunnus* and *Katsuwanus*) and swordfish. Blue marlin and white marlin are also specifically targeted in directed recreational and artisanal fisheries. Bycatch in pelagic longlines accounts for 80% of the total landings of Atlantic billfishes (Arrocha and Ortiz 2006). The maximum total reported landings for white marlin was 4906 metric tons (mt) in 1965, but rapidly dwindled to a low of 975 t by 1978 (Arocha and Ortiz 2006). Likewise, reported blue marlin landings peaked at over 9000 mt in 1963, but fell to 2500 mt by 2004 (Arocha and Ortiz 2006). The pelagic longline fishery originally targeted surface oriented yellowfin tuna with shallow longline sets. As demand for yellowfin tuna declined over the past 40 years, the fishery has shifted to deeper dwelling swordfish and bigeye tuna by fishing longlines at deeper depths (Goodyear *et al.* 2002, Arocha and Ortiz 2006).

Thirty-four countries have reported billfish catches from pelagic longline and purse seine fisheries in the Atlantic Ocean since 1956 (ICCAT 2006). International management of pelagic fisheries in the Atlantic Ocean is the responsibility of the member nations of the International Convention for the Conservation of Atlantic Tunas (ICCAT). The most recent stock assessment (2006) estimates current biomass (B) of blue marlin to be 43% of biomass of maximum sustainable yield (B_{MSY}), and the B of white marlin to be only 15% of B_{MSY} in the Atlantic Ocean (ICCAT 2003, Arocha and Ortiz 2006). The assessments of marlin stock status are made using Schafer production models that estimate total biomass from the fisheries-dependent catch-per-unit-effort (CPUE) data (ICCAT 2002, Restrepo *et al.* 2003, Goodyear *et al.* 2002). The majority of CPUE time series are of pelagic longline fisheries targeting tunas and swordfish, but also include recreational fisheries. The 2006 stock assessments applied a Bayesian surplus production model (BSP), a variant of the Schaefer production model (McAllister and Babcock 2003), which allowed increased flexibility over previous models in the weighting of different indices (Bolden *et al.* 2007).

The U.S. Atlantic pelagic longline fishery is heavily managed with quotas for swordfish and sharks, minimum size limits for swordfish, yellowfin tuna, bigeye tuna, and bluefin tuna *T. thynnus*, protected species take limits, area closures, reporting requirements, gear and bait requirements, and limited entry (Bolden *et al.* 2007). Since 1988, the U.S. Atlantic pelagic longline fishery has been prohibited from retaining any billfish and all billfish taken on the gear must be released, dead or alive. Only 5% of the mean reported catch of all of the Atlantic Ocean comes from dead discards of the U.S. pelagic longline fleet and the small recreational catch.

Selectivity of longline gear (i.e., interactions with bycatch species) can be affected by the depth and time the gear is fished. Gear targeting swordfish is fished relatively shallow at night, while gear targeting tunas is fished deeper during daylight (Boggs 1992, Nakano *et al.* 1997). As the depth fished by pelagic longlines changes, there can be a change in encounters between marlin and the fishing gear (Ward and Hindmarsh 2007), causing CPUE to be a poor estimator of abundance (Goodyear *et al.* 2002).

Changes in depth of longline fishing over time can be accounted for by standardizing catchability by depth (Hinton and Nakano 1996). This method, known as habitat-based standardization (HBS), modifies the effort of each hook on a longline by the proportion of time that fish spend at the depth the hook is fished. The effective effort for each hook is calculated and used to modify the effort component of the CPUE estimate. This technique was applied to blue marlin catch series from the Atlantic Ocean (Yokawa and Uozumi 2001) using habitat data from nine blue marlin tracked in the central Pacific Ocean with acoustic tags (Holland *et al.* 1990; Block *et al.* 1992), The application of the same standardization to Atlantic Ocean fishery data failed to account for some longline sets that actually did catch blue marlin at depth and resulted in very high CPUE values in areas with positive catch and low effective effort, artificially inflating overall CPUE estimates. ICCAT scientists deemed the use of HBS premature for assessments of Atlantic Ocean billfishes, especially with habitat data obtained from marlin from another ocean basin, and it was not implemented in the most recent stock assessments (Goodyear *et al.* 2002, Satoh *et al.* 2004, Andrade 2006, Goodyear 2006).

The deep diving behaviors of blue marlin bias the HBS CPUE estimates downward for shallow longline sets and upward for sets with hooks that are in or below the thermocline (Goodyear *et al.* 2002). Areas of research identified as necessary for implementation of HBS include investigations of the vertical distribution and movements of billfishes and pelagic longline hooks in the Atlantic Ocean (Goodyear *et al.* 2002).

Pop-up satellite archival tags

While physiological traits and diet studies provide indirect evidence that marlin are capable of extensive vertical movements, direct and quantitative evidence of the proportion of time spent at various depths can be obtained from electronic devices attached to the fish which record changes in depth. Prior to the advent of data recording tags, ultrasonic (acoustic) depth-sensitive tags were used to follow the vertical movements of individual fish using a boat equipped with a hydrophone. Ultrasonic tags have been used to track sailfish (Jolley and Irby 1979), striped marlin (Holts and Bedford 1990, Brill *et al.* 1993), black marlin (Pepperell and Davis 1999), and blue marlin (Yuen *et al.* 1974, Block 1990, Holland *et al.* 1990, Block *et al.* 1992, Kraus and Rooker 2007). These studies tracked fish caught with hook and line for time periods up to a few days, collecting high temporal resolution (seconds to minutes) data of the fish. Expendable bathythermograhs (XBTs) or conductivity, temperature and depth sensor (CTD) systems were often used to measure surrounding water profiles. In these studies, researchers stayed in close proximity to the fish, following its path in order to receive data about its movement and environmental variables. Thus tracks were limited in duration by sea conditions, man-power, vessel costs, and battery life of the acoustic transmitter (Holland *et al.* 1985).

Pop-up satellite archival tags (PSATs) provide an alternative for studying movements, mortality, and habitat utilization of billfishes. PSATs measure and record depth, temperature, and light levels encountered by a tagged fish. After a set time period the tag releases from the animal, floats to the surface, and transmits data to researchers independent of any additional contact with the fish. Data from many fish can be collected simultaneously with no need to recapture the fish to retrieve the data. PSATs have been used to study survival, horizontal movements, and habitat utilization of blue marlin (Graves *et al.* 2002, Kerstetter *et al.* 2003, Prince *et al.* 2005, Prince and Goodyear 2006, Goodyear *et al.* 2008), white marlin (Horodysky and Graves 2005, Prince *et al.* 2005, Prince and Goodyear 2006, Horodysky *et al.* 2007, Graves and Horodysky 2008), striped marlin (Domeier *et al.* 2003, Sippel *et al.* 2007), black marlin (Gunn *et al.* 2003, Prince and Goodyear 2006), and sailfish (Hoolihan 2004, Kerstetter and Graves 2006, Prince and Goodyear 2006, Hoolihan and Luo 2007). Confirming the results of previous acoustic telemetry studies, the data from PSATs also demonstrated that istiophorids spend the majority of the time in the upper uniform temperature surface layer.

While early PSAT studies were limited by the amount of data each PSAT could store, improvements in memory, batteries, data compression algorithms and other software have greatly increased the number of data points collected, archived, and transmitted, drastically improving the resolution of dive data collected. Horodysky *et al.* (2007) used PSATs collecting depth, light, and temperature data every 90 seconds for 10 days to characterize the habitat utilization of white marlin in the Atlantic Ocean. The study demonstrated considerable variation among individuals and differences in dive characteristics between tagging locations.

PSATs have proven themselves as an appropriate tool for tracking large pelagic fishes and measuring their habitat utilization the behaviors of blue marlin and white marlin in the western Atlantic Ocean. This information is necessary for the implementation of HBS of CPUE data series to obtain improved estimates of current and historical stock abundances. Accurate assessments are fundamental to proper management, and necessary to develop measures to rebuild populations of these important pelagic predators.

OBJECTIVES

In light of these issues, I used PSATs to elucidate the habitat utilization and diving behaviors of blue marlin and white marlin in the western Atlantic Ocean. The objectives of my study were to use data collected by high resolution PSATs to:

1. Characterize habitat utilization of blue marlin with respect to depth and temperature in the western Atlantic Ocean.

2. Characterize variables that influence dive behaviors of blue marlin.

3. Compare habitat utilization and dive characterization of blue marlin and white marlin across the western Atlantic Ocean.

METHODS

Tagging

The Microwave Telemetry PTT-100-HR model pop-up satellite tag was used in this study following the methods of Graves *et al.* (2002) and Horodysky *et al.* (2007). Individual PSATs measure 38 cm by 4 cm including a 22 cm antenna and weighs 65-68 g. The carbon composite body contains a lithium battery, a microprocessor, depth and pressure sensors, a temperature gauge, and a transmitter, with a bulb embedded with glass beads to provide flotation. The PSATs were programmed to record temperature, light, and depth data every 90 sec for the 10-day preset deployment period.

The tags were rigged for attachment to the fish with a tether comprised of 16 cm of 200 pound test Sea Striker® brand monofilament fishing line attached to a nylon intramuscular tag anchor. Metal crimps were used to attach the nylon anchor to the monofilament tether, and the tether to the tag. The entire assembly of monofilament and crimps was covered with heat shrink tubing to minimize abrasion with the marlin's body and corrosion of metal components. PSATs were deployed on 62 blue marlin and 40 white marlin caught in recreational fisheries using trolled baits and bait/lure combinations fished on standard fishing tackle (20 to 130 lb gear) and fought in a manner typical of the recreational fishery. At boatside, the fish were stabilized by grabbing the bill and dorsal fin to facilitate optimal tag placement.

PSATs were attached to the fish by inserting the nylon anchor into the dorsal musculature, interlocking with pterygiophore bones below the dorsal fin (Graves *et al.* 2002, Domeier *et al.* 2003, Horodysky *et al.* 2007). Tag heads were inserted with a stainless steel applicator attached to 0.3 to 2 m tagging poles. Marlin that were unable to maintain proper orientation at boatside were resuscitated by moving the fish through the water with the boat to allow water to pass over the gills until the fish's condition improved, a technique commonly employed by recreational anglers. Hooks were removed from the fish when possible. When removal was not feasible, the leader was cut as short as possible with the hook left in the fish (Horodysky *et al*. 2007). The locations of PSAT deployments were determined by the vessel's global positioning system (GPS).

After 10 day at liberty, PSATs released from the monofilament tether and floated to the surface. They then transmitted data to satellites of the ARGOS system for approximately 30 days. PSATs with the Satellite-in-View^{TM} software were preprogrammed to only transmit signals when a satellite was predicted to be above the horizon, minimizing battery usage. Coordinates of pop-up location and real time tracking of floating PSATs were obtained from the ARGOS system online data access. All of the data received by ARGOS was compiled by Microwave Telemetry, Inc. and sent to VIMS. PSATS that were recovered after they had washed ashore were returned to the manufacturer, where all archival data were downloaded.

Analysis

Data collected and archived by the tags included measurements of depth, temperature, and light taken every 90 sec for the 10 days the tags were attached to the marlin. Survival was inferred from the light, depth, and temperature profiles for the 10 days the PSATs were attached to the fish (Figure 1). Surviving fish showed continuous vertical movements as noted by varying pressures (depth), temperatures, and daily patterns of light level fluctuation. Net displacement over the 10-day period was measured for each fish from the geographic coordinates of the PSAT deployment location and the coordinates of the PSAT's location at first transmission of data using ARCGIS (ESRI Inc. 2008). Analysis of variance (ANOVA) tests were used to test for differences in the 10-day displacement between species and among locations for each species. All statistical analyses were performed in the statistical package R (R Development Core Team 2009).

All points of the depth and temperature tracks were simplified into 10 m and 1 °C histogram bins for day and night periods based on times of local sunrise and sunset. A two-sample Kolmogorov-Smirnoff test was used to compare the distributions obtained from histograms to assess species, location, and diel differences in habitat utilization (Horodysky *et al.* 2007). The null hypotheses for these tests were that there were no differences between distributions of time at depth or time at temperature within species, across locations, or between species. Marlin carrying a PSAT act as mobile temperature-depth recorders as they move through the water column. Therefore, pooled temperature-at-depth data from all fish tagged at a location were used to determine a mean sea surface temperature (SST) at each tagging location and determine a relative depth of the thermocline. The estimated thermocline was determined as the depth with the greatest decrease in temperature, generally around 20 °C.

The depth, temperature, and light tracks for each marlin were visually inspected for complete dives. Dives were considered complete if they originated at the surface (within the top 10m) and contained all expected data points (every 90 sec) as a fish moved through the water column and returned to within 10m of to the surface. Each complete dive was given a unique identifier and nine characterization variables were recorded, including: maximum depth, temperature change, total duration, descending time, ascending time, bottom time, wiggle count (the number of ascent/descent occurrences greater than twice the resolution, here 2.7 m), mean wiggle depth, and interdive interval (Figure 2). From these measured variables, the following composite variables were calculated: descent rate, ascent rate, percent bottom time, rate of change in temperature, and skew of ascent and descent. Complete vertical movements were measured from dawn of the second day until the end of the archival period to exclude behaviors possibly associated with recovery from angling stresses.

The mean maximum depth and total number of dives for each individual in day and night periods were determined from the total number of complete dives. To evaluate the diel periodicity, ANOVAs were performed with individual, diel period, and location as factors for both mean maximum depth and number of dives. These tests were conducted separately for blue marlin and white marlin. Student's *t* tests were performed on the maximum depth reached between diel periods for each individual. To reduce type I error, alpha level was reduced to 0.01 for these tests.

Using the variables recorded and calculated for each individual dive, multivariate analyses were used to determine the number of dive types and explore variation in these dive types among location and between species. Principal component analysis (PCA; prcomp in R) was used to simplify the variables into a smaller set of orthogonal factors that characterize dive types (Lesage *et al.* 1999, Baechler *et al.* 2002, Davis *et al.* 2005, Horodysky *et al.* 2007). Variables were log transformed and standardized with a mean of 0 and standard deviation of 1. A VARIMAX rotation was applied to the resulting factors to maximize the correlation of the variables within the factor.

Values for each factor were calculated for each dive based on the contribution of each of the original set of variables to the factors resulting from the PCA. Original variable values were weighted based on their contribution to the principal components for input into the cluster analysis

The orthogonal factors created by PCA were used in hierarchical K-means cluster analyses (kmeans in R) to determine an appropriate number of dive types, develop meaningful groups of dives, determine the number of different dive types, and put each dive into a group (Schreer and Testa 1995, Schreer *et al.* 2001, Horodysky *et al.* 2007). To remove outliers, the dives with the lowest 10% nearest neighbor densities were removed. The hierarchical clustering identified cluster centroids that were then used as seeds in subsequent non-hierarchical K-means clustering (pam in R). New clusters were formed with the closest Euclidian distances, refining the clusters produced previously (Hair *et al.* 1998).

Multivariate analysis of variance (MANOVA) was used to investigate the variation in orthogonal factors and dive types for different locations, diel periods, and between species (Horodysky *et al.* 2007). Due to differences in data recovery rates among PSATS and behaviors among fish, the number of complete dives per fish varied by more than an order of magnitude. To compensate for the wide range in number of dives per fish, means of all dives for a given dive type, diel period, and individual were used for the MANOVA. Dive variables selected by the PCA as explaining the maximum variation in dives were averaged for each individual over diel periods and dive types as defined by the previous cluster analysis. This allowed for each fish to serve as an independent observation (Hair *et al.* 1998, McGarigal *et al.* 2000, Horodysky *et al.* 2007).

RESULTS

Sixty-two blue marlin and 40 white marlin were tagged in five locations in the western Atlantic Ocean. Blue marlin were tagged off Porto Seguro, Brazil (n=9), La Guaira, Venezuela (n=21), Punta Cana, Dominican Republic (n=2), the U.S. Virgin Islands (n=27), and the US Mid-Atlantic (n=3). White marlin were tagged off La Guaira, Venezuela (n=18), Isla Mujeres, Mexico (n=3), and the US Mid-Atlantic (n=19; Table 1). Of these, 57 blue marlin and 36 white marlin survived and carried PSATs for the full 10-day deployment (Figure 1, Table 1). All 102 tags reported, and the average data recovery was 72% (range 18 - 100%; Table 2). Mean recovery rates were higher for blue marlin (80%, range = 18-100%) that for white marlin (62%, range = 44-79%) due to improvements in tag technology available when PSATs were deployed on the former, especially the incorporation of Satellite-in-View^{TM} software that maximized the battery life by relaying data only when a satellite was passing overhead. Mean data recovery rate was 84% when tags that ran aground while transmitting were omitted.

Displacement

The minimum straight-line 10-day (net) displacements were variable among individuals within a location and among locations. The average net displacement for both species combined was 242 km (range 9 to 943 km). The mean net displacement for all blue marlin was 230 km (range 22 km to 747.88 km) and 261 km for white marlin (range 9 to 709 km). The net displacements were not significantly different

(p=0.46) between species. However, there were significant differences (p<0.05) in net displacement among tagging locations for both species (Table 2).

Blue marlin tagged off the US mid-Atlantic had the highest mean net displacement at 733 km (range 547 to 943 km). Two of the three blue marlin tagged moved northeast, generally following the movements of the Gulf Stream, whereas the third moved south, against the prevailing currents (Figure 3). Blue marlin tagged off the US Virgin Islands and Dominican Republic were pooled as Caribbean Sea. The mean displacement in the Caribbean Sea was 258 km (range 20 to 646 km). These marlin radiated in all directions away from the tagging location (Figure 4). The average 10-day displacement of seven blue marlin tagged off Brazil was 212 km (range 19 to 329 km). The fish radiated in all directions away from the tagging sites and the coast (Figure 5). The average 10-day displacement of the blue marlin tagged off Venezuela was 126 km (9 to 336 km; Figure 6). As in the northern Caribbean and Brazil, these blue marlin radiated in all directions away from the tagging location. There was a significant difference ($p < 0.01$) in the minimum 10-day displacements among locations for blue marlin.

White marlin tagged off of Isla Mujeres, Mexico had the highest displacements of all white marlin tagged in this study. All three fish moved north into the Gulf of Mexico with a mean 10-day displacement of 466 km (range 234 to 714 km; Figure 7). White marlin tagged off the US mid-Atlantic had displacements averaging 316 km (range 79 to 748 km). Like the blue marlin tagged off the US mid-Atlantic, their bearing predominantly followed the currents of the Gulf Stream (Figure 3). The white marlin tagged off Venezuela demonstrated more northward movements with a mean displacement of 153 km (range 22 to 296 km; Figure 6). The minimum 10-day displacements for white marlin were significantly different among locations ($p = 0.01$).

Habitat Utilization

Time-at-depth and time-at-temperature histograms of marlin habitat utilization show that both species spent the majority of their time in the warmest waters available (i.e., well within the uniformed temperature surface layer). Blue marlin spent 62% of time in the top 10 m of the water column (Figure 8), and this did not vary significantly by location (p=0.55). Blue marlin tagged in the Caribbean spent the least amount of time in the upper 10 m (56 %, Figure 9), while blue marlin tagged off Brazil spent the highest proportion (69%, Figure 10). Blue marlin tagged off Venezuela and the US mid-Atlantic were intermediate with 66% and 67% of time spent in the upper 10 m, respectively (Figures 11 and 12). Blue marlin showed a secondary peak of higher occurrence at 40 -50 m depth (Figures 8-12). This peak was more pronounced during the day and was centered just shallower than the midpoint between the surface and the depth of the local thermocline.

Overall, white marlin spent significantly less time ($p < 0.05$) in the top 10 m of the water column (56%) than blue marlin (Figure 14). White marlin tagged off Mexico spent the least amount of time in the top 10 m (43%; Figure 15); whereas white marlin tagged off the US mid-Atlantic spent the highest proportion of time at the surface (67%; Figure 17). Those tagged off Venezuela spent 46% in the top 10 m

(Figure 16). Similar to blue marlin, white marlin exhibited a secondary peak at depth at 20 to 40 m in all locations, a shallower depth than blue marlin (Figures 13-17).

Analysis of time-at-temperature-relative to SST histograms indicated that blue marlin and white marlin spent the most time in the warmest waters. Blue marlin spent 65% of time in waters within 1 °C of the mean SST and over 99% of their time in temperatures within 8 °C of mean SST (Figure 18, 19). The proportion of time spent in the warmest water varied significantly with location (p=0.034). Blue marlin tagged off Brazil spent the greatest amount of time within 1 °C of the mean SST (75 %, Figure 20), while blue marlin tagged in the Caribbean Sea spent the lowest proportion (47%, Figure 21). Those tagged off the U.S. Mid-Atlantic and Venezuela were intermediate, spending 65% and 75% (respectively) within 1 °C of the mean SST (Figures 22 and 23).

White marlin spent 51% of time within 1 °C of mean SST and 95% of their time within 8 °C of mean SST (Figure 24). White marlin tagged off Venezuela spent the least amount of time within 1 °C of the mean SST (56%; Figure 25); whereas those tagged off Mexico spent the highest proportion (71%; Figure 27), and those tagged the U.S. Mid-Atlantic an intermediate amount of time 62% (Figure 26). Overall, there was no difference in the amount of time white and blue marlins spent within 1 °C of mean SST (*p*=0.07).

The mean SST was 26 °C off Venezuela, 27 °C off Brazil and the U.S. Mid-Atlantic, and 28 °C off Mexico and in the northern Caribbean Sea. The estimated thermocline depths ranged from the shallowest at 100 m off the U.S. mid-Atlantic, 150 m off Mexico, 150 m off Venezuela, 175 m in the northern Caribbean, and 175-200 m off Brazil (Figure 28).

