

PHYSIOLOGICAL STRESS AND POST-RELEASE MORTALITY OF
WHITE MARLIN (*Kajikia albida*) CAUGHT IN THE U.S.
RECREATIONAL FISHERY

A Thesis

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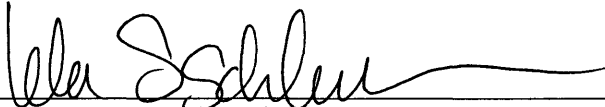
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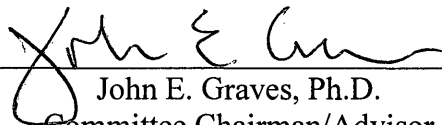
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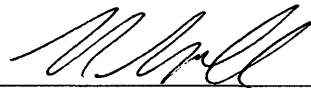
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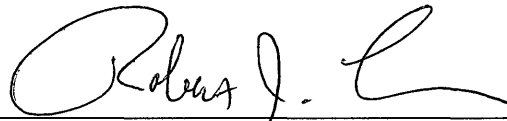
Master of Science


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DEDICATION

This thesis is dedicated to the memory of my grandmother, Eva Carlson Filbin, for
instilling in me a love and curiosity for the ocean.

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ABSTRACT

White Marlin (*Kajikia albida*) is a highly migratory species that occurs throughout temperate and tropical regions of the Atlantic Ocean and is the basis of a large sport fishery along the United States Atlantic coast. The single, Atlantic-wide stock is considered to be overfished, with less than one-third the spawning biomass estimated to be necessary for maximum sustainable yield. Billfish management measures adopted by the International Commission for the Conservation of Atlantic Tunas (ICCAT) and implemented in the U.S. by the National Marine Fisheries Service (NMFS), as well as increasing angler awareness of conservation, have resulted in the vast majority of White Marlin being released after capture. In 2003 it was estimated that more than 99% of the 4,000-8,000 White Marlin captured each year in the U.S. recreational fishery are released alive. Recent research aimed at estimating the rate of post-release mortality suggests that it may vary with hook type, hook location, angling time, air exposure, relative temperature change, and the size of the fish. Stress resulting from an angling event may also have sublethal physiological effects that negatively impact growth rates, reproductive output or investments, ability to evade predators, and disease resistance. I examined post-release mortality and post-angling physiological stress by collecting physiological data from blood samples and deploying pop-up satellite archival tags (PSATs) on recreationally angled White Marlin. Over two field seasons blood samples were collected from 68 recreationally caught White Marlin of which 22 were tagged with PSATs distributed over three stratified angling-time categories: short (0-10 min, n=8), medium (10-20 min, n=7), and long (>20 min, n=7). Plasma glucose, sodium, and cortisol increased significantly with fight time, plasma potassium decreased significantly with fight time, and plasma lactate and chloride increased significantly with fight time and water temperature. Habitat utilization following release was not affected by physiological status, angling time, lower jaw fork length (LJFL), or sea surface temperature. These results demonstrate that increased angling times and warmer water result in greater physiological stress in White Marlin. A 21% post-release mortality rate was inferred from PSAT data, and if non-reporting and early releasing tags are additionally assumed to be mortalities, post-release mortality could be as high as 32%. Post-release mortality was not related to fight time, LJFL, or sea surface temperature and was marked by elevated plasma potassium concentrations regardless of which mortality scenario was assumed. My estimates of post-release mortality rates in this study were more than an order of magnitude higher than had been previously assessed for White Marlin caught on circle hooks. This disparity in estimates may indicate that either blood sampling, removing fish from the water, or some combination of the two greatly increased post-release mortality. In order to maintain low rates of post-release mortality anglers should not remove White Marlin from the water and should resuscitate fish regardless of angling time.

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INTRODUCTION

More than 50% of marine fish caught in the United States are discarded alive and these individuals have experienced some level of physiological stress and physical injury (Bartholomew & Bohnsack 2005). Understanding the fate of released fishes (i.e. rates of post-release mortality) is critical for stock assessments and the development of effective fishing regulations. In order to reduce post-release mortality it is crucial to understand how angling practices affect survival. This is especially critical for large pelagic fishes; given that these fish support some of the largest and most valuable fisheries and have undergone a fifty percent reduction in biomass over the last century (Juan-Jordá et al. 2011).

White Marlin (*Kajikia albida*) are a highly migratory and relatively rare-event pelagic species; nevertheless, the vast majority of what we know about this species comes from fisheries dependent data. White Marlin are caught in directed recreational and artisanal fisheries, and as bycatch in commercial pelagic longline fisheries throughout the Atlantic. Landings data show that White Marlin populations, like populations of other billfish species, began to decrease rapidly in the 1960s with the onset of the pelagic longline fishery, and have remained low since that time (ICCAT 2012).

White Marlin are also the basis of a large multimillion dollar sport fishery along the U.S. Atlantic coast (Skomal 2007) and are additionally harvested for local consumption by artisanal drift gillnet and longline fisheries in Venezuela, Brazil, and the Atlantic coast of Africa. They are occasionally traded regionally throughout the Lesser

Antilles (Arocha & Bárríos 2009). The single Atlantic-wide White Marlin stock is overexploited, with a biomass well below the target for maximum sustainable yield. The most recent assessment for White Marlin conducted by the Standing Committee of Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) estimated the biomass of White Marlin at 32% of that necessary to produce maximum sustainable yield and very unlikely to rebuild in the next ten year period (ICCAT 2012). Billfish management regulations adopted by ICCAT and implemented in the United States by the National Marine Fisheries Service (NMFS) over the last decade have resulted in the vast majority of billfish being released after capture.

Following a management measure adopted by ICCAT in 2000 that restricted the U.S. recreational take of Blue Marlin and White Marlin to a total of 250 animals, NMFS adjusted the minimum size limit for both species, with the limit for White Marlin increasing to a lower jaw fork length of 168 cm. Anglers' increased awareness of the importance of protecting threatened billfish species has similarly led to an increase in live releases. Many billfish tournaments now support live releases of captured fish and it has been estimated that more than ninety-nine percent of the 4,000-8,000 White Marlin captured each year are released alive (Goodyear & Prince 2003; Cramer 2004).

Recreational fishing for White Marlin also occurs in the Straits of Florida, southeast Florida, the Bahamas, off the north coasts of Puerto Rico and the U.S. Virgin Islands, in the Mona Passage east of the Dominican Republic and in the Gulf of Mexico (White Marlin Biological Review Team 2007). The number of White Marlin captured and released each year appears to have increased since first documented by Cramer (2004); in 2013 it was estimated that approximately 10,000 White Marlin were captured

in the mid-Atlantic region (Graves, unpublished data). In fact, the mid-Atlantic recreational fleet, which extends from Cape Cod, Massachusetts to Cape Hatteras, North Carolina, has experienced several years of above average catch rates (Graves, unpublished data). White Marlin are often found at convergence zones and around bathymetric features such as drop-offs, canyons, and shoals where large numbers of prey items are available. Many recreational vessels target White Marlin around offshore submarine canyons from the shelf south of Norfolk Canyon off the coast of Virginia to Block Canyon off eastern New York.

Ecology and life history

White Marlin are a highly migratory pelagic species, distributed throughout tropical and sub-tropical waters of the Atlantic Ocean (Nakamura 1983). Information about their basic ecology and life history characteristics are limited due to the difficulty in obtaining large numbers of specimens as they typically occur in low densities over a wide distribution, and as a consequence of the reduction of their population size that has occurred over the last fifty years due to industrialized fishing. Their size and pelagic ecology additionally make it improbable that they could be kept in captivity.

What is known about the movements and habitat utilization of White Marlin largely comes from tagging studies that have used conventional tags, ultrasonic telemetry, and pop-up satellite archival tags (PSATs). White Marlin tagged with conventional tags have remained at large up to fifteen years, suggesting that longevity is likely at least two decades. Conventional tags have also shown that White Marlin are capable of trans-Atlantic movements and undertake migrations up to 6,517 straight-line kilometers (Ortiz et al. 2003). Very little ultrasonic tracking has been conducted on

White Marlin but data from active tracking have shown that they are capable of swimming up to 10.8 km/hour (Skomal 2006). In general, data from conventional tags and ultrasonic telemetry have provided important information about the life history of White Marlin but both of these techniques have limitations. Attempts to collect data using conventional tags are often hindered by low return rates (<2%) (Ortiz et. al 2003), and observations made of White Marlin (n=2) using ultrasonic telemetry are necessarily short-term (e.g. eight hours) due to the labor-intensive nature of active tracking (Skomal 2006).

Data collected from PSATs deployed for five and ten days have shown that White Marlin are capable of swimming up to 117 km per day (minimum straight line distance) and often have a strong association with surface waters, spending about half of their time in the top ten meters of the water column (Horodysky et al. 2007). Despite the fact that White Marlin are surface oriented and spend over 90% of their time within 8°C of the sea surface temperature (SST), PSAT data have shown that they can occupy a wide range of temperatures, with brief excursions to depth with as much as 13.5°C difference from SST. White Marlin, like all istiophorids, are primarily visual hunters with several unique adaptations to improve vision at depth (Fritsches et al. 2005); however, no diel differences in temperature or depth distributions have been observed (Horodysky et al. 2007). Typical behavior includes regular excursions to depth, presumably to forage, followed by a return to warm surface waters (Horodysky et al. 2007). Water more than 8°C colder than SST appears to affect the function of cardiac muscle and limit time at depth for many surface oriented pelagic fishes; this constraint necessitates that White Marlin return to the warmer surface waters after time at depth (Brill et al. 1999).

Recently, information from observer and port-sampling programs has begun to provide White Marlin life history data. A fishery dependent reproductive study using histological techniques demonstrated that White Marlin spawning in the southeastern Caribbean Sea primarily occurs from April to June (Arocha & Bárrios 2009). In this study spawning females were most frequently captured off northeast Dominican Republic in April and to the north-northeast of the Puerto Rico Trench in later months. This area has additionally been shown to be a spawning location for White Marlin by the presence of larvae 2-7+ days old (Prince et al. 2005). Other studies have hypothesized additional spawning areas based on the presence of White Marlin larvae northeast of Little Bahama Bank off the Abaco Islands, northwest of Grand Bahama Island, southwest of Bermuda, and in the Gulf of Mexico (Richardson and Rooker, unpublished data). In the South Atlantic White Marlin spawn primarily in the summer months off the southern coast of Brazil (Nakamura 1983).

