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Survival and Habitat Preferences of White Marlin (Tetrapturus albidus) Released from the Western North Atlantic Recreational Fishery

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SURVIVAL AND HABITAT PREFERENCES OF WHITE MARLIN (*Tetrapturus albidus*) RELEASED FROM THE WESTERN NORTH ATLANTIC RECREATIONAL FISHERY

A Thesis

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In Partial Fulfillment

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Master of Science

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by

Andrij Zenon Horodysky

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
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Approved March 2004.

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DEDICATION

This thesis is dedicated to the memory of my grandfather, John Zenon Horodysky, Ph. D. (1915-2002), who always made time to take me fishing and dreamed about seeing his grandson pursue a graduate education.

TABLE OF CONTENTS

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LIST OF TABLES

Page

CHAPTER 1: Application of Pop-up Satellite Archival Tag Technology to Estimate Postrelease Survival of White Marlin (*Tetrapturus albidus*) Caught on Circle and Straight-shank ("J") Hooks in the Western North Atlantic Recreational Fishery

CHAPTER 2: Habitat Preferences and Diving Behavior of White Marlin (*Tetrapturus albidus*) Released from Recreational Fishing Gear in the Western North Atlantic Ocean

LIST OF FIGURES

Page

CHAPTER 1: Application of Pop-up Satellite Archival Tag Technology to Estimate Postrelease Survival of White Marlin (*Tetrapturus albidus*) Caught on Circle and Straight-shank ("J") Hooks in the Western North Atlantic Recreational Fishery

CHAPTER 2: Habitat Preferences and Diving Behavior of White Marlin (*Tetrapturus albidus*) Released from Recreational Fishing Gear in the Western North Atlantic Ocean

ABSTRACT

The Atlantic-wide stock of white marlin (*Tetrapturus albidus*) is overexploited, with current biomass about 12% of that necessary for maximum sustainable yield. Member nations of the International Commission for the Conservation of Atlantic Tunas (ICCAT) are required to release all live white marlin from commercial fisheries (pelagic longline and purse seine), and the vast majority of these fish caught by the directed recreational fishery are released voluntarily. Whether these measures will significantly decrease white marlin fishing mortality is uncertain as relatively little is known of the fate of white marlin following release. Short-duration (5 or 10 day) deployments of pop-up satellite archival tags were used to estimate survival and elucidate the habitat preferences of white marlin released from the western North Atlantic recreational fishery.

Forty-one tags, recording temperature, pressure, and light level measurements approximately every two minutes for 5-day tags (n = 5) or four minutes for 10-day tags (n = 36), were attached to white marlin caught using dead baits rigged on straight-shank ("J") hooks (n = 21) or circle hooks (n = 20) offshore of the U.S. Mid-Atlantic region, the Dominican Republic, Mexico, and Venezuela. Forty tags (97.8%) reported to the satellites of the Argos system, and 33 reporting tags (82.5%) returned data consistent with survival over the deployment duration. Approximately 61% (range: 19-95%) of all archived data were successfully recovered from each tag. Survival was significantly ($p < 0.01$) higher for fish caught on circle hooks (100%) relative to those caught on straight-shank ("J") hooks (65%). Time-to-death ranged from 10 minutes to 64 hours following release for the seven documented mortalities, with five animals dying within the first six hours after release. These results suggest that a simple change in hook type can significantly increase the survival of white marlin released from recreational fishing gear.

Data from surviving white marlin suggest that this species appears to spend the majority of time associated with warm surface waters. The maximum depths attained by tagged white marlin varied across locations (Mid-Atlantic: 161m, Dominican Republic: 149 m, Mexico 210 m, Venezuela 199 m). All fish displayed repetitive short duration (mean: 26.8 min +/-17.1) diving behavior to depths averaging 51.2 m (+/- 20.3). An analysis of data from complete dives recovered from surviving white marlin revealed two major types of dives: one pattern was characterized by deep "v"-shaped excursions of relatively short duration (e.g., Type 1 dives) while the other featured dives that were more broadly "u"-shaped, showing behavior confined to a specific depth range for an extended period of time (e.g., Type 2 dives). Dive durations, depths, temperature gradients, and interdive intervals did not differ significantly between locations for Type 1 dives, but analysis of dive durations and interdive intervals of Type 2 dives revealed marginally significant differences among locations. Based on the frequency, persistence, and patterns of these dives, it is likely that the diving behavior observed in this species is associated with foraging. The nature and extent of observed diving behavior indicate that white marlin may direct a considerable proportion of foraging effort beyond surface waters, accounting for relatively high catch rates of white marlin on some pelagic longline deployments.

SURVIVAL AND HABITAT PREFERENCES OF WHITE MARLIN (*Tetrapturus albidus*) RELEASED FROM THE WESTERN NORTH ATLANTIC RECREATIONAL FISHERY

INTRODUCTION

Populations of Atlantic billfishes (Teleostei: Istiophoridae) are severely overexploited, with current harvests exceeding replacement yield. Recent assessments conducted by the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) suggest that the biomass of Atlantic blue marlin (*Makaira nigricans*) may be as low as 40% of that necessary for maximum sustainable yield (MSY) and white marlin (*Tetrapturus albidus*) biomass may be less than 12% of that required for MSY (ICCAT, 2001; ICCAT, 2002). Increasingly pessimistic population assessments, and declining catches despite increases in effective fishing effort, have led to serious concerns over the status of the Atlantic white marlin. A petition to list white marlin under the Endangered Species Act (ESA) was submitted to the National Marine Fisheries Service (NMFS) in 2001. NMFS did not list white marlin as an endangered species, and will reevaluate the need for an ESA listing in 2007.

Clearly, a more accurate understanding of the status of the white marlin stock is needed given increased exploitation of billfishes by commercial and recreational fisheries. Current international management measures in the Atlantic Ocean are intended to decrease fishing mortality by promoting the live release of blue marlin and white marlin from commercial and recreational gears. The efficacy of these measures cannot be evaluated because little is known about the survival of released billfishes. There is also currently a lack of data regarding depth and temperature preferences of Atlantic istiophorids, information which is critical for valid assessment of the stock abundances of these species. Short-duration (five or ten day) pop-up satellite tags (PSATs) were applied in this study to estimate the survival and elucidate the habitat preferences of white marlin released from the western North Atlantic recreational fishery.

White Marlin Biology

Generally, billfishes of the family Istiophoridae are considered to be large pelagic apex predators which inhabit tropical and subtropical epipelagic waters of the world's oceans (Graves and McDowell, 2003). Cosmopolitan representatives of this family include the sailfish (*Istiophorus platypterus* Shaw and Nodder, 1792) and blue marlin (*Makaira nigricans* Lacepede, 1802). The distributions of other istiophorids are confined to distinct ocean basins. Indo-west Pacific members of this family include the black marlin (*M. indica* Cuvier, 1832), striped marlin (*Tetrapturus audax* Phillipi, 1887), and shortbill spearfish (*T. angustirostris* Tanaka, 1915), and Atlantic representatives include white marlin (*T. albidus* Poey, 1860), Atlantic longbill spearfish (*T. pfluegeri* Robins and de Sylva 1963), and the Mediterranean spearfish (*T. belone* Rafinesque, 1810) (Nakamura, 1985). Along with the tunas and mackerels, these fishes represent important commercial and/or recreational fisheries in the world's tropical, subtropical, and temperate pelagic marine waters. White marlin are distributed throughout the tropical and temperate waters of the Atlantic Ocean from 45°N to 45°S.

A summary of white marlin biology is given in Nakamura (1985). Little is known of the age structure, reproductive ability, or recruitment of any istiophorid billfish. White marlin are believed to be very fast growing, attaining a maximum size of 80 kg, and a maximum age greater than 18 years (ICCAT, 2001). Female white marlin reach sexual maturity at around 20 kg and attain larger maximum sizes than males, although this effect is not nearly as pronounced as that seen in *Makaira*. The distribution of white marlin varies seasonally, reaching higher latitudes in both hemispheres during respective summers (ICCAT, 2001). Spawning is believed to occur in northern and southern hemispheres in their respective spring/summer, based on observation of gonad condition and presence of purported white marlin larvae (White Marlin Status Review Team, 2002). Although feeding behavior in all istiophorid billfishes is poorly understood, small temporal aggregations of white marlin have been observed where favorable water conditions promote concentrations of prey (Nakamura, 1985). Stomach contents of white marlin have included a variety of generally epipelagic prey such as *Illex* and *Loligo* squid, exocoetid flying fishes, *Scomber* spp., small tunas (*Thunnus*, *Euthynnus*, *Sarda*, and *Auxis*), monacanthid filefishes, dolphinfish (*Coryphaena hippurus*), blue runners (*Caranx crysos*), round herring (*Eutremeus teres*), and Atlantic moonfish (*Vomer setapinnis*) (Nakamura, 1985; Davies and Bortone, 1976).

White Marlin Fisheries

Throughout their range in the Atlantic Ocean, white marlin are taken in directed recreational and artisanal fisheries and occur as incidental bycatch in commercial pelagic longline gear targeting tunas and swordfish. White marlin bycatch comprises a small fraction of the total catch of the pelagic longline fishery, yet this gear accounts for the majority of fishing mortality by virtue of sheer magnitude (ICCAT, 2001). Throughout the Atlantic, total reported landings (recreational and commercial) of white marlin peaked at 4911 MT in 1965 and have fluctuated without tendency between 1000 and 2000 MT since 1980 despite substantial increases in effort (ICCAT, 2002). Since 1956, white marlin catches have been reported by 27 countries fishing in the Atlantic Ocean (ICCAT, 2002). Total Atlantic catches of white marlin in 2000 were distributed among international fleets as follows: Chinese Taipei (36%), EC-Spain (17%), Japan (8%), EC-France/Spain (8%), Venezuela (6%), Brazil (5%) (White Marlin Status Review Team, 2002). Combined, U.S. commercial and recreational fisheries account for less than 5% of the total reported fishing mortality (landings plus dead discards) for the Atlantic stock of white marlin (ICCAT, 2002).

Historically, the U.S. pelagic longline fishery has primarily targeted swordfish, yellowfin tuna, and bigeye tuna, and has also secondarily prosecuted fisheries on other marketable species including dolphin (*Coryphaena hippurus*), albacore (*Thunnus alalunga*), wahoo (*Acanthocybium solandri*), as well as several species of pelagic sharks (White Marlin Status Review Team, 2002). This multi-species fishery is opportunistic, switching gear style and deployment strategy to maximize the best available economic outcome of each trip (NMFS, 1999). Traditionally, longline gear is composed of a primary mainline, 5-40 miles in length, with roughly 20-30 hooks per mile connected to the mainline via gangions of monofilament (NMFS, 1999). The depth of the mainline and the fishing depths of hooks are determined by the length of the floatline, gangion length, ocean currents, and target species (NMFS, 1999). Longline sets targeting swordfish are generally deployed relatively shallow at night to capitalize on the epipelagic nocturnal feeding habits of swordfish. In contrast, longline sets targeting tunas are deployed in the morning and fish deeper in the water column. Longline gear is indiscriminate with respect to catch, and interacts with a variety of non-target species with little or no commercial value, including the istiophorid billfishes, and protected species such as sea turtles, marine mammals, and seabirds (NMFS, 1999). All undersized or protected species, including all billfishes, must be released dead or alive by U.S. commercial fishermen. White marlin dead discards from the U.S. pelagic longline fishery peaked at 107 MT in 1989, and have decreased to 40-60 MT in recent years (White Marlin Status Review Team, 2002).

Recreational sportfishing for billfish species has a long and storied history, with early 20th century writers including Zane Grey and Ernest Hemingway first popularizing angling pursuits of these animals (de Sylva, 1975). Sportfishing for Atlantic billfishes occurs on private recreational and charter vessels simultaneously trolling multiple lines rigged with dead baits or artificial lures (NMFS, 1999). Most of the recreational fishing effort targeting white marlin occurs seasonally in proximity to key fishing ports and tournaments along the U.S. East Coast, Gulf of Mexico, and in the Caribbean Sea (Prince et al., 1990). The white marlin fishing season begins in the early spring when concentrations of fish begin to arrive at locations in the Caribbean. White marlin move northward and are caught in large numbers along the U.S. East Coast as waters warm in late summer (NMFS, 1999). Autumn concentrations of white marlin are most notable in the southern Caribbean Sea. Landings of white marlin by U.S. recreational anglers are estimated through the combination of the Marine Recreational Fishery Statistics Survey (MRFSS), the Large Pelagics Survey (LPS), and the U.S. Atlantic Recreational Billfish Survey (RBS) (Goodyear et al., 2001). From 1960 to the mid 1980s, U.S. recreational landings of white marlin ranged between 40 and 110 MT. Since the late 1980s, the directed U.S. recreational fishery for white marlin interacts with an estimated 4,000-

8,000 individuals annually, with roughly 99% of those fish released (Goodyear and Prince, 2003). Over the same time period, 2-20 metric tons of white marlin have been landed by U.S. recreational fishermen (ICCAT, 2002).

Stock Status and Management

The increased exploitation of billfishes by commercial and recreational fisheries necessitates a more accurate understanding of the status of istiophorid stocks (Uozumi, 2003). International management of Atlantic tunas and billfishes falls under the purview of the International Commission for the Conservation of Atlantic Tunas (ICCAT). Population assessments of Atlantic istiophorids have historically applied a Schaefer non-equilibrium production model (Prager, 1995; ICCAT, 2002; Restrepo et al, 2003) that uses standardized sets of catch-per-unit-effort and landings data from several commercial and recreational fisheries to parameterize the stock (Goodyear, 2003; Uozumi, 2003).

Early assessments of white marlin (1992, 1996) conducted by the ICCAT Standing Committee for Research and Statistics (SCRS) modeled two separate stock scenarios: one incorporating separate northern and southern stocks with a 5 °N boundary and a single Atlantic-wide stock (ICCAT, 2001). Assessments using both approaches were conducted because of the absence of data elucidating the proper management unit. Inferences into the stock boundaries of white marlin have been obtained from longline catch data demonstrating their continuous distribution across the tropics during all quarters and from limited data recovered from conventional tagging programs. At least eight recaptured white marlin have shown trans-Atlantic movements (west to east) (Ortiz et al., 2003). Although no white marlin have demonstrated trans-equatorial movements, some have passed across the putative 5 °N two-stock boundary (Prince et al., 2001; Prince et al., 2003; Ortiz et al., 2003). Additionally, analysis of mitochondrial DNA and hypervariable nuclear microsatellite DNA loci suggests genetic connectivity of white marlin within the Atlantic Ocean and provides no evidence to suggest multiple stocks in this species (Graves and McDowell, 2001; Graves and McDowell, 2003).

Historic longline catch data demonstrating the distribution of white marlin across the tropics during all quarters, movements inferred from tag recoveries, and genetic data are all consistent with the management of *T. albidus* as a single Atlantic stock (ICCAT, 2001). In 2000 and 2002, white marlin population assessments were thus conducted with the assumption of a single Atlantic stock only. In the 2000 stock assessment for this species, the ICCAT SCRS estimated a biomass of 2,200 MT, less than 15% of that required for maximum sustainable yield (MSY), and a fishing mortality seven times greater than that expected at MSY (ICCAT, 2001). The 2002 SCRS white marlin stock assessment was even more pessimistic, indicating a biomass level less than 12% of that required for MSY and a current fishing mortality eight times greater than that expected at MSY under the continuity case (ICCAT, 2002). The assessment estimated the Atlantic stock of white marlin to be on the order of 200,000 adults subjected to recreational and commercial fisheries; however, there is a great deal of uncertainty about the assessment results (ICCAT, 2002).

There has been considerable debate surrounding the exact methodology used during assessments of billfish populations. The catch-per-unit-effort (CPUE) time-series used in these assessments have been affected by historical changes in fishing practices from shallow longline sets targeting yellowfin tuna to deeper sets targeting swordfish and bigeye tuna (Graves et al., 2003). The degree to which these changes have affected catch rates of target and bycatch species is presently unknown (Yokawa and Uozumi, 2001). Much controversy has centered around the specific methods used to account for these historical changes in fishing practices in the CPUE time-series used in assessments. Hinton and Nakano (1996) proposed a "habitat-based" model that standardizes catch rates in proportion to time billfishes spend at depth or temperature, an adjustment that accounts for historical differences in the depths of longline gear deployments. Data considered in this modeling procedure include billfish physiological and ecological parameters (depth and temperature preferences), oceanographic features, and longline fishing depths. Longline gear behavior parameters and billfish habitat data used in the model are from studies in the Pacific Ocean. The applicability of this modeling technique to Atlantic istiophorids is tenuous because there is currently a lack of data regarding depth and temperature preferences of Atlantic blue marlin and white marlin (Goodyear et al., 2003; Graves et al., 2003). This information is critical for valid assessment of the stock abundances of these species. Clearly, a better understanding of the manner in which white marlin use their habitat will improve the veracity of future population assessments, and the identification of methods to decrease white marlin fishing mortality will help slow the decline of the stock.

International and domestic management organizations rely on the release of live billfishes from commercial and recreational gears to reduce the fishing mortality on istiophorid stocks. The efficacy of these measures cannot be evaluated because little is known about the survival of released billfishes. Estimates of white marlin postrelease mortality are currently not incorporated into ICCAT landing statistics or assessments

(White Marlin Status Review Team, 2002), and all recreationally released billfish have been assumed to survive in the absence of better data (see Peel, 1995). For management measures which rely on live release to be successful in reduce the fishing mortality, an appreciable number of released white marlin must survive. Conventional tagging programs have not been successful in generating valid postrelease survival estimates for white marlin due to very poor reporting rates (Bayley and Prince, 1994; Jones and Prince, 1998; Ortiz et al., 2003). To date, neither acoustic tracking studies, nor those employing pop-up-satellite tags (PSATs) have assessed the survival of white marlin released from either recreational or commercial gears.

PSAT technology

The advent of satellite tracking technology has lead to the recent development of pop-up satellite archival tags, which measure and record environmental parameters while attached to an organism and then detach, float to the surface, and relay data to the satellites of the Argos system. Although fairly expensive, these tags eliminate the reliance on fishermen to return tags (conventional tags) or the need for a dedicated chase vessel to follow fish at sea (acoustic tracking). The development of pop-up satellite archival tag (PSAT) technology has significantly improved scientific understanding of the postrelease survival, behavior, and movements of highly migratory marine fishes including bluefin tuna, swordfish, blue marlin, striped marlin, and white sharks (Block et al., 2001; Sedberry and Loefer, 2001; Boustany et al., 2002; Graves et al., 2002; Domeier and Dewar, 2003; Kerstetter et al., 2003). PSAT technology was first used to study postrelease survival of billfishes by Graves et al. (2002), who demonstrated survival of at least eight of nine blue marlin for a period of five days after release from recreational sportfishing gear in the offshore waters of Bermuda. Kerstetter et al. (2003) subsequently applied this technology to blue marlin caught in the western north Atlantic on pelagic longline gear, and demonstrated that at least seven of nine blue marlin survived release for periods of five or thirty days.

Project objectives

This project has two main foci: an estimation of the survival of white marlin released from recreational fishing gear, and an elucidation of the habitat preferences and behavior of surviving white marlin. This study used the Microwave Telemetry PTT-100 HR tag model, which is programmed to record and archive a continuous series of temperature, light, and pressure (depth) measurements for fairly short intervals. Two tag types were used in this study: five tags were programmed to release after five days, recording measurements approximately every two minutes, while thirty-six tags were programmed to release after ten days, recorded measurements about every two minutes (n = 6 tags) or four minutes (n = 30 tags).

The first objective involved an overall estimation of the postrelease survival of white marlin. Survival of released white marlin was easily determined from three distinct lines of evidence provided by the satellite tags: water temperature and depth profiles, light level data, and net movement. Additionally, a secondary motivation of this objective was to assess differences in hooking locations and hook-induced trauma of white marlin caught on circle and straight-shank ("J") hooks to gain insights on the mechanisms affecting survival in this species. Recently, several studies have documented a reduction in hook-induced trauma and a concomitant increase in survival associated with the use of circle hooks in fisheries targeting a variety of fishes (see Lucy and Studholme, 2002). General working hypotheses for this objective are: (A) that most white marlin survive recreational release, and (B) the incidence of deep-hooking, tissue trauma, and mortality will be reduced with circle hooks.

The second objective of this project involved an elucidation of the habitat preferences and behavior of surviving white marlin. There is a lack of behavioral data from Atlantic istiophorids with which to test the applicability of recently-developed habitat-based standardization (HBS) models to assessments of white marlin and blue marlin. Goals of this objective are to elucidate the depth and temperature preferences, diving behavior, and diel patterns of white marlin across the four sampled locations. Null hypotheses for statistical analyses include: (A) there is no effect of diel period on dive depth, and (B) there are no differences in dive durations, depths, temperature gradients, or interdive intervals between locations.

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CHAPTER 1:

Application of Pop-up Satellite Archival Tag Technology to Estimate Postrelease Survival of White Marlin (*Tetrapturus albidus*) Caught on Circle and Straight-shank ("J") Hooks in the Western North Atlantic Recreational Fishery

INTRODUCTION

Atlantic white marlin (*Tetrapturus albidus* Poey 1860) are targeted by a directed recreational fishery and occur as incidental bycatch in commercial fisheries throughout the pelagic waters of the Atlantic Ocean. Total reported recreational and commercial landings of white marlin peaked at 4911 MT in the mid-1960s, declined steadily during the next 15 years, and have since fluctuated without trend between 1000 and 2000 MT despite substantial increases in fishing effort (ICCAT, 2002). Recent population assessments conducted by the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) indicate that the Atlantic-wide white marlin stock is currently at historically low levels and has been severely overexploited for over three decades (ICCAT, 2002). The 2002 white marlin assessment estimated the biomass in 2001 to be less than 12% of that required for maximum sustainable yield (MSY) under the continuity case (ICCAT, 2002). Current harvest is estimated to be more than eight times the replacement yield (ICCAT, 2002).

In response to the overfished status of white marlin, ICCAT has adopted binding international recommendations to decrease overall Atlantic landings of this species by 67% from 1996 or 1999 levels (whichever is greater) through the release of all live white marlin from commercial pelagic longline and purse seine gear (ICCAT, 2001). However, even these dramatic reductions may be ineffective in rebuilding the white marlin stock. Goodyear (2000) estimated that a 60% reduction from 1999 fishing mortality levels would be required to halt the reduction of Atlantic blue marlin (*Makaira nigricans*), and the more pessimistic white marlin population assessment suggests that the reduction in mortality required to stabilize this stock will likely be even greater.

Domestic management measures within the United States, established by the Atlantic Billfish Fishery Management Plan (FMP) (NMFS, 1988) and subsequent Amendment 1 (NMFS, 1999), have also been implemented to reduce white marlin fishing mortality. U.S. commercial fishermen have been prohibited from landing or possessing all Atlantic istiophorids since 1988. Dead discards of white marlin from the U.S. commercial pelagic longline fishery peaked at 107 MT in 1989, and decreased to 40-60 MT over the last several years (White Marlin Status Review Team, 2002). Management measures for U.S. recreational anglers include a minimum size of 66 inches lower jaw fork length (NMFS, 1999) and mandatory reporting of landed billfishes (NMFS, 2003). White marlin landings by U.S. recreational anglers ranged between 40 and 110 MT from 1960 to the mid-1980s (Goodyear and Prince, 2003) and decreased to about 2 MT in recent years. At present, over 99% of the 4,000-8,000 white marlin estimated to be caught annually by U.S. recreational fishermen are released (Goodyear and Prince, 2003).