The two deepest descents recorded for blue marlin were 590 and 561 m by different individuals tagged in the northern Caribbean. All other dives were less than 400 m, but blue marlin from all locations reached depths greater than 300 m. However, 97% of all blue marlin descents terminated at depths less than 200 m. The deepest descent recorded for a white marlin was 282 m by an individual tagged off the U.S. Mid-Atlantic. However, 99.8% of all white marlin descents terminated at less than 200 m.

Diel Patterns

Preliminary visual inspection of individual tracks supported the presence of diel periodicity for some blue marlin, with individuals making deeper dives during the day, and remaining shallower at night (Figure 29). Despite the pronounced pattern exhibited by some individuals; there were no significant differences (p =0.47 and p= 0.48 for white marlin and blue marlin, respectively) between the overall distributions in time at depth or time at temperature between diel periods for either species (Figures 8, 29). However, there were significant differences in the mean number of dives made between day and night periods for blue marlin ($p<0.01$; Table 3).

There were significant differences ($p < 0.01$) in maximum depth between diel periods for 29% of blue marlin (16 of 55 individuals), but only 3% white marlin (1 of 32 individuals). Significant diel differences in maximum depth ($p<0.01$) were seen in blue marlin from all four tagging locations, but this was not the case for white marlin (p=0.35; Table 3). The proportion of individual blue marlin showing significant diel periodicity was 11% off Brazil, 23% off Venezuela, 33% off the U.S. Mid-Atlantic, and 37% in the northern Caribbean. The single white marlin that showed significant diel differences in maximum depths was tagged off Venezuela. Vertical movement data for blue and white marlins were obtained during all moon phases. Individuals tagged at the same location, even on the same day, showed differences in diel patterns; hence moon phase was not related to diel differences in dive patterns.

Dive types

Overall, blue marlin vertical movements appeared more complex than those of white marlin. Visual inspections of blue marlin data revealed 4,228 complete dives with individuals making an average of 45 descents (range 5 – 126 descents) over 10 days. The number of dives varied among individuals and with the proportion of data recovered. The dives of blue marlin were not easily classified into discrete groups (i.e., "U", "V" shaped) as was done for white marlin by Horodysky *et al.* (2007). While some dives could be classified as “U” or “V” shaped, many appeared to have characteristics of both types, or included multiple visits to maximum depth. Time at maximum depth (i.e., bottom time) and rates of descent varied considerably within and among individuals, and it appears classification of dive types into discrete groups is inappropriate for blue marlin.

The variation in dives explained by the nine measured dive variables (total duration, descent time, bottom time, ascent time, maximum depth, change in temperature from the surface, number of wiggles, wiggle depth, and interdive interval) and five composite dive variables (descent rate, ascent rate, % bottom time, rate of change in temperature, and skew of ascent and descent) were investigated through PCA. The first four principal components explained 88% of the variation in dives and show separation into distinct clusters (Figure 30). The variables identified as explaining the most variation from the first four principal components were total duration, bottom time, ascent time, number of wiggles, wiggle depth, interdive interval, skew of ascent and descent, % time ascending, and % time descending. Five of the original 14 dive variables did not describe enough variation to be useful in classifying dives. The nine remaining dive variables were used to cluster the 4,228 dives into two dive types. High values of the agglomerative coefficient indicate joining of two very different clusters and a rapid decrease following the formation of two clusters suggests a two-cluster system. Subsequent visual inspection of dives within the two clusters revealed one cluster containing "simple dives", or standard "U" or "V" shaped dives, while the other contained "complex dives", those incorporating multiple ascents, descents, and plateaus, that preclude classification into simple, "letter shaped" dive types (Figure 31).

Significant differences were observed for blue marlin and white marlin among locations ($p< 0.01$), individuals ($p< 0.01$), diel periods ($p< 0.01$), dive types ($p< 0.01$), and interaction terms for diel period*location ($p< 0.01$), location*species ($p< 0.01$), location*individual ($p< 0.01$), and location*species*individual ($p< 0.01$) for all nine variables combined. When the nine variables were separated, many demonstrated significant differences between diel periods (seven of the nine variables), among locations (eight of the nine), and the interaction between individual and location (six of the nine). Significance of interaction terms limits interpretation of dive types but supports the inability to visually score dives *a priori.*

DISCUSSION

All 102 tags deployed in the study transmitted data to the ARGOS satellites, with only two tags releasing from the fish prematurely. Studies using identical tag models and deployment techniques reported 40 of 41 tags reporting with three premature releases (Horodysky and Graves 2005) and all tags reporting with three premature releases (Graves and Horodysky 2008). Other tag models deployed on striped marlin reported usable data from 66 of 80 tags, but premature releases from 70 of the 80 tags (Domeier et al. 2003). In my study, the lowest data recoveries were for PSATs that washed ashore while transmitting. PSATs that floated with the antennae in an upright position continued to transmit data for about 30 days, at which time the battery was exhausted.

The amount of data recovered from PSAT transmissions varied between species, likely due to differences in tag technology. The tags used on white marlin transmitted continuously once they reached the surface with an average data recovery rate of 62%. Using the same continuously transmitting tags (Microwave Telemetry PTT-100-HR), Horodysky *et al.* (2007) reported similar average data recovery (62%). The tags used for blue marlin incorporated Satellite-in-View^{TM} (SIV) technology. These tags were preprogrammed to only transmit data when an ARGOS satellite was predicted to be above the horizon, reducing battery usage and prolonging data transmission, with a net effect of increasing average recovery rates to 80%.

The number of complete dives measured per individual is directly related to data recovery rates. Data are transmitted in packets of eight sequential data points. As data recovery rates decrease, more dives are missing one or more of the data packets that make up the complete dive and as a result, the number of complete dives declines. The number of dives per individual varied between species, with a mean number of dives per individual for blue marlin 27 and white marlin 17. This variation, however, did not result from a behavioral difference between species, but was due to the differences in data recovery rates between PSATs with and without SIV technology. There was not a significant difference (p=0.66) in the number of dives between species through the overlapping data recovery range (50-85%).

As PSAT technology improves, more options for data collection are available to researchers. An important consideration in tagging studies employing PSATs is the duration of time a PSAT records data while attached to the fish. PSATs programmed to release from the fish after 10 days were used here for two primary reasons. First, the project was part of a study investigating post-release mortality of blue and white marlins caught on circle and J hooks in the recreational fishery. PSATs programmed to release after shorter duration are preferred in survival studies to limit observed mortalities to those that are directly attributable to the capture event, and not to subsequent events (natural or fishery mortality). Second, PSATs programmed to release after 10 days can collect data at higher resolutions (i.e., shorter time increments) than PSATs programmed to remain attached for longer periods. The PSAT model used in this study (Microwave Telemetry PTT-100-HR) can be programmed to record data for up to 30 days. When programmed for 10-day attachment, data are recorded every 90 s, but when programmed to remain attached for 30 days, data are recorded every 270 sec. Data with lower time resolution would not contain sufficient data points to accurately classify short duration dives

(Horodysky *et al.* 2007). PSATs programmed to be deployed for longer than 30 days store data in bins instead of providing actual point measures of depth, temperature, and light. Although still useful for studies of habitat utilization and survival, binned data do not provide information about individual dives and high resolution PSATs are necessary for dive classification studies.

As opposed to PSATs, implantable archival tags provide an opportunity to collect high resolution data over long periods of time, but are limited in their use on billfishes as individuals must be recaptured to recover the tags and download the data. Implantable archival tags have been deployed in tuna with return rates as high as 53.5% (Block *et al.* 2001, Schaefer and Fuller 2005, Schaefer *et al.* 2007, Schaefer and Fuller 2009). However, conventional tags in billfish have an average recovery rate of only 1% (Ortiz *et al.* 2003), so the deployment of implanted archival tags in billfish would likely have a very poor return on time and money invested.

To account for changes in behavior resulting from stresses related to capture, data points from the first day and night following PSAT deployment were not used in my analyses. This time period was considered sufficient to allow for recovery and avoid behaviors directly resulting from capture. Beginning on the second day, vertical movement followed patterns that were typically seen throughout the remainder of the 10-day period (Figure 1). Acoustic tagging studies reported returns to what was considered normal behaviors within hours following release (Yuen *et al.* 1974, Jolley and Irby 1979, Block 1990, Holts and Bedford 1990, Holland *et al.* 1990, Block *et al.* 1992, Brill *et al.* 1993, Pepperell and Davis 1999).

Displacement

Mean 10-day displacements varied among locations, but not between species. The largest displacements for both white and blue marlins were from fish tagged off the U.S. Mid-Atlantic that encountered and moved with the Gulf Stream. The Gulf Stream current varies from 5-150 cm sec^{-1}, and typically averages around 20-40 cm sec^{-1} (Gaskell 1973, Gross 1990). Thus, higher speeds, and larger displacements, of those fish that encountered the Gulf Stream are not unexpected. White marlin tagged off the U.S. Mid-Atlantic that did not follow the Gulf Stream had displacements typical of marlin in other locations. The shortest displacements for both blue marlin and white marlin were from individuals tagged off Venezuela, where some marlin apparently encountered favorable conditions and did not travel far from the tagging site during the 10 days. Other individuals of both species tagged off Venezuela had 10-day displacements typical of those observed at other locations.

Minimum speeds over ground (i.e., calculated from net displacements) ranged from 1 to 109 cm sec^{-1} for blue marlin and 2 - 87 cm sec^{-1} for white marlin. These speeds over ground are absolute minimums, and do not take into account any vertical movements or horizontal straying, and thus are expected to be consistently lower than directly measured swimming speeds (i.e., speed through the water). Blue marlin minimum net speeds calculated in this study were lower than the directly measured swimming speeds of blue marlin (50-150 cm sec^{-1}) using towed impellers and acoustic telemetry (Block et al 1992b). White marlin speed over ground had a larger range than, but encompassed previously calculated speed over ground (15-21 cm sec^{-1}, Horodysky et al 2007).

Habitat utilization

Time at temperature and time at depth histograms show that blue marlin and white marlin spend the majority of time in the warmest water available (i.e., closest to the surface and within the uniformed temperature surface layer). Time at temperature for both species varied by location and with the local thermocline depth. While spending the majority of time within the uniform temperature surface layer, a secondary peak was seen at depths for both species. This peak was around 20 to 40 m depth for white marlin, and slightly deeper (30 to 60 m) for blue marlin tagged at the same location. Mean maximum dive depths from this study (Table 3) and others (Horodysky *et al.* 2007), fall within these secondary peaks. These secondary peaks may be related to depths of high forage abundance, or depths where marlin can most efficiently detect and capture prey. Marlin may have a higher propensity to remain at these depths if they are exhibiting searching or feeding behaviors. Although more pronounced during the day for blue marlin, the peaks were seen during the day and night periods for both species, thus feeding behaviors may continue at all times. Shimose *et al.* (2006) reported a trend towards more empty Pacific blue marlin stomachs in the morning, suggesting limited feeding at night. Although the vast majority of fish's time was spent near the surface, these secondary peaks in proportion of time at depth may be important as depths where blue marlin and white marlin routinely feed and would encounter shallow longline gear (Bigelow *et al.* 2006).

Time at depth and time at temperature data fell within ranges reported in all other tagging studies of blue marlin and white marlin. Previous studies have shown that blue marlin and white marlin spend the vast majority of time in the uniform temperature surface layer, above the thermocline. Habitat utilization consistently varies more with location and local physical water parameters than between species, suggesting some absolutes that control the habitat utilization of billfishes (Yuen *et al.* 1974, Block 1990, Holland *et al.* 1990, Block *et al.* 1992, Graves *et al.* 2002, Kerstetter *et al.* 2003, Prince *et al.* 2005, Prince and Goodyear 2006, Prince *et al.* 2005, Prince and Goodyear 2006, Horodysky *et al.* 2007, Goodyear *et al.* 2008). While depth is easily measured, the temperature of the water occupied relative to the surface temperature may be more appropriate than depth or absolute temperature when classifying habitat utilization. While fish cannot directly sense absolute depths (Bernal *et al.* 2009), tunas do have a very acute sense of temperature change (0.1 °C) (Dizon *et al.* 1974, 1976, Streffel *et al.* 1976). Moreover, temperature directly limits cardiac output and swimming performance in tunas and billfishes (Brill *et al.* 1998). Because temperature at depth varies among locations, relative temperature allows for the incorporation of absolute physiological limits. Here, 99% of blue marlin dives and greater than 95% of white marlin dives stayed within an 8° C temperature change of SST, a physiological threshold that appears to limit the vertical movements of other pelagic fishes (Brill 1994, Brill and Lutcavage 2001). The vertical distribution of this warmest water varied with location, and along with it, the habitat utilized by blue marlin and white marlin. Both species tended to spend a higher proportion of time in the upper 10 m at locations with a shallow thermocline and cooler SST (US

Mid-Atlantic) while spending less time at the surface in locations with a deeper thermocline and warmer SST (Caribbean), a trend reported for white marlin in similar locations (Horodysky *et al.* 2007).

Diel patterns

Diel vertical movement patterns were suggested by preliminary visual inspection of blue marlin data. Significant differences in maximum dive depths were observed in some blue marlin individuals at each location, while only a single white marlin tagged off Venezuela showed diel patterns in the maximum dive depth. Blue marlin are visual predators and have specific adaptations to increase visual functionality (Fritsches *et al.* 2003). However, below some minimum light level threshold, blue marlin visual function must be light limited. Variation in available light at night with lunar period may explain some variation in diel dive patterns. A full moon would provide additional light at night, allowing fish to continue diving to depths at night, weakening diel patterns. The opposite would be expected during the new moon. Both blue marlin and white marlin were tagged in all locations during all moon phases and may explain why no diel patterns in dive behavior were apparent. Evidence of diel differences have been seen in some blue marlin tracking studies with deeper dives occurring during the day (Holland 1990, Block 1992, Kerstetter et al 2003, Goodyear et al 2008); however there has always been high variation within and among individuals (Prince et al. 2006, Kerststter *et al.* 2003). In sum, while present in some instances at all locations, diel patterns in diving behavior are not universal in blue marlin.

In contrast, swordfish and tunas show consistent diel patterns spending days venturing to greater depth and nights within the uniform temperature surface layer, movements that are closely linked to foraging (Carey and Robison, 1981, Brill *et al.* 1999, Sedberry and Loefer 2001, Musyl *et al.* 2003, Markaida and Hochberg 2005). Different species appear to partition the water column into multiple levels, minimizing competitive interactions between the species (Bernal et al 2009). These differences in behaviors are closely linked to physiological differences between species (Brill *et al.* 1999, Brill and Lutcavage 2001, Brill *et al.* 2005, Galli et al. 2009). Physiological differences have not been noted between blue marlin and white marlin due to the difficulty in conducting physiological studies on large billfishes.

There is considerable spatial habitat (horizontal and vertical) overlap between blue marlin and white marlin throughout their ranges and the results of this and other studies provide little evidence for niche partitioning based on habitat. Nakamura (1985) suggested potential ecological exclusion between blue marlin and white marlin, leading to local inverse abundances, but reasons for this are unknown. As both blue marlin and white marlin are opportunistic predators with overlapping ranges and habitat, there is opportunity for competition between the two species. Differences in diving behaviors may act as a mechanism to decrease competition between species (Baechler *et al.* 2002, Austin *et al.* 2006), and could be linked with different foraging strategies in areas of varying marlin densities or prey abundances.

Dive classifications

Attempts to classify dives and assign mechanistic explanations for the patterns have focused on air breathing pinnepeds (Schreer *et al.* 2001), cetaceans (Martin *et al.* 1994), sirenians (Chilvers *et al.* 2004), sea turtles (Fossette *et al.* 2008), and penguins (Wilson *et al.* 1996). Discrete dives can be separated by breathing events as these organisms are physiologically tied to the surface. Similar analyses can be used on fishes that frequently return to the warmest surface waters such as tuna and billfishes (Holland et al. 1992, Musyl *et al.* 2003, Malte *et al.* 2007, Horodysky *et al.* 2007, Wilson and Block 2009). Early studies of air breathing pinnipeds based dive classifications on maximum depth and duration (Kooyman 1968). As tagging technology improved and more data were available, visual classification of dive shapes was possible (Lesage *et al.* 1999, Schreer *et al.* 2001, Baechler *et al.* 2002, Malcolm & Duffus 2000). Biases caused by visually scoring dives can be limited by the use of multivariate statistical techniques to differentiate dives based on a suite of variables (Tinker *et al.* 2007, Schreer & Testa 1995, Baechler *et al.* 2002, Schreer *et al.* 1998). Comparative studies have suggested that manual classification methods may provide better explanations of biological significance than statistical methods to dive type classification (Schreer & Testa 1995, Malcolm & Duffus 2000). Hence, ecological studies have used visual classification to make biological inferences from dive data (Hays *et al.* 2000, Lescroël & Bost 2005, Hassrick *et al.* 2007, Schaefer *et al.* 2007, Elliott *et al.* 2008, Wilson and Block 2009). Several authors have suggested ecological explanations for the standard "U" and "V" dive shapes (Williams & Kooyman 1985, Baechler *et al.* 2002, Horodysky *et al.* 2007, Wilson and Block 2009). "V" shaped dives are typified by rapid descent followed immediately by a rapid ascent. These dives could represent exploratory foraging, traveling while reducing drag, or escaping predators. "U", or square shaped dives, occur when the diver spends extended time at the bottom and are thought to be characteristic of a predator exploiting a food source; whether demersal or limited to a narrow depth range (Lesage *et al.* 1999, Schreer *et al.* 2001, Baechler *et al.* 2002, Horodysky *et al.* 2007).

Statistical methods were used here to classify dives of blue marlin and white marlin. Preliminarily visual inspection classified some "V" and "U" shaped dives. However, most dives were not discretely classified, and would therefore be excluded from analysis (Figure 31). These complex dives included wiggles, hybrid dives, highly skewed dives, among other shapes. Multivariate statistical approaches simplified the original 14 dive variables into a set of nine that explained the greatest proportion of variables. These nine variables classified blue marlin and white marlin dives into two types. Visual inspection of those types did not line up with "U" or "V" dive types. Rather, dives separated into groups based on their complexity. The complex dives, which would be removed from analyses using only "letter shaped" dives with presumptive ecological significance, accounted for more than half of all dive variation (Figure 30) and should be taken into account for future studies of factors that influence diving behaviors. As multivariate techniques for classifying dives are refined, future work should strive to assign behaviors to dive types to make ecological inferences.

Application to HBS

Goodyear *et al.* (2003) reviewed the needs for appropriate incorporation of HBS to CPUE time series for blue marlin in the Atlantic Ocean. Three major areas of research were considered necessary before implementation of HBS to CPUE time series data: fish habitat and behavior, gear behavior, and physical oceanographic conditions. Incorporation of habitat utilization data of blue marlin from the Atlantic Ocean was a major necessity because the Hinton-Nakano analysis used data from nine blue marlin acoustically tracked in the Pacific Ocean up to five days in an area with a shallower thermocline than the locations studies here (Holland *et al.* 1990, Block *et al.* 1992). The findings from this study provide habitat utilization data including time at depth, time at temperature, and time at temperature relative to SST, for blue marlin from the western Atlantic Ocean. The habitat utilized by the blue marlin in this study from the Atlantic Ocean was similar to those of the Pacific Ocean, with most of the time spent within the uniforme temperature surface layer, and very few dives below the thermocline (Holland *et al.* 1990, Block *et al.* 1992). These data support claims that there are set physiological limits that govern the vertical habitat use of large pelagic fishes (Brill and Lutcavage 2001, Bernal *et al.* 2009, Weng *et al.* 2009). The proportion of time spent at depth seen here is similar to that seen in other tracking studies of blue marlin. All blue marlin seem limited by the same temperature range and associated depths, with exceptions in extreme situations (upwelling areas that limit oxygen, spawning areas) (Prince and Goodyear 2006).

This study provides information necessary to apply HBS methods to blue marlin and white marlin assessments. While an Atlantic Ocean wide assessment of blue marlin is planned for 2011 by ICCAT, habitat utilization data (this study and

Horodysky *et al.* 2007) applicable to white marlin stock assessments are now available once issues related to species misidentification with roundscale spearfish are resolved. However, more information is needed regarding the propensity of billfishes to feed at the depths they occupy, as marlin feeding rates may vary with depth. Validation of the ecological significance of dive types and an understanding of how fish behavior is related to time at depth, whether searching, moving, feeding, or escaping predators would help relate dive types with an individual's propensity to feed at various depths where it may encounter fishing gear. The exact position and behavior of longline gear must also be known to determine where marlin might interact with the gear. While billfishes spend the vast majority of time in the upper 10 m of the water column, the gear spends relatively little time in that depth layer except passing through as it is being deployed and hauled back. One must also consider that baits on longline gear are moved through the water during deployment and haulback, possibly increasing the likelihood that marlin will interact with the gear (Goodyear *et al.* 2003). The results of this study emphasize the need to understand local oceanographic conditions and how they could affect the habitat utilization and diving behaviors of blue marlin and white marlin. Clearly, differences in location lead to the greatest differences in behavior and habitat utilization, but there are still many assumptions of the model that need validation. This study provides high resolution data that is useful for implementation of HBS and furthering basic biological information about the physical, physiological, and potentially competitive forces that constrain blue marlin and white marlin habitat utilization and diving behaviors in the western Atlantic Ocean.