Arocha and Bárrios (2009) showed that spawning female White Marlin were primarily captured in water temperatures from 22.5 to 25.9°C and depths of 90 to 110 meters. Females in that study began to mature at 151 cm lower jaw fork length (LJFL) and generally attained full maturity by 185 cm LJFL. The authors further determined that an average 25 kg adult female could spawn 427,500 eggs per batch, with spawning taking place every 1.4-2.0 days over a period of about 90 days. Thus, average annual fecundity for a 25kg female was calculated to be 19.2-27.3 million oocytes between April and June.

White Marlin are known to be generalist predators, primarily preying on epipelagic fishes and cephalopods. In the Gulf of Mexico and off the United States Atlantic coast important prey items include herring, dolphinfish (*Coryphaena* spp.),

hardtail jacks (*Caranx crysos*), and squid (Nakamura 1983). Other studies have shown Scombrids (*Euthynnus* and *Auxis*), moonfish (*Selene setapinnis*) and Atlantic pomfret (*Brama brama*) to be important prey items (Davies & Bortone 1976, Júnior et al. 2004). White Marlin have high metabolic rates and may consume as much as 6.3% of their body mass daily (Júnior et al. 2004).

Age and growth patterns for White Marlin remain largely unknown; however, several researchers have attempted to use saggital otoliths and fin spines to age billfishes with mixed results. Current research suggests that growth rings deposited in anal fin spines may provide accurate age information for White Marlin and have the advantage of being easier to collect than saggital otoliths (Drew et al. 2006). As the fish grows, fin spine vascularization eventually obscures early forming rings; however, statistical techniques have been used to infer the number of obscured rings. Growth patterns appear to be sexually dimorphic with females obtaining larger sizes than males (De Sylva & Davis 1963, Lenarz & Nakamura 1972, Oliveira et al. 2007). Researchers have observed White Marlin ages one to thirteen across fish approximately 125-195 cm LJFL (Die & Drew 2008); however, data for this study were fishery dependent and smaller fish were poorly represented, which resulted in high average percent error and coefficient of variation for the data.

White Marlin and Roundscale Spearfish

After many years of confusion surrounding the identification of White Marlin and the morphologically similar Roundscale Spearfish, the Roundscale Spearfish was validated as a distinct species by researchers using genetic techniques in 2006 (Collette et al. 2006, Shivji et al. 2006). This discovery presents a challenge for both managers and

scientists. White Marlin landings reported to ICCAT most likely include significant numbers of Roundscale Spearfish, which may constitute as much as 27% of reported White Marlin landings, although these estimates vary greatly temporally and spatially (Beerkircher et al. 2009). Unknowingly managing these two species as a single group may also have had the unintended consequence of incorrect assumptions about the biology of White Marlin. Most significantly, White Marlin population size may be overestimated (Shivji et al. 2006).

Post-release survival of White Marlin

Recent research aimed at estimating post-release mortality in marine and freshwater fishes suggests that mortality may vary with fight time, gear type, the amount of time the fish is exposed to air, relative temperature change, and the size of the animal (Horodysky & Graves 2005, Suski et al. 2007, Cicia et al. 2012, Heberer et al. 2010). It is essential to quantify post-release mortality for White Marlin in order to accurately estimate levels of fishing mortality on this overfished species and to identify angling practices that result in the largest reduction in post-release mortality.

Ultrasonic telemetry has been used since the 1970s to estimate post-release mortality of large pelagic fishes; however, there have been few studies focused on billfish. Skomal (2006) used ultrasonic tracking to actively track two White Marlin for eight hours after they had been angled for 49 and 51 minutes and did not observe post-release mortality in either. For the past twelve years researchers have been using PSATs to quantify post-release mortality of large pelagic fishes as well as to examine behavior associated with recovery and survivorship. But the magnitude of post-release mortality for most fisheries and gear types that target highly migratory species remains unclear.

PSATs can be used to estimate post-release mortality over a longer period than with ultrasonic tracking, but obtaining statistical power for estimates requires large sample sizes (Goodyear 2002). Previous research on post-release mortality in billfishes using PSATs has shown that mortality may be significantly reduced with the use of circle hooks (Horodysky & Graves 2005, Graves & Horodysky 2010). Some uncertainty remains regarding the magnitude of post-release mortality for the species on this terminal gear. In order to examine multiple treatments within a study (fishing methods, gear types, etc.) high numbers of PSATs would be required and obtaining a sample size with any real statistical power for multiple treatments is cost-prohibitive based on the present cost (~\$4,000) per tag (Horodysky & Graves 2005, Kerstetter & Graves 2008, Musyl et al. 2011). Currently there is a need for a cost-effective way to estimate post-release mortality for robust sample sizes and to generate results with statistical power. Physiological samples can be collected at low cost from a large number of fish and may provide information about the fate of fish following release. Using PSATs in combination with physiological data may allow for a relatively low cost, statistically powerful, and empirically-based method to estimate post-release mortality in fishes.

Stress physiology

In addition to the physical damage caused by hooks, recreational fish experience various levels of stress resulting from the angling event, boatside handling, de-hooking, and release procedures. In many cases, billfish are so exhausted at the end of a fight that they cannot maintain equilibrium in the water column and need to be resuscitated prior to release. Stress can be defined as a state of threatened homeostasis that is re-established by a complex suite of adaptive responses (Barton 2002). It is generally recognized that fishes

react to stress from capture, handling, and exhaustive exercise with more exaggerated disruptions to their physiology than other higher vertebrates (Wells et al. 1986).

Physiological disturbances resulting from exhaustive exercise stress may be so severe as to cause the death of the animal several hours later (Wood et al. 1983). The grouped responses should be interpreted with the understanding that individual conditions, including species differences, genetic characteristics, and local environmental conditions, can affect nature and the severity of the response (Black 1958, Wood et al. 1983).

The stress response in fish has been broadly categorized into primary, secondary, and tertiary responses (Iwama et al. 2006), and they will be presented here in that manner. The primary stress response in fish is neuroendocrine and associated with rapid changes in circulating levels of stress hormones, predominantly catecholamines and corticosteroids (Skomal & Mandelman 2012). When real or perceived threats are detected, the central nervous system initiates the physiological stress response (Barton 2002). Neural signals trigger sympathetic nerve fibers that innervate chromaffin cells to immediately secrete catecholamines from chromaffin tissue (clusters of neurosecretory cells on the dorsal surface of the kidneys) via cholinergic receptors (Randall & Perry 1992, Barton 2002). Adrenaline (or epinephrine) and noradrenaline (or norepinephrine) are the dominant catecholamines released. Triggering stressors may include hypoxia, hypercapnia, and exhaustive exercise during capture and handling (Mazeaud et al. 1977, Randall & Perry 1992). Cortisol is the principle corticosteroid in actinopterygian fishes (Barton 2002). Although cortisol release in teleosts is delayed relative to catecholamine release (Iwama et al. 2006). The pathway for cortisol release begins in the hypothalamic-

pituitary-interrenal (HPI) axis with the release of corticotropin-releasing hormone, mainly from the hypothalamus in the brain, which stimulates the corticotrophic cells of the anterior pituitary to secrete adrenocorticotropin (ACTH). Circulating ACTH then stimulates the inter-renal cells embedded in the kidney to synthesize and release corticosteroids into circulation for distribution to target tissues. Chromaffin and inter-renal tissues lie in close proximity in fishes, suggesting a paracrine control for stress hormone regulation (Iwama et al. 2006).

The secondary stress response comprises a suite of various biochemical and physiological effects associated with stress and mediated by stress hormones. Effects typically include rapid mobilization of glucose into the blood stream to meet energy demands, and the onset of anaerobic glycolysis; resulting in the associated depletion of intramuscular glycogen, adenosine triphosphate (ATP), and creatine triphosphate reserves. This response is coupled with the accumulation of lactate in white muscle; the decrease in intracellular and extracellular pH due to metabolic accumulation of H^+ and/or respiratory acidoses (pCO_2 elevation); and a perturbation of osmotic and fluid volume homeostasis with internal fluid shifts driving potential hemoconcentration (Wood 1991, Kieffer et al. 1995, Skomal & Mandelman 2012). Fish erythrocytes possess nuclei and remain transcriptionally active and therefore retain the capacity to set heat shock protein 70 (Hsp70) gene expression in motion within red blood cells in response to stress (Curie et al. 1999). Elevations in hematocrit (i.e., the fraction of blood volume comprised by the red blood cells) can also occur due to splenic contractions and/or red blood cell swelling; both of these responses augment oxygen transport (Wendelaar Bonga 1997). These biochemical and physiological responses can be measured and used to quantify the

degree of physiological stress. This information can be used to predict post-release mortality and provide insight into capture stressors.

The tertiary stress response relates to whole animal and/or population responses to stress and is much more difficult to quantify than either the primary or secondary responses. Stress can negatively impact individuals and these negative effects may translate up to the population level (Cooke et al. 2002). Acute and chronic stressors can cause physiological changes at the organismal level, affecting growth rates, ability to evade predators, reproductive outputs or investments, and disease resistance (Iwama et al. 2006, Skomal & Mandelman 2012). Arocha and Bárríos (2009) noted that all but one female White Marlin caught in spawning condition (n=18) during observed long line sets were dead at haul-back, suggesting that females in spawning condition are especially susceptible to mortality. It should be noted however, that these authors did not identify the mortality rate of female White Marlin at other stages of reproduction, or males at any stage. Jackson and Farber (1998) found that, between 1987 and 1995, 56.1% of White Marlin caught in the Venezuelan pelagic longline fishery were dead at haul-back with female White Marlin comprising 51% of the White Marlin catch. However, these authors did not investigate spawning condition of fish nor report the sex composition of the fish that were dead at haul-back.