The benefit of current management measures that rely on the release of white marlin cannot be evaluated because levels of postrelease survival are not known for this species. Recaptures rates of billfishes tagged with conventional tags are very low (0.4-1.83%; Prince et al., 2003; Ortiz el al., 2003), which may result from high postrelease mortality, tag shedding, or failure to report recaptures (Bayley and Prince, 1994; Jones and Prince, 1998). Little acoustic tracking has been conducted on white marlin (Skomal and Chase, 2002; n = 2 tracks), but similar work on other istiophorid species suggest relatively high postrelease survival from recreational fisheries for periods ranging from a few hours to a few days (e.g., sailfish: Jolley and Irby, 1979; blue marlin: Holland et al., 1990; Block et al., 1992; black marlin: Pepperell and Davis, 1999). However, data from acoustic tracking studies bear limitations and biases that preclude their use in estimating billfish postrelease survival (discussed in Pepperell and Davis, 1999; Graves et al., 2002). In the absence of better data, all recreationally released billfish have been assumed to survive (see Peel, 1995), and estimates of white marlin postrelease mortality are currently not incorporated into ICCAT landing statistics or assessments (White Marlin Status Review Team, 2002).

Developments in pop-up satellite archival tag (PSAT) technology have greatly improved scientific understanding of the behavior, movements and postrelease survival of highly migratory marine fishes including bluefin tuna (Block et al., 2001), swordfish (Sedberry and Loefer, 2001), white sharks (Boustany et al., 2002), blue marlin (Graves et al., 2002; Kerstetter et al., 2003), black marlin (Gunn et al., 2003), and striped marlin (Domeier and Dewar, 2003). To estimate the postrelease survival of billfishes, researchers have used PSAT deployment durations ranging from five days to seven months (Graves et al., 2002; Domeier and Dewar, 2003; Kerstetter et al., 2003). Goodyear (2002) cautions that longer duration deployments increase the potential for tag shedding, tag malfunction, and data corruption, and may bias postrelease survival estimates by including additional sources of mortality other than the capture event. Graves et al. (2002) considered five days to be an appropriate window to detect mortality in blue marlin released from recreational gear offshore of Bermuda, citing recaptures of blue marlin tagged with conventional tags within five days of the initial tagging event as evidence that some istiophorids may recover sufficiently to resume feeding shortly after capture.

Survival estimates of other istiophorid species released from recreational fishing gear may not be applicable to white marlin. One reason may involve body size: recreationally caught blue marlin and striped marlin are generally larger than white marlin. Secondly, the angling techniques used to catch certain istiophorid species differ. Blue marlin often hook themselves in the mouth and head while aggressively pursuing high speed trolled lures (Graves et al., 2002). In contrast, as white and striped marlin approach a specific baitfish in the trolling spread, many anglers free-spool (i.e., "drop-back") rigged natural baits to feeding marlin to imitate stunned baitfish (described in Mather et al., 1975). The use of natural baits rigged on traditional straight-shank ("J") hooks raises the probability of hook-induced trauma in vital internal areas including the gills, esophagus, and/or stomach (Prince et al., 2002a).

Recently, several studies have documented a reduction in hook-induced trauma associated with the use of circle hooks in fisheries targeting estuarine and pelagic fishes (see Lucy and Studholme, 2002). However, there is little research specifically comparing levels of postrelease survival of pelagic fishes caught on circle and straight-shank ("J") hooks. Prince et al. (2002a) and Skomal et al. (2002) examined hooking locations and injuries in sailfish and bluefin tuna, respectively, caught on both hook types, but lacked postrelease survival data from study animals. Domeier and Dewar (2003) did not detect a significant difference between striped marlin caught on circle and straight-shank ("J") hooks, although the authors did observe significantly decreased rates of deep-hooking and tissue trauma with circle hooks relative to straight-shank ("J") hooks.

This study used data recovered from PSATs to estimate the survival of 41 white marlin that were caught on circle and straight-shank ("J") hooks in the recreational fishery and released in the western North Atlantic Ocean during 2002-2003. Differences in hooking locations and hook-induced trauma of white marlin caught on circle and straight-shank ("J") hooks were assessed.

MATERIALS AND METHODS

Tags

The Microwave Telemetry, Inc. (Columbia, MD, USA) PTT-100 HR model PSAT tag was used in this study. This tag is slightly buoyant, measures 35 cm by 4 cm, and weighs <70 grams. The body of the tag contains a lithium composite battery, a microprocessor, a pressure sensor, a temperature gauge, and a transmitter, all housed within a black, resin-filled carbon fiber tube. Flotation is provided by a spherical resin bulb embedded with buoyant glass beads. This tag model is programmed to record and archive a continuous series of temperature, light, and pressure (depth) measurements, and can withstand pressure equivalent to a depth of 3000 m. Tags programmed to release after five days (n = 5) recorded measurements approximately every two minutes, while tags programmed to release after ten days (n = 35) recorded measurements about every four minutes. Additionally, both 5-day and 10-day tag models transmitted archived and real-time surface temperature, pressure, and light level readings to orbiting satellites of the Argos system for 7-10 days following release from study animals.

PSATs were rigged with an assembly composed of 16 cm of 400 pound test Momoi® brand (Momoi Fishing Co., Ako City, Japan) monofilament fishing line attached to a large hydroscopic, surgical grade nylon intramuscular tag anchor following Graves et al. (2002). Anchors were implanted with 10 cm stainless steel applicators attached to 0.3 m, 1 m, or 2 m tagging poles (the length of the tagging pole varied depending on the distance from a boat's gunwhales to the water) and were inserted approximately 9 cm deep into an area about 10 cm posterior to the origin of the dorsal fin and 5 cm ventral to the base of the dorsal fin (Fig. 1). In this region, the nylon anchor has an opportunity to pass through and potentially interlock with pterygiophores supporting the dorsal fin but well above the coelomic cavity (Prince et al., 2002b; Graves et al., 2002). When possible, a conventional tag was also implanted posterior to the PSAT.

Deployment

White marlin were tagged in the waters offshore of the U.S. Mid-Atlantic Bight, the Dominican Republic, Mexico, and Venezuela (Table 1). These locations were chosen based on vessel availability and seasonal concentrations of white marlin. All tagging operations were conducted on private or charter recreational fishing vessels targeting billfishes and tunas. White marlin were caught on 20-40 lb class sportfishing tackle and fought to a level of exhaustion consistent with typical recreational fishing practice. The first 41 white marlin caught and successfully positioned boatside were tagged. Care was taken to sufficiently quiet fish to facilitate optimal tag placement without causing excessive stress to study animals. When possible, crew members secured white marlin for tagging by holding them by the bill and dorsal fin in the water alongside the boat, a technique often used when controlling a billfish to remove hooks. On boats with high gunwhales that prohibited the billing of marlin, fish were leadered to the boat's side and moved into position for tagging when calm. Six hooked white marlin escaped after capture but prior to tagging due to the breaking of frayed leaders or hook slippage during this process. Hooks were removed when feasible; otherwise, they were left in the fish and the leader was cut as close to the animal as possible prior to release. Both are common practices in the recreational billfish fishery. During capture and positioning alongside tagging vessels, six white marlin were lethargic, unable to maintain vertical position in the water, and lost color. These six white marlin were resuscitated alongside the moving boat for 1-5 minutes prior to release, also a common practice in the recreational fishery.

Gear type, time to leader, total fight duration, fight behavior, hooking location, overall condition, estimated weight, and GPS coordinates of release were recorded for each tagged white marlin. Following Prince et al. (2002a), straight-shank ("J") hooks were defined as those with a point parallel to the main hook shaft, whereas circle hooks were defined as having a point perpendicular to the main hook shaft. All circle and straight-shank ("J") hooks were rigged using dead ballyhoo (*Hemiramphus brasiliensis*) as bait. Size 7/0 Mustad straight-shank ("J") hooks (models 9175 and 7731) were rigged with the hook exiting the ventral surface of the ballyhoo. Two models of circle hooks were employed in this study: Mustad Demon Fine Wire (model C39952BL, size 7/0; 5° offset, n = 9) and Eagle Claw Circle Sea (L2004EL, sizes 7/0-9/0; non-offset, n = 11). All circle hooks were rigged pointing upwards from the head of the ballyhoo (see Prince et al., 2002a). The rigging designations and fishing techniques unique to each hook type were maintained in this study to reflect the usual application of circle and straight-shank ("J") hooks in the white marlin fishery. Other than these differences, all handling, tagging, and recording methods were the same for both treatments.

Hooking locations were pooled into two categories: jaw/externally visible (including all lip-hooked, foul-hooked, and bill-entangled white marlin) and deep/not externally visible (including all white marlin hooked in the palate, gills, esophagus, and everted stomachs). Bleeding was recorded as present or absent, and the general location of bleeding was recorded when it was possible to identify the source.

Data Analysis

Survival of released white marlin was determined from three distinct lines of evidence provided by the satellite tags: water temperature and depth profiles, light level data, and net movement. Time series of water temperature, depth, and light level measurements taken every 2 minutes (5 day tags) or 4 minutes (10 day tags) were used to discriminate surviving from moribund animals. Net movement was determined as a minimum straight line distance traveled between the coordinates of the initial tagging event and the coordinates of the first reliable satellite contact with the detached tag (inferred to be the location of tag pop-up) using Argos location codes 1, 2, or 3 for the first or second day of transmission. In cases where tags did not report more precise location codes, an average of all location code 0 readings for the first day of transmission were used as a proxy for the location of tag pop-up. To determine the directions (and magnitudes) of observed surface currents in areas where fish were tagged, GPS coordinates (Argos location codes of 1, 2, or 3, or a daily mean of location code 0, for tags lacking these) were plotted for the 7-10 days that the tags were floating at the surface and transmitting data to satellites. All maps, tracks, and distances were generated using MATLAB version 6.5 (release 13.1) (Mathworks Inc, Natick, Massachussetts).

Cochran-Mantel-Haenszel (CMH) tests were used to address the effect of circle and straight-shank ("J") hooks on survival, hooking location, and the degree of hook-induced trauma. A Yates correction for small sample size was applied when expected cell frequencies were less than 5 (Agresti, 1990). The effect of fight time on survival was assessed with a Wilcoxon-Mann-Whitney exact test, with the null hypothesis that there was no difference in fight time between surviving and moribund white marlin. All statistical analyses were conducted using SAS version 8 (SAS Institute, Cary, NC). The lone non-reporting tag observed in this study was excluded from all subsequent analyses.

Additionally, bootstrapping simulations were conducted using software developed by Goodyear (2002) to examine the effect of sample size on the 95% confidence intervals of the release mortality estimates. Distributions of estimates were based on 10,000 simulations with an underlying release mortality of 35% for experiments containing 10-200 tags and no sources of error (e.g., no premature release of tags, no tagging-induced mortality, and no natural mortality).

RESULTS

Forty-one white marlin were tagged in four locations during 2002-2003 (Table 1). Information for each fish is summarized in Table 2. Fight times were fairly typical for this fishery (mean: 15.8 min, range: 3-83 min), although two animals required more than 30 minutes before they were sufficiently calm at boatside for tag placement. Overall, forty tags (97.6%) reported to the satellites of the Argos system and of these, thirty-seven tags remained attached to study animals for the full five- or ten-day duration. One five-day tag released prematurely from a surviving white marlin after 2.5 days, presumably due to poor attachment. This individual showed behavior similar to other surviving white marlin while the tag was attached, and was presumed to have survived for the purposes of this study. Additionally, two ten-day tags attached to moribund white marlin released from the carcasses prior to the expected date after spending an extended amount of time at a constant depth/temperature on the seafloor. Approximately 61% of data (range: 19-95%) were successfully transmitted from reporting tags.

Overall, 33 of 40 tags (82.5%) returned data consistent with survival of tagged animals over the duration of tag deployment. Water temperature and depth data recorded by the tags of surviving white marlin showed high levels of variability over the course of the entire tag deployment duration (Fig. 2A). In contrast, moribund white marlin (Fig. 2B) sank to the seafloor (237-1307 m) and to constant water temperatures (3.7-12.5 C), where they remained until tags released and floated to the surface. Five of the seven moribund white marlin died within the first six hours of release, including four animals that died within the first hour (Table 2).

The two white marlin that experienced the longest fight times (46 and 83 min) died more than 24 hours following release. White marlin VZ03-13 had a fight time of 46 minutes and died 27 hours after tagging, and DR02-04 had a fight time of 83 minutes and died 64 hours after tagging (Fig. 3). There was no significant difference in fight time between surviving (mean: 13.6, ± 7.3) and moribund white marlin (mean: 26.3, ± 28.6) (Wilcoxon-Mann-Whitney exact test, $Z = 0.4996$, $p = 0.62$), largely due to the high variability in the latter.

Hook type had a highly significant effect on the postrelease survival of white marlin (Fig. 4). Fish caught on circle hooks experienced significantly higher survival (20 of 20; 100%) than those caught on straight-shank ("J") hooks (13 of 20; 65%) (CMH $\chi^2=7.386$, $P < 0.007$). There were also highly significant differences in hooking locations and hook-induced trauma between hook types (Fig. 4). Odds ratios reveal that white marlin caught on straight-shank ("J") hooks were 41 times more likely to be hooked deeply (CMH $\chi^2=11.48$, $P < 0.001$) and over 15 times more likely to sustain hook-induced tissue trauma resulting in bleeding (CMH $\chi^2=8.3$, $P < 0.005$) than fish caught on circle hooks. Of the white marlin caught on straight-shank ("J") hooks, half were hooked in deep locations, and 70% of these fish were bleeding. Four of the seven observed mortalities were deep-hooked and bleeding fish. Overall, 56% of bleeding, 40% of deep-hooked, and 57% of deep-hooked and bleeding white marlin perished following release. In contrast, all white marlin caught on circle hooks were hooked in the jaw, and bleeding was only evident in a single animal in which the hook point exited the edge of the eye socket but did not damage the eye. Additionally, 20% (8 of 40) of the white marlin in this study became entangled in the line during the fight and were brought to the boat tail-first, a condition known as "tailwrapped". This phenomenon was equally distributed with respect to hook type. Five tailwrapped white marlin required resuscitation, and two tailwrapped white marlin hooked in the jaw with straight-shank ("J") hooks died.

Using the model developed by Goodyear (2002), the results of 10,000 simulated experiments deploying 10-200 tags at an underlying true mortality rate of 35% indicate that a dramatic increased in sample size is needed to improve the precision of mortality estimates (Fig 5). Approximate confidence intervals for an experiment deploying 20 tags on white marlin caught on straight-shank ("J") hooks range from about 15-59% (± 22% of the true value). Doubling the sample size (n = 40) decreases the 95% confidence intervals to ± 15% of the true value while quadrupling the number of tags (n = 80 PSATs) would reduce confidence intervals to ± 10% of the true value. More than 200 PSATs would have to be deployed to lower the confidence intervals to ± 5% of the true value.

The net displacement of released white marlin was variable among individuals and across locations, and was used as an independent line of evidence to assess survival. Surviving white marlin demonstrated movement patterns that cannot be explained by surface currents alone. Distances and directions of displacement are summarized in Table 2, while straight-line tracks of tagged animals and drifting tracks of transmitting tags are presented in Figures 6 and 7. White marlin tagged with 10-day PSATs moved an average of 101 (± 84) nautical miles (nmi) or 188 km (± 155) while those tagged with 5-day PSATs moved an average of 38.8 nmi (± 15.6) or 72 km (± 29).

DISCUSSION

The results of this study clearly indicate that hook type significantly affects the survival of white marlin released from recreational fishing gear. White marlin caught on circle hooks were much more likely to survive recreational release than those caught on straight-shank ("J") hooks. These results concur with previous research across a broad range of fishes spanning diverse recreational fishing techniques (Muoneke and Childress, 1994; Diggles and Ernst, 1997; Lukacovic and Uphoff, 2002; Malchoff et al., 2002; Zimmerman and Bochenek, 2002; Skomal et al., 2002). However, the results of this study contrast with those of Domeier and Dewar (2003), who noted differences in deep-hooking and bleeding of the closely-related striped marlin caught on circle hooks or "J" hooks but did not detect a significant difference in mortality between hook types. Differences between the two studies may result from disparity between the two species, specific bait types (white marlin were caught on dead baits in the present study, Domeier and Dewar (2003) used live baits), and/or sampling error. It should be noted that Domeier and Dewar (2003) and the present study both used non-offset and 5° offset circle hooks.

The survival rate observed with straight-shank ("J") hooks in this study (65%) is slightly lower than that reported for other istiophorid species (blue marlin 89%, Graves et al., 2002; striped marlin 71%, Domeier and Dewar, 2003) caught on these hooks. This observation may result from the smaller body size of white marlin relative to blue marlin and striped marlin. In addition, differences in the recreational fishing practices for these species could also account for the variation in levels of istiophorid postrelease survival.

In fisheries targeting striped marlin and white marlin, longer drop-back durations with natural baits rigged on "J" hooks increase the probability of deep-hooking and internal damage, which influence mortality. The postrelease mortality rates of white marlin and striped marlin from drop-back fisheries are similar, and are notably higher than that of blue marlin caught on high speed trolled baits.

The results of this study also agree with previous research documenting increased deep-hooking and tissue trauma associated with the use of straight-shank ("J") hooks. Relative to circle hooks, "J" hooks are over 20 times more likely to cause bleeding in sailfish (Prince et al., 2002a), five times more likely to cause bleeding in striped marlin (Domeier and Dewar, 2003), and 15 times more likely to cause bleeding in white marlin (this study). Slightly more than half of the bleeding white marlin and less than half of the deep-hooked fish caught on "J" hooks died in this study. Combined with observations of rusted hooks in the viscera of otherwise healthy istiophorids (Prince et al., 2002a), these data suggest that deep-hooking locations are not necessarily lethal. Furthermore, the results of the present study results also suggest that jaw hooking locations are not exclusively nonlethal. Straight-shank ("J") hooks can cause lacerations to vital organs including the eye, brain, pharynx, esophagus, and stomach before detaching from the initial hooking location and re-hooking in regions that are typically considered less lethal, including the jaw and bill (Prince et al., 2002a). These internal injuries are difficult to record without additional handling and internal examination, and confound relationships between hooking location and mortality in the absence of other predictors. Regardless, the significantly higher survival of white marlin caught on circle hooks, coupled with reduced rates of deep-hooking and tissue trauma, suggest that this terminal gear may decrease postrelease mortality rates in drop-back fisheries that currently use "J" hooks.

None of the white marlin caught on circle hooks in this study were deep-hooked. Despite documenting significantly lower deep-hooking rates with circle hooks, previous studies have nonetheless observed that both non-offset and 5° offset circle hooks may occasionally hook fish deeply (Prince et al., 2002a; Skomal et al. 2002). This is especially true of severely offset (e.g., 15°) circle hooks, which are highly associated with increased levels of deep-hooking and may mitigate any conservation benefits associated with the use of this terminal gear (Prince et al., 2002a).

Resuscitation of exhausted istiophorids is a common practice in the recreational fishery. Five white marlin which were tailwrapped and unable to ram-ventilate during the fight were resuscitated in this study. For example, white marlin MX03-03 was tailwrapped for the final seven minutes of the 21 minute fight and appeared to be severely exhausted at boatside. This fish was unable to regulate its position in the water when the PSAT was implanted, and required the longest resuscitation of any white marlin in this study (~5 min.). After release, a diver confirmed that this marlin regained color and actively swam away upon reaching cooler water at a depth of about 20 m (G. Harvey, pers. comm.). Depth and temperature data show that this fish survived for the entire 10-day tag deployment duration. Failure to revive any of the exhausted or tailwrapped white marlin in this study would have biased the mortality estimate upwards if any of these animals perished as a result of exhaustion.

It is unlikely that trauma induced by boatside handling or tagging contributed to the difference between the mortality of white marlin caught on circle hooks and "J" hooks. Domeier and Dewar (2003) suggested that two striped marlin in their study died as a result of striking the side of the tagging vessel rather than from hook-induced injury. We observed only one white marlin (DR02-01) strike the side of a tagging vessel; this fish survived and exhibited behavior similar to other healthy white marlin for the full five-day tag deployment duration.

The majority of mortalities observed in this study occurred within the first six hours of release; however two mortalities occurred more than 24 hours following release. Delayed postrelease mortality in some teleosts may be associated with intracellular acidosis following exhaustive exercise (Wood et al., 1983). After release, white marlin DR02-04 spent the majority of the first day within a few meters of the surface (Fig. 3A). Similar prolonged surface associations have been documented in blue marlin (Block et al., 1992) and striped marlin (Brill et al., 1993), a behavioral pattern that has been attributed to that of a badly injured fish (Brill et al., 1993). After 20 hours, white marlin DR02-04 resumed diving behavior similar to that observed in healthy tagged fish (Fig. 3B), suggesting possible recovery from catch-and-release. Post-exertion recovery in istiophorid billfishes is poorly studied, but Skomal and Chase (2002) reported significant perturbations in blood chemistry, including elevation in blood cortisol levels in bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), and white marlin exposed to prolonged angling bouts (mean = 46 min). The authors observed recovery periods characterized by limited diving behavior for two hours or less after release in the acoustic tracks of these animals. The mortality of white marlin DR02-04 after apparent recovery (Fig. 3C) may suggest natural mortality, the influence of another capture event, or that the act of feeding disturbed the hook, which was left in the animal, and caused additional injury.

We also cannot discount predation as a possible cause of mortality in any of the white marlin that died in this study. Acoustic tagging studies have described predation of tagged and released sailfish (Jolley and Irby, 1979), blue marlin (Block et al., 1992) and black marlin (Pepperell and Davis, 1999) by sharks. Recently, Kerstetter et al. (in press) observed results consistent with scavenging and predation of PSAT-tagged white marlin and opah (*Lampris guttatus*) by sharks. Both Block et al. (1992) and Kerstetter et al. (in press) documented attacks on tagged marlin exhibiting prolonged postrelease surface associations, the same pattern shown by DR02-04 immediately following release and again prior to mortality.

One tag (MA04) in this study failed to report and was eliminated from all analyses. Early PSAT studies (Graves et al., 2002; Kerstetter et al., 2003) approached the subject of non-reporting tags conservatively, considering tags that failed to report as mortalities. However, these studies used tag models rated to withstand pressure equivalent to a depth of 650 m, and neither was able to infer mortalities of animals based on returned data. In contrast, more recent PSAT models are rated withstand pressure equivalent to a depth of 3000m. Studies using newer models of PSATs have clearly documented several mortalities and have chosen to eliminate nonreporting tags from analyses (Domeier and Dewar, 2003; this study). Treating non-reporting tags as mortalities will incorrectly bias mortality estimates upwards if tags had failed to report for reasons other than catch-and-release induced mortality (Goodyear, 2002).