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Table 1. Summary information of tagged blue marlin (BUM) and white marlin (WHM) including tagging location, data recovery, survival, and 10-day displacement. Location abbreviations indicate U.S. Mid-Atlantic (Mid Atl), Venezuela (VZ), and northern Caribbean (Carib).

Tag ID	Species	Date Released	Location	Data Recovery	Survival	Displacement (km)
4882	WHM	9-Sep-2005	Mid Atl		N	
24029	WHM	9-Sep-2005	Mid Atl	69%	Y	709.05
24033	WHM	9-Sep-2005	Mid Atl	73%	Y	237.13
24040	WHM	9-Sep-2005	Mid Atl	53%	Y	199.07
24520	WHM	9-Sep-2005	Mid Atl	70%	Y	313.18
24522	WHM	9-Sep-2005	Mid Atl	73%	Y	138.20
35689	WHM	9-Sep-2005	Mid Atl	73%	Y	584.81
40638	WHM	8-Nov-2005	VZ	49%	Y	101.26
41331	WHM	8-Nov-2005	VZ	44%	Y	221.00
40642	WHM	9-Nov-2005	VZ		N	
41334	WHM	9-Nov-2005	VZ	50%	Y	293.44
41329	WHM	10-Nov-2005	VZ	54%	Y	170.69
41330	WHM	13-Nov-2005	VZ	56%	Y	81.78
41332	WHM	13-Nov-2005	VZ	43%	Y	231.34
40641	WHM	31-May-2006	Mexico	63%	Y	714.10
41328	WHM	31-May-2006	Mexico	47%	Y	234.90
62106	WHM	1-Jun-2006	Mexico	76%	Y	449.28
62101	WHM	29-Jul-2006	Mid Atl	71%	Y	747.88
62112	WHM	29-Jul-2006	Mid Atl	74%	Y	428.69
62100	WHM	7-Aug-2006	Mid Atl	70%	Y	422.11
62121	WHM	7-Aug-2006	Mid Atl	79%	Y	124.41
62123	WHM	7-Aug-2006	Mid Atl	75%	Y	78.80
62122	WHM	13-Aug-2006	Mid Atl	74%	Y	290.02
62105	WHM	14-Aug-2006	Mid Atl	66%	Y	91.89
62110	WHM	23-Aug-2006	Mid Atl	59%	Y	122.92
62104	WHM	24-Aug-2006	Mid Atl	69%	Y	105.43
62113	WHM	24-Aug-2006	Mid Atl	64%	Y	475.73
62119	WHM	24-Aug-2006	Mid Atl	64%	Y	475.15
62120	WHM	4-Sep-2006	Mid Atl	70%	Y	141.93
62103	WHM	24-Sep-2006	VZ	57%	Y	28.37
62111	WHM	24-Sep-2006	VZ	54%	Y	179.08
62124	WHM	24-Sep-2006	VZ		N	
62107	WHM	25-Sep-2006	VZ	51%	Y	67.45
62108	WHM	25-Sep-2006	VZ	59%	Y	71.92
62116	WHM	25-Sep-2006	VZ	55%	Y	107.70
62117	WHM	25-Sep-2006	VZ	61%	Y	22.39

Table 1 continued.

Tag ID	Species	Date Released	Location	Data Recovery	Survival	Displacement (km)
62118	WHM	26-Sep-2006	VZ	48%	Y	152.22
62125	WHM	26-Sep-2006	VZ		N	
62114	WHM	30-Oct-2006	VZ	57%	Y	272.49
62109	WHM	8-Nov-2006	VZ	51%	Y	295.91
39800	BUM	7-Sep-2007	VZ	82%	Y	171.69
41333	BUM	17-Mar-2008	VZ	81%	Y	139.30
59081	BUM	28-Mar-2008	Carib	68%	Y	49.12
40644	BUM	29-Mar-2008	Carib	85%	Y	85.62
62113	BUM	14-May-2008	VZ	84%	Y	30.02
24523	BUM	15-May-2008	VZ	85%	Y	9.54
40640	BUM	16-May-2008	VZ	73%	Y	122.61
34233	BUM	17-May-2008	VZ	85%	Y	86.89
36436	BUM	15-Jun-2008	Mid Atl	85%	Y	546.49
35687	BUM	22-Jun-2008	Mid Atl	88%	Y	942.70
62112	BUM	8-Aug-2008	Carib	90%	Y	501.83
41328	BUM	10-Aug-2008	Carib	90%	Y	646.44
59083	BUM	10-Aug-2008	Carib	92%	Y	348.77
62117	BUM	11-Aug-2008	Carib	83%	Y	107.09
62118	BUM	11-Aug-2008	Carib	88%	Y	342.79
40634	BUM	12-Aug-2008	Carib	93%	Y	488.19
62119	BUM	12-Aug-2008	Carib	87%	Y	327.53
36435	BUM	17-Aug-2008	Mid Atl	90%	Y	708.71
84343	BUM	7-Sep-2008	Carib	91%	Y	190.72
84344	BUM	7-Sep-2008	Carib	68%	Y	20.07
84345	BUM	7-Sep-2008	Carib	92%	Y	318.82
84346	BUM	8-Sep-2008	Carib	90%	Y	120.40
84347	BUM	9-Sep-2008	Carib	93%	Y	237.90
84348	BUM	10-Sep-2008	Carib	72%	Y	68.10
84349	BUM	10-Sep-2008	Carib	88%	Y	264.13
84350	BUM	11-Sep-2008	Carib		N	
84351	BUM	11-Sep-2008	Carib	100%	Y	196.87
84352	BUM	15-Sep-2008	Carib	92%	Y	234.20
62116	BUM	25-Sep-2008	VZ	90%	Y	13.06
84341	BUM	2-Nov-2008	Brazil	85%	Y	118.67
62115	BUM	2-Nov-2008	VZ	84%	Y	336.33
84340	BUM	3-Nov-2008	VZ	94%	Y	170.78

Table 1 continued.

Tag ID	Species	Date Released	Location	Data Recovery	Survival	Displacement (km)
84354	BUM	4-Nov-2008	Brazil	74%	Y	283.76
62111	BUM	15-Nov-2008	VZ	18%	Y	262.85
62114	BUM	17-Nov-2008	VZ	87%	Y	135.08
84342	BUM	22-Nov-2008	VZ	79%	Y	114.79
84365	BUM	30-Nov-2008	VZ	86%	Y	83.43
84355	BUM	2-Dec-2008	Brazil		N	
84356	BUM	2-Dec-2008	Brazil	36%	Y	288.81
84362	BUM	9-Dec-2008	VZ	81%	Y	226.14
84339	BUM	9-Dec-2008	VZ	90%	Y	118.03
4869	BUM	9-Dec-2008	VZ		N	
35688	BUM	11-Dec-2008	VZ	83%	Y	106.61
84357	BUM	11-Dec-2008	Brazil	85%	Y	218.43
84358	BUM	13-Dec-2008	Brazil	90%	Y	232.65
84359	BUM	13-Dec-2008	Brazil	91%	Y	215.97
84361	BUM	2-Jan-2009	Brazil	88%	Y	19.24
84364	BUM	2-Jan-2009	Brazil	94%	Y	329.44
40641	BUM	7-Feb-2009	VZ	26%	Y	123.52
59080	BUM	18-Apr-2009	VZ	85%	Y	95.58
24527	BUM	6-May-2009	VZ	57%	Y	87.58
40637	BUM	9-May-2009	VZ	64%	Y	90.09
84366	BUM	6-Jul-2009	Carib		N	
41327	BUM	6-Jul-2009	Carib	80%	Y	196.00
40636	BUM	9-Jul-2009	Carib	86%	Y	143.47
40643	BUM	1-Aug-2009	Carib	38%	Y	109.47
24059	BUM	8-Aug-2009	Carib	31%	Y	378.60
84353	BUM	30-Aug-2009	Carib		N	
84337	BUM	2-Sep-2009	Carib	98%	Y	214.05
84338	BUM	4-Sep-2009	Carib	99%	Y	462.69
84363	BUM	30-Sep-2009	Carib	95%	Y	270.89
84360	BUM	7-Oct-2009	Carib	48%	Y	385.36

Table 2. Summary of 10-day displacement and data recovery for blue marlin (BUM) and white marlin (WHM) by location, displacement and % data recovery.

Species	Tagging Location	N	Mean displacement (km)	Range (km)	Mean data recovery (%)	Range (%)
BUM	Brazil	8	213.37	19.24-329.44	80.38	36-94
BUM	Northern Caribbean	26	258.04	20.07-646.44	82.00	31-100
BUM	Mid-Atlantic US	3	732.63	546.49-942.70	87.67	85-90
BUM	Venezuela	20	126.20	9.54-139.30	75.70	18-94
BUM	all	57	230.49	9.54-942.70	80.00	18-100
WHM	Mid-Atlantic US	18	315.91	78.80-747.88	69.22	53-79
WHM	Mexico	3	466.09	234.90-714.10	62.00	47-76
WHM	Venezuela	15	153.14	22.39-295.91	53.00	43-61
WHM	all	36	260.61	22.39-747.88	62.00	43-79
both	Mid-Atlantic US	21	375.44	78.80-942.70	72.00	53-90
both	Venezuela	35	137.74	9.54-336.33	66.00	18-61
both	all	93	242.15	9.54-942.70	71.78	18-100

Table 3. Mean values of all measured dive variables for each individual by species, locations (Mid-Atl= U.S. Mid Atlantic), and diel period.

Fish #	Species	Location	Diel Period	Complete dives	Duration (min)	Descent (min)	Bottom (min)	Ascent (min)	Interdive interval (min)	Max Depth (m)	Δ t (°C)	Wiggles	Wiggle depth (m)
84341	blue	Brazil	Day	12	48.33	10.83	27.42	10.25	25.50	70.27	2.71	1.08	10.83
84341	blue	Brazil	Night	18	29.89	10.44	6.89	12.56	13.60	62.23	2.08	0.17	10.00
84354	blue	Brazil	Day	3	30.00	10.67	5.33	14.00	42.00	49.80	1.63	0.00	
84354	blue	Brazil	Night	2	15.00	2.50	3.00	9.50		49.75	0.70	0.00	
84356	blue	Brazil	Day	29	57.93	13.45	30.10	14.10	33.15	112.17	2.94	0.69	26.67
84356	blue	Brazil	Night	13	59.54	11.15	31.00	16.46	36.00	83.03	1.58	1.00	31.00
84357	blue	Brazil	Day	25	44.32	14.68	8.48	21.20	53.90	94.99	3.57	0.08	57.50
84357	blue	Brazil	Night	18	24.94	9.28	2.56	13.11	79.00	69.40	1.76	0.00	
84358	blue	Brazil	Day	85	26.48	11.58	3.42	11.38	20.05	100.89	4.58	0.12	34.29
84358	blue	Brazil	Night	4	19.00	4.00	4.25	10.75	22.00	106.58	5.23	0.00	
84359	blue	Brazil	Day	15	61.60	19.20	24.93	17.47	34.77	90.65	3.43	0.33	30.00
84359	blue	Brazil	Night	7	33.57	9.00	8.43	16.86	29.40	64.23	2.01	0.00	
84361	blue	Brazil	Day	23	43.26	11.87	12.83	18.48	36.81	93.43	3.36	0.22	17.50
84361	blue	Brazil	Night	10	42.90	8.40	9.70	24.80	67.83	92.93	3.68	0.50	21.67
84364	blue	Brazil	Day	25	29.68	9.04	1.16	19.28	73.75	99.47	4.39	0.12	28.33
84364	blue	Brazil	Night	12	55.42	8.67	20.75	26.00	74.44	87.65	3.02	0.42	26.67
24059	blue	Caribbean	Night	17	45.68	10.82	16.68	17.00	53.30	94.30	3.85	1.07	28.50
24059	blue	Caribbean	Day	17	54.00	13.18	26.06	14.76	40.43	107.02	4.14	1.31	35.00
40634	blue	Caribbean	Day	43	65.93	21.56	29.56	14.74	9.53	121.07	4.44	1.35	26.60
40634	blue	Caribbean	Night	13	43.15	13.38	11.62	18.15	43.00	105.02	3.73	0.38	20.00
40636	blue	Caribbean	Day	42	40.26	10.88	19.86	9.52	19.49	51.66	1.04	0.40	15.50
40636	blue	Caribbean	Night	15	21.53	7.67	3.07	10.80	71.78	63.29	2.82	0.00	
40638	blue	Caribbean	Day	12	23.58	8.08	9.17	6.33	8.25	65.17	3.88	0.08	20.00
40638	blue	Caribbean	Night	1	39.00	4.00	33.00	2.00	4.00	91.50	3.90	0.00	
40643	blue	Caribbean	Day	2	16.50	6.00	0.50	10.00		65.25	2.20	0.00	
40643	blue	Caribbean	Night	5	20.20	7.40	7.40	5.40	9.50	59.72	2.14	0.00	
40644	blue	Caribbean	Day	35	21.51	7.71	5.80	8.17	42.47	46.81	0.07	0.29	20.00
40644	blue	Caribbean	Night	11	16.45	6.45	0.27	9.73	84.60	73.16	0.07	0.00	
41327	blue	Caribbean	Day	23	35.43	11.87	9.09	15.70	55.72	149.48	6.17	0.13	37.50
41327	blue	Caribbean	Night	21	30.57	11.00	5.24	15.05	57.43	129.03	5.85	0.14	56.67

Table 3. Continued.

Fish #	Species	Location	Diel Period	Complete dives	Duration (min)	Descent (min)	Bottom (min)	Ascent (min)	Interdive interval (min)	Max Depth (m)	Δ t (°C)	Wiggles	Wiggle depth (m)
41328	blue	Caribbean	Day	10	66.20	26.80	6.30	34.10	34.67	140.27	6.01	0.10	15.00
41328	blue	Caribbean	Night	41	39.98	12.39	10.02	18.29	28.63	71.19	3.36	0.07	13.33
59083	blue	Caribbean	Day	41	71.79	16.05	33.92	23.67	8.17	110.52	4.15	2.38	19.52
59083	blue	Caribbean	Night	11	38.00	10.91	19.73	8.00	14.67	87.16	2.56	1.27	27.50
62112	blue	Caribbean	Day	24	76.58	15.25	29.96	15.42	25.28	114.42	4.23	2.00	23.35
62112	blue	Caribbean	Night	21	28.10	6.14	13.43	8.00	32.47	50.01	11.25	0.05	2.50
62117	blue	Caribbean	Day	11	32.55	9.45	19.27	3.82	3.67	61.85	1.85	2.64	13.89
62117	blue	Caribbean	Night	22	38.18	9.77	19.05	9.36	11.33	97.87	3.24	2.23	20.00
62118	blue	Caribbean	Day	51	39.57	10.45	16.27	12.82	7.64	70.14	1.95	0.39	23.18
62118	blue	Caribbean	Night	19	21.74	9.89	2.21	9.63	46.67	54.71	1.37	0.05	15.00
62119	blue	Caribbean	Day	55	39.73	6.13	26.44	8.75	11.13	58.25	1.49	1.04	22.78
62119	blue	Caribbean	Night	34	31.24	8.35	10.44	12.44	42.90	74.49	2.39	0.41	18.57
84337	blue	Caribbean	Day	91	33.82	8.00	18.46	6.24	6.84	58.85	1.54	0.84	19.70
84337	blue	Caribbean	Night	25	47.28	9.20	19.40	18.56	58.61	68.82	2.80	0.28	20.00
84338	blue	Caribbean	Day	59	49.97	12.86	15.10	21.41	32.23	110.49	4.33	0.12	23.75
84338	blue	Caribbean	Night	53	33.42	8.25	4.19	14.43	30.08	70.84	2.60	0.11	23.33
84343	blue	Caribbean	Day	49	47.31	11.39	24.88	11.02	17.29	88.75	1.93	0.88	30.00
84343	blue	Caribbean	Night	26	40.27	10.08	9.23	22.12	59.65	116.77	3.87	0.15	73.75
84344	blue	Caribbean	Day	9	48.44	15.78	15.33	17.33	50.67	131.67	4.68	0.44	41.67
84344	blue	Caribbean	Night	4	29.50	14.75	0.50	14.25	24.00	105.90	3.28	0.00	
84345	blue	Caribbean	Day	96	37.96	7.81	23.35	6.91	7.74	63.23	1.78	0.95	24.23
84345	blue	Caribbean	Night	26	15.31	5.77	1.19	8.35	52.73	61.97	1.80	0.00	
84346	blue	Caribbean	Day	4	22.25	10.75	1.25	10.25	46.00	68.93	1.33	0.00	
84346	blue	Caribbean	Night	23	30.17	10.61	7.13	12.22	83.92	88.53	3.17	0.13	27.50
84347	blue	Caribbean	Day	62	35.35	10.21	16.97	8.29	13.85	77.35	2.33	0.37	31.67
84347	blue	Caribbean	Night	15	28.00	9.47	1.13	17.40	55.64	109.39	4.22	0.00	
84348	blue	Caribbean	Day	8	37.25	13.63	4.38	19.00	17.00	128.06	5.01	0.13	35.00
84348	blue	Caribbean	Night	10	22.80	8.20	2.10	10.50	81.00	78.23	2.93	0.00	
84349	blue	Caribbean	Day	25	34.00	12.16	7.08	14.76	56.13	100.76	4.28	0.24	28.33
84349	blue	Caribbean	Night	15	38.60	6.73	11.53	20.33	88.89	74.67	3.19	0.20	18.33

Table 3. Continued.

Fish #	Species	Location	Diel Period	Complete dives	Duration (min)	Descent (min)	Bottom (min)	Ascent (min)	Interdive interval (min)	Max Depth (m)	Δ t (°C)	Wiggles	Wiggle depth (m)
84351	blue	Caribbean	Day	49	63.33	20.55	19.98	22.63	11.38	113.82	4.10	0.57	39.12
84351	blue	Caribbean	Night	47	33.32	10.34	8.83	14.17	12.79	68.81	2.58	0.17	32.00
84352	blue	Caribbean	Day	12	39.00	11.42	0.83	26.75	98.43	112.97	3.98	0.00	
84352	blue	Caribbean	Night	23	39.13	8.61	8.74	21.78	67.42	76.78	2.62	0.17	26.67
84360	blue	Caribbean	Day	70	36.96	9.93	15.90	11.11	16.09	86.56	2.36	0.76	28.15
84360	blue	Caribbean	Night	19	28.95	8.21	8.42	12.21	16.42	72.57	2.16	0.16	35.00
84363	blue	Caribbean	Day	17	45.47	18.76	3.24	23.53	69.45	245.94	9.18	0.06	65.00
84363	blue	Caribbean	Night	15	30.73	13.07	1.67	16.00	94.22	120.36	4.51	0.13	22.50
35687	blue	Mid-Atl	Day	33	66.64	8.73	49.33	7.48	9.48	87.02	2.17	2.30	16.43
35687	blue	Mid-Atl	Night	18	29.22	7.22	11.83	9.50	27.54	55.49	1.18	0.61	10.00
36435	blue	Mid-Atl	Day	16	45.50	13.50	18.69	12.31	25.00	79.66	7.43	0.69	11.00
36435	blue	Mid-Atl	Night	2	13.50	3.50	3.50	6.50		40.35	3.05	0.00	
36436	blue	Mid-Atl	Day	47	44.87	11.70	18.02	14.40	24.75	97.93	16.27	0.72	14.38
36436	blue	Mid-Atl	Night	17	34.06	6.18	16.88	10.41	18.63	46.62	2.05	0.29	7.50
24523	blue	Venezuela	Day	97	19.01	4.53	10.72	3.52	7.02	47.80	1.05	1.19	14.29
24523	blue	Venezuela	Night	29	15.11	2.89	7.03	5.32	30.29	49.26	1.24	0.18	10.00
24527	blue	Venezuela	Day	16	18.50	7.75	5.38	5.94	12.40	59.73	1.55	0.31	11.67
24527	blue	Venezuela	Night	16	17.06	6.13	5.06	5.81	15.00	45.88	1.01	0.13	25.00
34233	blue	Venezuela	Day	52	23.33	4.37	15.21	3.92	7.45	29.98	1.46	0.73	8.25
34233	blue	Venezuela	Night	11	23.55	3.45	14.18	6.18	29.50	30.50	1.30	0.27	5.00
35688	blue	Venezuela	Day	31	36.06	7.39	20.35	8.39	27.83	60.04	2.17	0.55	17.00
35688	blue	Venezuela	Night	28	28.82	8.00	5.46	15.36	30.55	65.91	2.45	0.36	23.75
39800	blue	Venezuela	Day	46	26.30	10.39	5.17	10.37	26.60	87.04	5.49	0.04	12.50
39800	blue	Venezuela	Night	29	19.80	5.56	1.96	12.48	46.71	74.75	3.97	0.16	17.50
40637	blue	Venezuela	Day	61	21.34	6.18	8.33	6.74	32.20	44.20	1.06	0.28	12.78
40637	blue	Venezuela	Night	31	14.71	3.71	3.19	7.81	54.70	45.99	0.91	0.00	
40640	blue	Venezuela	Day	22	25.59	5.82	12.23	7.55	27.76	46.35	0.71	0.27	20.83
40640	blue	Venezuela	Night	22	15.50	5.68	0.82	9.00	44.79	53.05	1.49	0.00	
40641	blue	Venezuela	Day	3	16.67	3.67	9.67	3.33	27.00	39.90	0.40	0.33	10.00
41333	blue	Venezuela	Day	37	23.97	5.11	12.70	6.11	34.15	57.01	1.05	0.46	17.00

Table 3. Continued.