Recent molecular studies on the teleost response to stress suggest that acute stress can cause cellular damage that results in chronic stress affecting long term fitness and reducing survivorship (Curie et al. 1999, Iwama et al. 2006). The physiological and mechanical stress associated with catch-and-release fishing has been shown to alter swimming speed and ability to evade predators. Following rod and reel capture, Bonefish

(Albula vulpes) exhibit loss of equilibrium, which causes them to be more vulnerable to predation. Researchers found that loss of equilibrium was positively correlated with the duration of air exposure and handling stress (Danylchuck et al. 2007). Stress also alters the immune response in teleost fish; debilitated immune function has been observed following hypoxia and capture stress (Møllgaard & Nielsen 1995, Lupes et al. 2006).

Under conditions of exhaustive exercise, physiological stability is achieved through reallocation of energy systems toward those most critical to survival. This will temporarily result in increased fitness; the stress response can, however, ultimately result in decreased fitness and/or mortality. If the compensatory mechanisms (or the energy required to deal with the costs associated with these compensatory mechanisms) are not sufficient to correct for large homeostatic perturbations, mortality will ensue (Wendelaar Bonga 1997). Most significantly, the physiological effects that arise from the primary and secondary responses may persist for hours to days (Cooke et al. 2012).

The recovery process involves correcting ionic/osmotic balances, clearing lactate accumulation, and replenishing energy stores (Suski et al. 2006). The return to baseline levels is a slow process due to the need to restructure ion pumps in the gills, and increase bicarbonate to buffer lactate and decrease ion concentrations. The release of stress hormones in the primary response causes increased cardiac output, increased blood pressure, recruiting of gill lamellae, and increased gill diffusing capacity to facilitate oxygen uptake as fish attempt to meet elevated oxygen demands. These changes to gill morphology have been shown to facilitate ion permeability by disrupting tight junctions and decreasing the resistance to ion diffusion. The final result is that stress and exercise are typically associated with concomitant mineralization and water loss to the

environment (Wendelaar Bonga 1997). The prolonged physiological response has been demonstrated in the laboratory. Bonefish exposed to exhaustive exercise and air exposure required between two to four hours to return to resting lactate and glucose levels and more than four hours for ion levels to return to resting values (Suski et al. 2007). Additionally, heart rate and other cardiac variables have been shown to remain elevated up to 18 hours after the stressor has ended (Cooke et al. 2012).

A large proportion of effort in recent physiological research has been directed at quantifying the physiological response to exhaustive exercise (Iwama et al. 2006). Researchers have used blood samples from fish in the field (Moyes et al. 2006, Heberer et al. 2010, Marshall et al. 2012) as well as in the lab (Mazeaud et al. 1977, Suski et al. 2007) to categorize the stress response for species that are frequently released following capture because of size, season, or area restrictions or fisheries that are based on catch-and-release. Stress effects are well documented for many fishes and a long-standing goal of research centered on exhaustive exercise is to identify physiological predictors for mortality; however, the stress response has been shown to be species specific and dependent on the duration and nature of the stressor (Skomal & Mandelman 2012). Additionally, studies often observe low rates of mortality, which limit statistical inferences regarding a specific cause of death (Cooke et al. 2012).

For studies conducted in the field the relative contribution of stress to post-release mortality has been difficult to quantify because it occurs in combination with the mechanical damage caused by fishing gear. Consequently, strategies to limit stress and reduce post-release mortality (the importance of fight times, line strength, resuscitation, etc.) are very difficult to evaluate for pelagic fishes. However, in the White Marlin

fishery, the broad acceptance of circle hooks [the vast majority of which lodge in the corner of the fish's jaw (Graves & Horodysky 2008)] greatly reduces the variance in hook location and provides an opportunity to evaluate the relative importance of stress to post-release mortality in this important recreational fishery.

Project goals and experimental design

My research goals were to combine a suite of physiological measurements with information from PSATs to better understand the condition of White Marlin captured and released from the recreational fishery. By linking data from PSATs and physiological analysis I set out to derive physiological predictors for post-release mortality and to estimate the fishing mortality of the U.S. recreational fishery for White Marlin. My hypotheses were that elevated physiological stress and post-release mortality would be predicted by increased angling times, warmer water temperatures, and larger White Marlin. To estimate predictors for mortality, 22 recreationally angled White Marlin were sampled for blood and tagged with PSATs distributed over three stratified angling time categories to follow behavior and survival over a 30-day period. An additional 46 White Marlin were sampled for blood to expand the understanding of the physiological response to angling and estimate the fishing mortality of the fishery.

MATERIALS AND METHODS

Species capture & tag deployment

Sampling and PSAT deployments were conducted on recreational and charter fishing vessels between August 2012 and September 2013. Sampling was conducted 60 to 100 miles off Ocean City, Maryland and Virginia Beach, Virginia in Norfolk Canyon and areas south, Washington Canyon, and Baltimore Canyon along the U.S. mid-Atlantic coast. Sixty-eight White Marlin were captured in the normal course of fishing operations using trolled ballyhoo (*Hemiramphus brasiliensis*) rigged with a circle hook on 30 pound test main line and with a 60 to 100 pound test leader 30 feet in length. White Marlin were caught during the course of normal fishing operations and angling times were not extended or altered; however, some additional time past when the fish would normally have been considered caught (i.e. touching the leader) was often necessary in order to maneuver the fish into position to be safely brought into the vessel.

Angled White Marlin were maneuvered alongside the vessel and carefully lifted by the bill over the gunwale and placed on deck. Fish were immobilized by holding the bill and tail securely to the deck, while a damp rag was placed over the fish's eyes to keep it calm. When possible, a saltwater deck hose was placed into the fish's mouth so that oxygenated water was delivered to the gills. Once immobilized on deck, lower jaw fork length (LJFL) and hooking location were recorded and the hook was removed. Fish condition was assessed on a ten-point scale that assigned zero, one, or two points (poor, average, or excellent condition) for each of the following categories: coloration, activity,

eye condition, injuries, and whether or not the stomach was everted. Fish were then sampled for approximately 5 mL of blood drawn from the ventral aorta by lifting the operculum and inserting an 18-gauge heparinized needle attached to a 10 mL heparinized syringe ventral to the gills. Approximately 1g of white muscle was collected from the caudal region using an 8.0 mm tissue biopsy punch.

Geographic location, sea surface temperature, fight description, fight time, and handling time were recorded. Fight time was defined as the time from when the fish was hooked to when the fish was brought alongside the vessel, while handling time was defined as the time the fish was kept on the vessel. Time on deck was minimized and kept to less than two minutes for most individuals, though a few individual handling times were as long as three and a half minutes.

The first White Marlin that were hooked in the corner of the jaw and captured in each of three angling-time categories: short (0-10 min, n=8), medium (10-20 min, n=7), and long (>20 min, n=7), were tagged with 30-day High-Rate X-Tags from Microwave Telemetry Inc. (Columbia, MD). White Marlin were tagged following blood sampling and immediately returned to the water after the tagging procedure. PSATs were programmed to release prematurely if depth values remained constant (± 3 meters) for four days or if a depth of 1,250 meters was reached. In the event of post-release mortality the programmed premature release helps to protect the tag against damage from scavengers or being crushed by pressure at depth. The rigging and deployment of PSATs followed the protocol outlined in Graves et al. (2002). Fish that did not receive satellite tags were returned to the water following blood sampling. Fish were resuscitated alongside the boat by holding the bill so the fish remained under the water and oriented

into the current alongside the slowly moving vessel and oxygenated water was flowing over the gills. Fish were released once they regained some coloration and showed signs of trying to swim away from the vessel. Resuscitation time ranged from approximately 15-180 seconds.

Physiological samples

Blood and muscle samples were stabilized following the release of the fish. White muscle samples were immediately frozen in liquid nitrogen and subsequently stored at -80°C . Hematocrit was assessed in the field from a subsample of whole blood following centrifugation at $12,000 \times g$ for five minutes. The remaining whole blood sample was centrifuged at $12,000 \times g$ for five minutes. Following centrifugation, plasma was decanted; and it and the remaining red blood cell pellet were frozen separately in liquid nitrogen for the duration of the time in the field. All samples were subsequently stored at -80°C .

Plasma samples were thawed and analyzed for sodium (Na^+), chloride (Cl^-), potassium (K^+), calcium (Ca^{++}), magnesium (Mg^{++}), glucose, lactate, and cortisol. Plasma electrolytes and metabolites were analyzed using an automated blood chemistry analyzer [NOVA CCX Statprofiler (Waltham, MA, USA)]. Cortisol was assessed using a competitive enzyme-linked immunosorbent assay (ELISA) following the protocol outlined in Carey and McCormick (1998). Cortisol values were determined using a Tecan GENios plate reader that read absorbance at 450nm and Magellan software (6.55). Plasma samples analyzed for cortisol were run in duplicate and the mean concentration was used for analysis. Samples were reanalyzed if duplicates had a coefficient of variation greater than ten percent.

White muscle tissue and red blood cells were collected to assess muscle lactate and heat shock protein 70 (Hsp70), respectively. Unfortunately, during the period that samples were stored at -80°C a freezer failure resulted in the complete thawing of all collected plasma, tissue, and red blood cells. Concentrations of electrolytes, metabolites, and hormones in plasma samples were validated by reanalyzing previously assessed samples and were not significantly different before and after the thaw occurred. Rapid degradation of muscle lactate and mRNA prevented the analysis of muscle lactate and Hsp70 as originally planned.