Relatively small sample sizes and fairly limited spatial coverage in this study preclude the use of these data to infer Atlantic-wide estimates of postrelease mortality rates in white marlin. Given the need to account for geographical differences in body sizes of white marlin, fishing gears, drop-back durations, angler skill level, habitat variables, predator densities, and locations, the sample size needed to generate an accurate estimate of postrelease mortality for the entire Atlantic recreational sportfishery could easily require more than a thousand tags (Goodyear, 2002). Results of simulated experiments suggest that if the true underlying J-hook mortality rate is 35%, more than 200 PSATs would have to be deployed on white marlin caught on this terminal tackle to reduce the 95% confidence intervals to ± 5% of the true value. The cost of such an experiment (~ $1million for tags alone) is presently prohibitive, especially considering that these estimates are derived under the assumption of ideal conditions (no premature releases, no tag-induced mortality, and no natural mortality) (Goodyear, 2002). The presence of any confounding factors would increase the necessary sample size and the total cost of such an experiment (Goodyear, 2002).

Despite a small sample size, the present study clearly demonstrates the importance of hook type to the postrelease survival of white marlin. Our results suggest that a highly significant proportion of released white marlin caught on straight-shank ("J") hooks perish, and that these hooks are significantly more likely to hook fish deeply and cause internal damage. In contrast, the survival of all white marlin caught on circle hooks suggests that a simple change in terminal tackle can significantly reduce postrelease fishing mortality in the recreational fishery.

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Table 1. Summary of white marlin (*Tetrapturus albidus*) tagging operations during 2002-2003.

Location	Dates of tagging	Tag deployment duration	Number deployed
Mid-Atlantic Coast, USA (MA)	2002: 18-22 Aug, 5-21 Sept	10-day	11
	2003: 22 Aug	10-day	1
Punta Cana, Dominican Republic (DR)	15-19 May, 2002	5-day	5
Isla Mujeres, Mexico (MX)	10-12 June 2003	10-day	3
La Guaira, Venezuela (VZ)	2002:23-25 Nov	10-day	6
	2003:12-13 Sept, 1 Oct.	10-day	15

Table 2. Summary information for tagged white marlin (*Tetrapturus albidus*) released from recreational fishing gear in the western North Atlantic Ocean. “D/N” refers to deep/not externally visible locations, “foul” refers to a white marlin hooked in the dorsal musculature. Tailwrapped fish are denoted with the symbol “^{T}”, resuscitated marlin are denoted with the symbol “^{R}”.

Tag #	Est. weight (kg)	Fight time (min)	Hook Type	Hook Location	Bleeding (Y/N)	Survive (Y/N)	Movement (nmi / km dir)
DR02-01	23	19	"J"	D/N	N	Y	23 / 43 NW
DR02-02	20	29	"J"	D/N	N	Y	39 / 72 NW
DR02-03	20	29	"J"	D/N	Y	Y	33 / 61 NE
DR02-04	25	83	"J"	D/N	Y	N	-
DR02-05	20	6	"J"	D/N	N	Y	60 / 111 SE
MA01	18	7	"J"	D/N	Y	N	-
MA02	20	24	"J"	jaw	N	Y	63 / 117 S
MA03	18	9	"J"	D/N	Y	Y	51 / 94 S
MA05	20	17	"J"	D/N	Y	Y	24 / 44 S
MA06	18	7	"J"	D/N	Y	N	-
MA07	20	7	"J"	jaw	Y	N	-
MA08$^{T, R}$	25	17	"J"	jaw	N	N	-
MA09	23	9	"J"	jaw	N	Y	103 / 191 NE
MA10	23	13	"J"	jaw	Y	Y	102 / 189 SE
MA11^{T}	27	16	"J"	jaw	N	Y	260 / 482 SE
MA12^{R}	23	5	"J"	jaw	N	Y	59 / 109SE
VZ02-01	27	8	circle	jaw	N	Y	118 / 219 NW
VZ02-02	23	12	circle	jaw	N	Y	80 / 148 NE
VZ02-03$^{T, R}$	20	4	circle	jaw	N	Y	69 / 128 NW
VZ02-04	18	9	circle	jaw	N	Y	63 / 117 NE
VZ02-05	20	7	circle	jaw	N	Y	67 / 124 N
VZ02-06	23	9	circle	jaw	N	Y	98 / 181 NW
MX03-01^{T}	27	15	circle	jaw	N	Y	172 / 319 NW
MX03-02	18	15	circle	jaw	N	Y	422 / 782 NW
MX03-03$^{T, R}$	23	21	circle	jaw	N	Y	211 / 391 NW
VZ03-01	20	3	circle	jaw	N	Y	85 / 157 NE
VZ03-02	30	6	circle	jaw	N	Y	127 / 235 NE
VZ03-03	23	12	circle	jaw	N	Y	16 / 30 N
VZ03-04	27	10	circle	jaw	Y	Y	114 / 211 NE
VZ03-05	34	23	circle	jaw	N	Y	40 / 74 W
VZ03-06	23	9	circle	jaw	N	Y	49 / 91 NE
VZ03-07	23	15	circle	jaw	N	Y	23 / 43 NE
VZ03-08	23	7	circle	jaw	N	Y	39 / 72 NE
VZ03-09^{T}	23	10	circle	jaw	N	Y	127 / 235 NE
VZ03-10$^{T, R}$	23	28	"J"	jaw	N	Y	81 / 150 NE
VZ03-11$^{T, R}$	23	46	"J"	foul	N	N	-
VZ03-12	18	23	"J"	jaw	N	Y	19 / 35 NW
VZ03-13	16	17	"J"	D/N	Y	N	-
VZ03-14	20	14	circle	jaw	N	Y	131 / 243 NW
VZ03-15	20	8	circle	jaw	N	Y	128 / 237 NE

Figure 1. White marlin (*Tetrapturus albidus*) tagged with a Microwave Telemetry PTT-100 HR pop-up satellite tag (A) and conventional streamer tag (B).

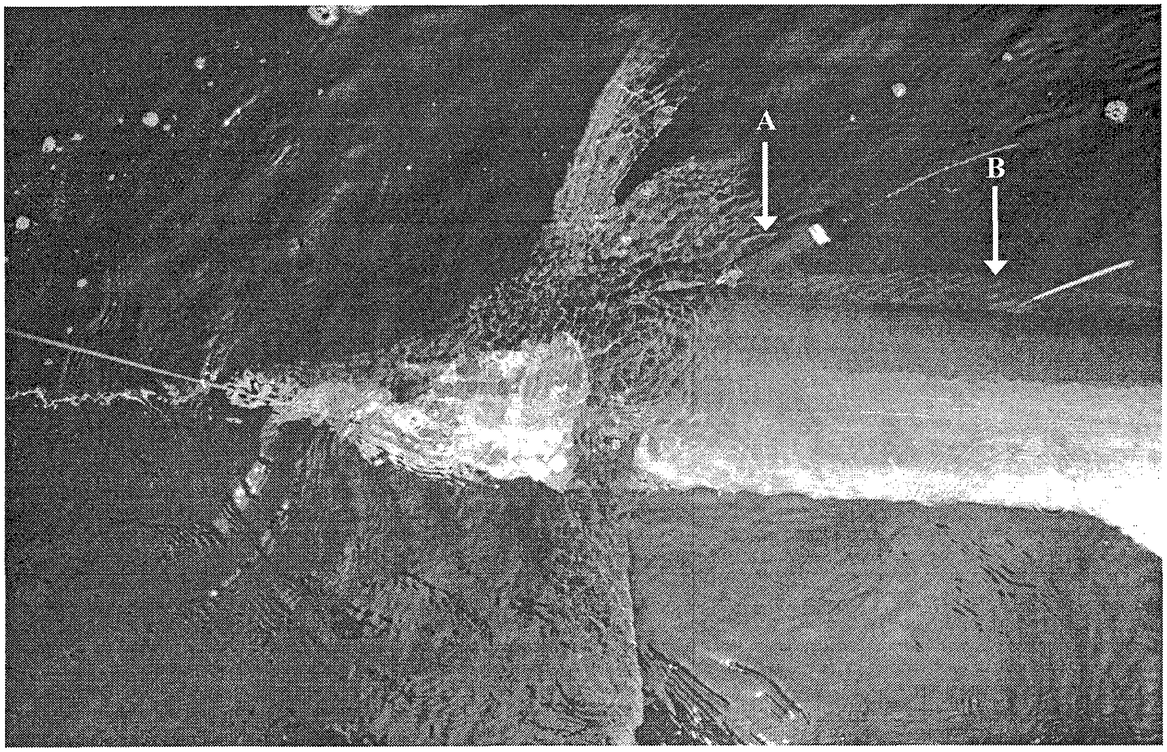
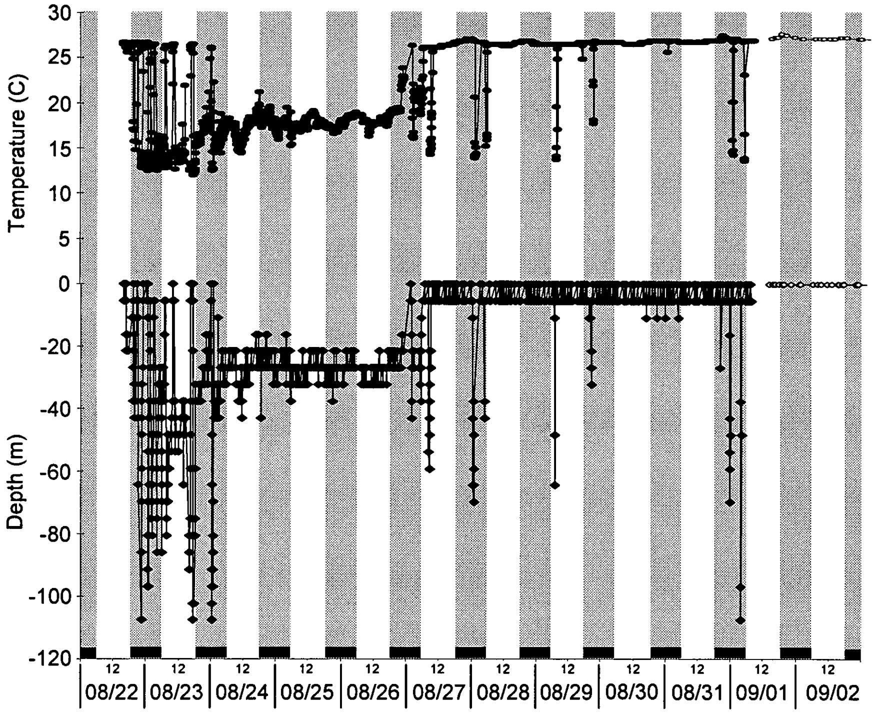

A
B

Figure 2. Depth and temperature tracks for a surviving (a: MA12) and a moribund (b: MA01) white marlin. Filled symbols correspond to two-minute or four-minute interval point measurements taken while tags were attached to animals, hollow symbols refer to measurements taken after tags released from the fish and were at the surface transmitting data to Argos satellites. Grey bars denote periods of local night.

a) Surviving white marlin



b) Moribund white marlin

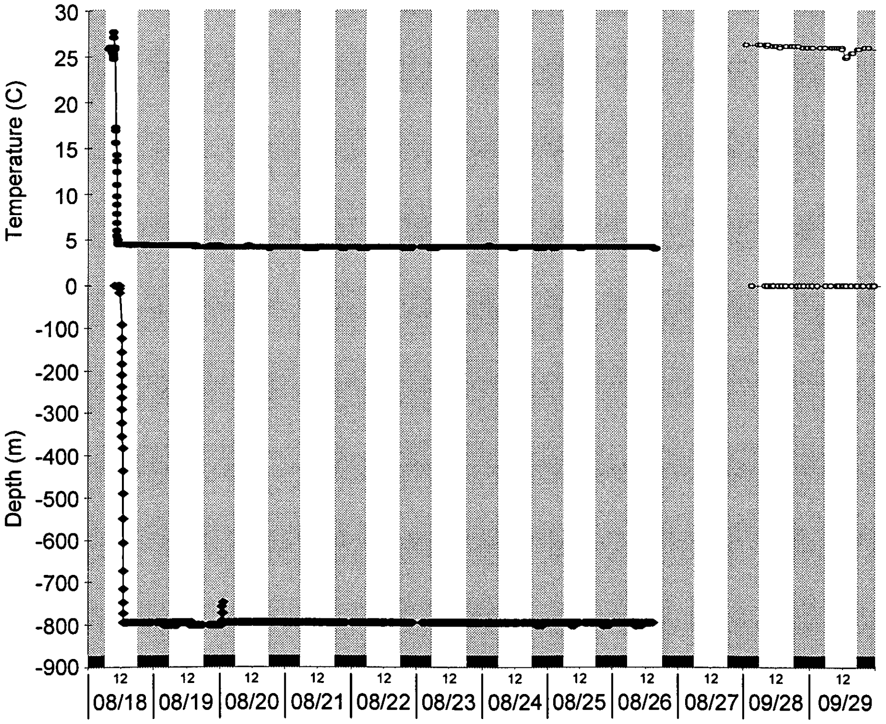


Figure 3. Track of DR02-04 showing mortality 64 hours after release, including (A) the first 20 hours following release, (B) the next 40 hours showing behavior similar to other surviving tagged marlin, and (C) the four hours prior to mortality.

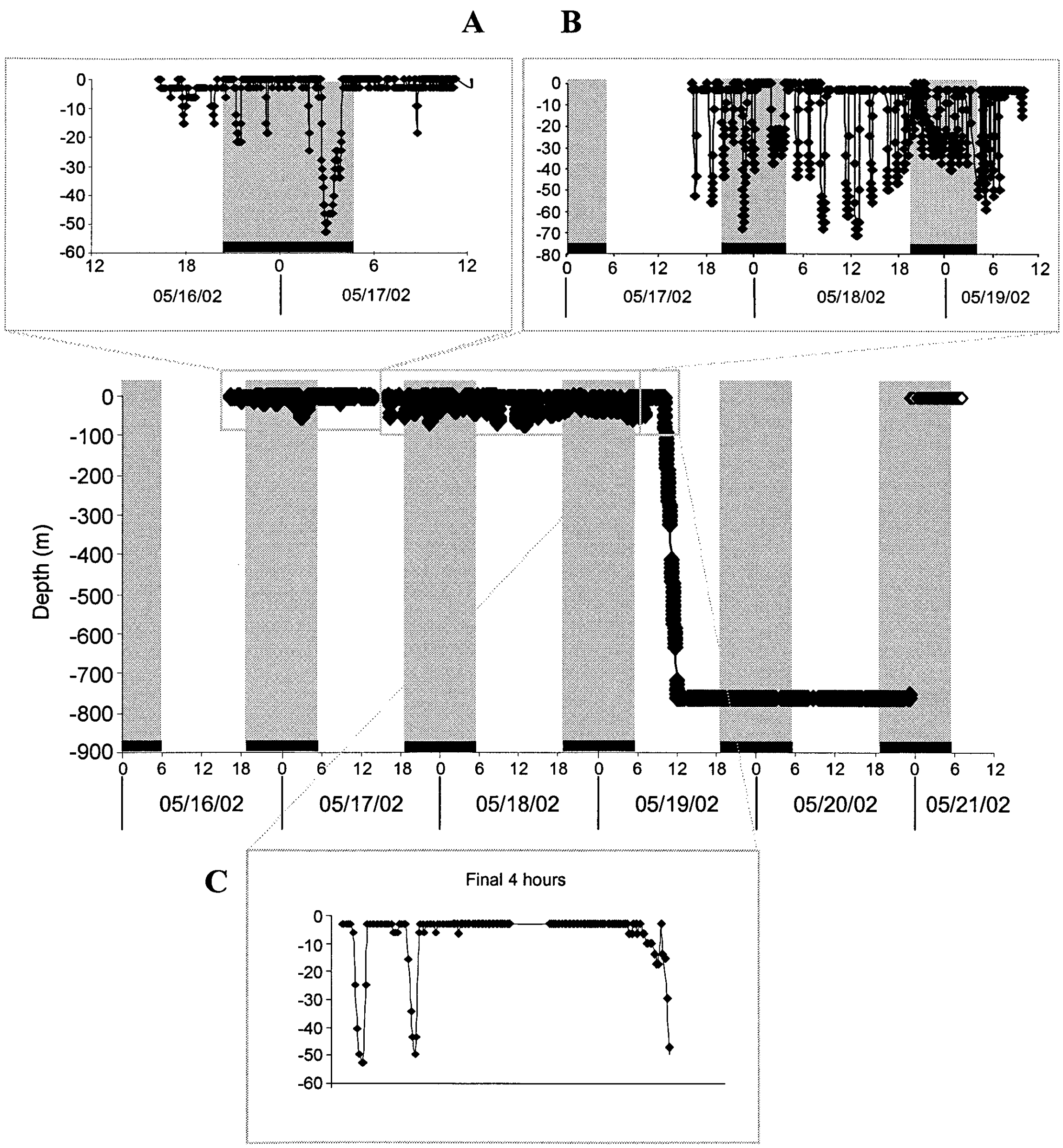

A
B
0
-10
-20
-30
-40
-50
-60
12
18
0
6
12
05/16/02
05/17/02
0
-10
-20
-30
-40
-50
-60
-70
-80
0
6
12
18
0
6
12
18
0
6
12
05/17/02
05/18/02
05/19/02
Depth (m)
0
-100
-200
-300
-400
-500
-600
-700
-800
-900
0
6
12
18
0
6
12
18
0
6
12
18
0
6
12
18
0
6
12
18
0
6
12
05/16/02
05/17/02
05/18/02
05/19/02
05/20/02
05/21/02
C
Final 4 hours
0
-10
-20
-30
-40
-50
-60

Figure 4. Effects of circle and straight-shank ("J") hooks on hooking location, trauma, and fate.

Hook Type	Hook Location	Bleeding	Fate	
"J" hook 20	Jaw/ext. visible 10 (50%)	No 8 (80%)	Live	6
			Dead	2
		Yes 2 (20%)	Live	1
			Dead	1
	Deep/ not ext. visible 10 (50%)	No 3 (30%)	Live	3
			Dead	0
		Yes 7 (70%)	Live	3
			Dead	4
Circle hook 20	Jaw/ext. visible 20 (100%)	No 19 (95%)	Live	19
			Dead	0
		Yes 1 (5%)	Live	1
			Dead	0
	Deep/ not ext. visible 0	No n/a	Live	n/a
			Dead	n/a
		Yes n/a	Live	n/a
			Dead	n/a

Figure 5. Effect of sample sizes ranging from 10-200 PSATs on the 95% confidence intervals for estimates of release mortality. Estimates were derived from 10,000 simulations per 10 or 20 tag increment using software developed by Goodyear (2002). The dashed line represents the underlying true value of 0.35.

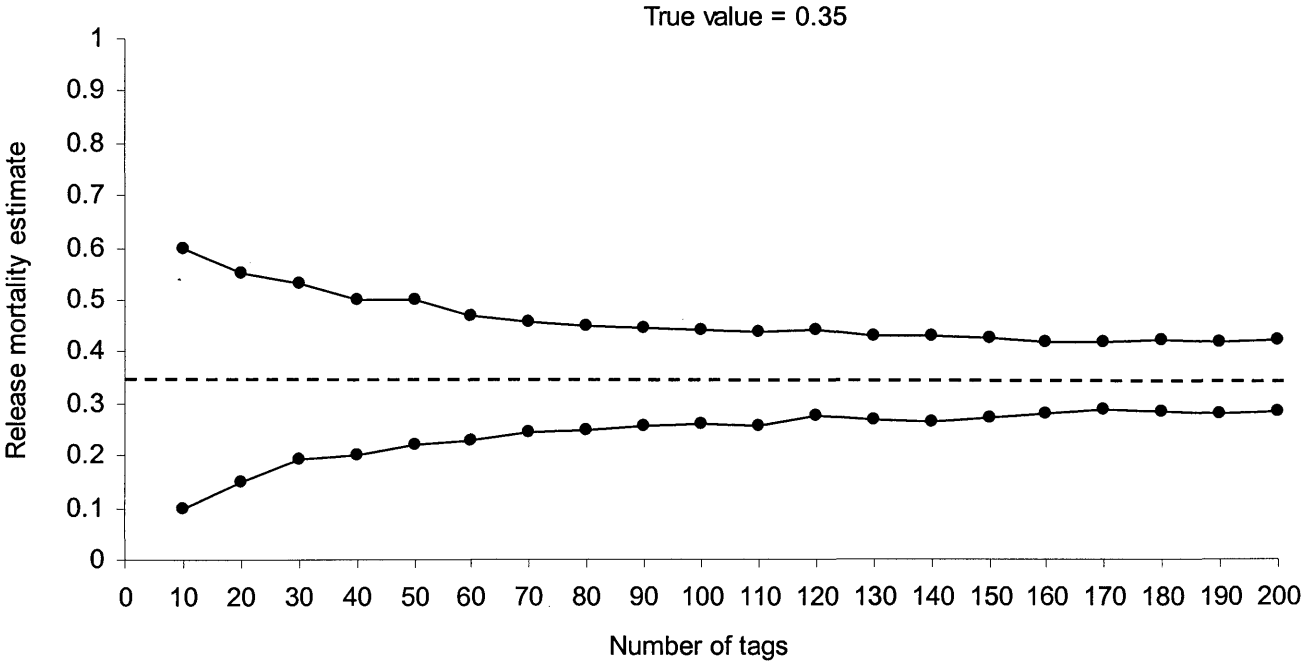
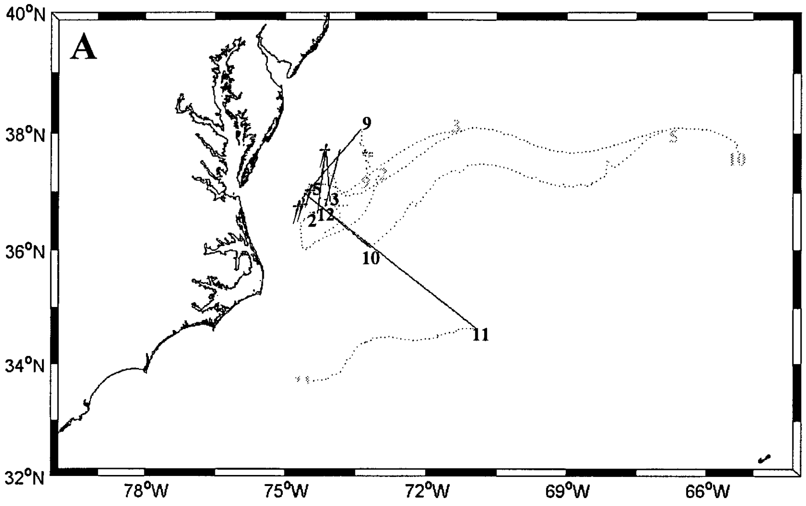
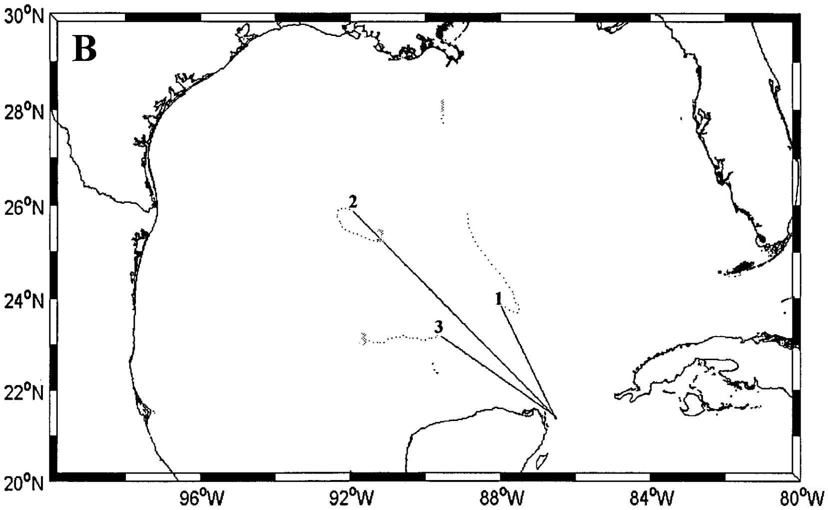

True value = 0.35
Release mortality estimate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
Number of tags

Figure 6. Minimum straight line distances traveled by white marlin (solid lines) and drifting tracks of transmitting tags (dotted lines) offshore of (A) the U.S. Mid-Atlantic (2002-2003), (B) Isla Mujeres, Mexico (2003), and (C) Punta Cana, Dominican Republic (2002). Crosses denote mortalities in A ($n = 4$) and C ($n = 1$).