Fish #	Species	Location	Diel Period	Complete dives	Duration (min)	Descent (min)	Bottom (min)	Ascent (min)	Interdive interval (min)	Max Depth (m)	Δ t (°C)	Wiggles	Wiggle depth (m)
41333	blue	Venezuela	Night	57	24.02	6.61	8.05	9.37	41.96	65.59	1.75	0.16	22.22
59080	blue	Venezuela	Day	40	38.28	10.88	17.18	10.15	14.63	99.53	4.13	0.45	59.55
59080	blue	Venezuela	Night	7	13.14	4.14	3.00	6.00	30.40	43.80	0.40	0.00	
62111	blue	Venezuela	Night	1	10.00	2.00	0.00	8.00		67.20	2.00	0.00	
62114	blue	Venezuela	Day	36	23.72	5.64	11.17	6.94	24.86	50.25	2.21	1.08	11.84
62114	blue	Venezuela	Night	16	15.31	4.75	2.63	7.94	28.00	64.23	2.94	0.19	16.67
62115	blue	Venezuela	Day	20	41.10	9.00	15.10	14.65	33.67	97.71	5.63	0.75	20.00
62115	blue	Venezuela	Night	28	31.75	7.57	8.18	15.57	27.86	64.26	3.51	0.57	8.13
62116	blue	Venezuela	Day	65	36.18	14.31	14.35	7.08	11.00	75.42	4.16	1.68	20.95
62116	blue	Venezuela	Night	49	27.49	9.27	6.57	11.69	38.81	77.28	4.57	0.16	20.00
84339	blue	Venezuela	Day	42	26.76	6.81	10.50	9.74	46.54	53.85	1.50	0.29	18.57
84339	blue	Venezuela	Night	25	20.60	5.96	5.68	9.00	79.17	61.47	2.10	0.08	17.50
84342	blue	Venezuela	Day	26	35.69	11.77	3.96	19.58	55.38	148.27	6.42	0.12	25.00
84342	blue	Venezuela	Night	12	15.58	5.00	1.58	9.00	72.25	49.99	1.94	0.00	
84362	blue	Venezuela	Day	11	24.00	5.82	4.09	13.91	32.75	46.45	0.50	0.00	
84362	blue	Venezuela	Night	17	38.47	6.65	10.59	21.18	54.29	57.94	0.96	0.18	17.50
84365	blue	Venezuela	Day	25	21.08	9.88	2.40	8.76	36.81	65.95	2.44	0.20	20.00
84365	blue	Venezuela	Night	35	23.14	6.29	2.00	14.34	33.30	67.79	2.82	0.14	18.00
59081	blue	Caribbean	Day	15	29.47	6.93	8.13	14.53	37.75	102.66	1.07	0.13	55.00
59081	blue	Caribbean	Night	17	19.41	6.29	2.06	10.94	50.75	84.01	0.79	0.06	10.00
84340	blue	Venezuela	Day	48	67.96	20.17	33.15	14.65	9.73	90.78	3.35	0.48	33.67
84340	blue	Venezuela	Night	18	19.67	6.22	0.72	13.28	109.46	68.88	2.69	0.00	
24029	white	Mid-Atl	Day	24	38.08	8.25	13.79	5.00	3.45	37.38	0.89	0.96	13.85
24029	white	Mid-Atl	Night	43	25.58	6.16	12.21	6.67	25.08	41.40	1.72	0.40	11.93
24033	white	Mid-Atl	Day	29	38.31	4.83	21.41	5.41	9.65	39.38	1.64	1.31	9.23
24033	white	Mid-Atl	Night	12	44.25	9.42	21.08	13.42	16.70	58.73	2.24	0.17	5.00
24520	white	Mid-Atl	Day	49	30.78	6.78	19.39	4.55	8.50	41.62	3.44	2.31	16.56
24520	white	Mid-Atl	Night	30	22.83	5.67	9.93	7.90	16.31	35.84	2.42	1.00	15.00
24522	white	Mid-Atl	Day	36	45.94	5.78	33.92	6.31	31.56	40.12	3.81	0.75	14.38
24522	white	Mid-Atl	Night	22	33.79	7.17	20.54	7.33	22.55	47.91	4.63	0.91	18.75

Table 3. Continued.

Fish #	Species	Location	Diel Period	Complete dives	Duration (min)	Descent (min)	Bottom (min)	Ascent (min)	Interdive interval (min)	Max Depth (m)	Δ t (°C)	Wiggles	Wiggle depth (m)
35689	white	Mid-Atl	Day	34	42.74	5.91	32.62	4.21	22.58	44.93	1.79	1.03	22.27
35689	white	Mid-Atl	Night	16	21.44	7.94	7.75	5.75	34.91	92.39	0.97	0.25	11.67
62100	white	Mid-Atl	Day	31	17.97	4.16	10.19	3.65	16.62	37.62	3.67	0.06	10.00
62100	white	Mid-Atl	Night	9	18.00	3.00	9.33	5.67	28.33	27.04	3.28	0.00	
62104	white	Mid-Atl	Day	33	19.88	5.64	9.06	6.03	18.84	37.07	3.66	0.27	16.00
62104	white	Mid-Atl	Night	15	22.60	4.00	6.47	12.13	32.42	42.45	4.89	0.00	
62105	white	Mid-Atl	Day	16	16.88	6.38	5.44	5.06	15.08	63.73	9.58	0.13	15.00
62105	white	Mid-Atl	Night	1	12.00	3.00	0.00	9.00		32.30	10.50	0.00	
62110	white	Mid-Atl	Day	34	21.38	5.79	8.00	7.59	6.70	36.74	3.97	0.32	16.43
62110	white	Mid-Atl	Night	19	18.37	5.68	5.32	7.37	22.30	34.49	3.64	0.00	
62112	white	Mid-Atl	Day	31	23.58	5.87	10.10	7.61	17.85	31.31	5.10	0.10	17.50
62112	white	Mid-Atl	Night	14	23.43	7.21	4.79	11.43	27.86	32.28	5.76	0.00	
62113	white	Mid-Atl	Day	9	19.67	3.44	12.89	3.33	47.75	27.19	4.60	0.22	15.00
62113	white	Mid-Atl	Night	5	44.00	4.80	33.80	5.80	19.00	39.00	7.00	0.60	15.00
62119	white	Mid-Atl	Day	12	25.92	6.58	9.83	9.75	32.50	37.66	4.70	0.08	15.00
62119	white	Mid-Atl	Night	12	22.42	4.25	5.25	12.92	17.40	30.49	3.54	0.00	
62120	white	Mid-Atl	Day	3	19.00	5.67	8.33	5.00	2.00	29.60	2.10	0.00	
62120	white	Mid-Atl	Night	13	16.00	3.69	7.23	5.08	6.43	26.70	0.72	0.00	
62121	white	Mid-Atl	Day	6	13.50	5.00	0.67	7.83	17.50	30.50	6.35	0.00	
62121	white	Mid-Atl	Night	8	16.63	4.38	1.00	11.25	11.75	27.41	6.10	0.00	
62122	white	Mid-Atl	Day	60	19.37	5.83	8.42	4.92	8.58	26.46	2.85	0.02	15.00
62122	white	Mid-Atl	Night	10	20.70	8.10	5.20	7.30	36.00	30.12	4.96	0.00	
62123	white	Mid-Atl	Day	3	24.67	17.67	1.33	5.67	29.00	29.60	6.70	0.00	
62123	white	Mid-Atl	Night	11	19.73	4.82	6.27	8.64	21.14	25.56	8.34	0.00	
40641	white	Mexico	Day	7	28.14	11.43	6.14	10.57	21.75	107.54	4.37	0.14	20.00
40641	white	Mexico	Night	7	23.86	8.29	2.71	12.43	43.00	114.31	3.11	0.00	
41328	white	Mexico	Day	4	21.50	7.00	8.00	6.50	9.33	75.33	6.83	0.00	
41328	white	Mexico	Night	4	19.25	7.75	4.50	7.00	9.00	80.00	2.78	0.00	
62106	white	Mexico	Day	21	38.05	4.05	19.95	5.43	13.88	40.87	4.20	0.81	9.44
62106	white	Mexico	Night	34	24.41	6.32	11.62	6.50	14.57	41.09	3.56	0.41	13.33

Table 3. Continued

Fish #	Species	Location	Diel Period	Complete dives	Duration (min)	Descent (min)	Bottom (min)	Ascent (min)	Interdive interval (min)	Max Depth (m)	Δ t (°C)	Wiggles	Wiggle depth (m)
41329	white	Venezuela	Day	16	20.19	5.06	10.81	4.31	5.89	61.26	3.01	0.25	15.00
41329	white	Venezuela	Night	10	25.50	4.60	12.20	8.60	16.67	58.84	3.24	0.20	15.00
41330	white	Venezuela	Day	11	21.82	7.73	7.09	6.82	3.50	57.78	2.69	0.00	
41330	white	Venezuela	Night	17	19.76	5.76	4.76	9.12	3.00	52.02	14.29	0.00	
41331	white	Venezuela	Day	10	16.90	4.50	6.30	6.10	19.60	61.59	4.08	0.20	22.50
41331	white	Venezuela	Night	5	32.60	5.60	15.00	12.00	14.00	63.74	4.76	0.00	
41332	white	Venezuela	Day	8	15.00	5.13	5.50	4.75	3.00	59.40	2.25	0.38	27.50
41332	white	Venezuela	Night	1	25.00	3.00	19.00	3.00		96.80	4.00	0.00	
41334	white	Venezuela	Day	15	17.67	6.33	6.73	4.60	7.67	58.70	2.01	0.33	17.50
41334	white	Venezuela	Night	5	34.00	12.80	12.20	11.00	16.50	73.16	5.68	0.00	
62103	white	Venezuela	Day	26	19.81	8.62	3.08	7.88	17.63	89.40	5.38	0.12	21.67
62103	white	Venezuela	Night	15	24.53	7.07	7.20	10.27	27.25	73.89	4.52	0.07	70.00
62107	white	Venezuela	Day	27	15.26	6.48	2.78	6.19	21.48	48.77	2.62	0.00	
62107	white	Venezuela	Night	7	21.14	6.57	3.57	10.86	35.00	61.01	4.51	0.00	
62108	white	Venezuela	Day	26	20.31	6.69	6.58	7.04	22.27	70.15	4.92	0.00	
62108	white	Venezuela	Night	18	29.67	5.06	7.39	17.33	29.50	73.51	4.78	0.00	
62109	white	Venezuela	Day	11	19.82	9.27	1.27	9.27	35.86	91.32	5.45	0.18	25.00
62109	white	Venezuela	Night	13	27.31	8.31	5.15	13.85	19.60	110.19	6.30	0.00	
62114	white	Venezuela	Day	7	26.57	9.43	5.00	12.14	25.33	53.84	7.61	0.00	
62114	white	Venezuela	Night	1	27.00	9.00	0.00	18.00		35.00	4.70	0.00	
62116	white	Venezuela	Day	17	23.41	9.00	0.88	13.53	60.40	96.49	6.91	0.00	
62116	white	Venezuela	Night	5	43.40	16.80	4.60	20.80	30.50	130.70	9.72	0.00	
62117	white	Venezuela	Day	27	24.19	8.78	4.11	10.74	19.25	57.74	6.14	0.00	
62117	white	Venezuela	Night	22	22.59	7.77	3.23	11.59	20.45	49.69	5.40	0.05	15.00
62118	white	Venezuela	Day	16	18.50	6.69	4.56	7.25	18.67	40.94	3.81	0.06	20.00
62118	white	Venezuela	Night	6	23.00	8.83	2.50	11.67	6.00	57.60	7.60	0.00	

Figure 1. Dive profiles showing depth and temperatures for blue marlin that survived (top) and perished following release (bottom). Grey shaded regions represent nighttime.

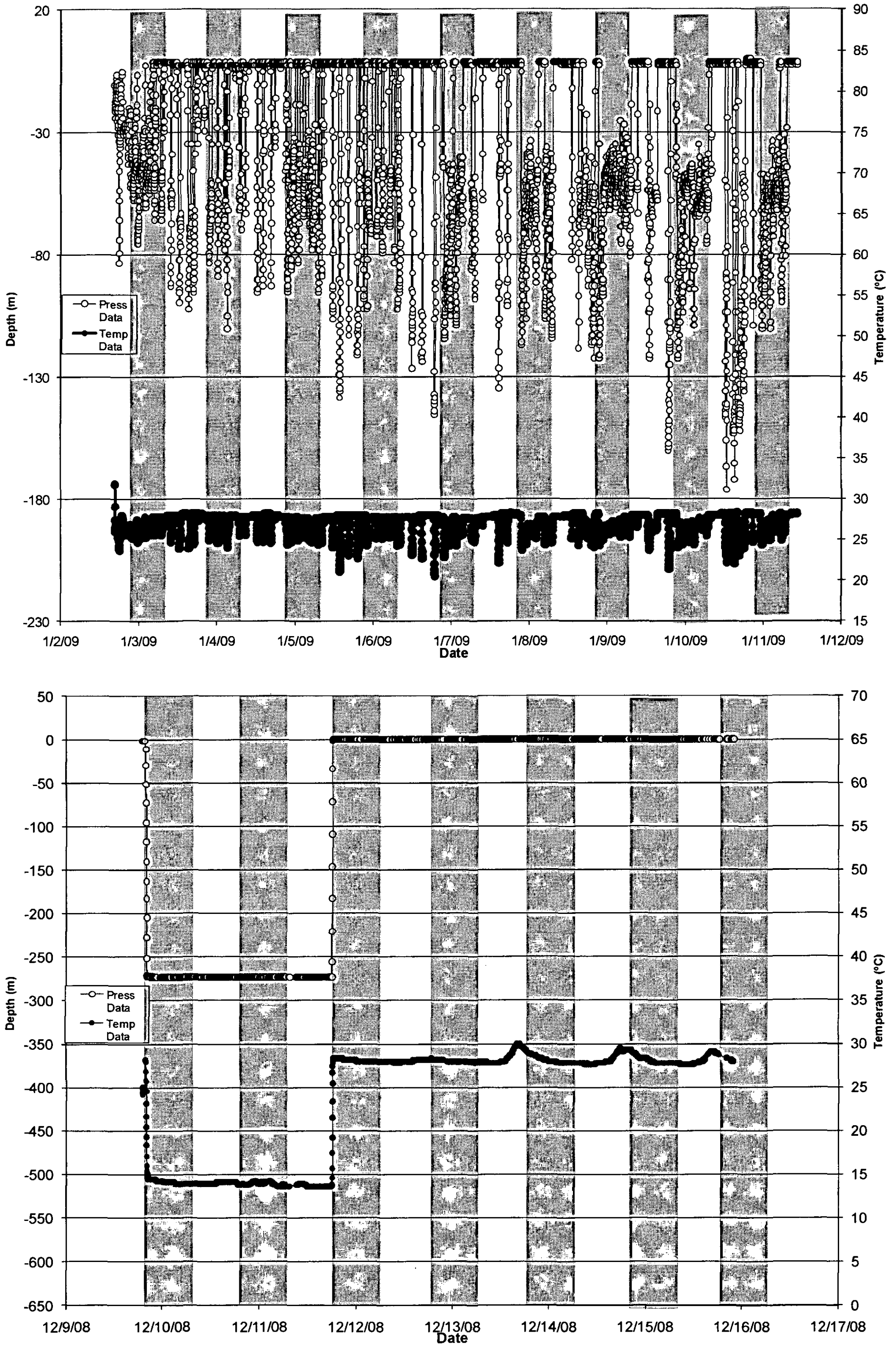


Figure 2. Representative dive demonstrating measured variables: total duration (minutes, A), interdive interval (minutes, B), wiggle depth (m, C), maximum depth (m, D), descent duration (minutes, E), bottom duration (minutes, F), and ascent duration (minutes, G).

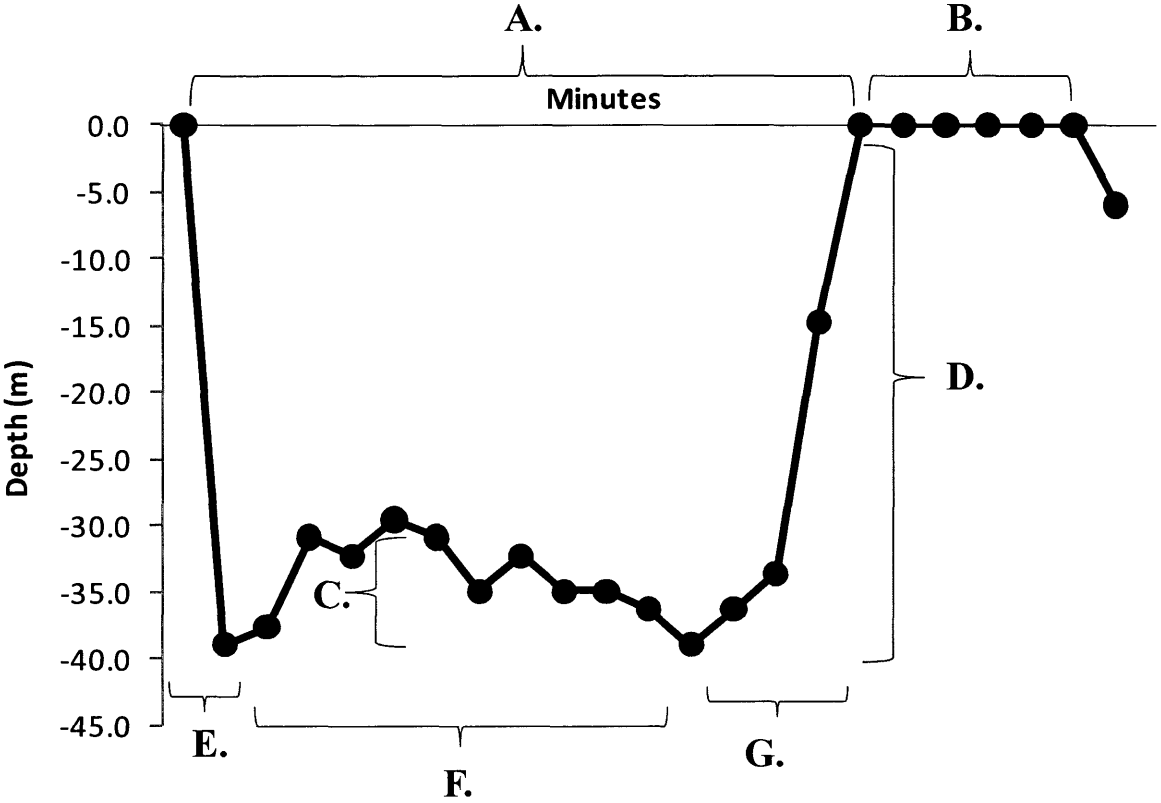


Figure 3. Minimum straight line displacements of blue marlin (BUM) and white marlin (WHM) tagged off the U.S. Mid-Atlantic Coast.

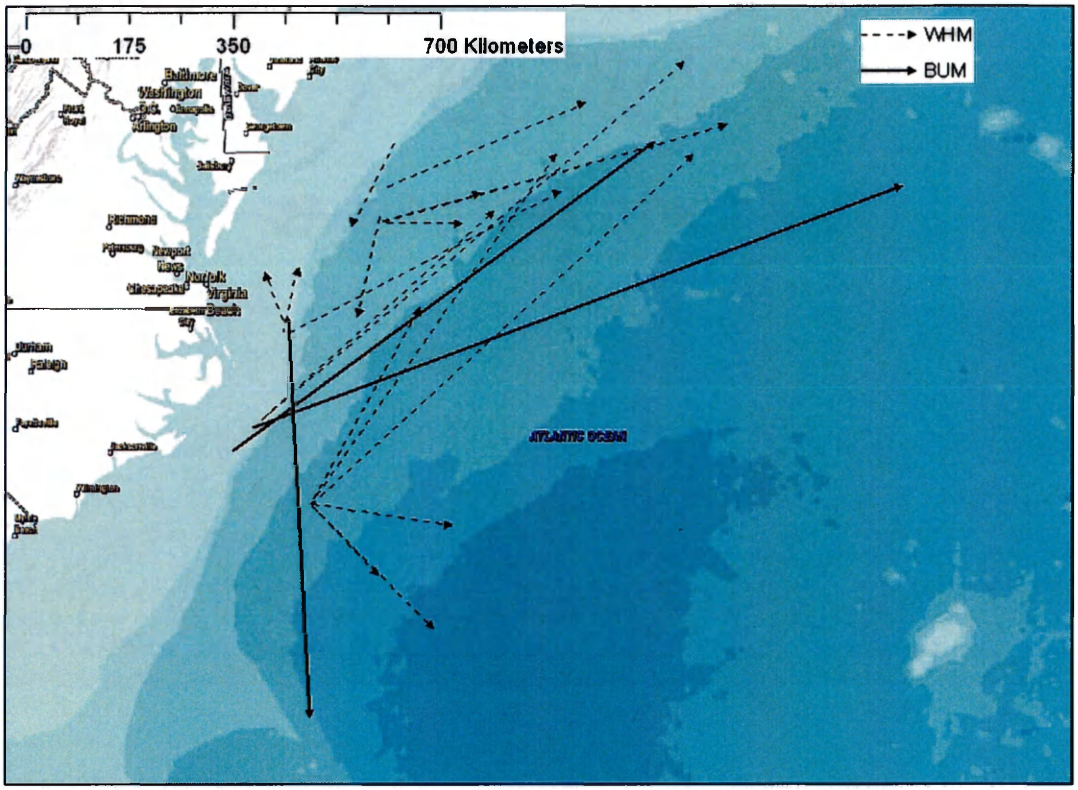


Figure 4. Minimum straight line displacements of blue marlin (BUM) tagged off the U.S. Virgin Islands and Dominican Republic in the northern Caribbean.