Data analysis

The minimum straight line distance travelled by each fish was calculated by determining the distance between the tagging location and the first reliable satellite contact with the floating tag [ARGOS codes 1, 2, or 3] using ArcGIS (10.0) and Geospatial Modeling Environment (0.7.2.0). Analyses of net movements, as well as time series of light levels, water temperature, and depth measurements, were used to assess habitat utilization, migration strategies, and mortality (Horodysky & Graves 2005). Software developed by Goodyear (2002) was used to assess 95% confidence intervals for estimates of post-release mortality. Distributions of estimates were based on 10,000 simulations and no tagging-induced mortality or natural mortality. To determine if physiological stress was related to angling time, LJFL, or sea surface temperature, measured physiological variables were modeled with generalized linear models using a Gaussian distribution. To assess the influence of physiological stress on habitat utilization following release, physiological variables were again modeled with generalized linear models using a Gaussian distribution to predict for median temperature in the first four

hours following release. To determine predictors for post-release mortality, physiological variables and survival status were analyzed using generalized linear models with a binomial distribution. Models were selected based on Akaike's Information Criterion (AIC) and goodness of fit. The variance inflation factor (VIF) of physiological variables was examined for the generalized linear models predicting habitat utilization and highly correlated variables were eliminated from the models. For all analyses significance was set at $\alpha=0.05$ and all statistical analyses were run in R (3.1.0) (R Core Team 2014).

RESULTS

Species capture & tag deployment

Sixty-eight White Marlin were caught on recreational fishing vessels over 36 days at sea spread over two field seasons (2012-2013). An average of 1.89 White Marlin were captured for each day at sea, with the number of fish sampled ranging from zero (six occurrences) to six (one occurrence). Blood and white muscle tissue samples were obtained for all 68 fish and 22 individuals were tagged with 30-day high rate PSATs.

Fish size ranged from 122-175 cm LJFL; however, the majority of fish did not vary greatly and the average size of 158 cm LJFL was fairly representative of sampled fish (Fig. 1). Angling times extended from 3-41 minutes, encompassing both extremes for the fishery, and the average angling time was 15 minutes. Surface water temperatures in the locations that fish were captured ranged from 23.1-26.7°C with an average of 25°C.

Of the 22 PSATs deployed, 19 tags remained attached for at least ten days or reported data sufficient to determine mortality, two tags detached the day they were put out, and one tag never reported. Fifteen of the 19 tags recorded data consistent with survival and 13 of those tags remained attached for the full 30-day deployment, while two tags released prematurely after 11 and 12 days. For the 19 tags that remained attached for at least ten days or recorded a mortality event, 78-96% of the data was recovered.

Habitat utilization data from PSATs showed that fish utilized water temperatures ranging from 10.0-30.5°C with a mean water temperature of 25.1°C. In general, White

Marlin spent the majority of their time in water that was 24-28°C and spent less than five percent of their time below 22°C (Fig. 2). Excursions to depth ranged from the surface to 254.2 meters with a mean depth of 26.6 meters below sea surface. White Marlin spent the majority of their time in the top 100 meters of the water column with just over 40% of their time in the top ten meters (Fig. 3).

White Marlin tagged for 30 days traveled between 91 and 2,643 km away from the tagging point with an average of 1,181 km travelled. Fish exhibited a variety of migration patterns as they left the mid-Atlantic coast with some fish moving directly southward, others taking a more eastward trajectory, and one fish likely riding the Gulf Stream and moving northeast (Fig. 4).

All White Marlin were tagged in the months of August and September in 2012 and 2013. There did not appear to be any relationship between when a fish was tagged and how far it travelled. The fish that travelled the furthest distance from the tagging location (2,643 straight-line km) was also the earliest fish tagged (August 8, 2013) while the fish that travelled the shortest distance (91 straight-line km) was tagged only 15 days later (August 23, 2013). Similarly, there did not appear to be a consistent time period when White Marlin left the coastal zone and crossed the Gulf Stream, as determined by a rapid increase in sea surface temperature followed by a return to lower sea surface temperatures. Some fish left the coastal zone as early as mid-August while others did not cross the Gulf Stream until early October.

Based on analysis of tag data, a total of four mortalities were inferred out of 19 tags that transmitted unambiguous data for a post-release mortality rate of 21.1% with 95% confidence intervals ranging from 5.3-36.8% post-release mortality. When the non-

reporting tag and the two tags that released within 24 hours of deployment were considered mortalities, post-release mortality was calculated to be 31.8% with 95% confidence intervals of 13.6-45.5% post-release mortality.

All four mortalities sank to the bottom immediately following release. Two mortalities remained resting on the sea floor for the remainder of the time the tags were attached while the other two mortalities were apparently scavenged by predators after spending several hours on the sea floor. Scavenging was indicated by PSATs registering darkness and recording behavior divergent from what would be expected for surviving White Marlin (Fig. 5). The tags deployed on White Marlin 120583 and 110289 recorded a period of several hours of inactivity at more than 200 meters depth immediately following release. For both fish this period of inactivity was followed by temperature and depth measurements incongruous with White Marlin behavior, and constant darkness as the tag moved up and down in the water column suggesting that the tags had been consumed and were recording data from inside the stomachs of predators.

White Marlin 120583 was hooked while cutting through a school of baitfish at the surface, angled for 16 minutes, measured 137 cm LJFL, and was held on deck for approximately three minutes. Immediately following release it sank to a depth of 234 meters where it presumably died and remained resting on the sea floor for a period of three hours. Tag data suggests that a predator swallowed the tag following this period of inactivity as it began to register temperature and depth changes as the predator moved up and down in the water column. The predator had a diurnal behavior pattern of slow descents to 400-600 meters during the day and slow ascents up to 200 meters in the evening which, along with temperature data reflecting ambient water temperatures (e.g.,

not an endothermic predator), suggests that the predator was likely a six-gill shark (*Hexanchus griseus*) (Fig. 6). Tag120583 continued to collect data inside the predator's stomach for eight days before it was presumably regurgitated. Over the eight-day period the tag was displaced 678 km.

White Marlin 110289 was hooked while cutting through a school of baitfish at the surface, angled for five minutes, measured 165 cm LJFL, and was held on deck approximately two minutes. It sank to a depth of 225 meters immediately following release. Over a period of seven hours the tag did not register a depth change greater than three meters, suggesting that the fish had died and was resting at the bottom. Following this period of inactivity, the tag registered continuous darkness and temperature and depth data incongruent with White Marlin behavior indicating that the tag had been consumed. This predator, similar to the predator of White Marlin 120583, was not endothermic and had a diurnal behavior pattern, making daytime excursions to depths around 350-400 meters where it spent up to ten hours at depth and slowly returned to the surface (Fig. 7). Tag 110289 continued to collect data for 19 days in the predator's stomach before regurgitation. Over the 19-day period the tag was displaced 276 km.

White Marlin 120577 died and sank to the sea floor following release but was not scavenged. This fish was angled for six minutes, measured 165 cm LJFL, was kept on deck for two minutes, and despite being resuscitated did not swim away strongly or maintain its position in the water column following release. Immediately following release White Marlin 120577 sank to a depth of approximately 350 meters and remained at that depth until the tag detached from the fish 13 days later and floated to the surface (Fig. 8). The tag should have automatically detached after registering constant depth for a

four-day period but the pre-programmed premature release mechanism apparently did not function correctly.

White Marlin 120565 died and sank to the sea floor following release. This fish was caught feeding on a bait ball and still had baitfish in its mouth when it was caught. It was angled for ten minutes, measured 165 cm LJFL, was kept on deck for two minutes, and despite being resuscitated did not swim away strongly following release.

Immediately following release White Marlin 120565 sank to a depth of approximately 100 meters and remained at that depth until the tag detached from the fish five hours later and floated to the surface. The tag presumably became dislodged from the dorsal muscle tissue of the fish as scavengers began feeding on the fish.

One mortality was noted for a White Marlin that was sampled after all available PSATs had been deployed and therefore was not tagged. White Marlin 67 was angled for ten minutes, measured 152 cm LJFL, and was kept on deck for two minutes. It became wrapped in the line during angling which may have restricted the fish's ventilation during angling. The fish had lost color by the time it was brought into the boat, remained moribund on deck, and was not resuscitated following sampling. This fish was observed to float belly up at the surface following release and presumably died shortly thereafter. For the subsequent physiology analyses White Marlin 67 will be considered a mortality though it cannot be definitively shown that this was the case.

Physiological samples

Plasma sodium, potassium, chloride, magnesium, glucose, lactate, cortisol, and whole blood hematocrit were analyzed for all 68 White Marlin (Table 1). In general, plasma sodium, chloride, glucose, and lactate increased with angling time. Plasma

calcium, magnesium, and whole blood hematocrit did not change markedly with angling time and plasma potassium had a decreasing trend with increased angling time.

Physiological variables were analyzed with generalized linear models using a Gaussian distribution. Angling time, surface water temperature, and fish size were used to predict hematocrit and plasma ion values, glucose, lactate, and cortisol (Fig. 9-11). Plasma sodium, glucose, and cortisol increased significantly with fight time, while plasma potassium decreased significantly with fight time. Plasma lactate and chloride increased significantly with fight time and surface water temperature. Hematocrit, plasma magnesium, and plasma calcium did not have a significant relationship with any of the predictor variables, but the best possible model for these variables was based solely on fight time (Table 2).

To determine if physiological stress influenced White Marlin habitat utilization, generalized linear models with a Gaussian distribution were used. Models assessed if angling time, surface water temperature, fish size, and/or physiological variables could predict for White Marlin median water temperature registered by PSATs in the first four hours following release. The best model to predict median temperature in the first four hours after release was of the form: Median Temperature ~ Plasma calcium + LJFL (Fig. 12). This model approached significance with a p-value of 0.055 for plasma calcium and $p=0.121$ for LJFL.

The physiological status, fight time, LJFL, and surface water temperature of the 19 White Marlin for which survival or mortality could be determined was modeled using a generalized linear model with a binomial distribution for which each fish was entered as a survivor or a mortality. Two scenarios were examined, the first where only five

mortalities were evaluated (White Marlin 120583, 110289, 120577, 120565, and 67), and the second where the one non-reporting PSAT and the two PSATs that detached within several hours were additionally considered mortalities. The best model to predict mortality of the sampled White Marlin for both model scenarios was of the form: Mortality ~ Plasma potassium. The standard model using five White Marlin mortalities approached significance with a p-value of 0.0509 (Fig. 13), while the more conservative model that additionally assumed non-reporting PSATs as mortalities was significant with a p-value of 0.0342 (Fig. 14). The point of 50% mortality was calculated for both the standard and the more conservative mortality models. For the standard model using five mortalities, 50% mortality occurred at 4.57 mmol/L plasma potassium. The more conservative model using eight mortalities shifted the point of 50% mortality down to 4.42 mmol/L plasma potassium.