Mid Atlantic White Marlin 2002-2003



Mexico White Marlin - June 2003



Dominican Republic White Marlin - May 2002

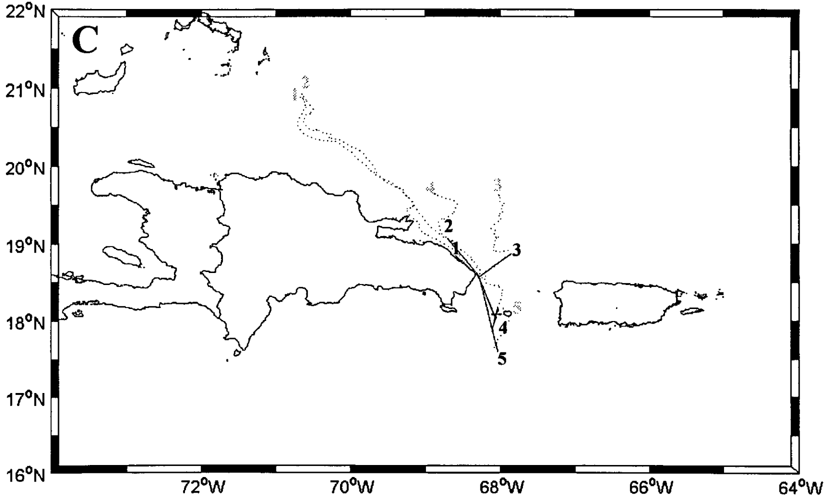
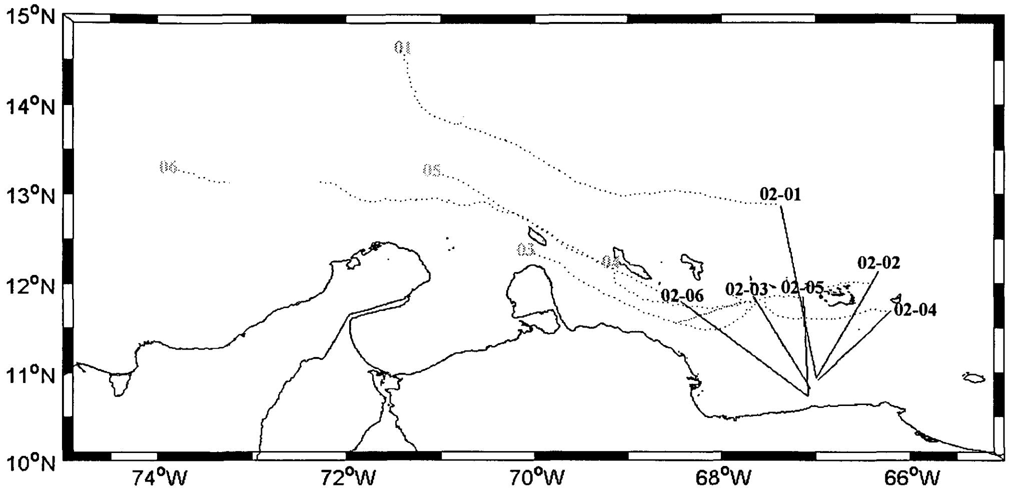
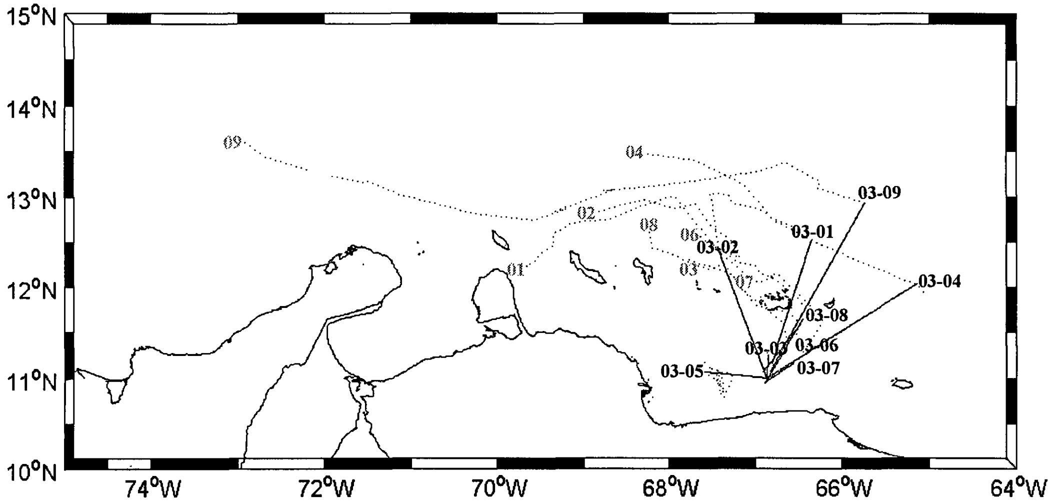


Figure 7. Minimum straight line distances traveled by white marlin (solid lines) and drifting tracks of transmitting tags offshore (dotted lines) of Venezuela in September, October, and November. Crosses denote mortalities in October (*n* = 2).

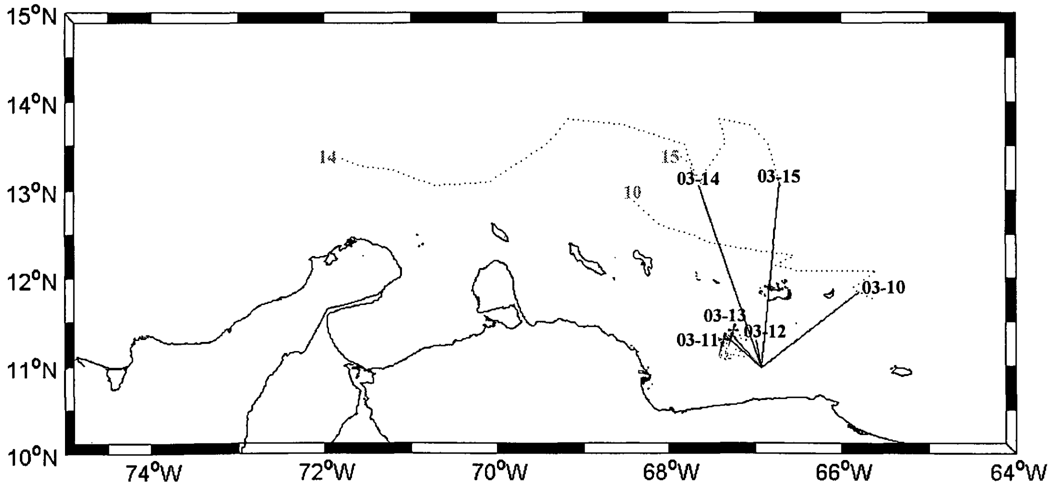
Venezuela White Marlin - November 2002



Venezuela White Marlin - September 2003



Venezuela White Marlin - Oct 2003



CHAPTER 2:

Habitat Preferences and Diving Behavior of White Marlin (*Tetrapturus albidus*) Released from Recreational Fishing Gear in the Western North Atlantic Ocean

INTRODUCTION

Billfishes are taken in directed recreational and artisanal fisheries and occur as incidental bycatch in commercial pelagic longline gear targeting tunas and swordfish. Although billfish bycatch comprises a small fraction of the total catch of the pelagic longline fishery, this gear accounts for the majority of istiophorid fishing mortality (ICCAT, 2001; Kerstetter et al., 2003). Within the Atlantic Ocean, stocks of several billfish species are considered to be overfished, with harvests exceeding replacement yield (ICCAT, 2001; ICCAT, 2002). For example, Atlantic blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) populations decreased dramatically in the 1960s, declined steadily during the next 15 years, and have since fluctuated without trend despite substantial increases in fishing effort (ICCAT, 2001). Recent assessments conducted by the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) suggest that the biomass of Atlantic blue marlin may be as low as 40% of that necessary for maximum sustainable yield (MSY) and white marlin biomass may be less than 12% of that required for MSY under the continuity case (ICCAT, 2001; ICCAT, 2002).

The increased exploitation of billfishes by commercial and recreational fisheries necessitates a more accurate understanding of the status of istiophorid stocks (Uozumi, 2003). Population assessments of Atlantic istiophorids have historically applied a Schaefer non-equilibrium production model (Prager, 1995; ICCAT, 2002; Restrepo et al, 2003) that uses standardized catch-per-unit-effort and landings time-series from five commercial fisheries (including pelagic longline, gill net, and purse seine) and two recreational rod-and-reel fisheries (Goodyear, 2003; Uozumi, 2003). Changes in CPUE in these time-series presumably reflect changes in the relative abundances of blue marlin and white marlin stocks (Goodyear, 2003). However, the CPUE time-series used in these assessments may be affected by historical changes in fishing practices. Specifically, pelagic longline gear deployments shifted from shallow sets targeting yellowfin tuna to deeper sets targeting swordfish and bigeye tuna in the 1970s (Graves et al., 2003). The degree to which these changes have affected catch rates of target and bycatch species is presently unknown (Yokawa and Uozumi, 2001).

There has been considerable debate during recent assessments of Atlantic istiophorids on the appropriate methods to standardize CPUE for historical changes in fishing practices. Most of the data series used in the assessments have been standardized with generalized linear models (GLM) to remove the possible effects of spatial changes in the fishery, target species, and gear-use parameters; however, it should be noted that resulting CPUE data do not always fit well to the Schaefer production model (Babcock and McAllister, 2003). Hinton and Nakano (1996) proposed a "habitat-based standardization" (HBS) model to weight CPUE in proportion to the amount of time target and bycatch species, such as billfishes, spend at the depth or temperature at which pelagic longline gear is set. This model incorporates oceanographic features, longline fishing depth, and billfish physiological and ecological parameters (depth and temperature preferences), and makes the fundamental assumption that feeding motivation is constant over time, all depths, and all temperatures (Graves et al., 2003). In simulations, the HBS model approach has produced results comparable to those of GLM modeling when assumptions used in the analyses were explicitly correct, but has produced strongly biased results when assumptions in the model were incorrect (Goodyear, 2003). Currently, the application of the HBS model to assessments of Atlantic istiophorids is a tenuous endeavor because it is based on limited habitat data from Pacific billfish species.

Studies using acoustic and pop-up satellite tags (PSATs) have shown that Pacific istiophorids spend the majority of their time in the upper 10 m of the water column in temperatures generally ranging from 25-27 °C (blue marlin *Makaira nigricans*: Holland et al., Block et al. 1992a; striped marlin *Tetrapturus audax*: Brill et. al, 1993; black marlin *Makaira indica*: Pepperell and Davis, 1999; Gunn et al., 2003). There is currently a paucity of data regarding depth and temperature preferences of Atlantic istiophorids. Two studies using acoustic telemetry have tracked white marlin (*T. albidus*: Skomal and Chase, 2003) and Atlantic sailfish (*Istiophorus platypterus*: Jolley and Irby, 1979) to assess recovery from exhaustion and evaluate postrelease survival, respectively, but provided little information regarding the habitat-use of study animals. Preliminary data from PSAT tagging studies conducted on Atlantic blue marlin have generally supported the association of this species with warm surface waters, but differences have been noted within and among individuals (Graves at al., 2002; Kerstetter et al., 2003). Until further information regarding habitat preferences and feeding behavior of Atlantic istiophorids is available, results from HBS modeling should be viewed with caution (Graves et al., 2003).

This study presents habitat-use data from 33 surviving white marlin caught on recreational fishing gear in the western North Atlantic Ocean between 2002-2003. The model of PSAT deployed in this study archived and reported sequential point measurements of depth and temperature over short time intervals, allowing the reconstruction of actual time-series tracks of tagged fish. These time-series were analyzed for insight into the habitat preferences and diving behavior of white marlin. The applicability of these results to recent attempts at developing a habitat-based stock assessment model for istiophorid billfishes in the Atlantic are discussed.

MATERIALS AND METHODS

The Microwave Telemetry, Inc. (Columbia, MD, USA) PTT-100 HR model PSAT tag was used in this study. The design and rigging of tags are discussed in Chapter 1. Tags recorded all times as Greenwich Mean Time (GMT); time-series were thus adjusted to reflect the local time at each respective tagging location. This model of tag is programmed to record and archive a time-series of temperature, light, and pressure (depth) measurements, and can withstand pressure equivalent to a depth of 3000 m. Pressure sensors recorded data in 5.4 m intervals and were accurate to within ± 2.5 m. Temperature sensors were accurate to ± 0.2 °C. Tags programmed to release after five days (n = 5) recorded measurements approximately every two minutes (mean 1.6 min), while tags programmed to release after ten days recorded measurements about every two minutes (n = 6, mean: 1.6 min) or four minutes (n = 29, mean: 3.2 min). Additionally, both 5-day and 10-day tag models transmitted archived and real-time surface temperature, pressure, and light level readings to orbiting satellites of the Argos system for 7-10 days following release from study animals. Archived data were transmitted from tag to satellite serially in clusters of nine consecutive data points.

Forty-one PSATs were attached to white marlin released from recreational fishing gear from May 2002 to October 2003. White marlin were tagged in the waters offshore of the U.S. Mid-Atlantic Bight, the Dominican Republic, Mexico, and Venezuela (Table 1). Fish were caught using dead ballyhoo (*Hemiramphus brasiliensis*) rigged on either circle (*n* = 20) or straight-shank ("J") hooks (*n* = 21) and were fought to a level of exhaustion consistent with typical recreational fishing practice on 20-40 lb class sportfishing tackle. Fish were brought alongside of the vessel, and tags were implanted in the musculature below the dorsal fin but above the body cavity. Forty tags (97.6%) reported to the satellites of the Argos system, and 33 tags returned data consistent with survival of tagged animals over the duration of tag deployment (see Chapter 1). All moribund animals were excluded from habitat analyses.

Data Analysis

Net movement was estimated as a minimum straight line distance traveled between the coordinates of the initial tagging event and the coordinates of the first reliable satellite contact with the detached tag (inferred to be the location of tag pop-up) using Argos location codes 1, 2, or 3 for the first or second day of transmission. In cases where tags did not report more precise location codes, an average of all location code 0 readings for the first day of transmission were used as a proxy for the location of tag pop-up. Directions (and magnitudes) of observed surface currents at all tagging locations were determined from the GPS coordinates (Argos location codes of 1, 2, or 3, or a daily mean of location code 0, for tags lacking these) of floating, transmitting tags. All maps, tracks, and distances were generated using MATLAB version 6.5 (release 13.1) (Mathworks Inc., Natick, Massachussetts). Sea surface temperature data from the U.S. Mid-Atlantic Coast were obtained from Pathfinder Advanced High Resolution Radiometry (AVHRR) satellites, and were assembled as a composite monthly image for September 2002. These data were obtained via the Physical Oceanography Distributed

Active Archive Center's (PO.DAAC) online PO.DAAC Ocean ESIP Tool (POET), maintained by the NASA Jet Propulsion Laboratory, Pasadena, CA. http://podaac.jpl.nasa.gov/poet.

Depth and temperature preferences were summarized in 10 m and 1°C interval histograms. Overall time-at-depth and time-at-temperature distributions featured data pooled from all 33 surviving white marlin. Time-at-depth and time-at-temperature histograms were also generated for each tagging location by pooling the distributions of all fish tagged at that location. In both cases, frequency data for each individual fish was weighted to equalize the contribution of each individual. This was done by comparing the number of archived data points successfully transmitted from a respective tag to the total number of data points transmitted by all white marlin tags included in a respective analysis. Standard errors were calculated from the weighted frequencies.

Potential diel differences in diving behavior were characterized for each surviving white marlin. Day and night designations were defined from light level data recovered from tags and were referenced against times of local sunrise and sunset for accuracy. Crepuscular periods featuring a change in ambient light levels readings corresponding to a transition from daylight to nightfall or vice-versa (e.g., sunrise and sunset) were removed from this analysis following Kerstetter et al. (2003). These periods generally lasted about an hour. Minimum, maximum, and mean depths were recorded for each day and night. Diel differences in diving behavior were assessed with Student's *t* tests performed on mean depths for all days and nights for each individual. One time-series that violated the homogeneity of variance assumption of Student's *t* test was assessed with a modified *t* test using Satterthwaite's degrees of freedom correction (Satterthwaite, 1946). The Satterthwaite *t* test is robust to violations of variance assumptions, especially if sample sizes are equal or nearly equal (Ramsey, 1980; Johnson, 1995; Zar, 1999). These statistical analyses were conducted using SAS version 8 (SAS Institute, Cary, NC). Days for which all data in a diel bin (day or night) were missing, and days featuring badly unbalanced distributions of data points in diel bins (more than three times as many data points in one bin) were removed from analyses. Because 33 total diel analyses were performed, significance was assessed at an alpha level of 0.01 to decrease Type I error.

Daily diving behavior was also characterized for each individual. A cursory visual examination of time-at-depth tracks revealed two classes of diving behavior, arbitrarily called Type 1 and Type 2 dives. Type 1 dives were characterized as deep "v"-shaped excursions of relatively short duration (3-83 minutes) with white marlin generally spending less than 10 minutes at the maximum depth. Type 2 dives were more broadly "u"-shaped, showing behavior confined to a specific depth range (±30 m) for an extended period of time (17-1140 minutes). The time spent on the surface between dive events was considered to be the interdive interval. It should be noted that interdive intervals did not always precede or succeed every dive. Figure 1 provides examples of these daily dive patterns observed in white marlin. The entire five or ten day track of each animal was surveyed for complete dives; excursions with missing packets of data were excluded from all analyses. The sample 24 hour period represented in Figure 1 featured three complete Type 1 dives, two complete Type 2 dives, and five complete interdive intervals. It should be noted that there were differences in the frequency and nature of daily dive patterns within the track of a given individual and among individuals. Additionally, data reporting rates varied between tags, thus not all diving events were successfully transmitted. Four surviving animals tagged with ten-day PSATs were also excluded from dive behavior analyses because their tags recorded data every two minutes and transmitted few complete dives, potentially biasing the transmission rates of longer dives.

Dive type, duration, maximum depth, temperature gradient encountered on a dive, and interdive interval were recorded for all complete dives undertaken by every surviving white marlin. Means and standard deviations of these observations were calculated for each fish. These data were then pooled by location, and mean and standard deviation values were weighted by the proportion of dives contributed by a specific animal out of the total number of dives undertaken by all white marlin at a given location. Kruskal-Wallis tests were used to examine differences in dive durations, dive depths, temperature gradients, or interdive intervals among locations. Tests were repeated for both Type 1 and Type 2 dives. The frequency data were subsequently pooled across all surviving white marlin and weighted by the percentage of dives contributed by a specific animal out of the total number of dives (n = 1918 complete Type 1 dives, n = 141 complete Type 2 dives) undertaken by all surviving white marlin. All statistical analyses were conducted using SAS version 8 (SAS Institute, Cary, NC).

Additionally, the relative change of water temperature with depth was assessed as the difference between sea surface temperature and the minimum temperature reached on every completely transmitted Type 1 and Type 2 dive. The resulting temperature distribution was summarized in a 1°C interval histogram.

RESULTS

Forty-one white marlin were tagged in four locations in the western North Atlantic Ocean during 2002-2003 (Table 1). Overall, forty tags (97.6%) reported to the satellites of the Argos system and of these, thirty-seven tags remained attached to study animals for the full five- or ten-day duration. One five-day tag released prematurely from a surviving white marlin after 2.5 days, presumably due to poor attachment. This individual exhibited behavior similar to other surviving white marlin while the tag was attached, and the data from this fish was included in habitat analyses for the purposes of this study. Based on analyses of depth, temperature and light level data, it was inferred that 33 of 40 (82.5%) reporting tags returned data consistent with survival. All moribund animals were excluded from analyses. An average of 61percent (range: 19-95%) of the total archived data points were recovered for each tag.

Movements

The magnitude of movement away from tagging coordinates was variable among individuals and between locations. Analysis of minimum straight line distances revealed that tagged white marlin dispersed 16-422 nautical miles (mean: 9.56 nmi/day) from tagging coordinates. Fish tagged with five-day tags moved an average of 0.3 nmi/hr (7.75 nmi/day average; range: 4.6-12 nmi) while those tagged with ten-day tags moved an average of 0.42 nmi/hr (9.8 nmi/day average; range: 1.6-42.2 nmi). The magnitude of displacement varied between locations.

Offshore of the U.S. Mid-Atlantic, surviving white marlin tagged with ten-day tags dispersed 24-260 nautical miles (2.4-26 nmi/day) from tagging locations (Fig 2). Fish tagged in August (mean displacement: 49.3 nmi ± 17.6) tended to move in a southerly direction while the heading of those tagged in September (mean displacement 155 nmi ± 90.9) was greater in magnitude and assumed a more easterly component. Drifting tracks of tags transmitting in the waters of the U.S. Mid-Atlantic were variable in heading and magnitude. Tags MA03, MA05, and MA10 became entrained in the Gulf Stream system, and most Mid-Atlantic tags drifted northeast while transmitting data. Exceptions include tag MA09, which presumably became entrained in an eddy and drifted due south, and tag MA11, which drifted southwest. Tags MA01 and MA06, attached to moribund white marlin, were recovered along the beaches of Oregon Inlet, North Carolina nearly a month after they ceased transmitting.

White marlin tagged offshore of Isla Mujeres, Mexico exhibited the largest minimum straight line distances in this study, displacing 172-422 nautical miles (17.2-42.2 nmi/day) in a northwesterly direction (Fig 3) over ten days. Coordinates of drifting tags suggest that tag MX03-01 was entrained in a strong northerly current. Tag MX03-02 appeared to be entrained in an eddy and drifted southeast. Tag MX03-03 moved nearly due west as it transmitted.