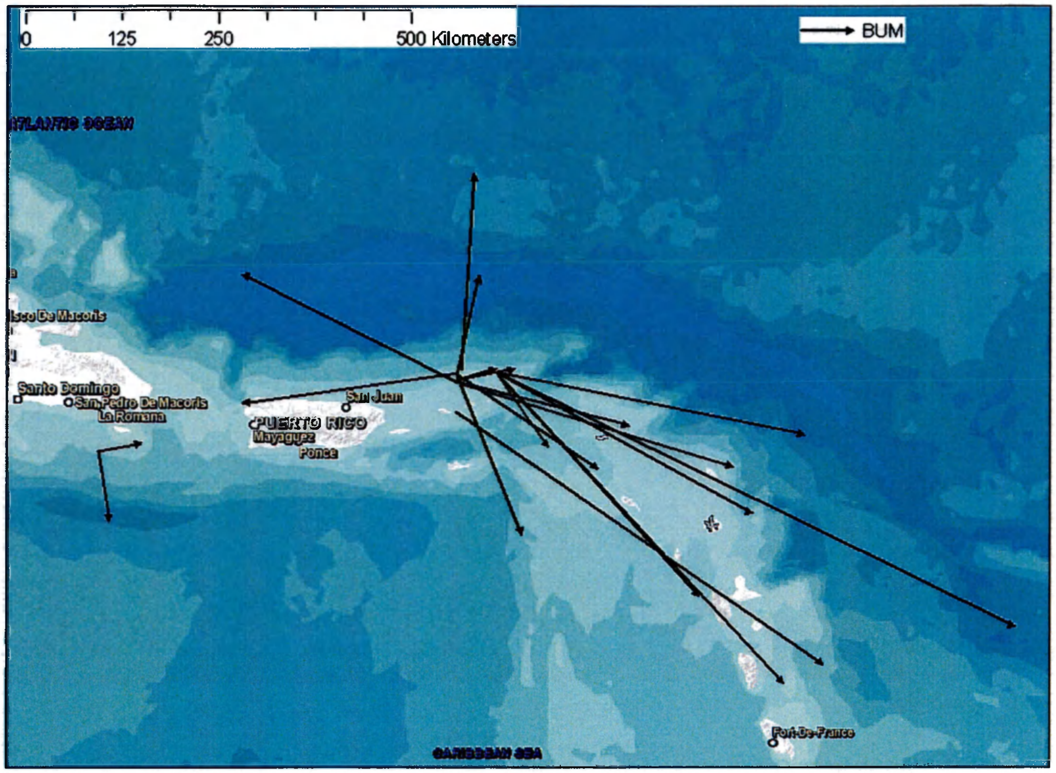


Figure 5. Minimum straight line displacements of blue marlin (BUM) tagged off Brazil.

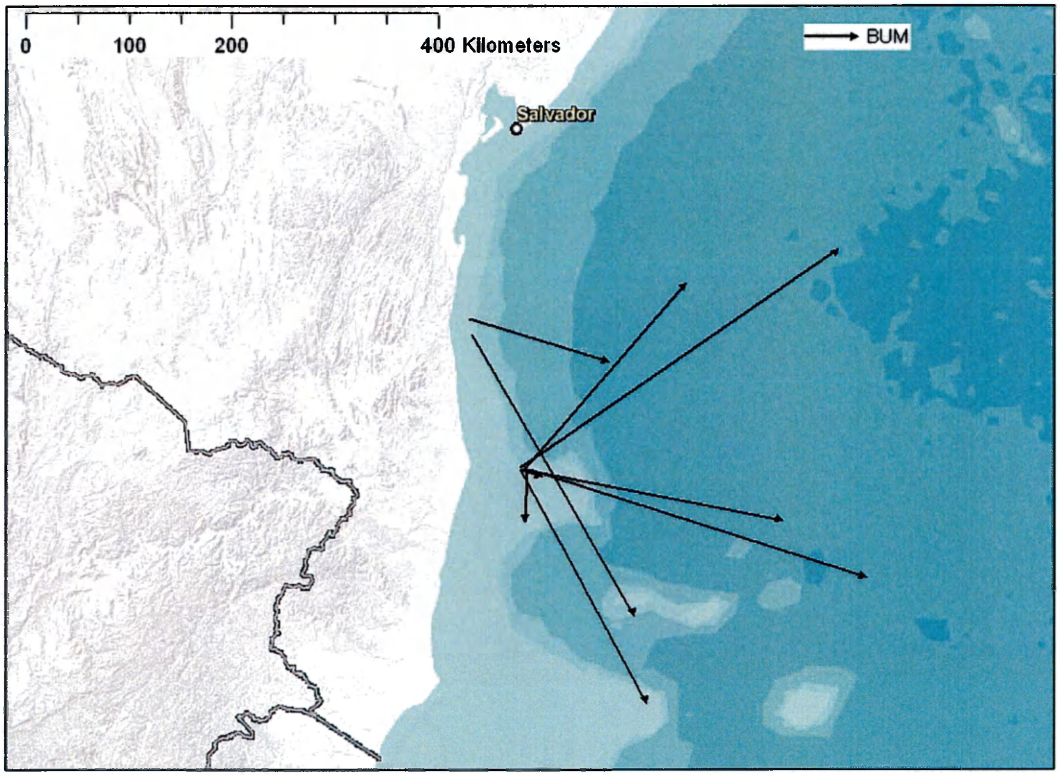


Figure 6. Minimum straight line displacements of blue marlin (BUM) and white marlin (WHM) tagged off Venezuela.

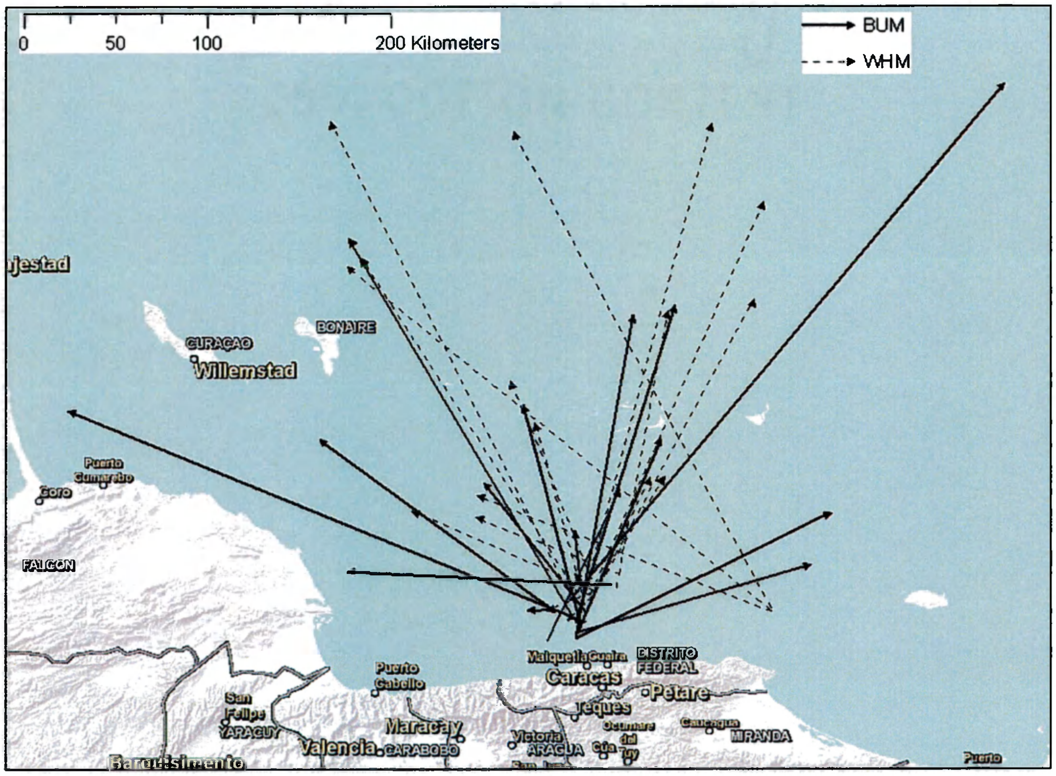


Figure 7. Minimum straight line displacements of white marlin (WHM) tagged off Mexico.

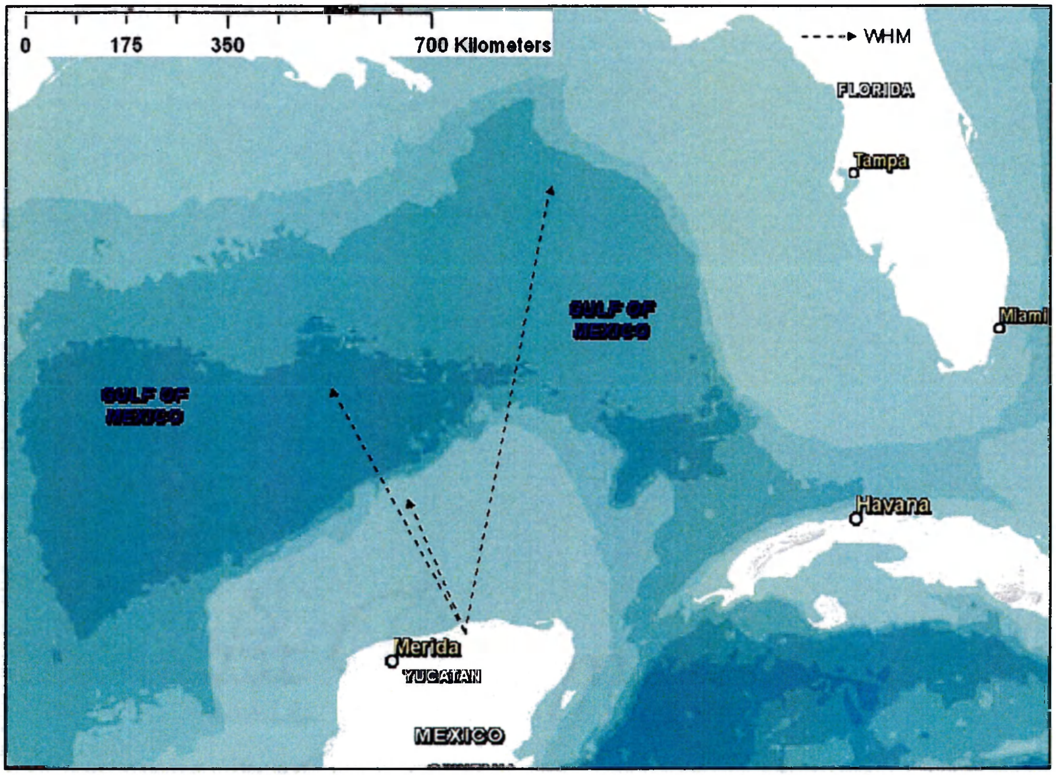


Figure 8. Time-at-depth histogram for all blue marlin separated into nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of the total time are shown.

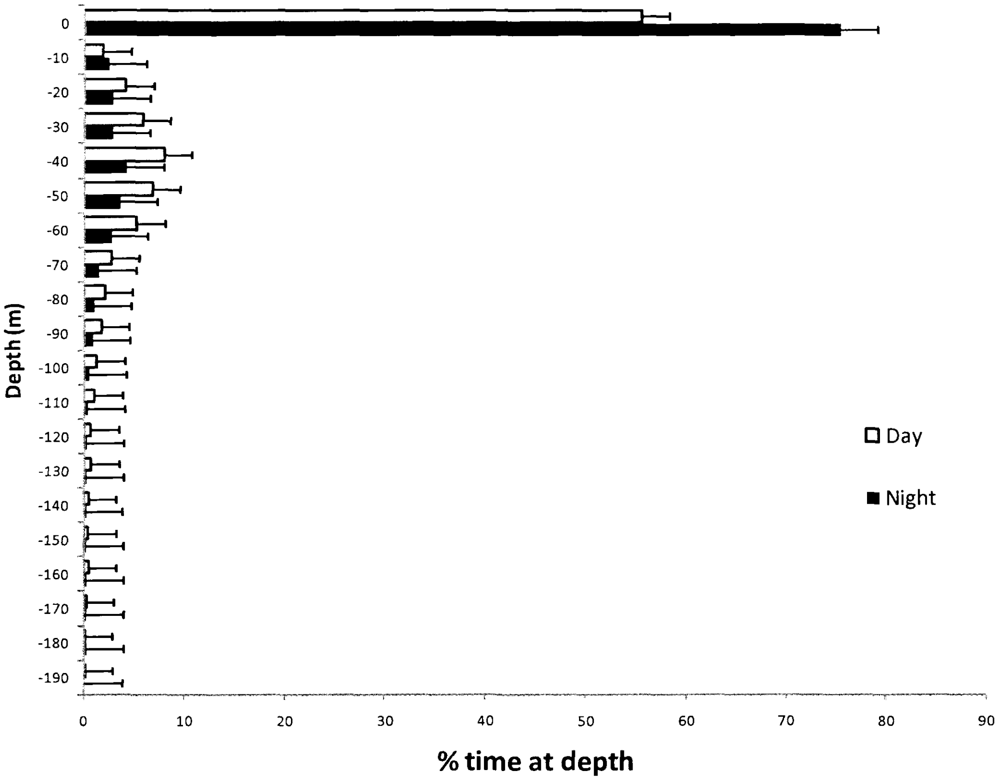


Figure 9. Time-at-depth histogram for blue marlin tagged off the U.S. Virgin Islands and Dominican Republic, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

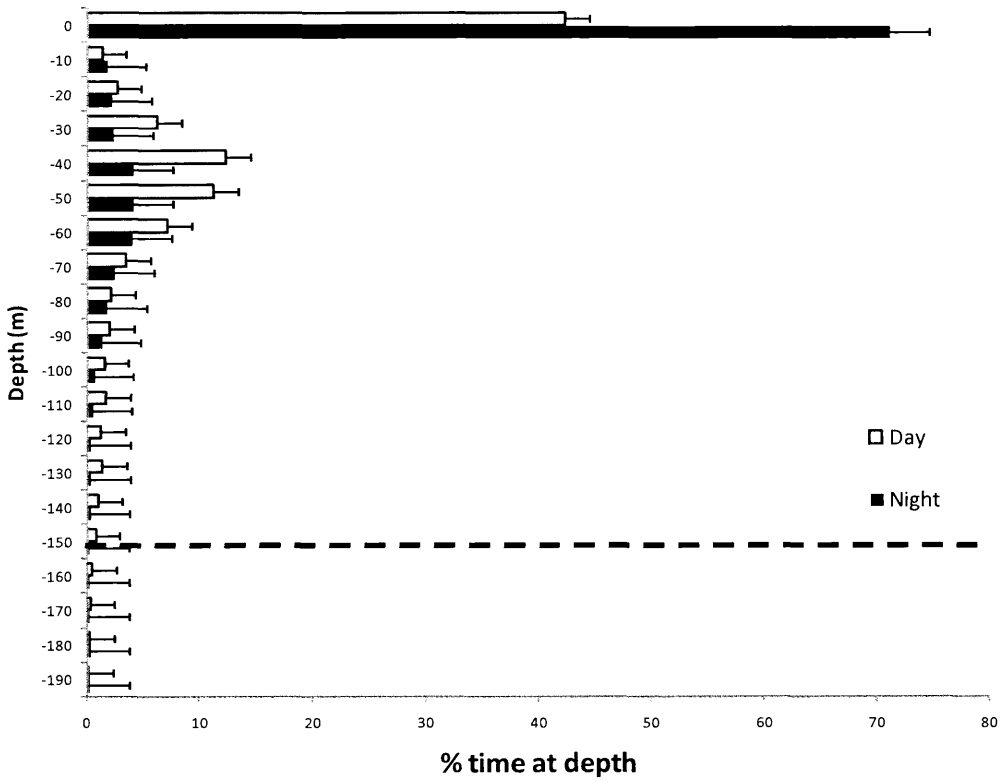


Figure 10. Time-at-depth histogram for blue marlin tagged off Brazil, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

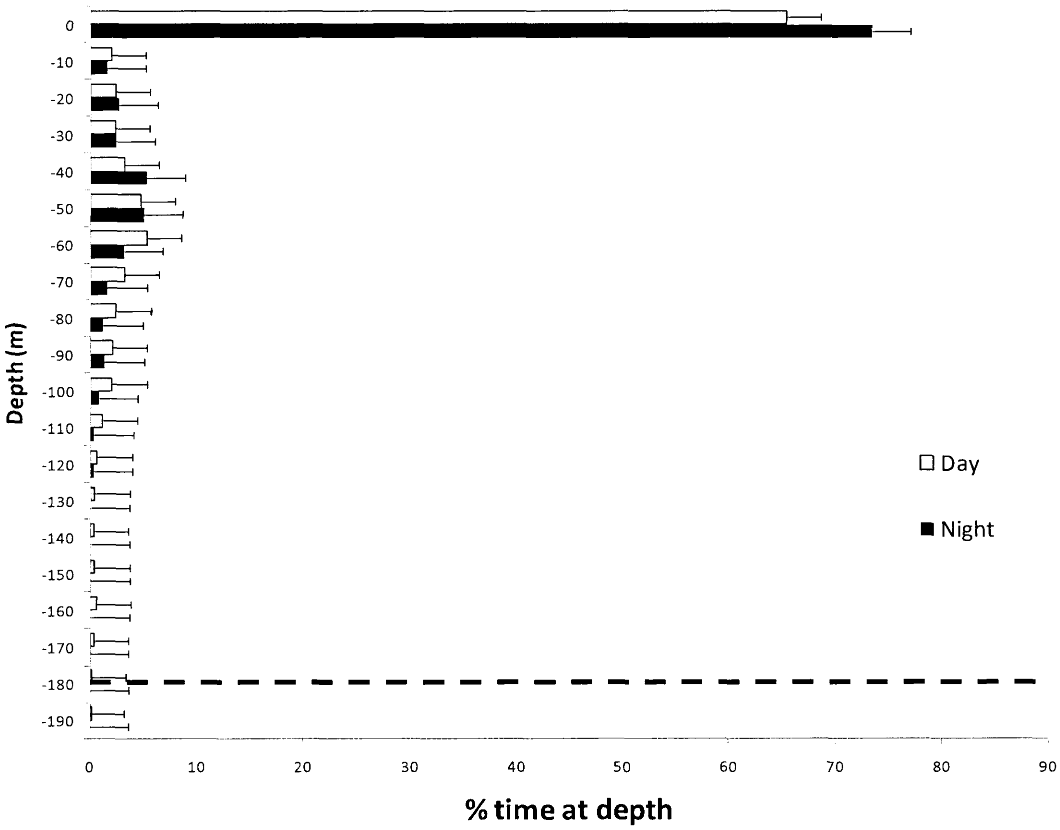


Figure 11. Time-at-depth histogram for blue marlin tagged off Venezuela, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

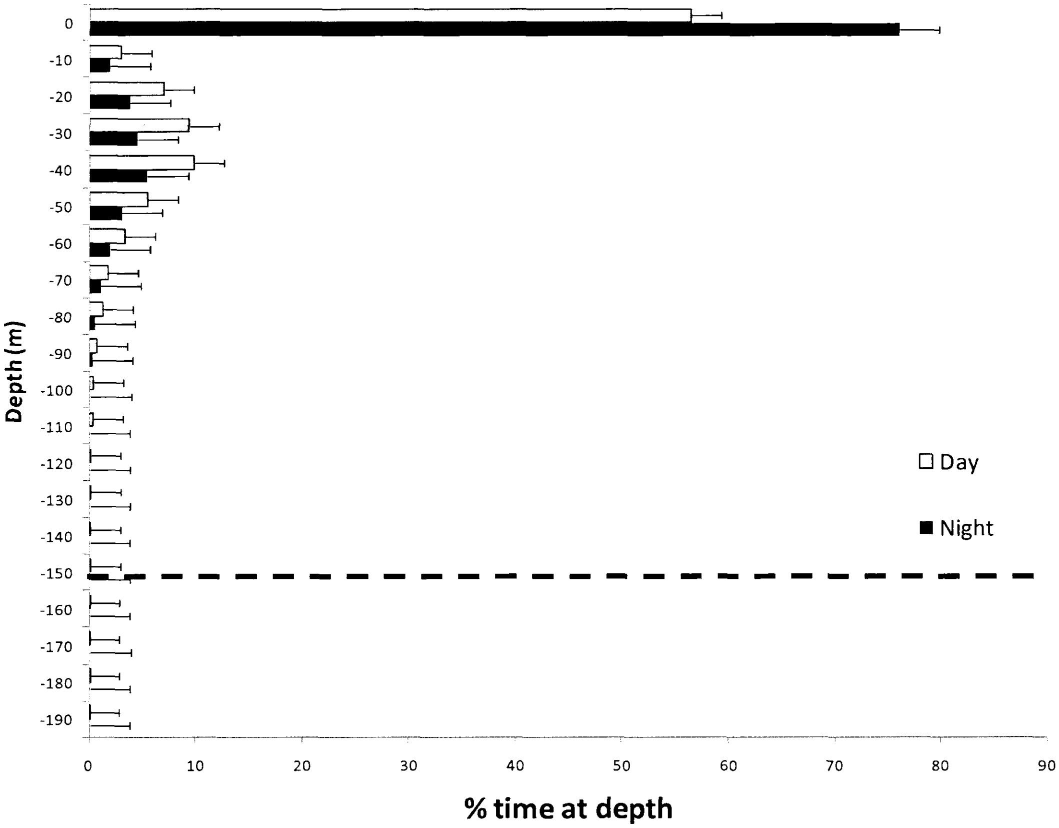


Figure 12. Time-at-depth histogram for blue marlin tagged off the U.S. Mid-Atlantic, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