Both model scenarios demonstrated that fish with elevated plasma potassium were at an increased risk of dying following release. Applying the standard mortality model to the 46 fish that were blood sampled but not tagged demonstrated that 16 of the 46 fish (34.8%) had plasma potassium concentrations above the 4.57 mmol/L point of 50% mortality. Using the more conservative mortality model that assumed the non-reporting tag and the two tags that detached within hours of release were mortalities, 22 of the 46 fish (47.8%) had plasma potassium concentrations above the 4.42 mmol/L point of 50% mortality.

DISCUSSION

Highly migratory pelagic species are both overfished and highly sought after by both commercial and recreational fisheries worldwide (Skomal 2007, Juan-Jordá et al. 2011). Releases of pelagic species captured by recreational and commercial gear are increasing both because of regulations mandating release and a growing conservation ethic among recreational anglers (Skomal 2007). It is therefore imperative to understand the role of physiological stress in order to more accurately estimate the sublethal effects and the true fishing mortality for released large pelagic fishes (Skomal 2007, Heberer et al. 2010). Assessing the effects of capture on the physiological stress of pelagic fishes presents several unique challenges. In particular, many pelagic fishes cannot be easily kept in captivity, have a low rate of recapture, and are impossible to obtain unstressed (Wells et al. 1986, Ortiz et al. 2003, Cooke et al. 2012). Therefore, control values cannot be determined, repeated physiological measurements are not possible, and long-term survival must be assessed through the use of archival tag technology (Skomal 2007, Cooke et al. 2012). Several studies looking at the effect of catch-and-release fishing on physiology, survival, and behavior have taken blood samples from fish and tagged conspecifics that were not sampled to make inferences about the relationship between stress and post-release mortality (Heberer et al. 2010, Gallagher et al. 2014). My study is one of the few to collect physiological samples and deploy tags to follow survival on the same fish (Thompson et al. 2008, Rapp et al. 2012, Skomal 2006).

The most significant finding from my research is that post-release mortality of

White Marlin caught on circle hooks can be much higher than previously reported. Physiological stress was elevated with increased angling time, and in some cases, with warmer water temperatures. Surprisingly, physiological stress, sea surface temperature, angling time, and/or fish size did not predict White Marlin habitat utilization following release. Angling time, sea surface temperature, and fish size also did not predict mortality. Elevated concentrations of plasma potassium proved to be the sole predictor for mortality regardless of whether a low- or high-mortality scenario was considered. In the following discussion I will present the habitat utilization data from White Marlin tagged with PSATs, the physiological stress response of White Marlin to catch-and-release fishing, the influence of physiological stress on behavior following release, estimates of White Marlin post-release mortality, and the effect of physiology on post-release mortality.

White Marlin habitat utilization & migration

Although I used PSATs primarily to assess survival status following release, they also provided important information on the habitat utilization of White Marlin. Habitat utilization data from 30-day PSATs demonstrated that White Marlin are capable of excursions to depths exceeding 200 meters and below 10°C, although they spent the majority of their time in the top 100 meters of the water column in 24-28°C water, and over 40% of their time in the top ten meters. White Marlin have previously been shown to have a strong association with surface waters, spending as much as 48% (± 3) of their time in the top ten meters of the water column, although this may vary by season and location (Horodysky et al. 2007). Similarly, White Marlin have previously been shown to spend 87% (± 11) of their time between 24 and 29°C (Horodysky et al. 2007). Acoustic

and PSAT studies have also reported an association with near-surface waters for other istiophorids (Holland et al. 1990, Brill et al. 1993, Gunn, Patterson, & Pepperell 2003, Hoolihan et al. 2011).

White Marlin are surface oriented but they have also been observed to frequently make short duration excursions to depths exceeding 100 meters, with a maximum depth between 161 and 368 meters depending on location (Prince et al. 2005, Horodysky et al. 2007). Habitat utilization data from my study are consistent with data on temperature and depth from previous White Marlin tagging studies (Prince et al. 2005, Horodysky et al. 2007, Hoolihan et al. 2012). Vertical movements of White Marlin may be limited by temperature (Brill et al. 1999), with fish making only short excursions to depths below 100 meters, although individuals have been shown to spend substantial time at depths between 20 and 80 meters (Horodysky et al. 2007). These repeated excursions to depth are presumed to be for feeding or to increase olfactory or visual cues to aid in acquiring prey as White Marlin move from depth to the surface.

Many of the details concerning the timing and cues for long distance migrations undertaken by White Marlin remain unknown. Historically, September is when the largest numbers of White Marlin are caught off of the U.S. mid-Atlantic coast and also when White Marlin begin to leave the region. Temperature has been shown to influence the vertical and horizontal movements of istiophorids (Holland et al. 1990, Block et al. 1992, Brill et al. 1993, Graves et al. 2002), which may be due to the effect of water temperature on cardiac function (Brill et al. 1999, Brill & Lutcavage 2001). White Marlin only inhabit the northern portion of their range in the western North Atlantic during the summer months (White Marlin Biological Review Team, 2007) so the seasonal

movements away from the mid-Atlantic region in the fall are likely influenced by temperature.

My data show that White Marlin migration cues consist of more than cooling water temperatures. White Marlin did not leave the coastal zone at one consistent time or sea surface temperature, or exhibit distinct migration routes when leaving the U.S. mid-Atlantic region. The 13 PSATs that remained attached for 30 days showed that White Marlin travelled from 91 to 2,643km between the months of August and October. The White Marlin that travelled the furthest distance was tagged from August 8 to September 8, 2013 while the White Marlin that travelled the shortest distance was tagged from August 23 to September 23, 2013; a period when water temperatures were cooling and most other tagged White Marlin had already started migrations.

White Marlin in my study moved between 0.126 and 3.67 km/hr, corresponding closely to the range of 0.129 to 4.815 km/hr reported by Horodysky et al. (2007) and comparable with published rates of speed for other istiophorids (Holts & Bedford 1990, Pepperell & Davis 1999, Graves et al. 2002). However, Skomal (2006) reported White Marlin moving as fast as 10.8 km/hr over an eight-hour period of active tracking. The reported rates of speed in my study, as well as published rates of speed for other istiophorids, vary greatly. This is due to the fact that, unless obtained from active tracking, these rates are likely underestimates because they are derived from the straight-line horizontal distance traveled between the tagging site and pop-up location divided by the time at liberty. Moreover, some fish remain close to the tagging location and others move thousands of kilometers. These estimates of rates of speed are not likely representative of true travel speeds, but do provide useful comparisons between studies.

Conventional tags with fisheries dependent recoveries have demonstrated White Marlin movements up to 6,517 straight-line km, with time at large up to 15 years (Ortiz et al. 2003). Conventional tags have documented a few instances of White Marlin from the U.S. East coast crossing the Atlantic and being recaptured off the northern coast of Africa (Ortiz et al. 2003). There are also many records from conventional tags of fish migrating from the U.S. mid-Atlantic region to the Gulf of Mexico, Caribbean, and northern coast of South America. To date, no trans-equatorial or inter-oceanic movements have been observed; however, genetic evidence currently supports a single Atlantic-wide stock, and these results are consistent with at least limited numbers of trans-equatorial migrations per generation (Graves and McDowell 2006). The 30-day tag deployments used in this study cannot provide many insights on long-term movements, but two fish did display directed movements to the Caribbean in a 30-day period.

Six- and 12-month PSATs deployed on White Marlin caught off the U.S. mid-Atlantic coast in another study also illustrate the importance of regional connectivity between the mid-Atlantic and the Caribbean (Loose, unpublished data). Geo-locating tags revealed that White Marlin spent time in and around the Caribbean over the winter and spring months. One White Marlin tagged with a 12-month tag retained the tag for the full deployment. This fish migrated south to the Caribbean for the winter and spring and then returned to the mid-Atlantic in the summer where the tag popped up very close to the location where the fish had been tagged one year earlier. In contrast, another White Marlin that was tagged for 325 days did not appear to demonstrate directed movements and instead moved North and South along the U.S. east coast over the winter months. In the spring this fish migrated to the waters off Bermuda, where the tag released due to

reaching maximum pressure suggesting that the fish had died and was sinking to depth. Reproductive histology and larval studies have shown that White Marlin spawn in and around the Caribbean and Bermuda April through June, which is one possible explanation for these long distance migrations (Prince et al. 2005, Arrocha & Bárríos 2009, S. Heppel, unpublished).

Physiological Stress

The present study is one of the few to examine the physiological effects of catch-and-release fishing on billfish and very little published information exists on the physiological effects of exhaustive exercise in billfish. Skomal (2006) examined the physiological response of five White Marlin to angling, but was not able to sample sufficient numbers to make statistical inferences. Wells and Davie (1985), Dobson et al. (1986), and Wells et al. (1986) published work on Striped Marlin and Blue Marlin and concluded that exhaustive exercise caused respiratory and metabolic acidosis that impaired oxygen transfer by the cardiorespiratory system and the function of vital organs. Blue Marlin and White Marlin have been shown to possess a high white muscle buffering capacity, but the extent to which this aids post-exercise recovery is not understood (Dobson et al. 1986, Skomal 2006).

The current study found that plasma lactate and chloride increased significantly with angling time and sea surface temperature; plasma glucose, sodium, and cortisol increased significantly with angling time; plasma potassium decreased significantly with angling time; and plasma magnesium, plasma calcium, and hematocrit did not change markedly in response to angling time, sea surface temperature, or LJFL. The general physiological patterns observed in this study are similar to what has been observed in

other fishes following exhaustive exercise with plasma electrolytes, metabolites, and hormones generally increasing with angling time (Wood, Turner & Graham 1983, Suski et al. 2007, Heberer et al. 2010, Brooks et al. 2012). The effect of increased water temperature has similarly been found to augment patterns of physiological stress (Suski et al. 2006) and may interact with air exposure to increase post-release mortality (Gingerich et al. 2007).