Data recovered from five-day tags deployed offshore of the Dominican Republic indicate that white marlin traveled a minimum of 23-60 nautical miles (4.6-7.8 nmi/day) from their tagging locations. Two white marlin moved northwest in the direction of the prevailing current, one moved northeast and two moved southeast (Fig. 4). Tags DR02-01 and DR02-02 appear to have been entrained in the same northwesterly current after release. Tags DR02-03 and DR02-04 drifted in a northerly direction while transmitting. Tag DR02-05 appears to have drifted onto the southern shore of Isla Mona, Puerto Rico on 4 June 2002, which presumably explains why this tag abruptly ceased transmitting data on that date.

White marlin carrying ten-day tags offshore of Venezuela displaced 16-127 nautical miles in September (mean 68.9 ± 44.8), 128-131 nautical miles in October, and 63-118 (mean 82.5 ± 21.5) nautical miles in November (Fig. 5). Venezuelan white marlin moved an average of 1.6-13.1 nmi/day over the ten day period. The prevailing direction of travel for most fish in September was northeasterly, and ranged from northeast to northwest in October and November. Drifting tracks of transmitting tags suggest that the predominant current direction along the shores of Venezuela is easterly, and that the dominant current direction offshore of La Guaira Bank is westerly.

Depth and Temperature Preferences

White marlin demonstrated a strong association with warm surface waters. Differences in depths and temperatures selected by white marlin were noted between days in the tracks of individuals. Pooled depth data suggest that white marlin generally spent over 40 percent (range: 17.5-67.8%) of their time in the upper 10 m of the water column (Fig. 6), but the time-at-depth distributions varied between locations (Fig. 7 A-D). The marlin tagged offshore of the U.S. Mid-Atlantic (Fig. 7A) spent the largest amount of time (55 %) in the upper 10 m of the water column. Fish tagged offshore of the Dominican Republic (Fig. 7B: 41.6%), Mexico (Fig. 7C: 34.5%) and Venezuela (Fig 7D: 41%) spent considerably less time associated with the upper 10 m. At all locations, white marlin spent less time in the 10-20 meter strata (range: 4.8-11.4%) than in the 20-

30 m range (9.5-17.3%). This difference was most pronounced in the Mid-Atlantic (Fig. 7A) and Venezuela (Fig. 7D). White marlin spent 30.3-48.2 percent of their time at depths ranging from 20-80 m.

Pooled temperature data suggest that white marlin spend 85.1 percent of their time in water temperatures ranging from 24-29ºC (Fig. 8), which encompasses the range of sea surface temperatures (SST) during tagging activities (Table 1: 24.0-29.7 ºC). Time-at-temperature distributions varied by location, and modal temperatures generally increased southward. Mid-Atlantic white marlin (Fig. 9A) featured a slightly bimodal temperature distribution, spending over 69 percent of their time between 23-26 ºC (mode: 26 ºC, 32.8%), and 8.4 percent of their between 16-18 ºC. Temperature preferences of marlin tagged offshore of the Dominican Republic (Fig. 9B) were the most constrained of any location in this study, with 91.8 percent of all observations between 23-27 ºC (mode: 27 ºC, 29.4%). White marlin tagged offshore of Mexico (Fig. 9C), spent 59.4 percent of their time in temperatures between 25-28 ºC (mode: 28 ºC, 24.7%). Finally, Venezuelan white marlin (Fig. 9D) spent 79.8 percent of their time in waters ranging from 24-28 ºC (mode: 27 ºC, 23.8%).

With respect to depth, significant diel patterns were evident for six of 33 individuals (Table 2). Of these, mean depths of four white marlin were significantly deeper during daylight hours and two animals were significantly deeper at night. All of the white marlin showing significant diel differences in mean depth were tagged offshore of Venezuela. It should be noted that contrasting patterns (deeper at night, shallower during the day and vice versa) were often observed within and among individuals, and that a particular diel dive pattern rarely persisted throughout the entire track for any individual. One exception to this observation was white marlin DR02-02 (Fig 10), which moved extensively throughout the water column during the day and directed the majority of its efforts between 20-60 m during night hours for the entire five day tracking period.

Data recovered from some white marlin tags reveal other distinct subsets of behavior. White marlin MA12 (Fig. 11) showed three distinct patterns of behavior during its ten-day track. During the first two days of this animal's track, it moved extensively through the upper 100 m of the water column. Subsequently, three consecutive days were spent almost exclusively between 20-40 m, and then this white marlin rarely left the upper 10 m of the water column during the final five days of the tag deployment. The track of white marlin MA09, which displaced 260 nmi southeast of the tagging location, shows elevated temperature readings despite increases in dive depth on the ninth day of the tag deployment (Fig 12). Combined, the depth, temperature, and net displacement data strongly suggest that this fish appeared to change its diving behavior as it moved from cooler coastal waters off Virginia into the warmer, oceanic waters of the Gulf Stream.

Analysis of daily dives indicate that all surviving white marlin exhibited Type 1 and Type 2 dive behaviors. All white marlin made frequent, short duration dives, many of which exceeded 100 m in depth. The maximum depths attained by tagged white marlin varied with location (Mid-Atlantic: 161 m, Dominican Republic: 149 m, Mexico 210 m, Venezuela 199 m). For Type 1 dives, mean dive duration, dive depth, temperature gradient, and interdive intervals did not vary significantly between locations (Fig. 13 A-D). When the weighted dive data were pooled for all surviving white marlin, the mean duration of Type 1 dives was 26.8 min (S.D. 17.1) to an average depth of 51.2

m (S.D. 20.3). Type 1 dives were longest offshore of Mexico (mean 30.7 min ± 19.3) and shortest offshore of Venezuela (mean 26.1 min ± 14.4) (Fig. 13A). Mean dive depths were shallowest offshore of the U.S. Mid-Atlantic (mean: 41.6 ± 17.0) and deepest offshore of Mexico (mean: 58.7 ± 30.6) (Fig. 13B). The mean range of temperatures encountered on Type 1 dives was 3.8 °C (S.D. 2.1). Minimum temperatures encountered by white marlin also varied between locations (Mid-Atlantic: 11.7 °C, Dominican Republic: 20 °C, Mexico 13.4 °C, Venezuela 17.1 °C). Mean temperature gradients encountered on Type 1 dives were highest offshore of Mexico (mean: 5.8 °C ± 4.0) and lowest offshore of the Dominican Republic (mean: 2.2 ± 1.1) (Fig. 13C). Between Type 1 dives, white marlin returned to the surface for interdive intervals averaging 33.2 min (S.D. 37.8). Interdive intervals following Type 1 dives were greatest offshore of the Mid-Atlantic (mean: 54.3 min ± 63.4) and were lowest offshore of Mexico (mean: 23.1 min ± 20.3) (Fig. 13D).

Type 2 dives occurred when fish confined their behavior to specific depth ranges for relatively long time intervals (mean: 141 min +/- 107.1). Analysis of Type 2 dive characteristics revealed marginally significant differences between locations with respect to dive duration ($\chi^2 = 8.21$, df = 3, p = 0.042) and interdive intervals ($\chi^2 = 8.08$, df = 3, p = 0.044) (Fig. 14 A-D). Type 2 dive durations were longest offshore of the U.S. Mid-Atlantic (mean: 207 min ± 188) and decreased southward to Venezuela (mean: 91.4 min ± 17.1) (Fig 14A). Mean depths (Fig. 14B) and mean temperature gradients (Fig. 14C) did not differ significantly between locations for Type 2 dives. Interdive intervals were greatest offshore of the U.S. Mid-Atlantic (54.3 min ± 73.2) and shortest offshore of Mexico (14.5 min ± 10.6) (Fig. 14D).

Additionally, analysis of the relative change of water temperature with depth during both Type 1 and Type 2 dives revealed that 95.02% of white marlin vertical movements occur within the upper 8 °C of the water column (Fig. 15). It appears that the relative change of water temperature with depth, rather than a preference for a specific depth, regulates white marlin diving behavior. For example, during the first five days of its track, maximum dive depths of white marlin MA02 (Fig. 16) varied by 90 m (40-150 m), but all of the vertical behavior was confined to water temperatures between SST and 8 °C below SST (e.g., the upper 8 °C of the water column).

DISCUSSION

Analyses of net movement data revealed that the directions and magnitudes of displacement patterns varied among individual white marlin and between locations. The majority of fish tagged in the waters of the U.S. Mid-Atlantic Bight, the Dominican Republic, and Mexico generally demonstrated straight-line movements following oceanographic currents; however, net displacements of several individuals at these locations were perpendicular to or directly opposing local current patterns. Offshore of Venezuela, most white marlin appeared to move perpendicular to the local current patterns. These displacements are generally consistent with results from prior tagging studies which indicate offshore movement away from tagging locations (Graves et al., 2002; Kerstetter et al., 2003), and in relation to current patterns or land masses (striped marlin: Brill et al., 1993; black marlin: Pepperell and Davis, 1999; blue marlin: Holland et al., 1990; Block et al., 1992b; Graves et al., 2002; striped marlin: Holts and Bedford, 1990; Brill et al., 1993; sailfish: Jolley and Irby, 1979). It should be noted that inferences into the horizontal movements of white marlin in this study were limited to minimum straight-line distances between the coordinates of the tagging location and coordinates of tag pop-up.

Minimum straight-line distances traveled by white marlin tagged in this study are similar to results for other istiophorids. Generally, comparisons between the telemetered swimming speeds of tracked istiophorids with those calculated from net displacements of conventionally tags billfishes have yielded very consistent results (Brill et al. 1993).

White marlin in this study moved between 0.07-1.76 nmi/hr, similar to the 0.73 nmi/hr and 0.95 nmi/hr average speeds reported by Graves et al (2002) and Kerstetter et al. (2003) respectively for Atlantic blue marlin. These results are also comparable to the average speeds reported for striped marlin (1.18nmi/hr, Holts and Bedford, 1990), black marlin (1.35-1.98 nmi/hr, Pepperell and Davis, 1999) and Pacific blue marlin (1-2 nmi/hr, Holland et al., 1990; 0.29-4.37 nmi, Block et al., 1992b). Magnitudes of mean hourly displacement for white marlin in this study varied between locations. Analyses of minimum straight line distances revealed that white marlin offshore of the U.S. Mid-Atlantic, the Dominican Republic, and Venezuela, moved at similar speeds (0.3-0.39 nmi/hr). In contrast, white marlin tagged offshore of Isla Mujeres, Mexico moved far more rapidly (1.12 nmi/hr), presumably due to the influence of a strong northerly current. Similar influences of current speeds on the horizontal displacements of striped marlin and blue sharks have been described (Carey and Scharold, 1990; Brill et al., 1993). Some difference between mean hourly displacements between locations may have also been due to natural patterns of movement associated with seasonal migrations of white marlin.

The results of this study strongly suggest that white marlin associate with the epipelagic zone and spend the majority of their time (mean: 40%) in the upper 10 m of the water column. While comparative behavioral data are not available for this species, data from prior acoustic and PSAT studies demonstrate that other istiophorids mostly associate with near-surface waters. For example, blue marlin tagged offshore of Hawaii and Bermuda frequented the upper 10 m of the water column for 50 and 80 percent of their time, respectively (Block et al., 2002a; Graves et al., 2002). Striped marlin offshore of Hawaii spent nearly 30 percent of their time in the upper 10 m of the water column (Brill et al., 1993).

The depths preferences of white marlin are similar, but not identical, to those of striped marlin and Atlantic blue marlin. White marlin in this study did not spend much time between 10-20 m but frequented depths ranging from 20-80 m for notable, although variable amounts of time (mean: 42.6 % ± 15.3). Atlantic blue marlin tagged with 30-day PAT tags also spent little at depths from 3-25 m and greater amounts of time between 25-> 100 m depth (Kerstetter et al., 2003). Striped marlin tagged offshore of Hawaii associate with depths between 51 and 90 m for a comparable amount of time (40%) (Brill et al., 1993). These results suggest that istiophorids may spend appreciable time beyond surface waters.

Generally, maximum reported depths of tagged istiophorids range between 100 and 270 m (Block et al., 1992a; Brill et al., 1993; Pepperell and Davis, 1999; Kerstetter et al., 2003), far less than excursions in excess of 600 m by broadbill swordfish (*Xiphias gladius*) (Carey and Robinson, 1981). Maximum depths of white marlin dives at each location in this study (149-210 m) fell within the range for other tagged istiophorids; however, these results should be viewed with some caution because sampling intervals in this study were limited to roughly every 1.6 or 3.2 minutes. As evidenced by the change in depth of 170 m in 3 minutes by white marlin VZ02-01, deep dives may occur rapidly, and maximum dive depths may not have always been successfully recorded with the sampling intervals used in this study.

White marlin depth distributions are likely more influenced by water temperature than by an absolute depth preference. The results of this study demonstrate a strong association of white marlin with warm waters within a few degrees of sea surface temperature (SST). White marlin spent over 85 percent of their time in waters ranging from 24 to 29 °C, similar to the range of temperatures frequented by Atlantic blue marlin (26-31 °C, Graves et al., 2002; Kerstetter et al., 2003). Temperature distributions of Pacific blue marlin and black marlin are also comparable (Holland et al., 1990; Block et al., 1992a; Gunn et al., 2003). The striped marlin tracked by Brill et al. (1993) offshore of Hawaii spent about 80% of their time in waters between 25 and 27 °C, while those tracked by Holts and Bedford (1990) offshore of California spent the majority of their time in cooler water (20 and 21 °C). This disparity is presumably due to differences in surface and mixed-layer temperatures between respective tagging locations (Brill et al., 1993). A similar phenomenon may be driving the time-at-temperature distributions of white marlin at the four tagging locations in this study. Mean SST values during tagging operations at each of the four locations concur strongly with modal temperatures selected by tagged white marlin, suggesting that this species may spend the majority of its time in the warmest waters available. White marlin tagged in the three Caribbean locations in this study experienced warmer surface temperatures and spent less time in the upper 10 m of the water column. In contrast, fish offshore of the U.S. Mid-Atlantic Bight experienced the lowest sea surface temperatures and spent the longest amount of time in the upper 10 m of the water column.

Analyses of the diel depth preferences of tagged istiophorids have yielded contrasting results. Most istiophorid tagging studies have suggested a tendency towards deeper diving behavior during daylight hours (Holland et al., 1990; Block et al., 1992a; Pepperell and Davis, 1999; Kerstetter et al., 2003), although some have demonstrated deeper dives at night (Holts and Bedford, 1990), and others have not revealed any diel differences (Brill et al., 1993; Gunn et al., 2003). In the present study, diel trends rarely persisted for more than a few days, and the vast majority of white marlin did not show significant differences in depth between day and night periods. Six animals did show significant diel patterns, of which four animals dove deeper during daylight hours, and two dove deeper at night. Diel behavior in white marlin and other istiophorids is thus far less distinct than that observed in broadbill swordfish (Carey and Robinson, 1981; Sedberry and Loefer (2001). Some white marlin maintained clear diel patterns throughout the entire tracking duration, while others demonstrated highly distinct subsets of behavior that seem largely independent of photoperiod and were likely related to prey abundance or physical properties of the water column. Results from these diel analyses demonstrate the broad diversity of white marlin behavior. Comparable levels of variation within and among individuals have been noted for other billfishes in previous acoustic and PSAT studies (Holland et al., 1990; Holts and Bedford, 1990; Block et al., 1992a; Pepperell and Davis, 1999; Graves et al., 2002; Domeier and Dewar, 2003; Kerstetter et al., 2003). Investigations into the diel preferences of istiophorids have thus generally defied species-level, let alone family-wide, generalizations.

Characteristics of Type 1 and Type 2 dives reveal some striking similarities in the manner in which white marlin exploit their habitat. All white marlin undertook frequent short-duration dives to depths of 60-100 m. Similar patterns of short duration descents to variable depths have been observed in blue marlin and striped marlin (Block et al., 1992a;

Brill et al., 1993; Pepperell and Davis, 1999; Graves et al., 2003; Kerstetter et al., 2003). Results of an analysis of Type 1 dives reveal that neither habitat variables (depth or temperature gradients) nor duration variables (length of dives and interdive intervals) differ between locations. Similarly, Type 2 dives did not differ significantly with respect to depths or temperature gradients between locations. Both Type 1 and Type 2 dives were roughly 50 m in depth, and through temperature gradients around 4 °C at most locations. Combined, these results suggest that the physical bounds of white marlin habitat and the manner in which these fish exploit this habitat are fairly consistent across the geographic range sampled in this study.

The duration, patterns, and periodicity of white marlin diving behavior suggests that Type 1 dives may represent short-duration feeding excursions and Type 2 dives may reflect prolonged foraging efforts beyond surface waters. Graves et al. (2003) reached similar conclusions regarding the purpose of short duration dives in Atlantic blue marlin. Based on the nature and persistence of daily dive patterns, it is probable that a considerable proportion of white marlin foraging occurs at depth. These observations are supported by high CPUE values for white marlin and sailfish at calculated hook depths of 105-125 m in the Caribbean Sea (Gonzalez and Gaertner, 1990) and high CPUE values of blue marlin at hook depths of 130-170 m (Maksimov, 1970). Stomach contents of white marlin have occasionally supported foraging beyond surface waters. In addition to epipelagic prey such as halfbeaks, flying fishes, filefish, and dolphinfishes, stomach contents of white marlin have also included various scombrids, squid (*Loligo* and *Illex* sp.), Atlantic moonfish (*Vomer setapinnis*), butterfish (*Peprilus* sp.), cutlassfish

(Trichuridae) (Nakamura, 1985; Davies and Bortone, 1976), lancetfish (*Alepisaurus* sp.), and even benthic rays (J. Graves, pers. obs).

Prey concentrations in the pelagic realm are fairly unpredictable and transient, and the varying breadth and intensity with which Type 2 behavior occurs suggests that this pattern may be reflective of marlin locating schooling prey and directing their efforts to exploit that resource for extended amounts of time. If white marlin diving behavior is motivated by foraging, they may dive to depth to either feed directly on deeper-dwelling prey, or to silhouette concentrations of epipelagic prey above them against downwelling light. The silhouetting hypothesis is supported by the typical occurrence of Type 2 behavior following the ascent from a Type 1 dive and the prevalence of Type 2 dives during daylight hours and on nights with brighter moon phases. Similar foraging strategies involving the silhouetting of prey have been described for a number of marine animals (McFarland and Munz, 1975; Davies et al., 1999; Ponganis et al., 2000; Fistrup and Harbison, 2002). If dives are motivated by foraging, significant differences in the dive durations and interdive intervals of Type 2 dives between locations may shed insight into foraging success white marlin at different locations. Alternatively, since current PSAT models cannot record feeding events, these differences may have a physiological basis. Absent data linking diet and patterns of diving behavior, the relationship of depth and istiophorid feeding motivation remains inferential.

Istiophorids possess several adaptations which are consistent with foraging excursions at depth. Recent investigations into the vision of blue marlin demonstrate that the marlin eye is specifically adapted for sensitivity at low light levels during deep foraging dives (Fritsches et al., 2003a). Additionally, regional variation in spectral resolution of the striped marlin eye suggests color vision above and ahead of the animal, and visual pigments optimal for contrast against monochromatic upwelled light were found on the lower part of the retina (Fritsches et al., 2003b). White marlin, like other istiophorids and broadbill swordfish, also feature a specialized thermogenic organ beneath the brain that generates and maintains elevated temperatures in the eye/brain (Block, 1986); however, they lack the ability to maintain body muscle temperatures above ambient water levels (Brill and Lutcavage, 2001).

While white marlin appear to be well adapted for searching at depth, they may not be adapted for staying in cooler, deeper waters for extended periods of time. Diving behaviors of blue, striped, and black marlin (Holland et al., 1990; Holts and Bedford, 1990; Brill et al., 1993; Pepperell and Davis, 1999) also suggest limited abilities to stay at depth for extended amounts of time; these species appear to be largely constrained to a maximum temperature gradient of 8 °C. The relative change in temperature with depth also affects white marlin diving behavior. Over 95% of white marlin dives were in the range of temperatures between SST and 8 °C below SST, although rare and very brief excursions resulted in water temperature differences as great as 13.5 °C. Vertical movements of individual white marlin often varied greatly with respect to maximum depth, yet minimum water temperatures at the deepest points on dives usually remained within the 8°C range. Brill et al. (1999) and Brill and Lutcavage (2001) suggest that temperature-induced reductions in cardiac function are responsible for generally limiting the depth distributions of yellowfin tuna and, by analogy, the istiophorid billfishes to an 8 °C range. Additionally, the prevalence of interdive intervals following white marlin dives also support these conclusions. Thus while time-at-temperature distributions suggest that white marlin spend the majority of their daylight and night hours in the warm surface waters of the upper 10m, some motivation for surface association may also lie in increasing core temperature and restoring cardiac function between frequent foraging dives rather than for feeding alone.

Habitat-based standardization (HBS) models used in recent assessments of billfishes weight catch-per-unit-effort rates in proportion to the time istiophorids spend at depth or temperature, an adjustment that accounts for historical changes in the depths of longline gear deployments. A fundamental assumption of the HBS approach is that istiophorid feeding motivation is constant over time as well as all depths and temperatures (Graves et al., 2003). Clearly, time-at-depth distributions of most istiophorids, including white marlin, suggest that they are predominantly surface-oriented, thus the HBS approach assumes that their catchability is greatest in these waters. Directed recreational fisheries exploit the surface orientation of billfishes, further supporting this assumption. However, the shift to deeper fishing longlines has not always consistently reduced billfish catch rates. In fact, catch rates of billfishes on some deep-set longlines have exceeded those on shallow-set longlines (Graves et al., 2003). Dive patterns of white marlin in this study, in concert with limited investigations into istiophorid diet, vision, and thermal physiology, suggest that billfishes are well adapted for foraging at depth and may associate with near-surface waters for purposes other than explicit foraging. Graves et al. (2003) conclude that standardization of catch rates on the basis of time-at-depth data, but devoid of considerations of feeding motivations, will lead to biased estimates of abundance.

Results of simulations show that the validity of results from HBS models depends heavily on the explicit specification of the true distributions and behaviors of istiophorids and accurate data regarding specific gear distributions (Goodyear 2003). These data are largely lacking for Atlantic billfishes. The HBS model is based on data from acoustic tracking studies of Pacific blue marlin and striped marlin (Brill et al., 1993; Holland et al., 1990; Block et al., 1992a), and assumes that inferences into the habitat preferences of Pacific istiophorids are correct despite being based on few observations (Goodyear et al., 2003). Application of this model to Atlantic istiophorids assumes that the temperature and depth preferences, physiology, and behavior of billfishes are constant across all locations, ages, sexes, and sizes and between ocean basins. Only recently has preliminary data regarding the habitat preferences of Atlantic become available, thus many of these assumptions have not yet been tested.