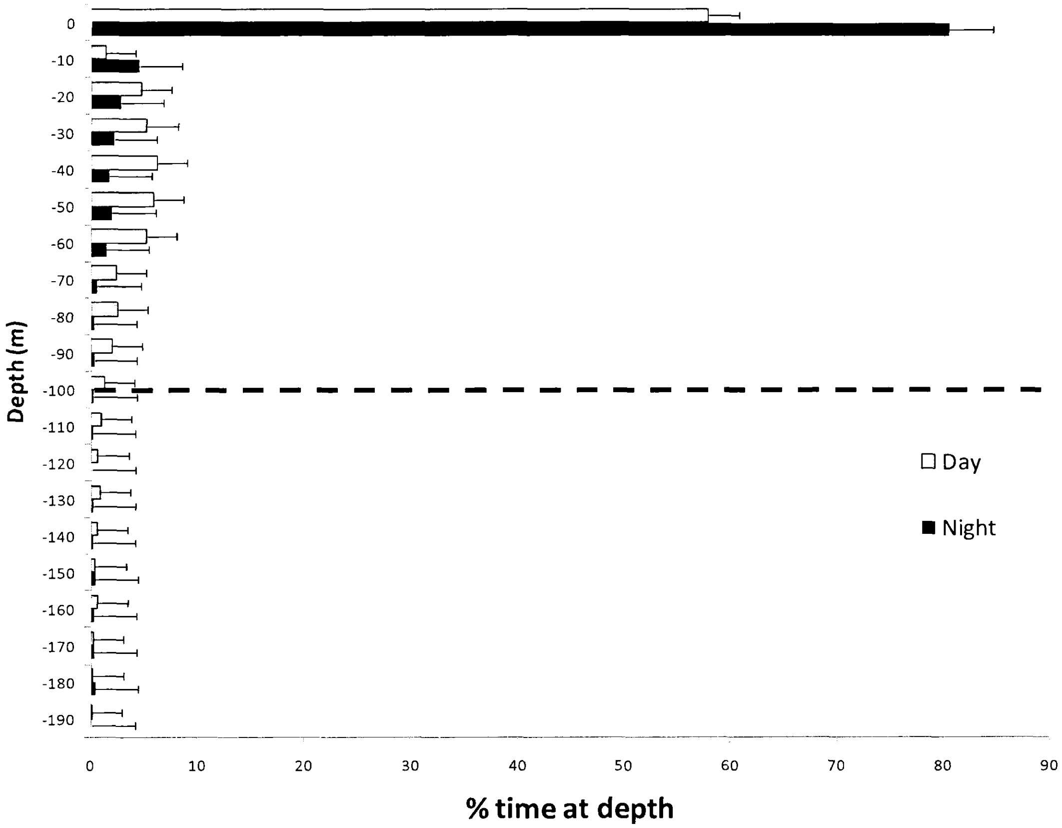


Figure 13. Time-at-depth histogram for all white marlin separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

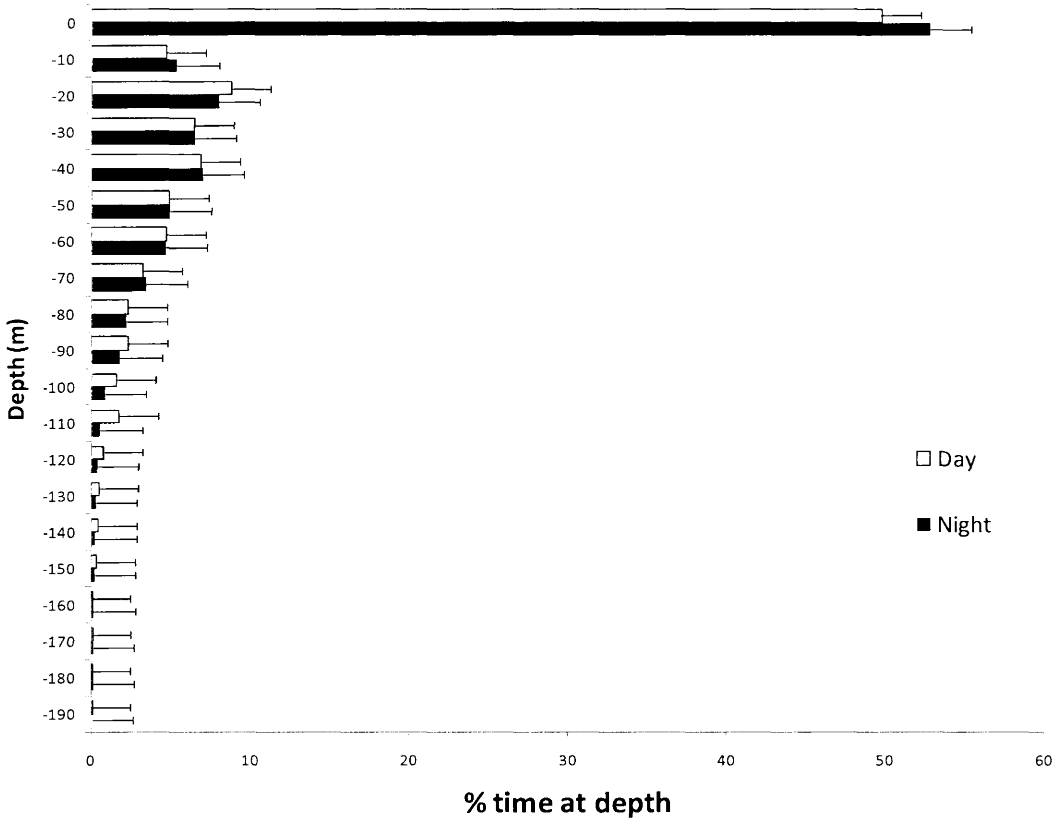


Figure 14. Time-at-depth histogram for white marlin tagged off Mexico, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

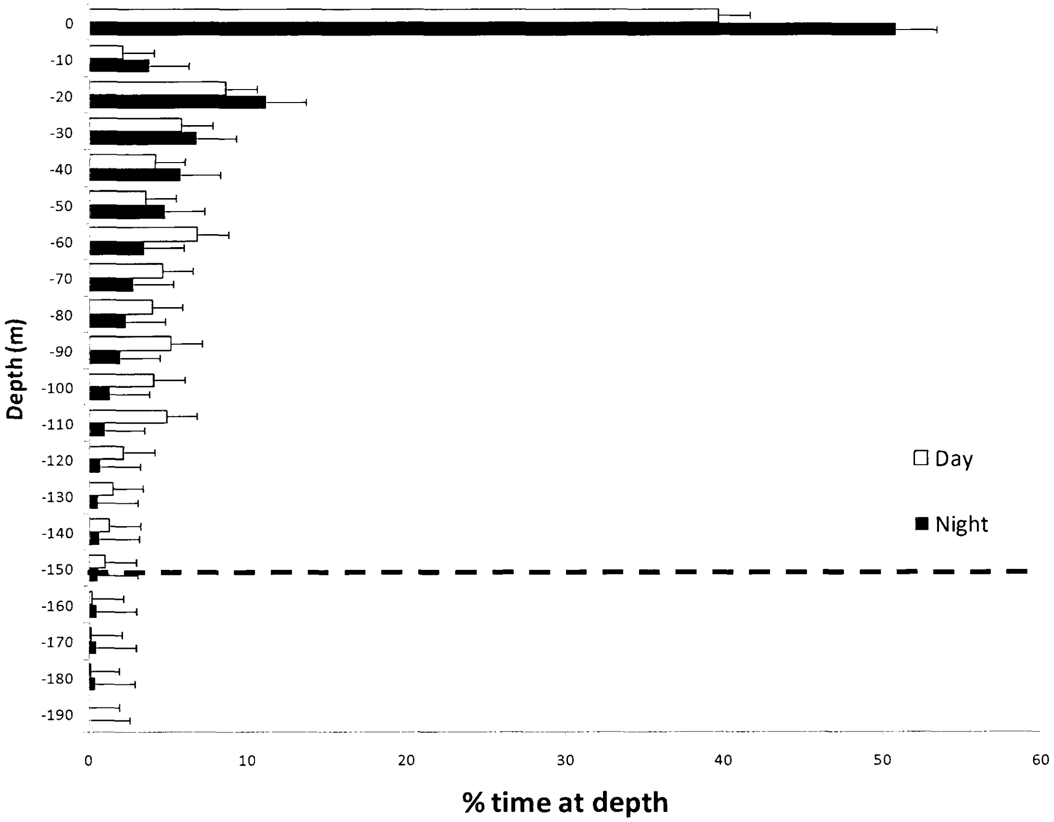


Figure 15. Time-at-depth histogram for white marlin tagged off the U.S. Mid-Atlantic, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

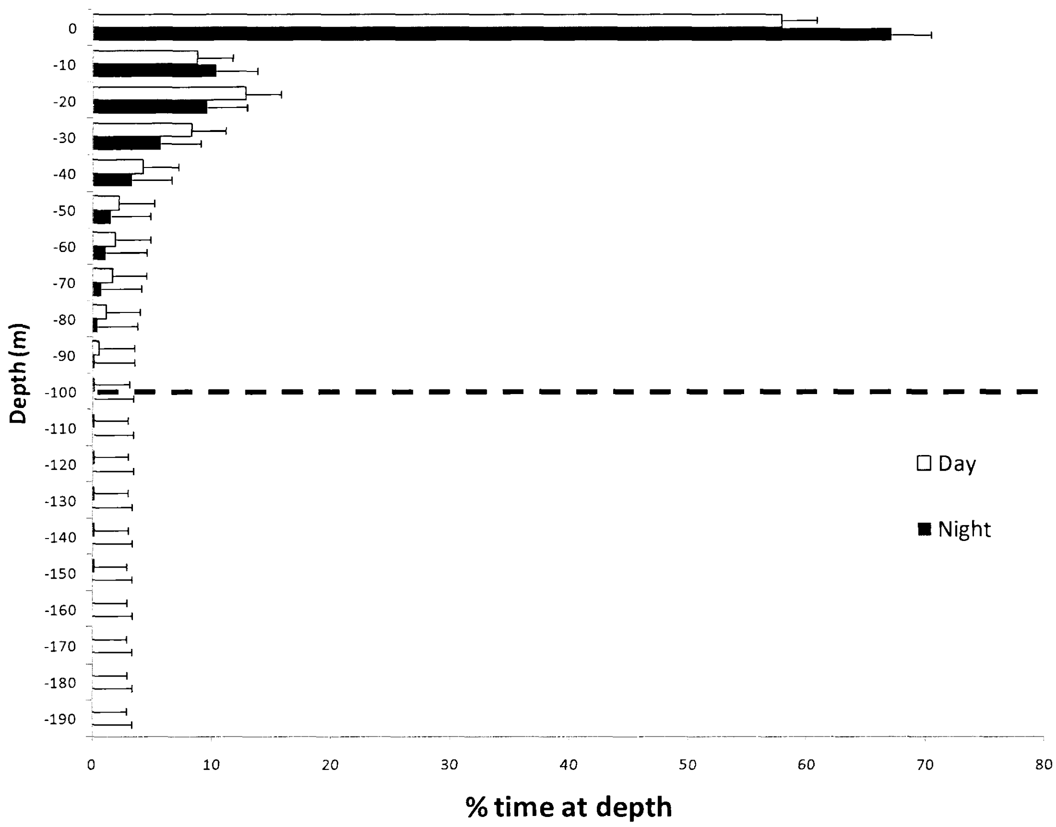


Figure 16. Time-at-depth histogram for white marlin tagged off Venezuela, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown. The dashed line represents the estimated thermocline depth.

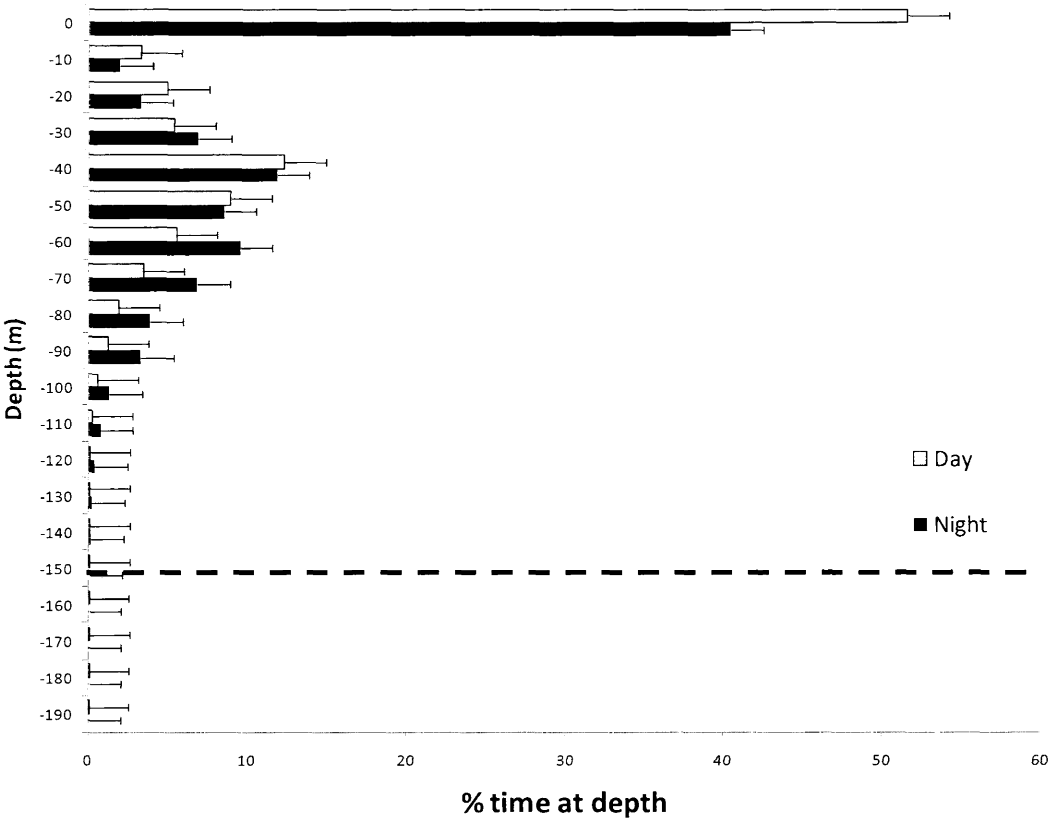


Figure 17. Time-at-depth histogram for blue marlin (black bars) and white marlin (grey bars). Only depth bins that contained >1% of total time are shown.

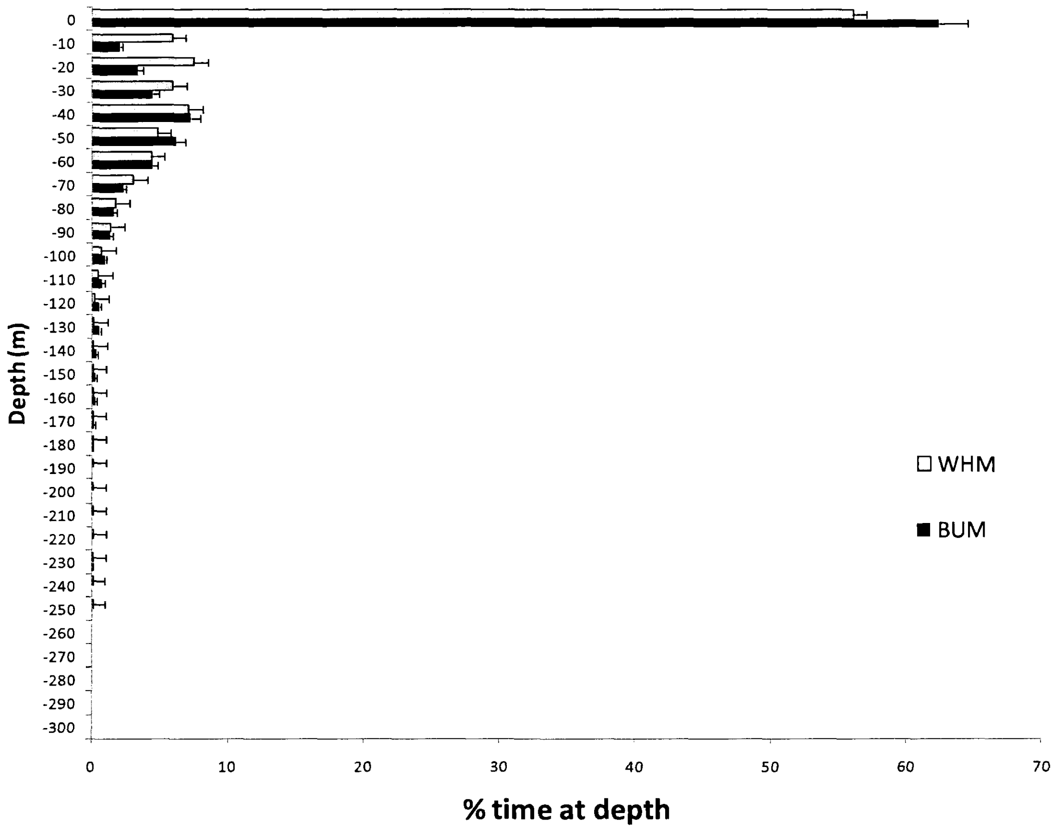


Figure 18. Time-at-temperature relative to sea surface temperature histogram for blue marlin (black bars) and white marlin (grey bars). Only depth bins that contained >1% of total time are shown.

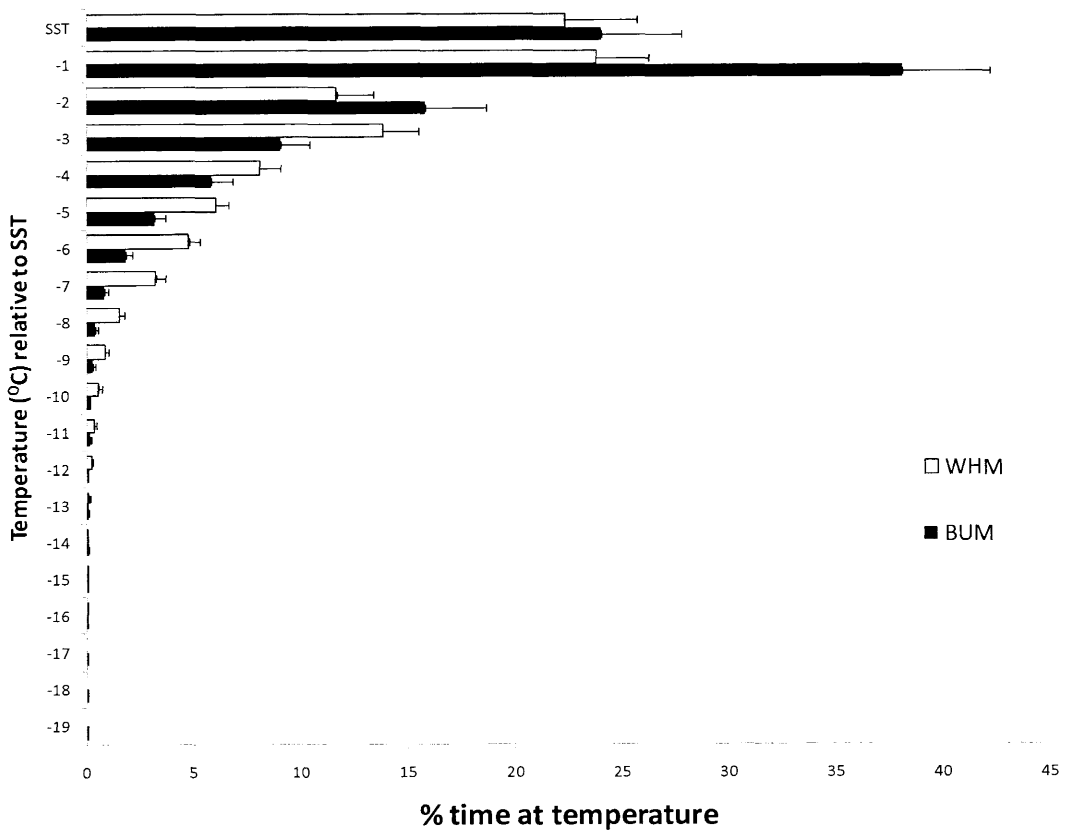


Figure 19. Time-at-temperature relative to sea surface temperature histogram for all blue marlin separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of time are shown.