In my study plasma calcium, magnesium, and hematocrit did not vary significantly with angling time, a pattern that contrasts with the results of others (Moyes et al. 2006, Suski et al. 2007, Heberer et al. 2010, Brooks et al. 2012). One possible explanation for the lack of a significant relationship between fight time and these physiological variables is that in some instances responses may have occurred rapidly and reached a plateau rather than continuing to increase over time (Skomal & Bernal 2010). Surprisingly, in my study plasma potassium tended to be lower in plasma samples from fish with longer fight times. This pattern may be due to a few plasma potassium outliers driving the observed relationship. Several studies have shown fish size to be an important variable in predicting physiological status (Davis & Parker 2004, Heberer et al. 2010, Skomal 2006); however, in my study the measured physiological variables did not vary significantly with LJFL, which may be due to the limited size range of sampled fish.

Skomal (2006) found that glucose, sodium, and chloride increased with angling time in White Marlin. In the current study observed mean plasma lactate, glucose, chloride, potassium, and sodium concentrations were slightly lower than those Skomal (2006) observed, while the mean hematocrit and plasma calcium concentration were

slightly higher. The physiological variables I observed did not differ greatly from those measured by Skomal (2006), with the exception of plasma cortisol.

Skomal (2006) found that White Marlin had higher cortisol levels than any of the nine tuna species investigated. In teleosts, cortisol concentrations following exhaustive exercise typically range from 50-60 ng/mL in inactive fishes to as high as 400-600 ng/mL in active salmonids (Milligan 1996). Skomal (2006) found a mean cortisol concentration of 769 ng/mL in White Marlin, while I found a range of cortisol values from 22 ng/mL to 1,250 ng/mL, with mean and median concentrations of 158.8 ng/mL and 73.9 ng/mL, respectively. I found the highest cortisol concentration in the White Marlin with the longest fight time, (>40 minutes). In Skomal's (2006) study, fish were angled for considerably longer times (range: 11-51 minutes, mean=37 minutes) than in my study (range: 3-41 minutes, mean=15 minutes). This may explain the differences in cortisol concentrations. Furthermore, cortisol concentrations in most fishes tend to peak thirty minutes to one hour following the stress event, so fish that are angled for shorter periods may not show peak cortisol concentrations (Barton & Iwama 1991). High levels of cortisol that occur at longer angling times are a concern and may prevent muscular glycogen synthesis after exhaustive exercise (Pagnotta et al. 1994, Milligan 2003). Over prolonged periods, high levels of cortisol may increase susceptibility to disease, depress growth rates, and interfere with reproduction (Mommensen et al. 1999).

Influence of physiological stress on behavior

Preliminary visual analysis of PSAT data from my study suggested that in the first 2-20 hours following release White Marlin spent time at cooler water temperatures.

Researchers have hypothesized that istiophorids seek cooler temperatures as a physiological response to severe anaerobic debt associated with capture (Block et al. 1992). Blue Marlin off Hawaii have been observed to descend to depth for four to six hours following recreational angling (Holland et al. 1990, Block et al. 1992). Conversely, it has also been observed that injured or stressed fish spend time at the surface following release (Block 1992, Brill et al. 1993, Horodysky & Graves 2005). Skomal (2006) acoustically tracked two White Marlin that were angled for 49 and 51 minutes and observed that over an eight-hour period following release they spent the majority of time at the surface; both of these fish survived the eight-hour tracking period. Horodysky and Graves (2005) inferred from PSAT data that two White Marlin caught on J-hooks spent extended periods at the surface prior to dying more than 24 hours following release. In contrast, all of the mortalities in my study occurred within one hour following release, and fish sank immediately. In addition to the stress and trauma associated with catch-and-release, the process of tagging fish with PSATs has been hypothesized to affect behavior. A meta-analysis of the behavior of 183 large pelagic fishes tagged with PSATs revealed that 36.6% of all individuals, and 20% of White Marlin, exhibited irregular behavior from 3 to 60 days following release, which the authors attributed to the stress of capture as well as the attachment of the PSAT (Hoolihan et al. 2011). Further, these authors found a significant difference in behavior between small and large Blue Marlin following release. In my study, models evaluating whether physiological status, LJFL, and/or angling time could predict time at temperature in the first four hours following release were not significant; however, given the breadth of information suggesting behavior modification of large pelagic fishes following release this question merits further research.

Several studies have suggested that billfish recovering from exhaustive exercise are more vulnerable to shark predation. Jolly and Irby (1979), Block et al. (1992), and Pepperell and Davis (1999) observed shark predation of Sailfish, Blue Marlin, and Black Marlin after capture on recreational gear. Kerstetter et al. (2004) observed post-release mortality of a White Marlin caught on commercial longline gear to shark predation and one White Marlin that died and was then scavenged by a predator. Several surviving White Marlin in my study utilized a narrow portion of the water column for several hours following release, which might suggest an increased vulnerability to predation. Neither Graves and Horodysky (2008) nor I observed any shark predation on live White Marlin; however, I did observe two White Marlin that were scavenged by predators following post-release mortality.

White Marlin post-release mortality

White Marlin post-release mortality inferred from my PSAT data ranged from 21-32%. These variable estimates of White Marlin post-release mortality were based on assumptions of tag data. If only PSAT data that clearly indicated mortality were used, post-release mortality was 21%; while if non-reporting tags and tags that detached within hours of deployment were also considered mortalities, post-release mortality was 32%. Furthermore, depending on which mortality scenario was selected, models that used plasma potassium as a predictor for mortality placed 35 or 48% of the White Marlin that were sampled but not tagged above the point of 50% mortality. Regardless of which scenario was used, post-release mortality in my study was more than an order of magnitude higher than previously assessed (Graves & Horodysky 2008).

In a previous study examining post-release mortality of White Marlin caught on circle hooks in the recreational fishery, 60 ten-day PSATs were deployed off the U.S. mid-Atlantic (n=19); Isla Mujeres, Mexico (n=6); and La Guaira, Venezuela (n=35) (Graves & Horodysky 2008). Only one mortality was inferred from the tag data, resulting in a post-release mortality rate of 1.7%. Of the 60 tags deployed, three tags detached early, one after a single day and two after five days. The tag that was only attached for a single day was excluded from analyses while the two five day deployments were included as surviving White Marlin. Angling times in Graves and Horodysky (2008) ranged from 4 to 40 minutes and had an average fight and handling time of just over 13 minutes. The current study had angling times ranging from 3 to 41 minutes and an average angling and handling time of 15 minutes. Post-release mortality of White Marlin in my study was more than an order of magnitude higher than Graves and Horodysky (2008) despite using the same type of gear, the same style of fishing, similar tag deployment, fishing in one of the same locations, and resuscitating White Marlin similarly prior to release. Sampling methods between Graves and Horodysky (2008) and my study were highly similar, even fishing with some of the same captains. Unlike previous efforts, I removed White Marlin from the water and took blood samples. This suggests that air exposure, blood sampling, or a combination of the two may greatly increase post-release mortality.

Air exposure has been shown to affect behavior and increase physiological stress and post-release mortality in fishes. Time out of water can cause the collapse of gill lamellae preventing the diffusion of oxygen to red blood cells and the offloading of carbon dioxide. The latter may result in an increase in blood pCO₂ causing extracellular

acidosis (Ferguson & Tufts 1992), an increase in blood metabolites (Arends et al. 1999, Davis & Schreck 2005, Suski et al. 2007), cardiovascular alterations (Cooke et al. 2003), and osmotic/ionic disruptions (Waring et al. 1996, Milston et al. 2006, Hur et al. 2007). Air exposure has also been shown to have cumulative effects with longer periods of time out of water resulting in larger physiological disturbances (Davis & Schreck 2005).

Suski et al. (2007) reported that Bonefish exercised in a laboratory for four minutes and air exposed for three minutes required over ten times as long to regain equilibrium than Bonefish that were air exposed for one minute and not exercised. Similarly, Bonefish handled and exposed to air following recreational capture were found to have difficulty maintaining equilibrium in the water column (Cooke & Philipp 2004, Danylchuk et al. 2007). Following recreational capture, longer durations of handling and air exposure were also found to positively influence the loss of equilibrium, and fish that had lost equilibrium were six times more likely to suffer predation (Danylchuk et al. 2007). Loss of equilibrium may also take hours to correct. Air exposure for a period of ten minutes was found to affect startle behavior and the ability of Sablefish (*Anoplopoma fimbria*) to orient themselves upright for at least 24 hours following air exposure (Davis & Parker 2004).

Davis and Schreck (2005) found that concentrations of plasma cortisol, lactate, glucose, sodium, and potassium increased relative to control values following air exposure in Pacific Halibut (*Hippoglossus stenolepis*). Cicia et al. (2012) found that concentrations of whole blood lactate were directly proportional to air exposure and plasma potassium increased significantly with air exposure in Little Skates (*Leucoraja erinacea*). Mortality rates also increased according to the duration of aerial exposure.

Similarly, Suski et al. (2007) found that blood lactate concentrations in Bonefish exercised for four minutes and air exposed for one minute were nearly three times greater than in fish exercised for four minutes without air exposure. Additionally, the group that was both exercised and air exposed had blood lactate values following a two-hour recovery that were almost twice as high as those that were exercised but not air exposed. The lone mortality in the study was a fish that was exercised four minutes and air exposed for three minutes.