The applicability of the habitat-based standardization method clearly needs to be evaluated, particularly given the observation that this approach has produced strongly biased results when assumptions in the model were incorrect (Goodyear, 2003). In some instances, biases inherent in incorporating inaccurate data into the HBS model has increased the probability of the conclusion that the stock is severely overfished (Goodyear et al., 2003). Some researchers have concluded that until it is possible to accurately describe istiophorid habitat, feeding motivation, and fishing depth of historic and current gears, the results of HBS modeling should be viewed with great caution (ICCAT 2001; Graves et al., 2003; Goodyear, 2003). Clearly, further investigations of habitat preference data for Atlantic istiophorids and vertical distribution of longline fishing gears are needed. These data, in concert with recently developed length-based, age-structured statistical models (Klieber et al., 2003) and fully-integrated habitat-based population dynamics models (Hinton et al., 2003), hold promise for improving habitat standardization of CPUE indices for Atlantic billfishes (Uozumi, 2003).

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Table 1. Locations and dates of PSAT deployments on white marlin during 2002-2003, with mean sea surface temperature (SST) at each location.

Location	Dates of tagging	Tag deployment duration	Number deployed	Mean SST
Mid-Atlantic Coast, USA (MA)	2002: 18-22 Aug, 5-21 Sept 2003: 22 Aug	10-day 10-day	11 1	26.1 ºC 26.6 ºC
Punta Cana, Dominican Republic (DR)	15-19 May, 2002	5-day	5	27.5 ºC
Isla Mujeres, Mexico (MX)	10-12 June 2003	10-day	3	28.2 ºC
La Guaira, Venezuela (VZ)	2002:23-25 Nov 2003:12-13 Sept, 1 Oct.	10-day 10-day	6 15	27.0 ºC 29.0 ºC

Table 2. Results of Student's T-tests for diel differences in diving behavior. Only white marlin showing significant diel differences were included. "Day" and "night" refer to time periods during which mean depths were significantly greater. Significance was assessed using an alpha level of 0.01. The inclusion of the symbol "S" after a p-value indicates that the p-value was adjusted using the Satterthwaite correction for unequal variances (Satterthwaite, 1946).

Analysis	Fish	Diel period	T-statistic	DF	p-value
Mean depth	VZ02-01	Night	-5.80	18	0.0001
	VZ02-06	Night	-3.50	16	0.003
	VZ03-02	Day	5.46	18	0.0001
	VZ03-04	Day	3.92	20	0.001
	VZ03-07	Day	3.62	20	0.002
	VZ03-14	Day	3.30	9.5	0.009^{S}

Figure 1. Representation of daily dive patterns of a sample day from white marlin MA02, tagged in the Mid-Atlantic in August 2002. Type 1 dives were defined as an excursion to an identifiable maximum depth and the subsequent return to the surface. Type 2 dives were more broadly "u"-shaped, showing behavior confined to a specific depth range for an extended period of time. Interdive intervals were defined as the amount of time spent at the surface between Type 1 and Type 2 dives.

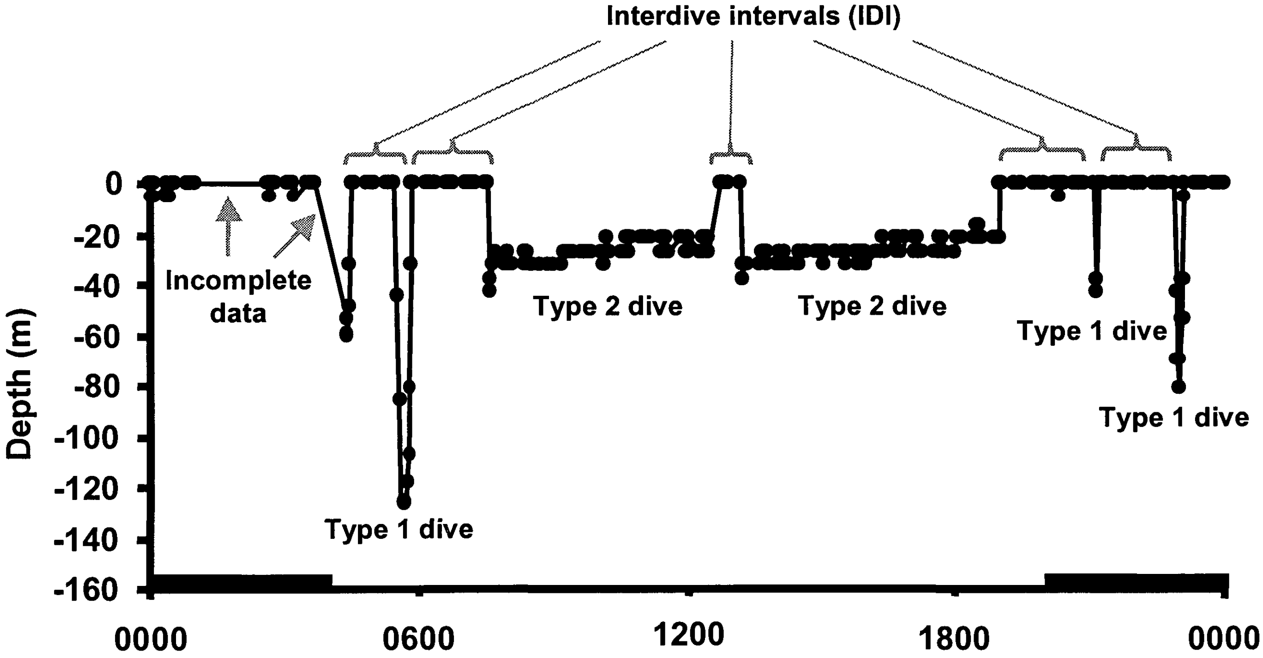

Interdive intervals (IDI)
Incomplete data
Type 1 dive
Type 2 dive
Type 2 dive
Type 1 dive
Type 1 dive
Depth (m)
0
-20
-40
-60
-80
-100
-120
-140
-160
0000
0600
1200
1800
0000

Figure 2. A) Minimum straight line distances traveled by white marlin (solid lines) and drifting tracks of transmitting tags (dotted lines). B) Sample sea surface temperatures (SST; colored figure) offshore of the U.S. Mid-Atlantic (August - September 2002-2003). SST data from Advanced High Resolution Radiometry (AVHRR) satellites were assembled as a composite monthly image for September 2002. These data were obtained via the Physical Oceanography Distributed Active Archive Center's (PO.DAAC) online PO.DAAC Ocean ESIP Tool (POET), maintained by the NASA Jet Propulsion Laboratory, Pasadena, CA. http://podaac.jpl.nasa.gov/poet.

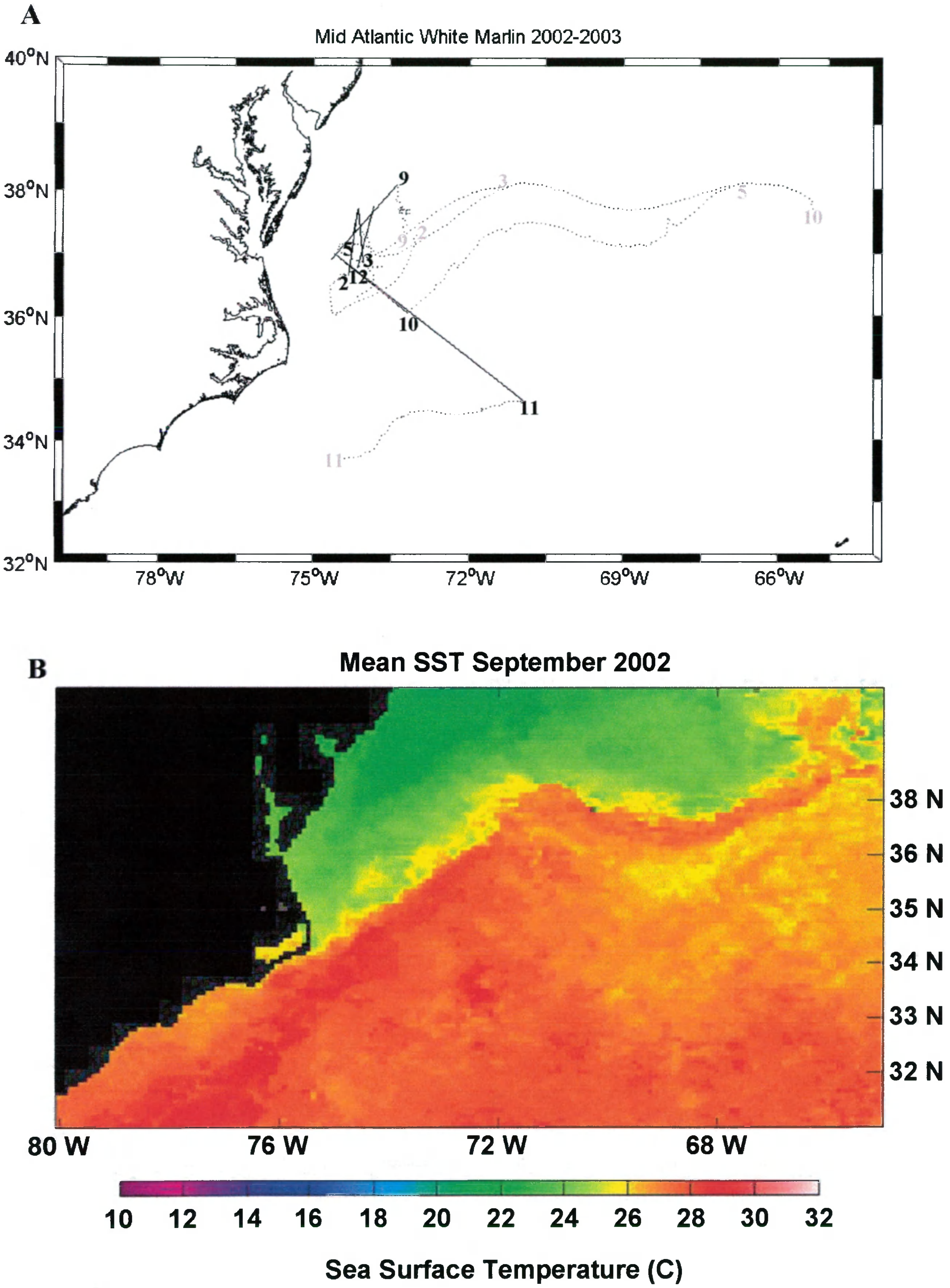

A
Mid Atlantic White Marlin 2002-2003
40°N
38°N
36°N
34°N
32°N
78°W
75°W
72°W
69°W
66°W
9
3
5
10
9
2
5
3
2
12
10
11
11
B
Mean SST September 2002
38 N
36 N
35 N
34 N
33 N
32 N
80 W
76 W
72 W
68 W
10
12
14
16
18
20
22
24
26
28
30
32
Sea Surface Temperature (C)

Figure 3. Minimum straight line distances traveled by white marlin (solid lines) and drifting tracks of transmitting tags (dotted lines) offshore of Punta Cana, Dominican Republic (May 2002).

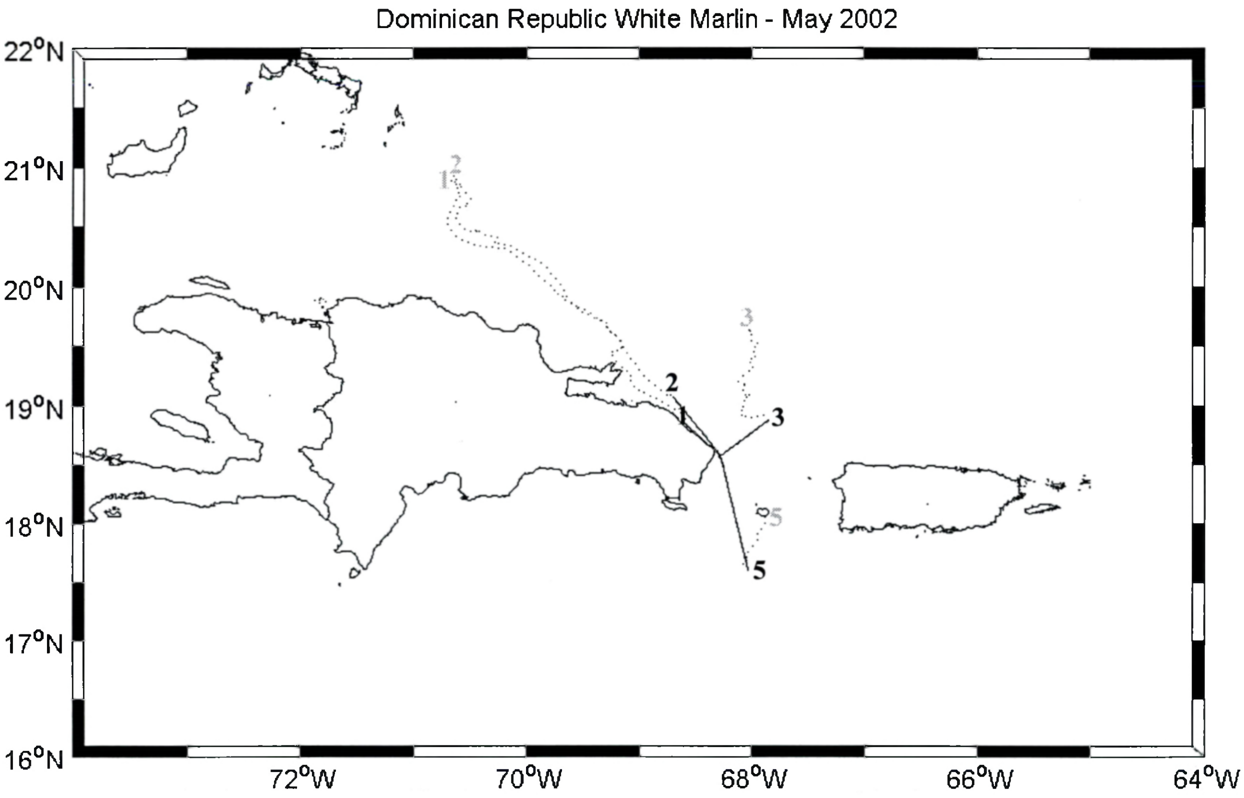

Dominican Republic White Marlin - May 2002
22°N
21°N
20°N
19°N
18°N
17°N
16°N
72°W
70°W
68°W
66°W
64°W
1
2
3
5
1
2
3
5

Figure 4. Minimum straight line distances traveled by white marlin (solid lines) and drifting tracks of transmitting tags (dotted lines) offshore of Isla Mujeres, Mexico (June 2003).

Mexico White Marlin - June 2003

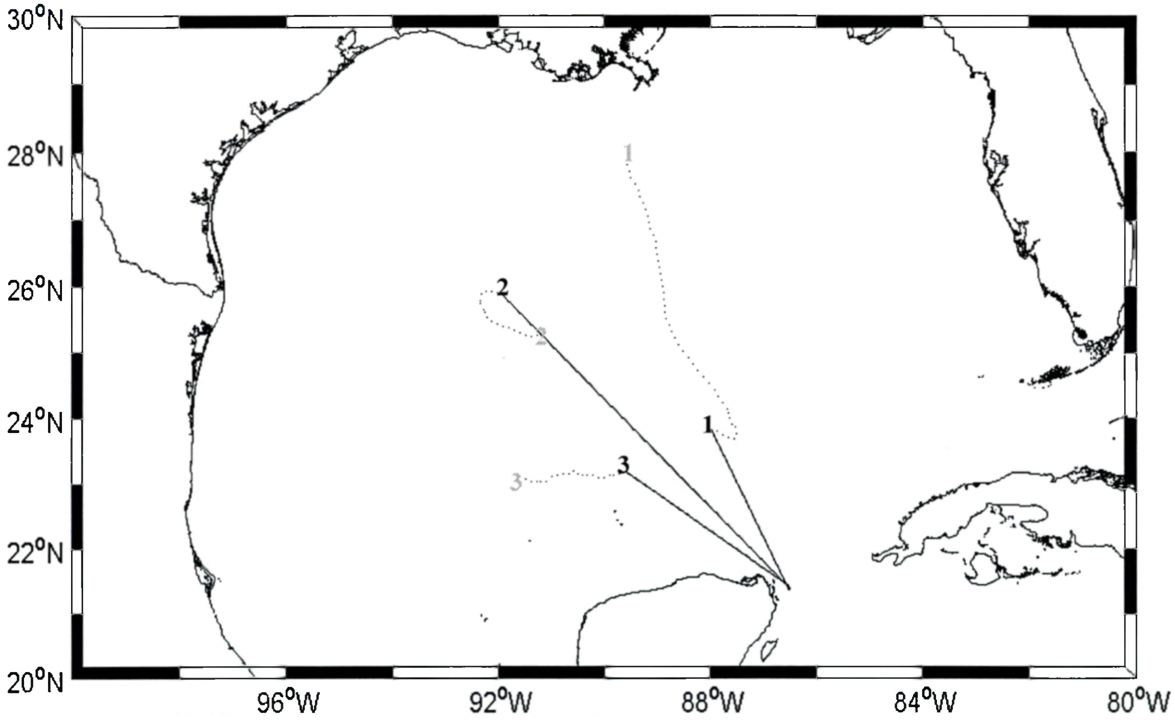
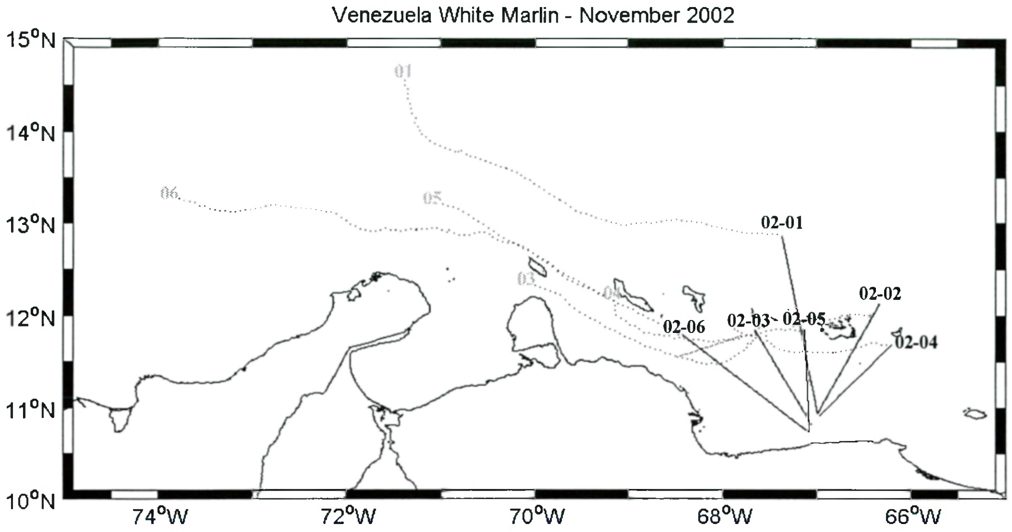
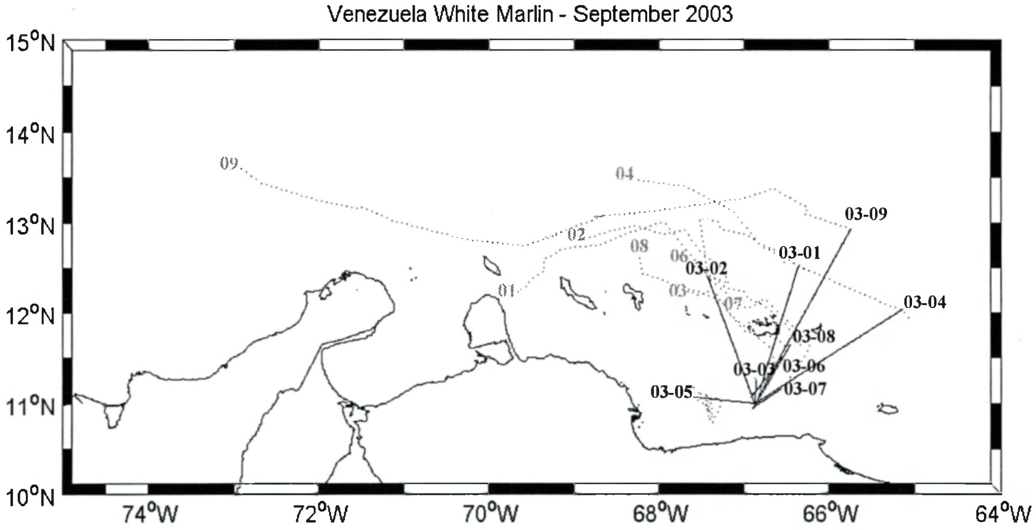


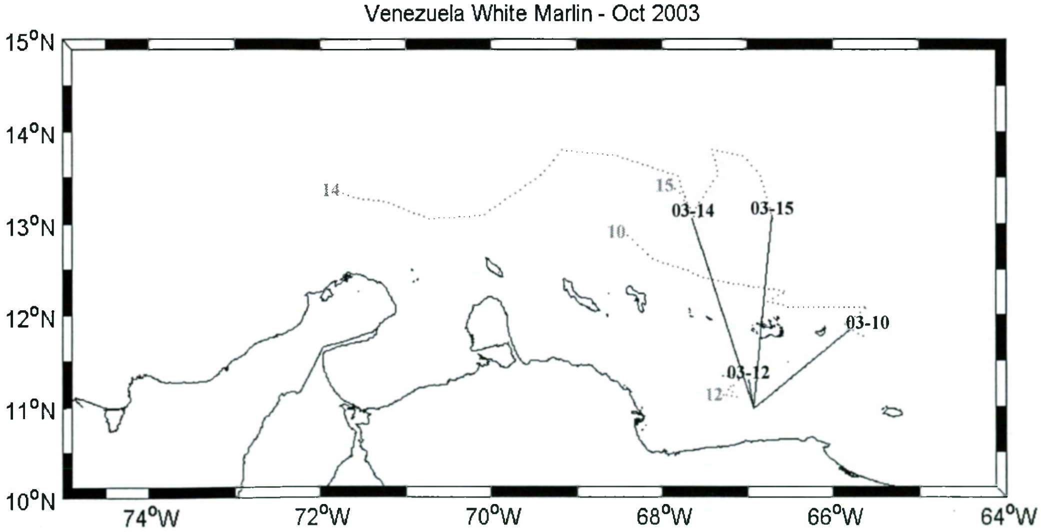
Figure 5. Minimum straight line distances traveled by white marlin (solid lines) and drifting tracks of transmitting tags (dotted lines) offshore of Venezuela in November 2002, September 2003, and October, 2003.



Venezuela White Marlin - November 2002



Venezuela White Marlin - September 2003



Venezuela White Marlin - Oct 2003

Figure 6. Pooled time-at-depth preferences from all surviving white marlin (n = 33). Frequency data for each individual fish were weighted by comparing the number of archived data points successfully transmitted from its respective tag to the total number of data points transmitted by all 33 tags included in this analysis. Standard errors were calculated from the weighted frequencies. Error bars are ±1 SE.