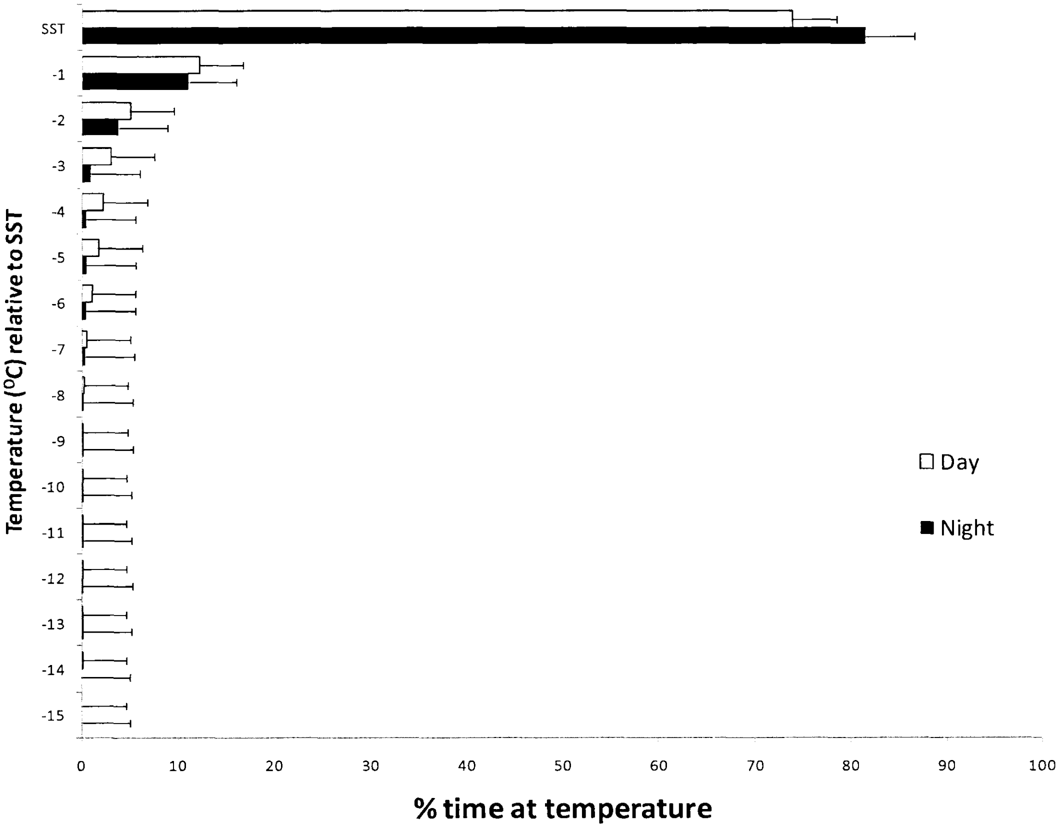


Figure 20. Time-at-temperature relative to sea surface temperature histogram for blue marlin tagged off Brazil, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

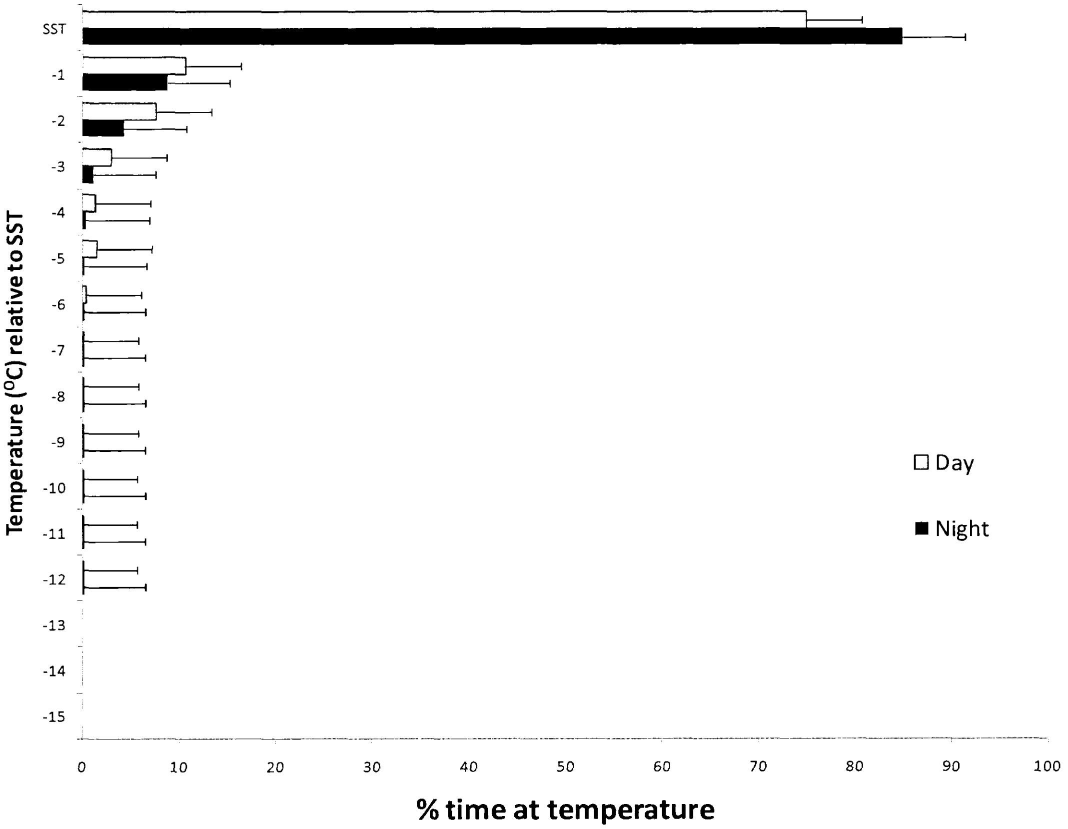


Figure 21. Time-at-temperature relative to sea surface temperature histogram for blue marlin tagged off the U.S. Virgin Islands and Dominican Republic, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

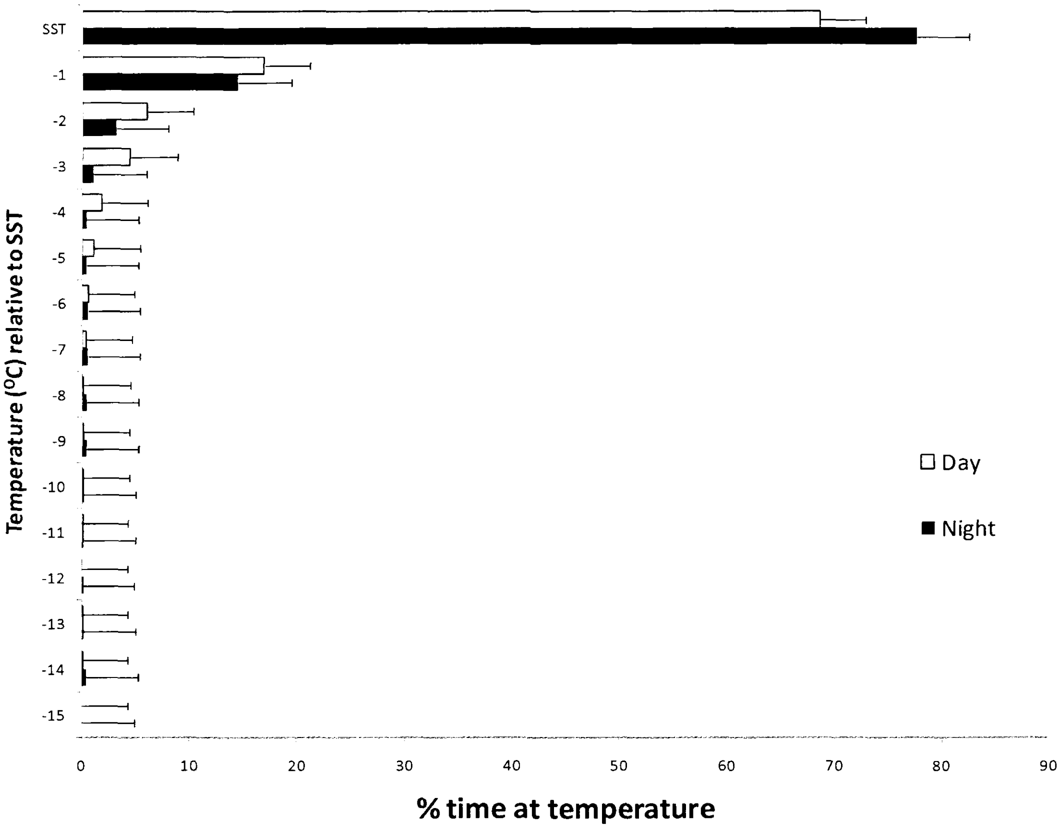


Figure 22. Time-at-temperature relative to sea surface temperature histogram for blue marlin tagged off the U.S. Mid-Atlantic, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

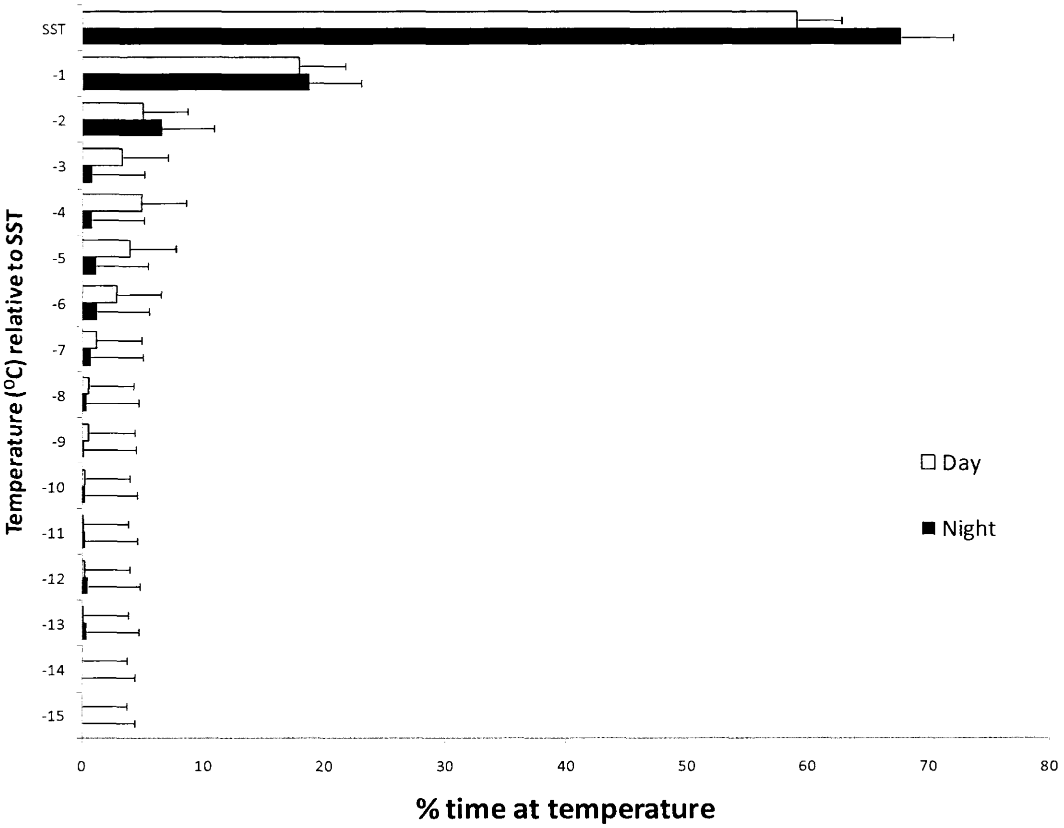


Figure 23. Time-at-temperature relative to sea surface temperature histogram for blue marlin tagged off Venezuela, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

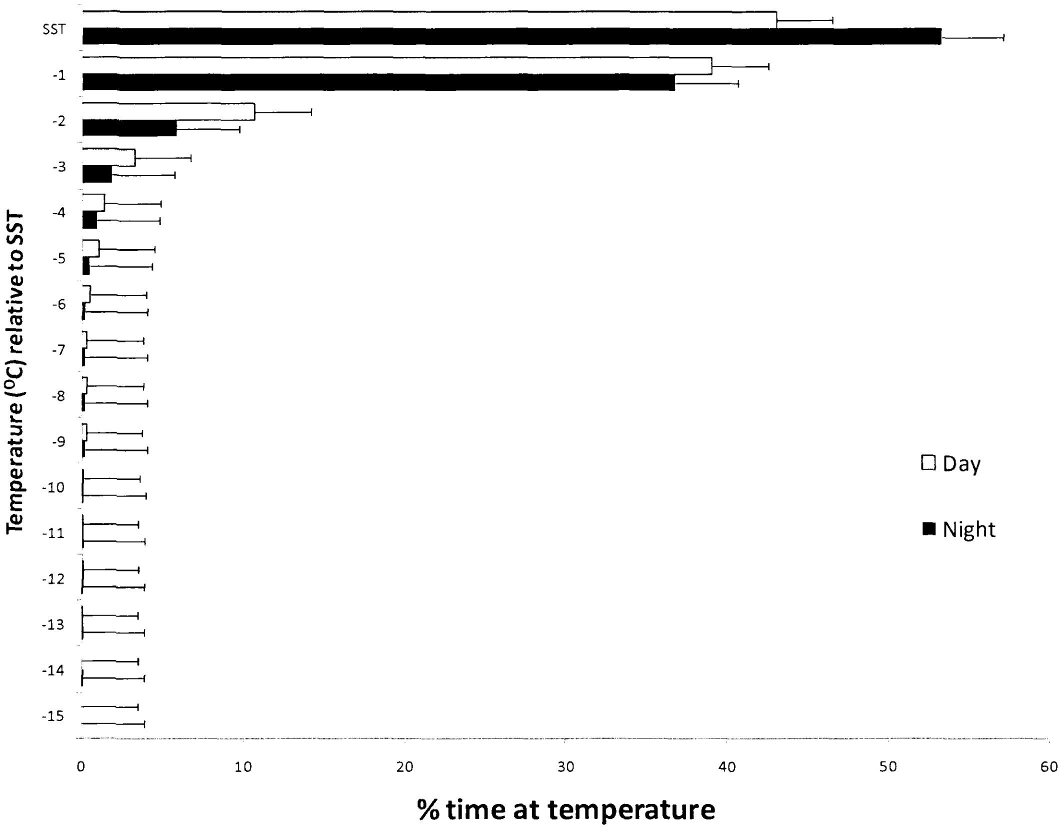


Figure 24. Time-at-temperature relative to sea surface temperature histogram for all white marlin separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

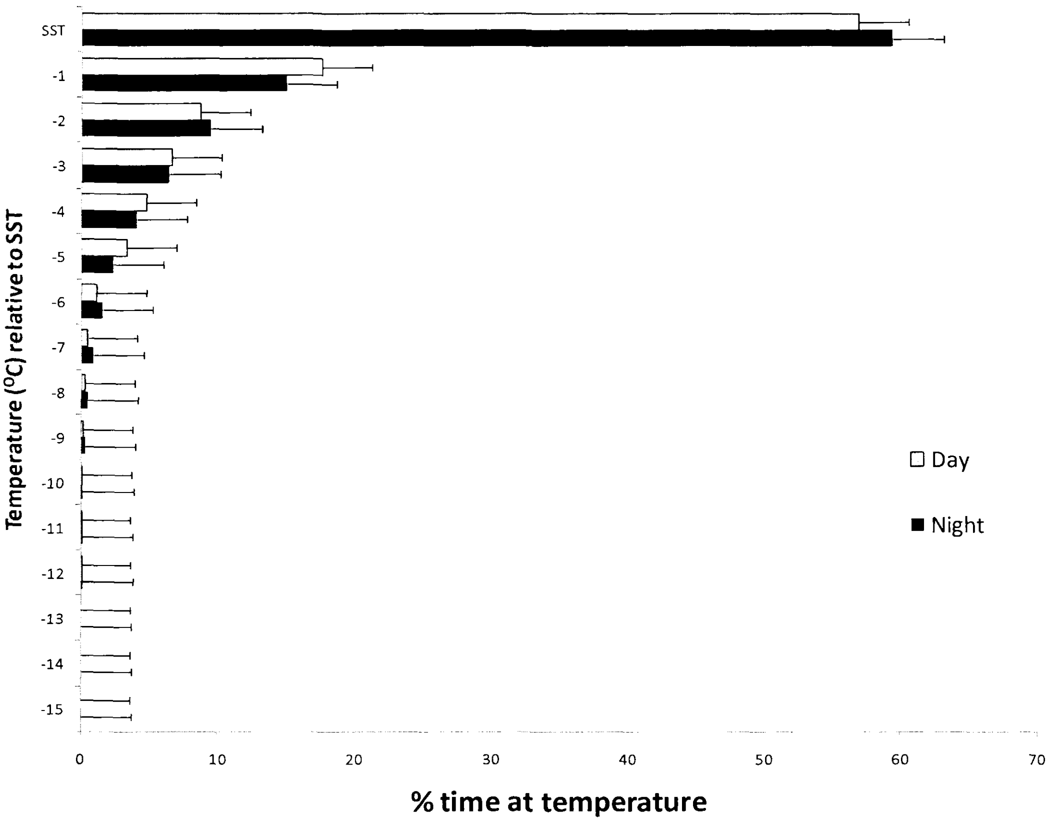


Figure 25. Time-at-temperature relative to sea surface temperature histogram for white marlin tagged off Venezuela, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

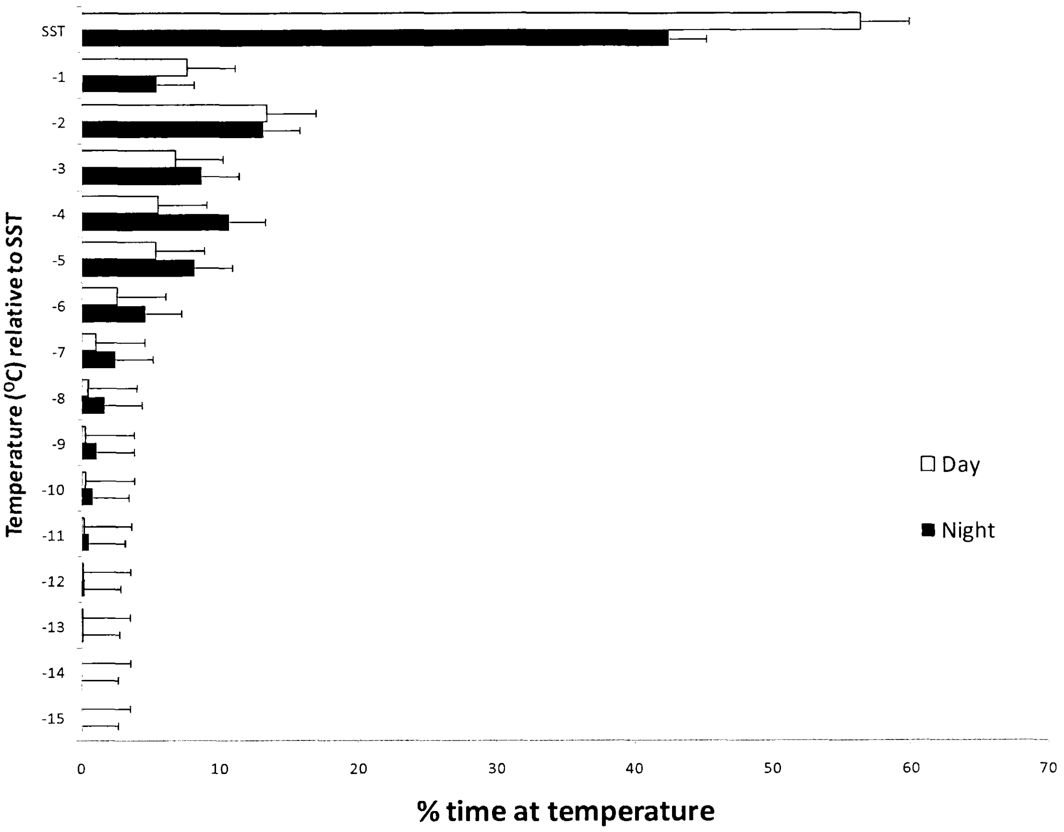


Figure 26. Time-at-temperature relative to sea surface temperature histogram for white marlin tagged off the U.S. Mid-Atlantic, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

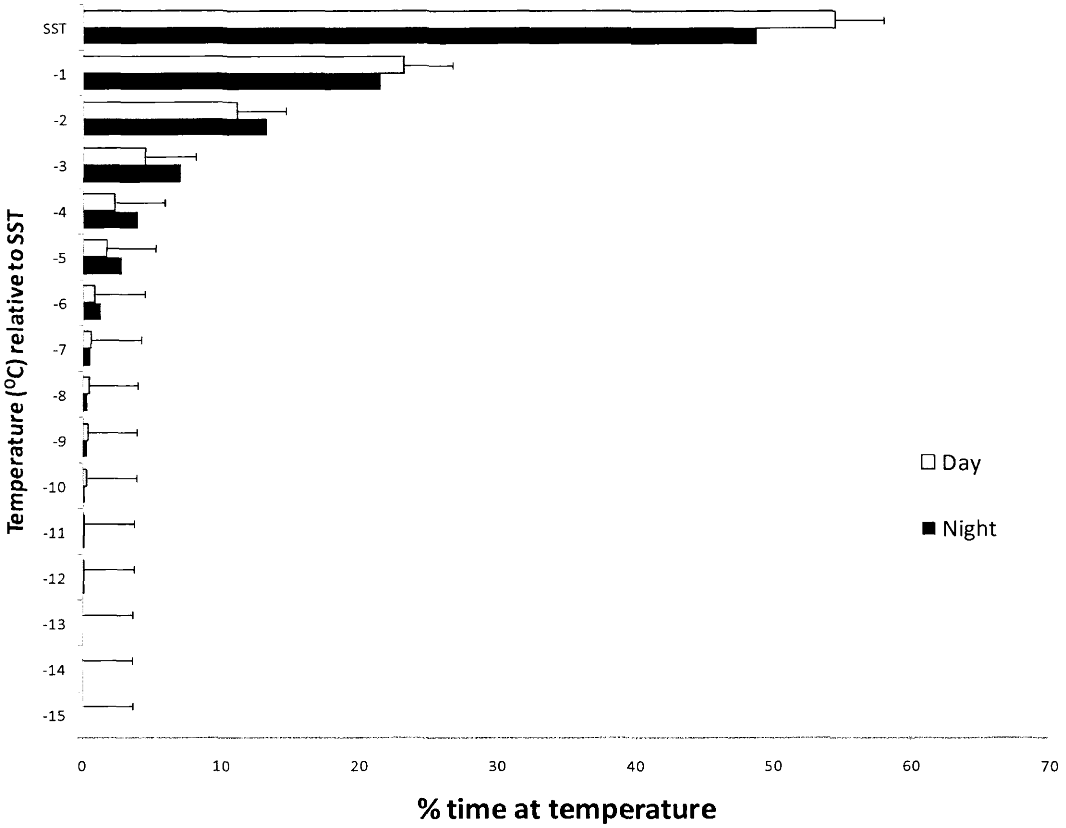


Figure 27. Time-at-temperature relative to sea surface temperature histogram for white marlin tagged off Mexico, separated by nighttime (black bars) and daytime (grey bars). Only depth bins that contained >1% of total time are shown.