An inherent problem in all physiological stress studies is that collecting blood and tissue samples from fish increases physiological stress (Cooke et al. 2012). The independent effect of blood sampling on physiological stress is difficult to assess; however, Langkilde and Shine (2005) used measurements of plasma corticosterone to assess stress related to blood sampling in a study with the lizard *Eulamprus heatwolei*. The study lizards were sampled for blood immediately upon capture and allowed to acclimate to a laboratory setting for fourteen days before the start of the experiment. Researchers sampled the lizards for blood at the onset of the experiment and one hour later when corticosterone was determined to reach peak levels. Corticosterone levels of blood-sampled lizards were significantly higher than concentrations measured immediately following capture and at the beginning of the experiment, and they remained elevated for up to two hours. Researchers working with Cliff Swallows (*Petrochelidon pyrrhonota*) evaluated the effect of blood sampling and reported a 21-33% decrease in survival due to the sampling (Voss, Shutler, & Werner 2010). Despite these findings, direct blood sampling of fishes may be less stressful than surgical implantation of cannula in a lab setting, which is often assumed to provide unstressed baseline blood

samples since fish are sampled while they are relatively undisturbed (Cooper & Morris 1998). In a study using Port Jackson Sharks (*Heterodontus portusjacksoni*) researchers sampled individuals for blood both by anesthetizing them and surgically implanting cannulae into the caudal artery and vein, and by removing non-anesthetized sharks from tanks and sampling the caudal vein directly with a needle and syringe. Results showed that blood sampling by caudal puncture reduced hematological and ionic perturbations relative to those resulting from surgery. While it is not possible to determine how blood sampling affected post-release mortality, it can be assumed that White Marlin in my study experienced some degree of physiological stress due to being removed from the water, restrained, and sampled for blood from the ventral aorta.

White Marlin physiology & post-release mortality

Elevated concentrations of plasma potassium proved to be the sole predictor for mortality in my study regardless of whether a low- or high-mortality scenario was considered. Several studies have noted elevated plasma potassium in response to stress events (Cliff & Thurman 1984, Wells et al. 1986, Manire et al. 2001, Mandelman & Farrington 2007, Frick et al. 2010), and several researchers have correlated high plasma potassium with mortality (Moyes et al. 2006, Marshall et al. 2012). Marshall et al. (2012) found a positive relationship between plasma lactate and potassium concentrations and literature values for mortality at haulback for several species of longline-captured sharks, but they did not determine the fate of sharks that were sampled and released. Additionally, Moyes et al. (2006) found that concentrations of plasma potassium, magnesium, calcium, lactate, and erythrocyte heat shock protein were significantly different in surviving and moribund Blue Sharks (*Prionace glauca*), but they did not tag

sharks that appeared moribund to confirm whether mortality occurred. Plasma potassium has been shown to be a significant predictor for mortality in the Sandbar Shark (*Carcharhinus plumbeus*) and the Dusky Shark (*C. obscurus*) (Marshall & Bernal, unpublished data). For both species the concentration of plasma potassium that represents the mortality threshold is significantly higher than in my study. Potassium is largely an intracellular ion and the presence of potassium in the blood (i.e. hyperkalemia) may result from cellular damage releasing intracellular contents, as well as acidosis, which can itself induce cellular damage, modify electrochemical gradients, and affect locomotor and heart muscle function (Cliff & Thurman 1984, Moyes et al. 2006). Results from my study and the unpublished data from Marshall and Bernal are the first investigations to demonstrate that plasma potassium is a significant predictor of mortality using physiological and PSAT data. These findings suggest the role of physiological stress in mortality extends between fishes as diverse as carcharinids and istiophorids.

Future research

While it is well documented that White Marlin undertake long distance movements, little is known about when and why they migrate thousands of miles. I observed differences in timing and migration patterns for fish leaving the mid-Atlantic region in the fall when White Marlin presumably headed for warmer waters. There is evidence for spawning in the Caribbean Sea, off of Bermuda, and southern Brazil in late spring but there may also be other spawning areas and fish may not necessarily spawn each year. The fish that I sampled tended to be similar in size with most approaching the size of 50% maturity. My data suggest that White Marlin utilize the mid-Atlantic region for foraging and growth before moving south to spawn in the spring (when they have

reached maturity). More work remains to be done investigating habitat utilization in and around spawning areas and the connectivity of different regions.

My research is the first study to evaluate the physiological response of White Marlin to catch-and-release angling with a sample size sufficiently large for statistical inferences. My research focused on fish caught off the U.S. mid-Atlantic region on one gear type, and future studies would benefit by examining the stress response of White Marlin over different seasons, locations, and gears.

Based on the divergence of estimates of White Marlin post-release mortality between my study and estimates in Graves and Horodysky (2008), it would appear that air exposure, blood sampling, or some combination of the two significantly increased the rate of post-release mortality. In the future, the effects of air exposure on mortality should be specifically investigated in White Marlin, and while it is improbable that White Marlin could be kept in captivity to test the physiological effects of blood sampling with repeated measurements, this could be evaluated for another related species that can be successfully maintained in captivity. Understanding the stress involved in blood sampling is an important consideration that should not be overlooked in physiological studies. Moreover, understanding the isolated effect of air exposure on White Marlin has important implications for the catch-and-release fishery.

Conclusions

White Marlin is an overfished species that is both highly migratory and sparsely distributed. These factors make White Marlin challenging to study, but also highlight the necessity of expanding our understanding of White Marlin ecology, habitat utilization, and response to stress associated with capture. Temperature and depth data from PSATs

in my study largely confirm published habitat utilization data. My results further demonstrate the differences in timing and direction that migrating White Marlin take as they leave the mid-Atlantic region in the fall, the capacity of White Marlin to undertake large migrations in short time periods, and the connectivity between the mid-Atlantic and the Caribbean regions. The mid-Atlantic fishery has expanded in the last few years and this area likely represents important foraging grounds for some members of the stock.

Physiological results revealed that White Marlin become more stressed the longer they are on the line and, in some instances, warmer water exacerbated physiological stress. Interestingly, angling time, LJFL, and/or physiological status did not affect habitat utilization following release, although a model predicting median temperature in the first four hours after release from LJFL and plasma calcium approached significance. The question of how stress affects habitat use should be examined further. Angling time, LJFL, and/or surface water temperature did not predict for mortality, but mortality was predicted by elevated concentrations of plasma potassium. Elevated concentrations of plasma potassium have also been shown to predict mortality in two carcharinid shark species, which may suggest a commonality in the physiological response between fish that succumb to post-release mortality. My results illustrate the importance of paired physiological and tagging research to better understand the relationship between stress, mortality, and catch-and-release fishing practices.

The most significant finding my study was that post-release mortality of White Marlin caught on circle hooks in the recreational fishery was more than an order of magnitude higher than previously estimated. This finding suggests that air exposure, blood sampling, or some combination of the two led to elevated rates of post-release

mortality. This is an important finding both because it illustrates the stress that sampling can have on fish and because it provides an important recommendation for recreational anglers. White Marlin are not typically removed from the water in the recreational fishery, but anglers do occasionally bring fish into the boat for pictures. This research suggests that bringing a fish into the boat could elevate the rate of post-release mortality from less than 2% to up to 32%. Many offshore anglers are conservation oriented and providing a recommendation on how to reduce post-release mortality as a guide to “best practices” may benefit the survival and conservation of White Marlin.

Table 1. Measured physiological variables for 68 sampled White Marlin.

Physiological Variable	Range	Mean	Standard Deviation
Plasma Sodium (mmol/L)	168.8-238.4	206.3	14.2
Plasma Potassium (mmol/L)	2.47-11.72	4.4	1.5
Plasma Chloride (mmol/L)	147.8-221.0	168.9	10.3
Plasma Calcium (mmol/L)	0.92-1.84	1.5	0.2
Plasma Magnesium (mmol/L)	0.47-1.19	0.8	0.1
Plasma Glucose (mmol/L)	2.8-11.8	6.7	2.4
Plasma Lactate (mmol/L)	4.4-29.8	15.2	5.1
Plasma Cortisol (ng/mL)	22.0-1249.9	158.8	189.2
Hematocrit (%)	30.5-48.5	41.4	3.0

Table 2. Generalized linear models evaluating the relationship between fight time, water temperature, lower jaw fork length, and measured physiological variables in 68 sampled White Marlin. Starred predictor variables indicate model significance.

Physiological Variables	Predictor Variables	P-value
Plasma lactate	Fight time* + water temp*	p<0.001, p<0.01
Plasma chloride	Fight time* + water temp*	p<0.05, p<0.001
Plasma glucose	Fight time* + water temp	p<0.001, p>0.05
Plasma potassium	Fight time* + water temp	p<0.05, p>0.05
Plasma sodium	Fight time*	p<0.001
Plasma cortisol	Fight time*	p<0.001
Plasma magnesium	Fight time	p>0.05
Plasma calcium	Fight time	p>0.05
Hematocrit	Fight time	p>0.05

Figure 1. Length frequency histogram of 68 sampled White Marlin. The dashed line marks estimated sexual maturity (L_{50}) at 160.46 cm LJFL for female White Marlin determined by Arocha and Bárríos (2009) in a study that examined reproductive histology of White Marlin captured by the Venezuelan long line fleet.