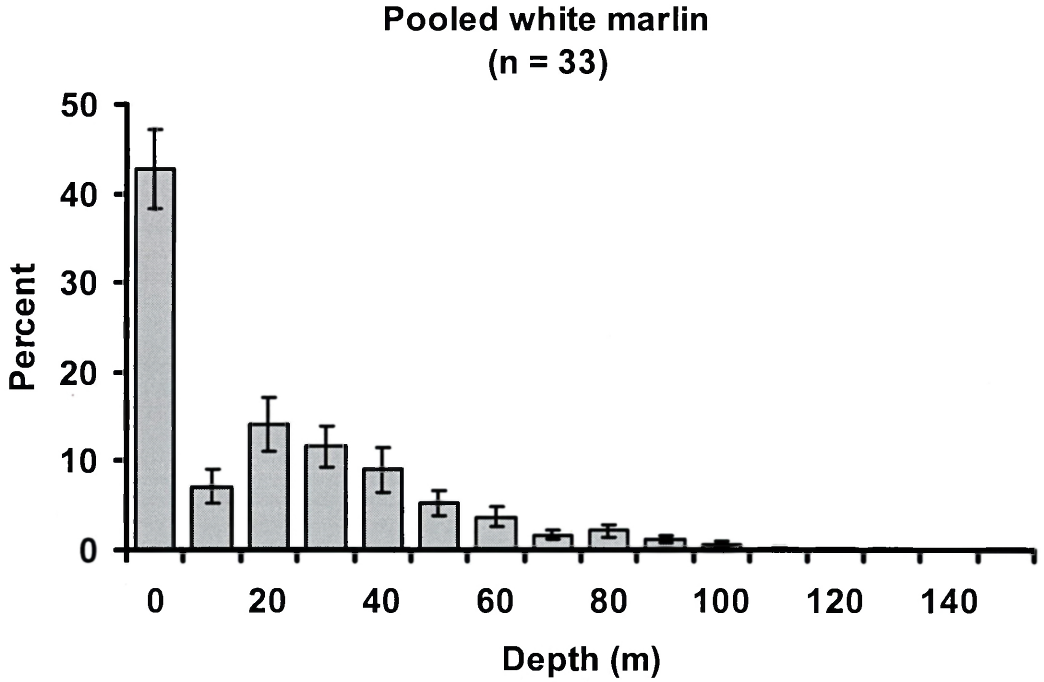

Pooled white marlin
(n = 33)
Percent
50
40
30
20
10
0
0
20
40
60
80
100
120
140
Depth (m)

Figure 7. Time-at-depth histograms for each tagging location: A) U.S. Mid-Atlantic, B) Dominican Republic, C) Mexico, and D) Venezuela. Frequency data for each individual fish were weighted by comparing the number of archived data points successfully transmitted from its respective tag to the total number of data points transmitted by all tags attached to surviving white marlin at a location. Sample sizes are given. Standard errors were calculated from the weighted frequencies. Error bars are ±1 SE.

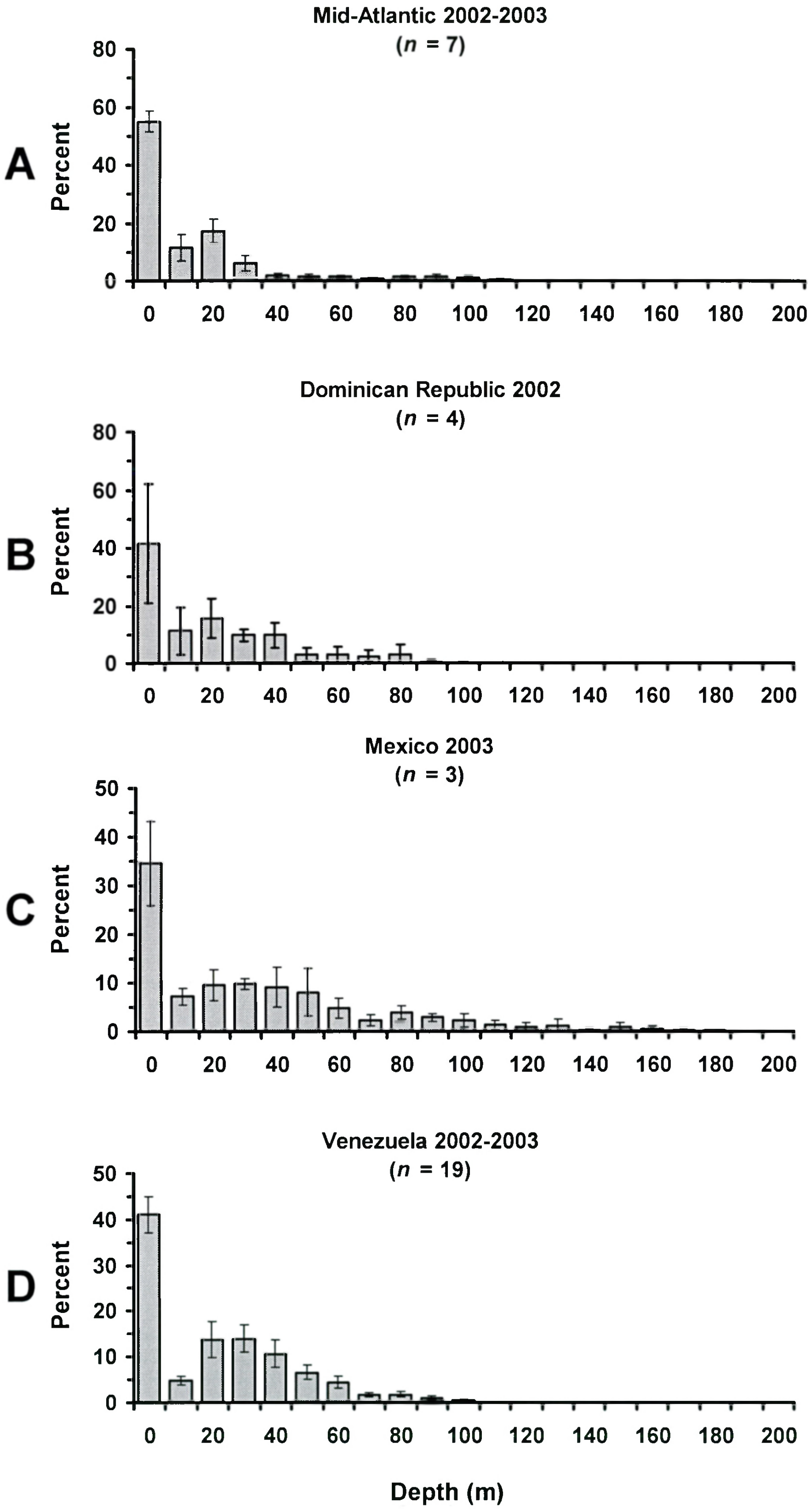

Mid-Atlantic 2002-2003
(*n* = 7)
A
Percent
80
60
40
20
0
0
20
40
60
80
100
120
140
160
180
200
Dominican Republic 2002
(*n* = 4)
B
Percent
80
60
40
20
0
0
20
40
60
80
100
120
140
160
180
200
Mexico 2003
(*n* = 3)
C
Percent
50
40
30
20
10
0
0
20
40
60
80
100
120
140
160
180
200
Venezuela 2002-2003
(*n* = 19)
D
Percent
50
40
30
20
10
0
0
20
40
60
80
100
120
140
160
180
200
Depth (m)

Figure 8. Pooled time-at-temperature preferences from all surviving white marlin (n = 33). Frequency data for each individual fish were weighted by comparing the number of archived data points successfully transmitted from its respective tag to the total number of data points transmitted by all 33 tags included in this analysis. Standard errors were calculated from the weighted frequencies. Error bars are ±1 SE.

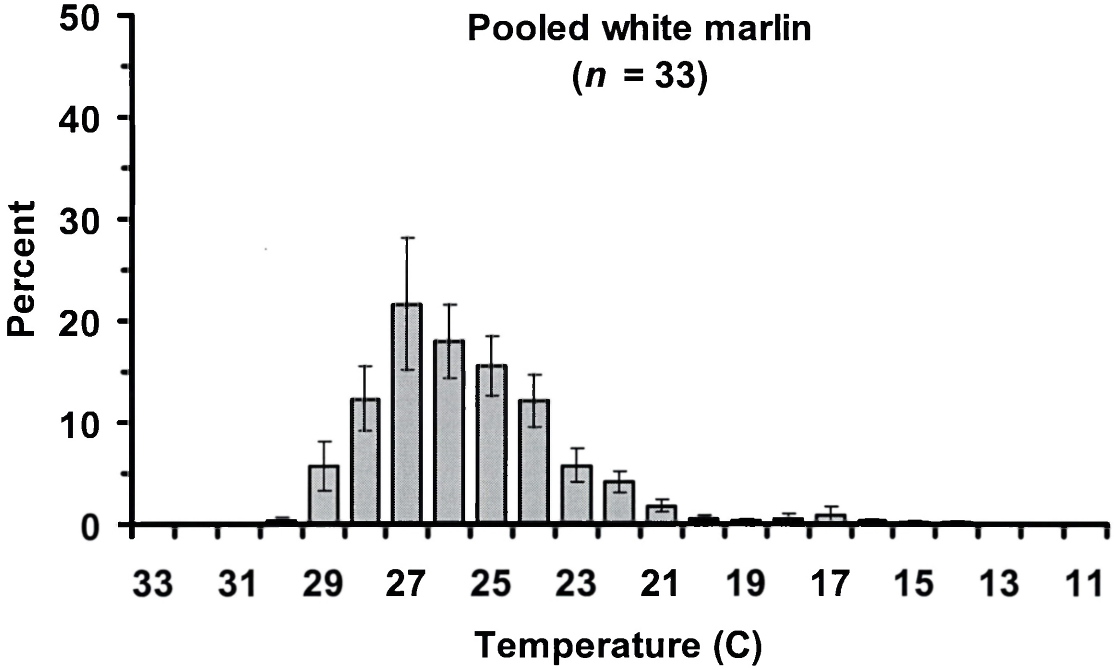
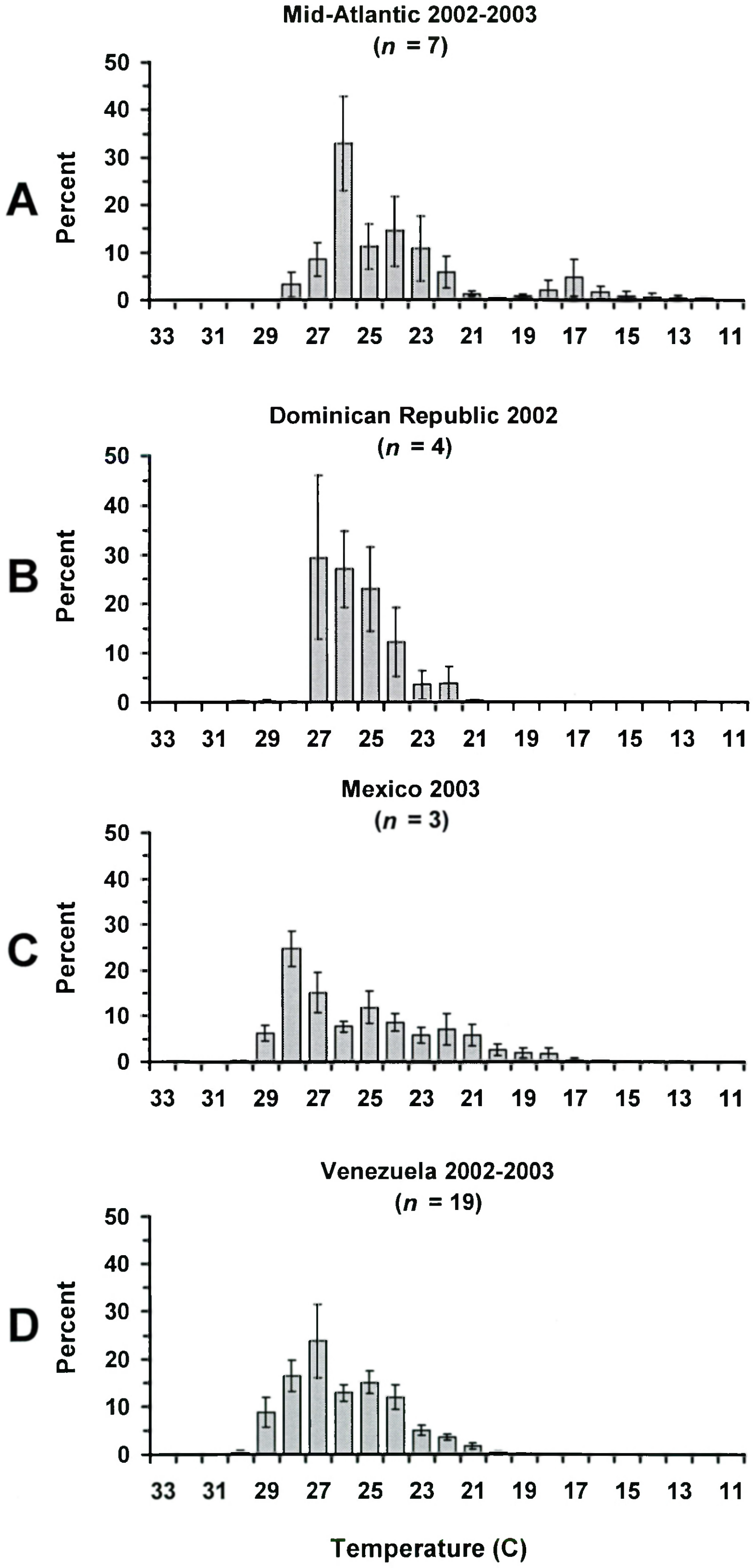

Pooled white marlin
(*n* = 33)
Percent
50
40
30
20
10
0
33
31
29
27
25
23
21
19
17
15
13
11
Temperature (C)

Figure 9. Time-at-temperature histograms for each tagging location: A) U.S. Mid-Atlantic, B) Dominican Republic, C) Mexico, and D) Venezuela. Frequency data for each individual fish were weighted by comparing the number of archived data points successfully transmitted from its respective tag to the total number of data points transmitted by all tags attached to surviving white marlin at a location. Sample sizes are given. Standard errors were calculated from the weighted frequencies. Error bars are ±1 SE.



Mid-Atlantic 2002-2003
(*n* = 7)

Dominican Republic 2002
(*n* = 4)

Mexico 2003
(*n* = 3)

Venezuela 2002-2003
(*n* = 19)

Figure 10. Consistent diel pattern of white marlin DR02-02, which moved extensively throughout the water column during the day and directed the majority of its efforts between 20-60 m during night hours for the entire five day tracking period.

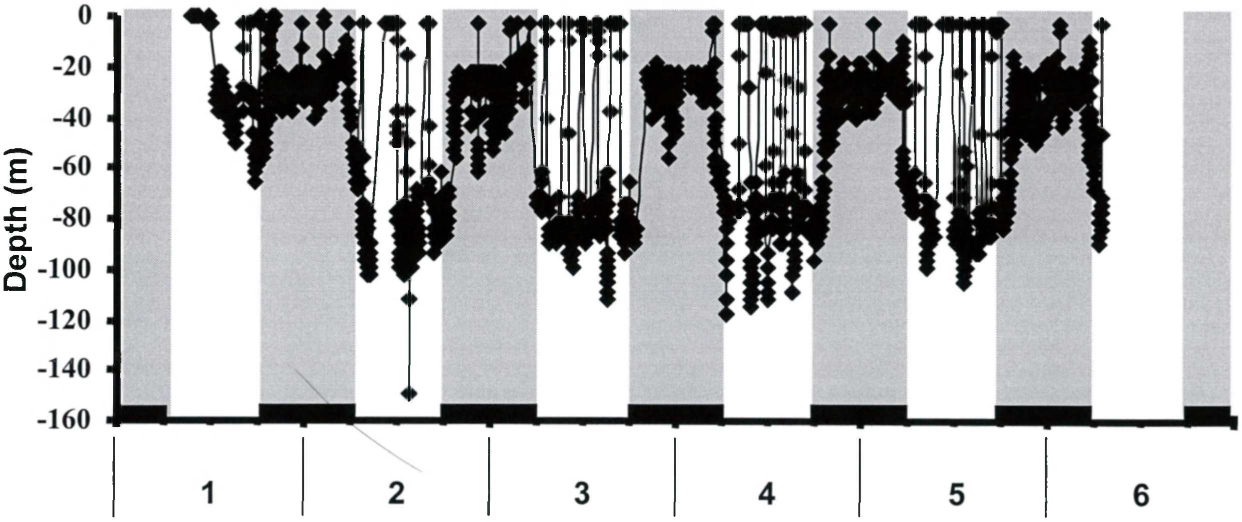

Depth (m)
0
-20
-40
-60
-80
-100
-120
-140
-160
1
2
3
4
5
6

Figure 11. Three distinct patterns of behavior of white marlin MA12 during its ten day track. This fish moved extensively through the upper 100 m of the water column during the first two days of the track. The dive behavior of this animal was more confined for the remainder of the ten day tag deployment duration. Three consecutive days were spent almost exclusively between 20-40 m and this fish rarely left the upper 10 m of the water column during the final five days of the tag deployment duration.

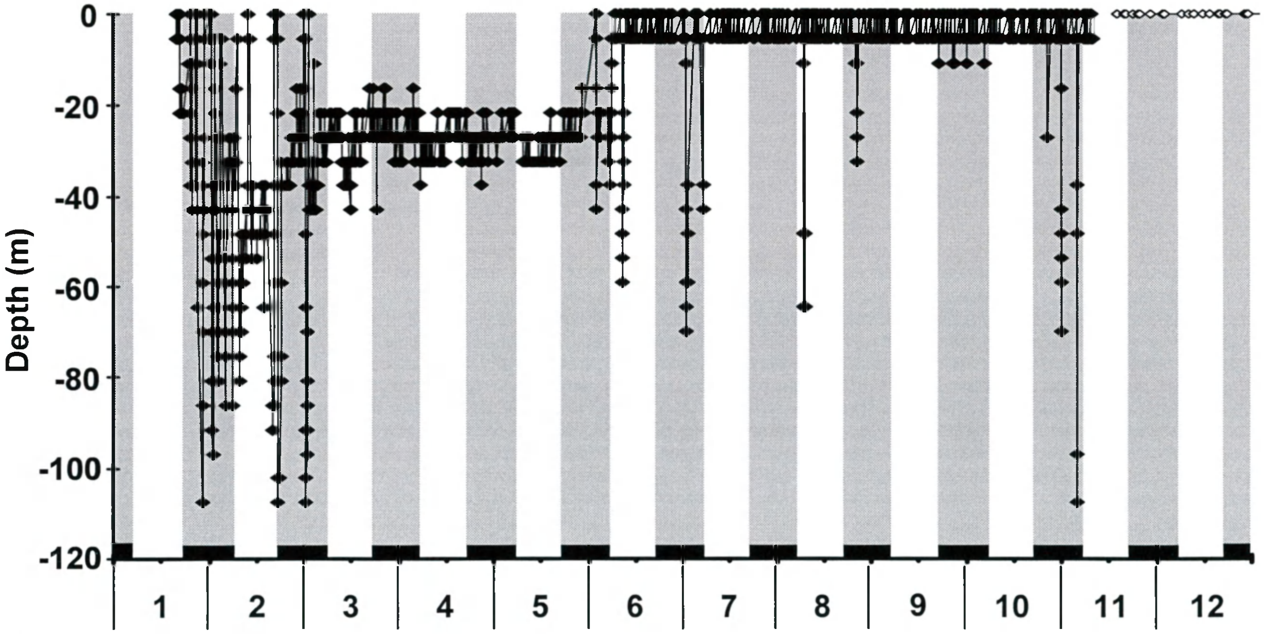

0
-20
-40
-60
-80
-100
-120
Depth (m)
1
2
3
4
5
6
7
8
9
10
11
12

Figure 12. Track of white marlin MA09, which shows elevated temperature readings despite increases in dive depth. This result suggests that this fish appeared to change its diving behavior as it moved from cooler coastal waters off Virginia into the warmer, oceanic waters of the Gulf Stream.

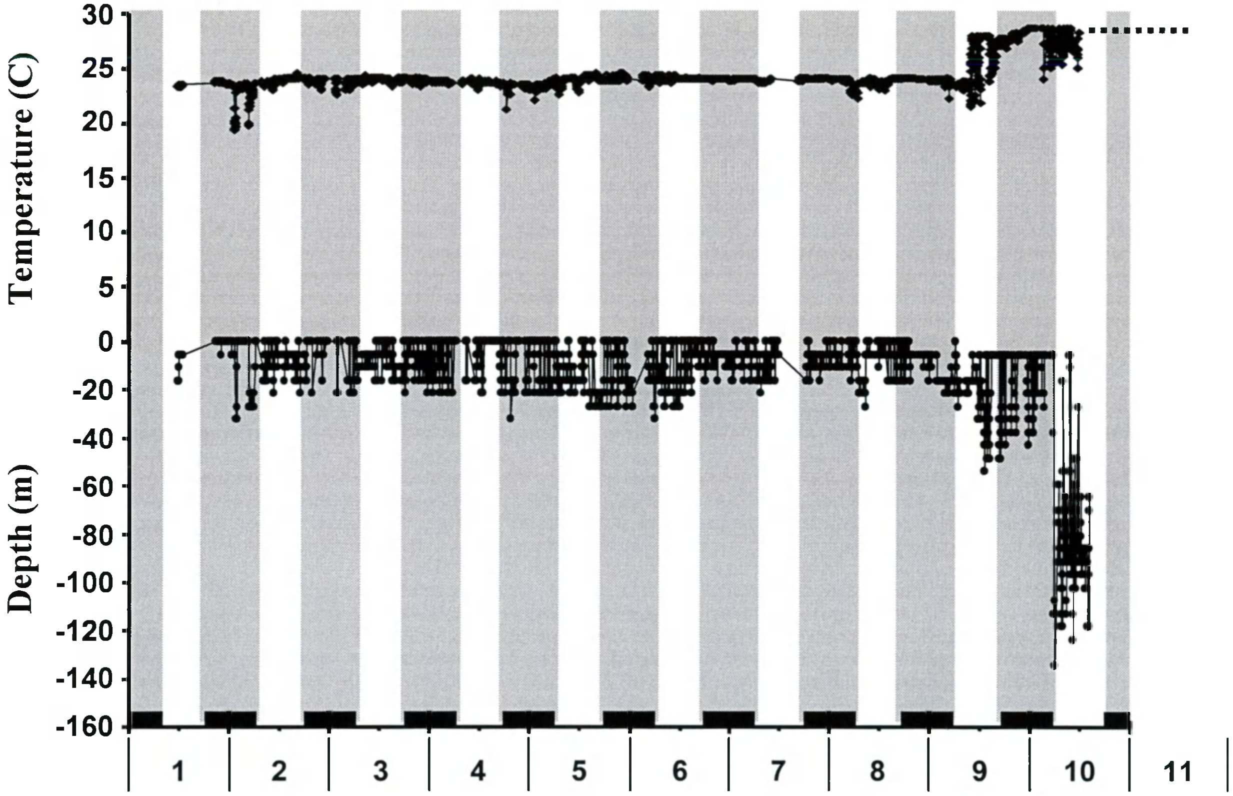

30
25
20
15
10
5
0
-20
-40
-60
-80
-100
-120
-140
-160
Temperature (C)
Depth (m)
1
2
3
4
5
6
7
8
9
10
11

Figure 13. Characteristics of Type 1 dives, including: A) mean dive duration (min), B) mean dive depth (m), C) mean temperature gradient (°C), and D) mean interdive interval (min). For each location, mean and standard deviation values were weighted by the proportion of dives contributed by a specific animal out of the total number of dives undertaken by all white marlin at a given location. The frequency data were subsequently pooled across all surviving white marlin and weighted by the percentage of dives contributed by a specific animal out of the total number of dives (n = 1918 complete Type 1 dives) undertaken by all surviving white marlin. Standard errors were calculated from the weighted data. Error bars are ±1 SE.