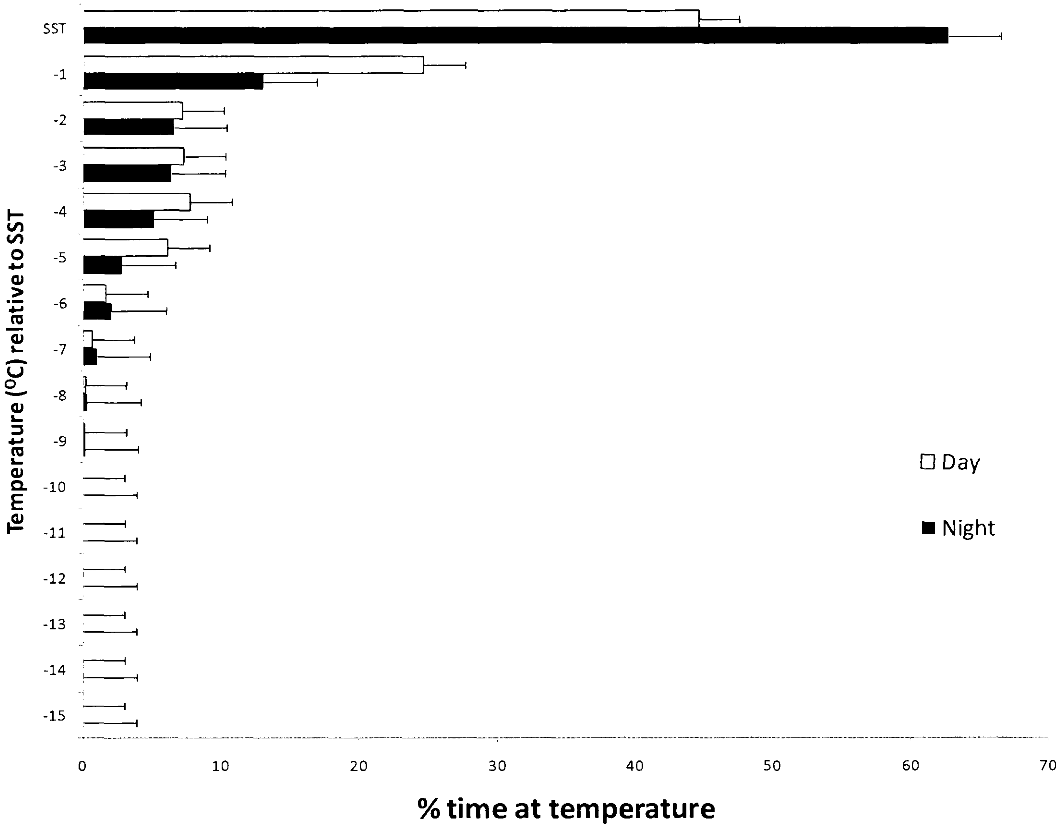


Figure 28. Temperature-at-depth plots for each tagging location using data from PSATs acting as mobile temperature-depth recorders.

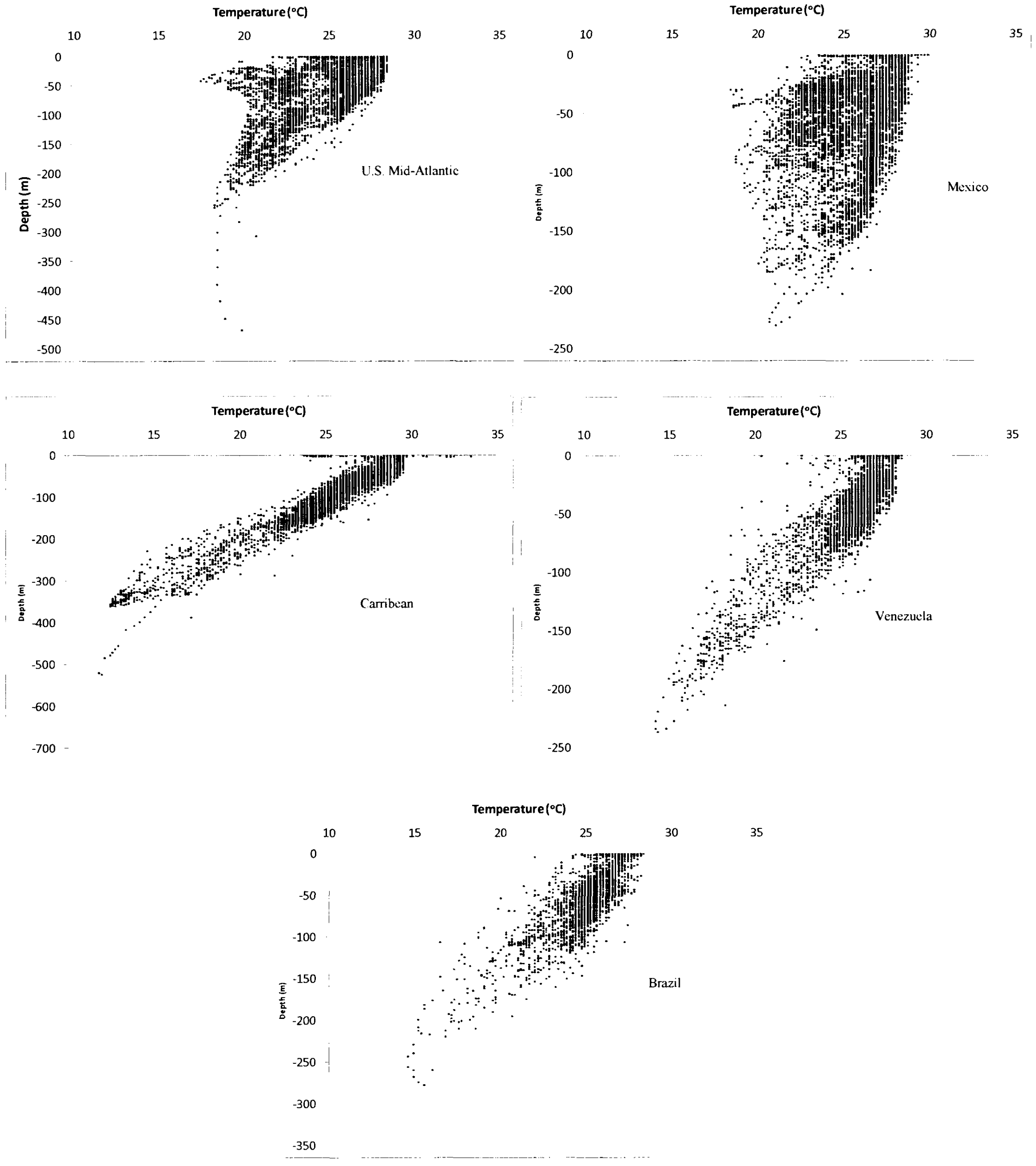
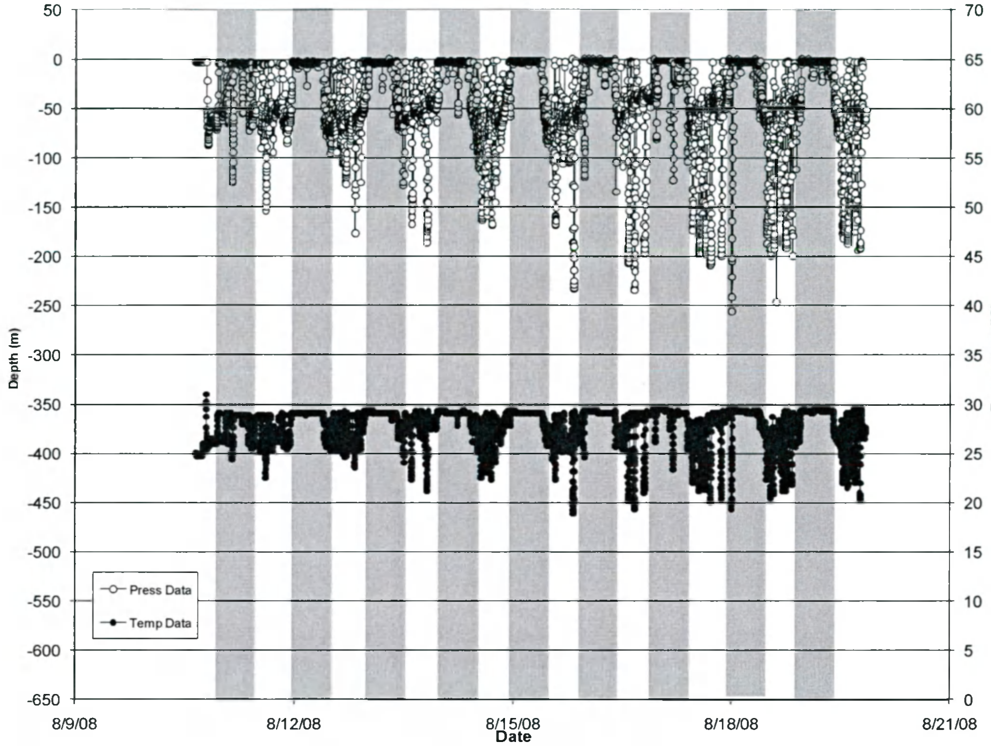


Figure 29. Dive profiles showing depth and temperatures for blue marlin exhibiting diel periodicity (top) and no diel periodicity (bottom). Grey shaded regions represent nighttime.



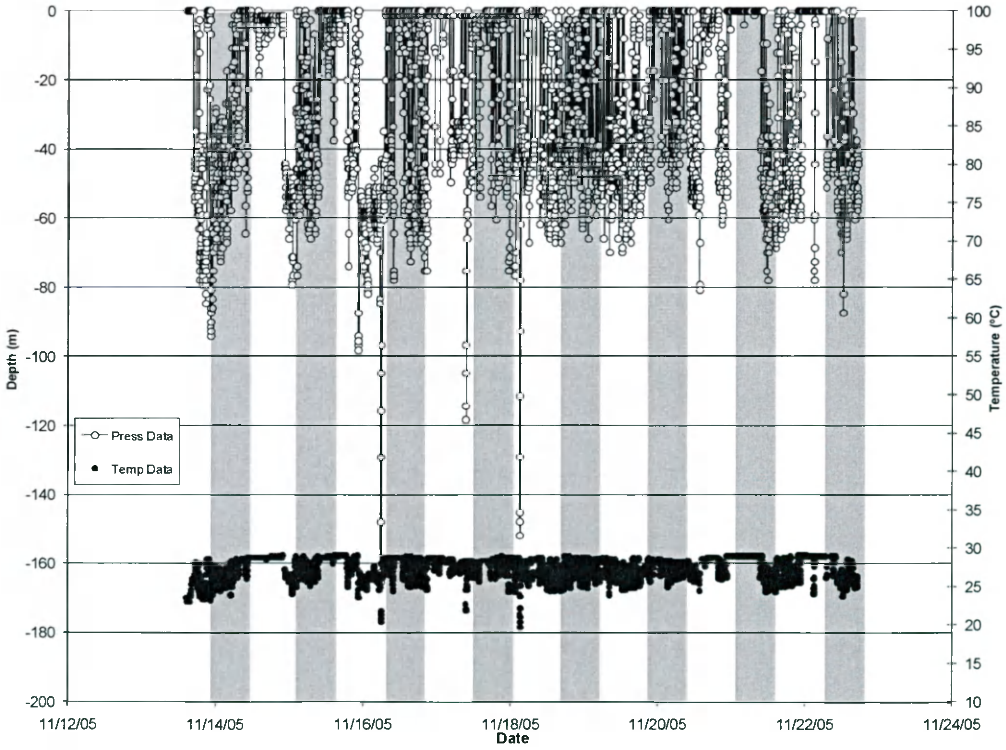
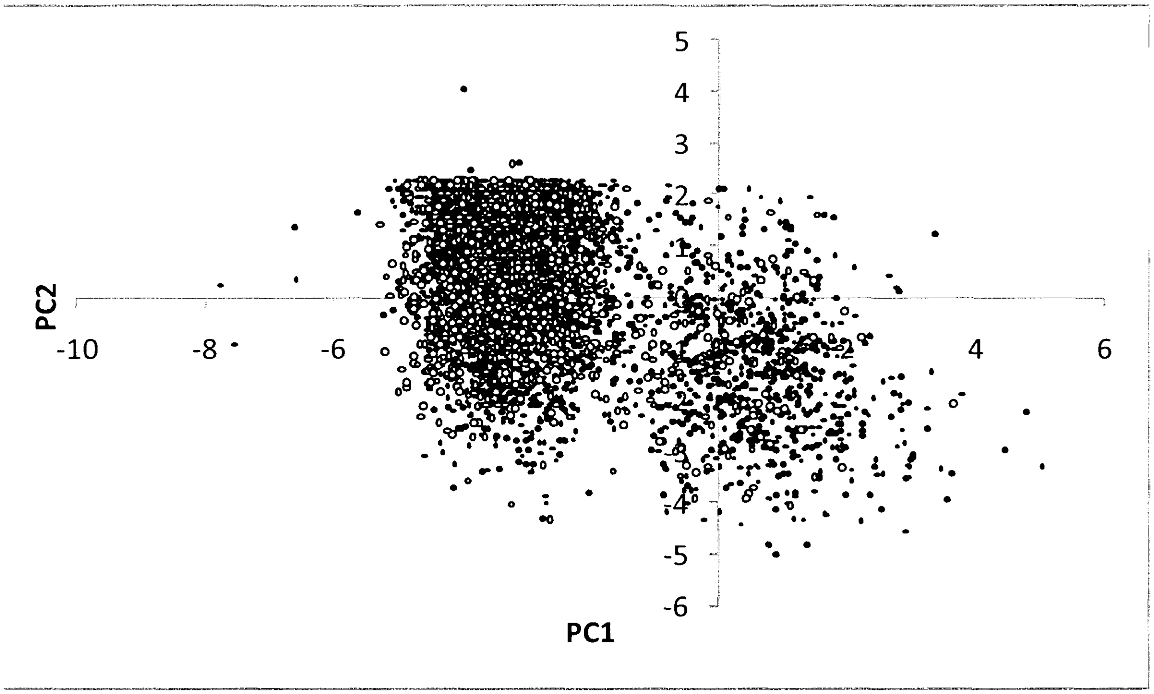


Figure 30. Score plots of orthogonal factor scores from each complete dive for blue marlin (solid) and white marlin (hollow) showing substantial overlap between species. PC1 vs PC2 (above) and PC1 vs PC3 (below).



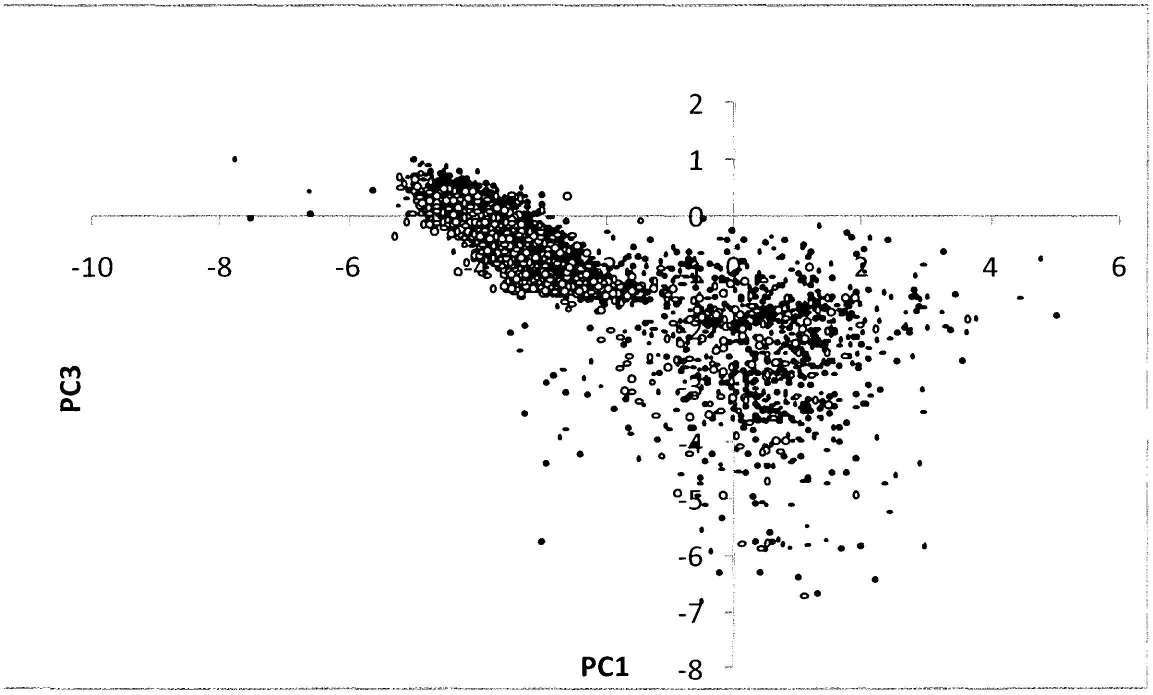
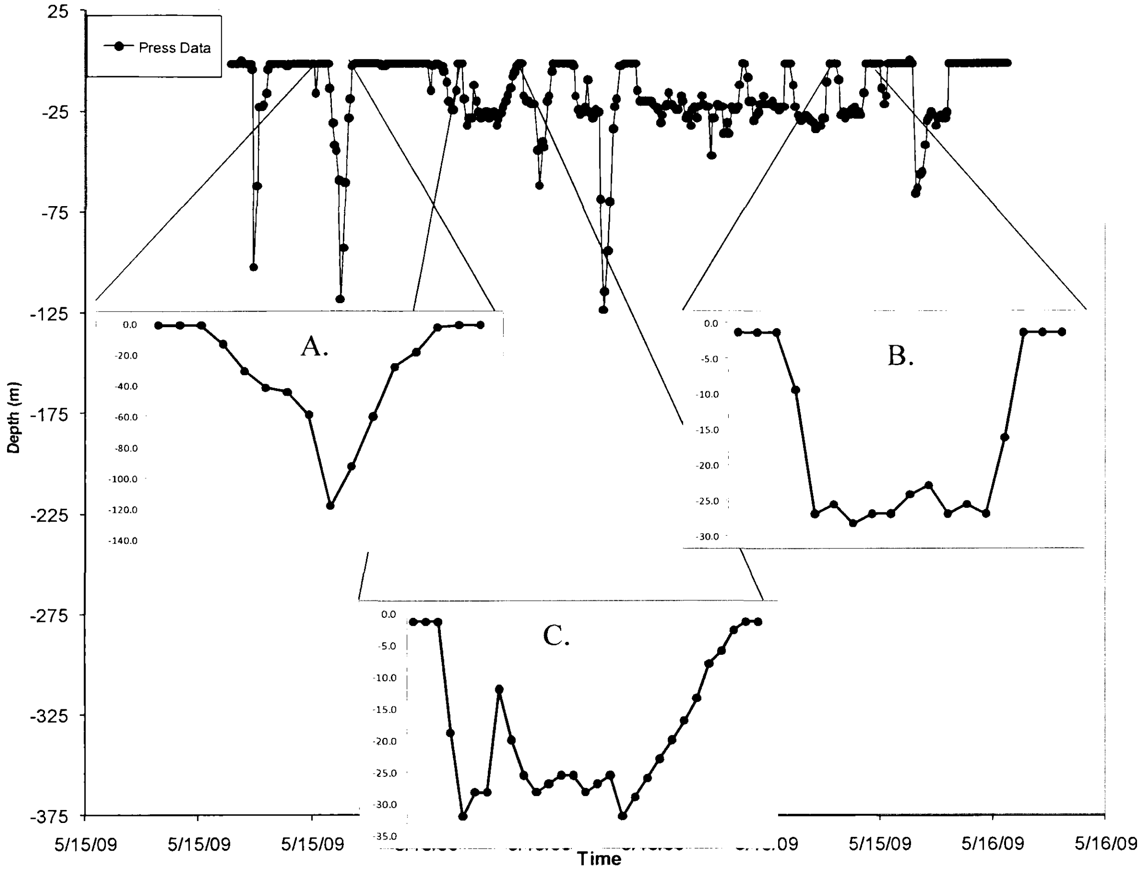


Figure 31. Representative dive patterns for a single day from a blue marlin tagged off Venezuela showing visually classified "V" (A) and "U"-shaped (B) dives as well as a complex dive (C).



VITA

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