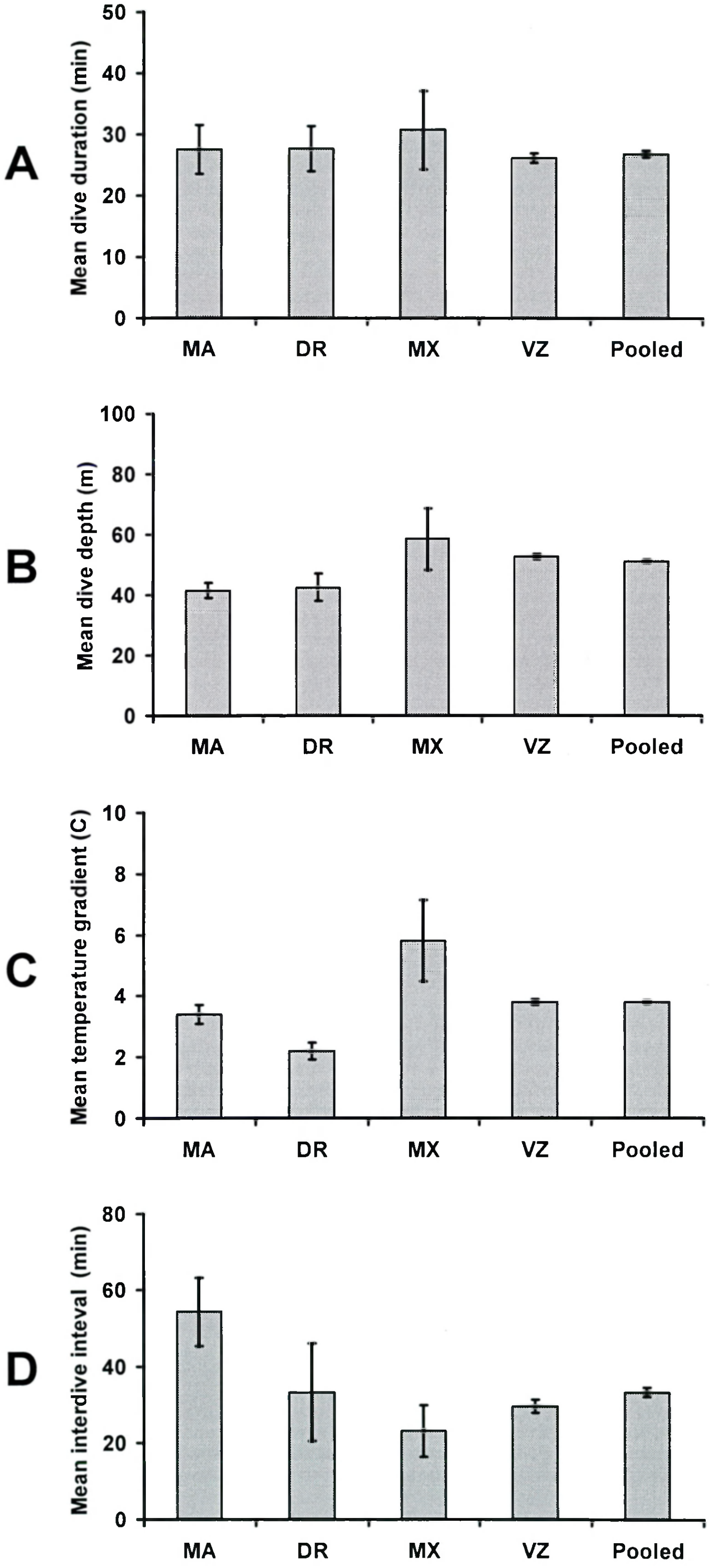

A
Mean dive duration (min)
0
10
20
30
40
50
MA
DR
MX
VZ
Pooled
B
Mean dive depth (m)
0
20
40
60
80
100
MA
DR
MX
VZ
Pooled
C
Mean temperature gradient (C)
0
2
4
6
8
10
MA
DR
MX
VZ
Pooled
D
Mean interdive inteval (min)
0
20
40
60
80
MA
DR
MX
VZ
Pooled

Figure 14. Characteristics of Type 2 dives, including: A) mean dive duration (min), B) mean dive depth (m), C) mean temperature gradient (ºC), and D) mean interdive interval (min). For each location, mean and standard deviation values were weighted by the proportion of dives contributed by a specific animal out of the total number of dives undertaken by all white marlin at a given location. The frequency data were subsequently pooled across all surviving white marlin and weighted by the percentage of dives contributed by a specific animal out of the total number of dives (*n* = 141 complete Type 2 dives) undertaken by all surviving white marlin. Standard errors were calculated from the weighted data. Error bars reflect standard error. Error bars are ±1 SE.

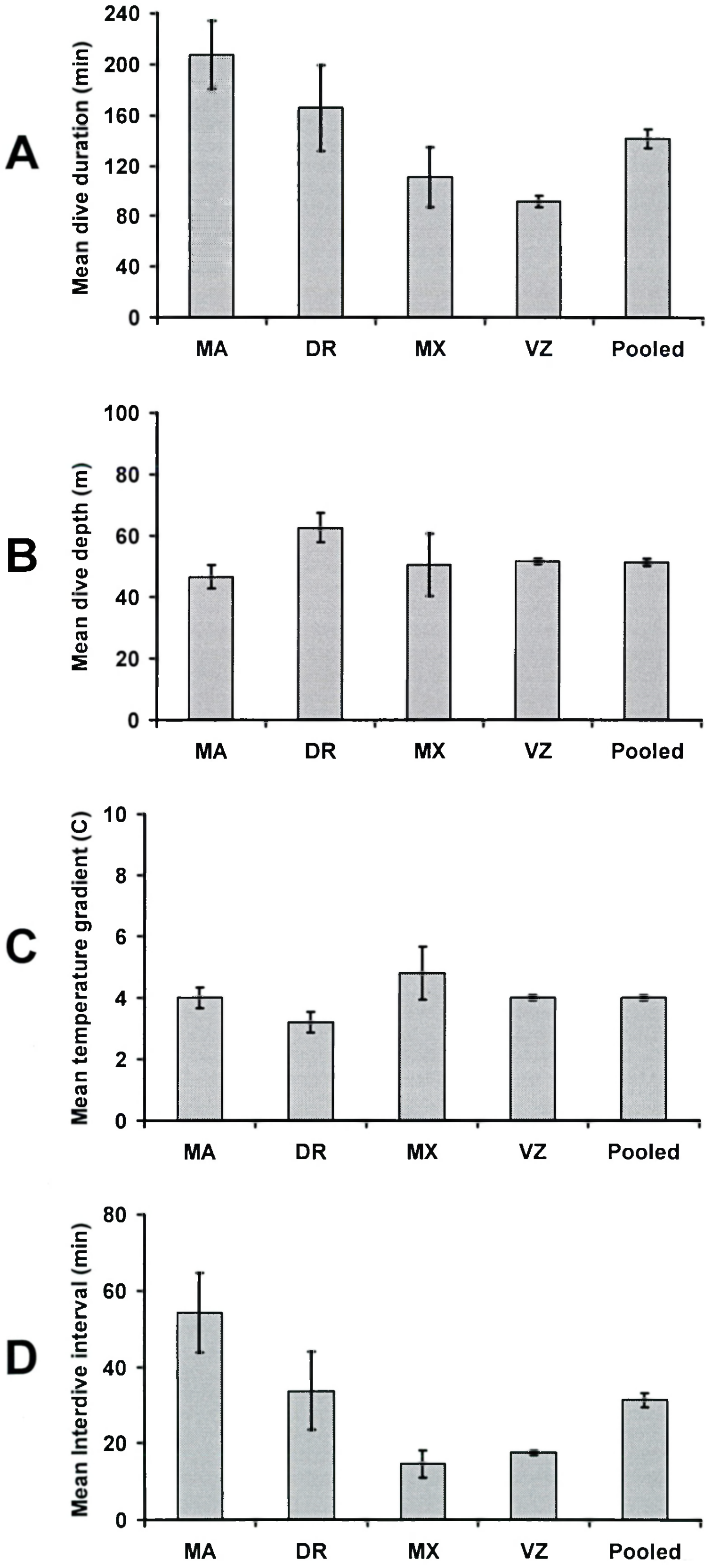

A
Mean dive duration (min)
0
40
80
120
160
200
240
MA
DR
MX
VZ
Pooled
B
Mean dive depth (m)
0
20
40
60
80
100
MA
DR
MX
VZ
Pooled
C
Mean temperature gradient (C)
0
2
4
6
8
10
MA
DR
MX
VZ
Pooled
D
Mean Interdive interval (min)
0
20
40
60
80
MA
DR
MX
VZ
Pooled

Figure 15. Frequency distribution of the relative change of water temperature with depth, assessed as the difference between sea surface temperature and the minimum temperature reached on every completely transmitted Type 1 and Type 2 dive. Error bars are ± SE. The dotted line denotes a cumulative sum of 95%.

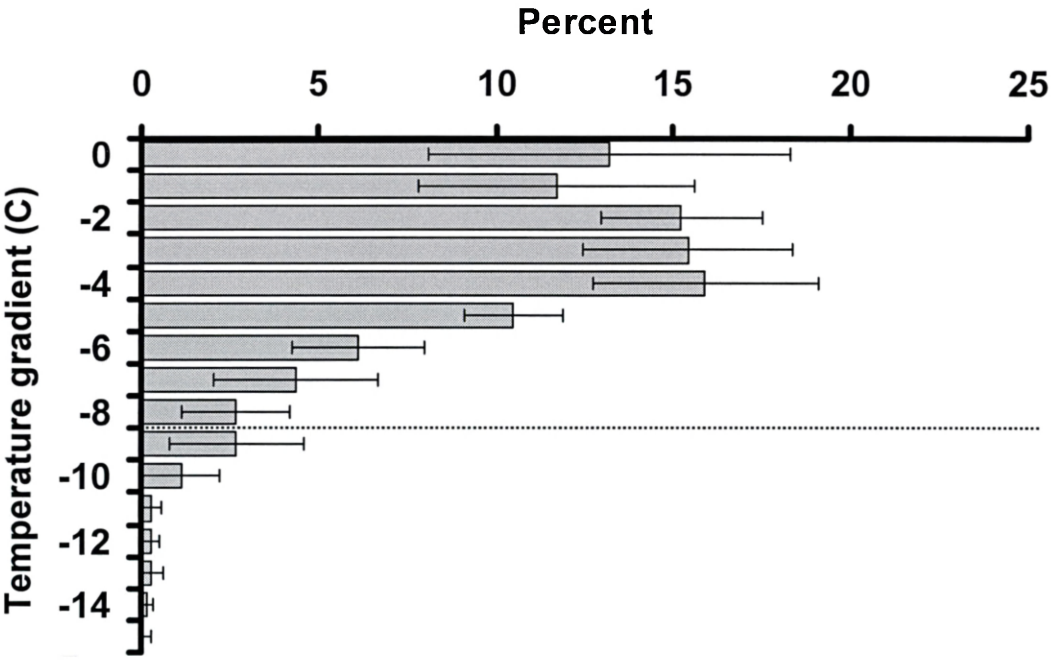
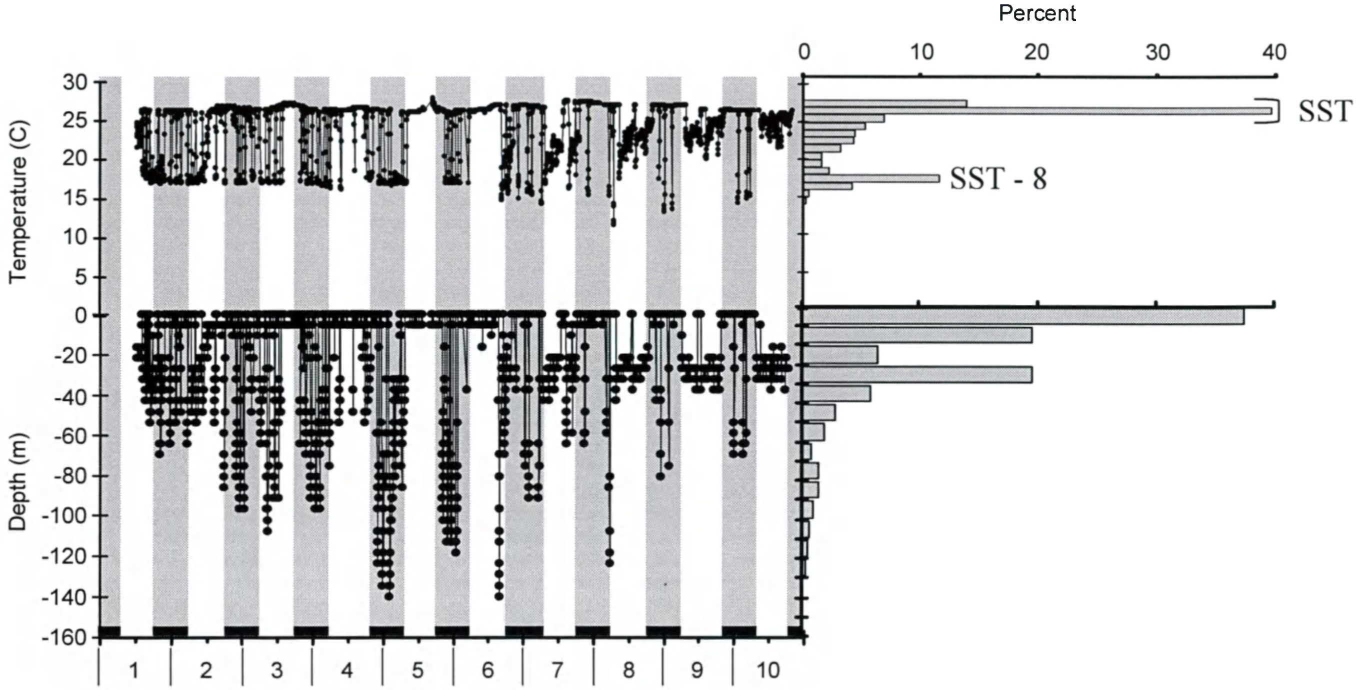

Percent
0
5
10
15
20
25
Temperature gradient (C)
0
-2
-4
-6
-8
-10
-12
-14

Figure 16. Track of white marlin MA02, showing movements largely constrained within the upper 8 °C of the water column despite highly variable maximum dive depths.


Percent
0
10
20
30
40
SST
SST - 8
Temperature (C)
30
25
20
15
10
5
0
Depth (m)
-20
-40
-60
-80
-100
-120
-140
-160
1
2
3
4
5
6
7
8
9
10

CONCLUSION

White marlin represent an important commercial, recreational, and ecological resource throughout the Atlantic Ocean. Population levels of white marlin are at historically low levels, with current harvests greatly exceeding replacement yield (ICCAT, 2002). Increasingly pessimistic population assessments necessitate the identification of mechanisms to reduce white marlin fishing mortality and methods to implement them. While over 99% of the white marlin caught annually by U.S. recreational fishermen are released (Goodyear and Prince, 2003), the results of this study demonstrate that a significant proportion of those fish caught on straight-shank ("J") hooks perish. Additionally, fish caught on this hook type were significantly more likely to be hooked deeply and incur hook-induced trauma. In contrast, all of the white marlin caught on circle hooks survived, and the overwhelming majority were hooked in the corner of the mouth and incurred no trauma resulting in bleeding. Relatively small sample sizes and fairly limited spatial coverage in this study preclude the use of these data to infer Atlantic-wide estimates of postrelease mortality; however, results of this study clearly demonstrate that a simple change hook type can significantly reduce the postrelease mortality of white marlin from the recreational fishery.

At present, "J" hooks are the dominant terminal tackle in the white marlin fishery. Mechanisms to increase the use of circle hooks in recreational fisheries targeting billfish should be strongly considered by management agencies. Possible examples of such mechanisms include, but are not limited to: (A) synopses of scientific investigations into the performance of circle and straight-shank "J" hooks in popular literature articles and presentations at fishing club meetings, trade shows, and tournaments, (B) accelerated outreach programs disseminating information about proper bait rigging and hook-setting techniques when using circle hooks, (C) state or federal certificate programs for the release of billfishes caught on circle hooks, (D) tournament divisions with cash prizes for fish caught on circle hooks, and/or (E) circle hook-only tournaments. Alternatively, management agencies could decide to mandate circle hooks, although enforcement of such a regulation is likely to be problematic.

Increasingly pessimistic population assessments also require a more accurate understanding of the true status of istiophorid stocks (Uozumi, 2003). At present, the relationship between white marlin abundance, feeding motivation, and physical properties of the water column are poorly understood, and the applicability of a habitat-based standardization is questionable, at best. The results of this project provide preliminary insights into the habitat preferences and behaviors of white marlin. However, given the relatively small sample sizes per location in this study, the large geographic range of this species, and the countless habitat variables which likely govern white marlin behavior, the results of the habitat investigations in this study should be viewed as preliminary and descriptive.

The frequency, persistence, and patterns of white marlin dives, in concert with limited investigations into istiophorid diet, thermal physiology, and vision by other researchers (Davies and Bortone, 1976; Block, 1986; Fritsches et al., 2003a; Fritsches et al., 2003b), suggest that white marlin are well adapted for foraging at depth. As such, their associate with near-surface waters may be for purposes other than explicit foraging, and their feeding motivation in shallow surface waters may not be proportional to the time spent in this region. Deep-set pelagic longline gear targeting bigeye tuna and broadbill swordfish may thus increase billfish bycatch by placing baits within, rather than beyond, the depths of many of the repetitive foraging dives of some billfish species. These results suggest that the assumption that feeding motivation is constant across all depths and temperatures (thus it is proportional to time-at-depth distributions) is likely inaccurate, and the incorporation of this assumption will lead to biased results. Until billfish feeding motivation is better understood, it may be premature to apply habitat-based stock assessment models to billfishes in the Atlantic Ocean.

Future Research

Clearly, increasing the accuracy of istiophorid population assessments should be a major priority of researchers and managers alike. Investigations into appropriate methods to weight catch-per-unit-effort data should be accelerated, and other statistical models based on biological data should also be considered. The Hinton-Nakano (1996) habitat standardization model shows promise, but effort should be devoted to ensure that this model produces robust estimates of CPUE. Specifically, more research should be devoted to investigating the basic life history and behavior of Atlantic istiophorids. Current knowledge of diving behavior, time-at-depth, and time-at-temperature preferences of Atlantic istiophorids is limited to two species and only a few locations. Whether these behaviors are similar at other locations in the Atlantic Ocean, and for all billfishes regardless of age, sex, size, and time of the year remains to be seen (Goodyear et al., 2003).

The association between depth distributions and istiophorid feeding motivation is uncertain. This relationship harbors important implications for the fundamental assumption of the HBS modeling approach that feeding motivation is proportional to time spent as a specific depth. Feeding habits of Atlantic billfishes are poorly known, thus analyses of stable isotope ratios and stomach contents at locations spanning their range will shed greater insights into billfish trophic ecology. Additionally, little is known about the specific behavior of longline fishng gear, and how the distribution of longline hooks is affected by the structure of the water column, subsurface currents, and other fish on the line. The adequacy (or lack thereof) of the gear model is perhaps the weakest link of the HBS model (Goodyear et al., 2003). One potential means of addressing these questions may be to combine paired shallow and deep longline sets bearing GPS units and time/depth recorders. This research would allow the comparison of catch rates at various depths to the stomach contents of the resulting billfish catch and prey abundance data in the region sampled.

In addition to increasing the accuracy of the data input into assessment models, methods to continue reductions in istiophorid postrelease mortality must be refined and promulgated to allow stocks to recover. For commercial fisheries, the identification of mechanisms to decrease the interaction of bycatch species, including billfishes, with longline gear should be explored. These investigations may include the effects of longline set durations and depths on bycatch:target species ratios, analyses of catch rates as a function of different bait types, and studies of chemical and visual bycatch repellents or target species attractants. To be effective, deterrents would have to decrease bycatch while not affecting, or possible even increasing target species catch. Recent investigations into istiophorid vision show potential (Fritsches et al., 2003a; Fritsches et al., 2003b), and future investigations into billfish physiology may yield mechanisms to minimize interaction of these species with pelagic longline gear.

For predominantly catch-and-release recreational fisheries, research should be centered around minimizing postrelease mortality. Preliminary investigations (Prince et. al., 2002; Domeier and Dewar, 2003; this study) show that circle hooks decrease internal trauma and increase survival. However, there is little research on the performance of offset circle hooks, and no single study has examined survival while documenting the effects of circle hooks on internal organs. Are these hooks really causing no internal damage to internal organs, or are these merely injuries which cannot be readily observed boatside? A simple, but highly effective means of assessing this relationship is a paired comparison of non-offset circle hooks with circle hooks of varying degrees of offset. To be most effective, such a study should combine the benefits of highly specific anatomical investigations of hooking locations on a large sample size (Skomal et al., 2002; Prince et al., 2002) with simultaneous PSAT tagging of a subset of animals for whom hooking location was estimated without causing additional stress to study animals (such as with this study). Resulting data would provide highly specific hook performance information for a large sample size while also validating survival for a subset of individuals. Additional investigations into the effect of fight time on blood chemistry and survival will shed insight into mechanisms to decrease white marlin postrelease survival.

Advances in technology will provide future researchers with many exciting improvements to current PSAT models. Clearly, smaller tags, more powerful batteries, more frequent data sampling intervals, longer tag deployment durations, and better data transmission rates will enhance the utility of PSAT tags and generate greater insights into the habitat preferences and behavior of istiophorids and a variety of smaller species. The recent addition of satellite-in-view (SIV™) technology will increase battery life and should also increase data transmission rates. Given the desire to increase tag deployment durations, investigations into the effects of stress and torque on the physical components of tags and refinement of attachment protocols will identify mechanisms to decrease premature releases of tags from study animals. Research into the drag effects of towed tags will provide researchers with an understanding of the metabolic costs of outfitting study animals with data-logging microcomputers. Additionally, continued improvements in filtering programs to decrease latitudinal errors in geolocation algorithms will improve estimates of "real-time" positions of study animals – it is easy to see how such improvements will dramatically broaden possible research applications.

Finally, given the high costs of this technology, increased applicability of PSAT technology to a wider range of species is not a cure-all panacea. Researchers should think carefully about sampling design and selecting the appropriate components of this technology to match specific research hypotheses. Properly designed studies using PSAT technology can yield powerful insights into animal behavior and survival and can directly affect management decisions.

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Entered the Master of Science program at the School of Marine Science, Virginia Institute of Marine Science, College of William and Mary in August 2001. Became a member of Umpqua Feather Merchants' Signature Fly Designer Program in 2001. Caught first white marlin on May 19, 2002 and first blue marlin on September 5, 2002.