Length Frequency of 68 Sampled White Marlin

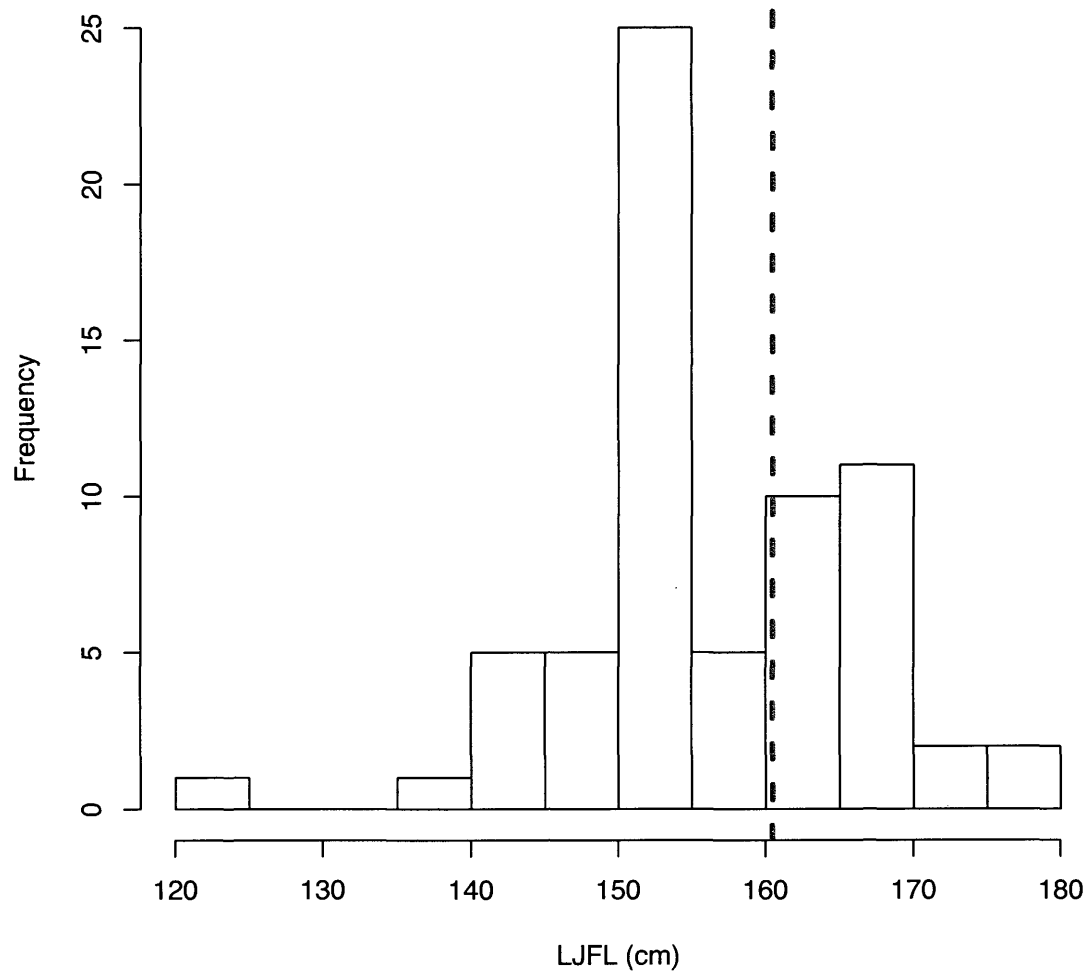


Figure 2. Percent time at temperature for 15 White Marlin tagged off the U.S. mid-Atlantic coast with thirty-day PSATs 2012-2013.

White Marlin Time at Temperature

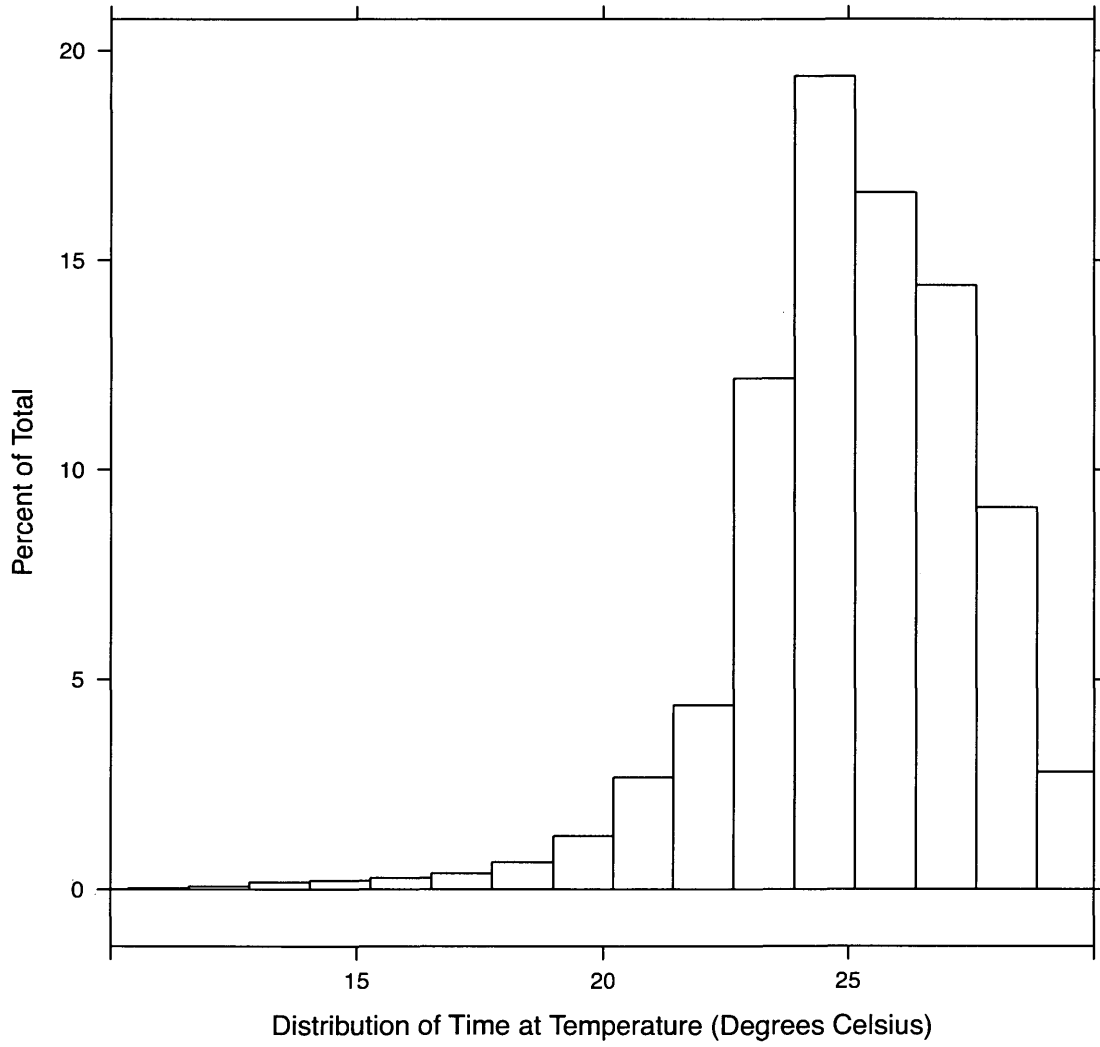


Figure 3. Percent time at depth for 15 White Marlin tagged off the U.S. mid-Atlantic coast with thirty-day PSATs 2012-2013.

White Marlin Time at Depth

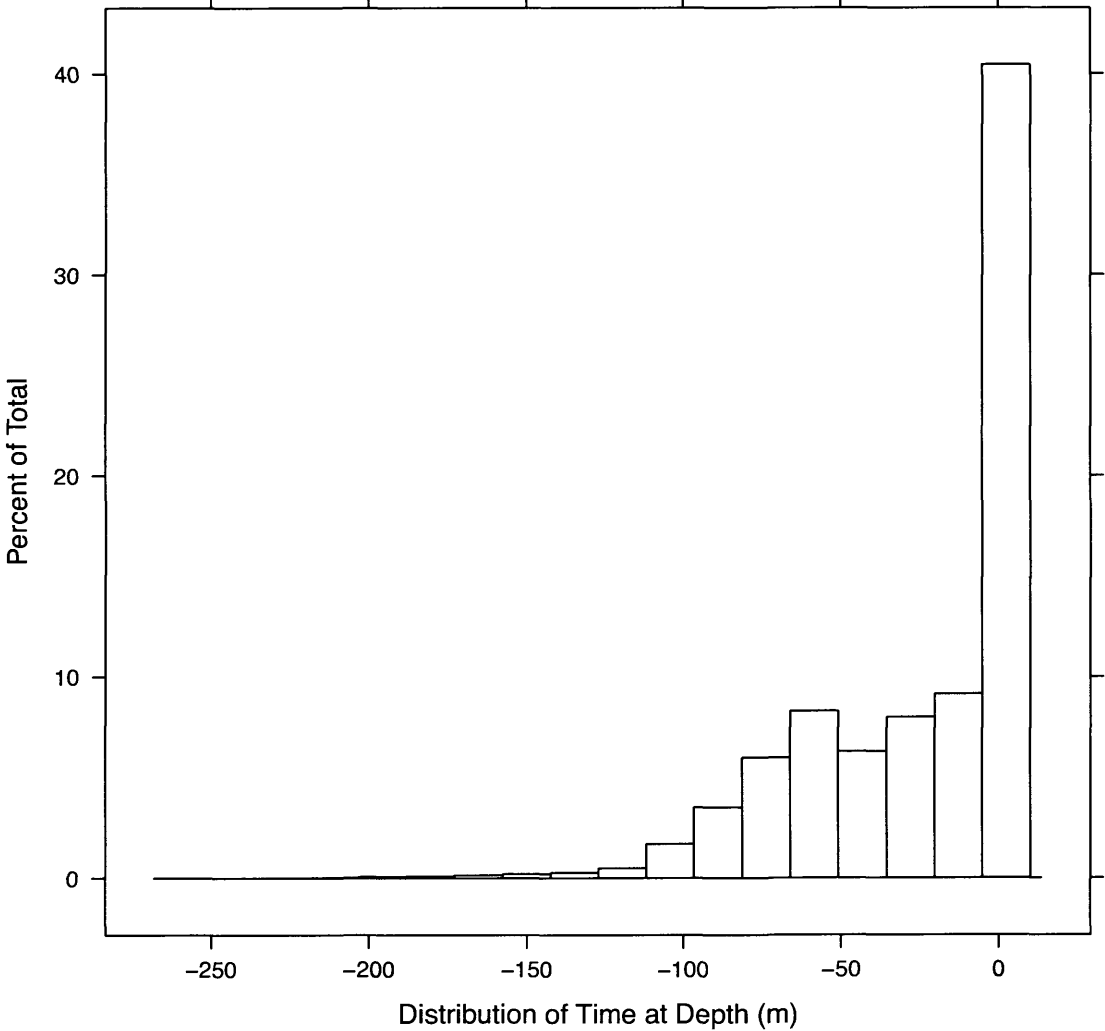


Figure 4. Pop-up locations of thirty-day PSATs deployed on White Marlin off the U.S. mid-Atlantic coast. Two tags that released prematurely after 11 and 12 days and four mortalities observed from tagging data are denoted on the map.

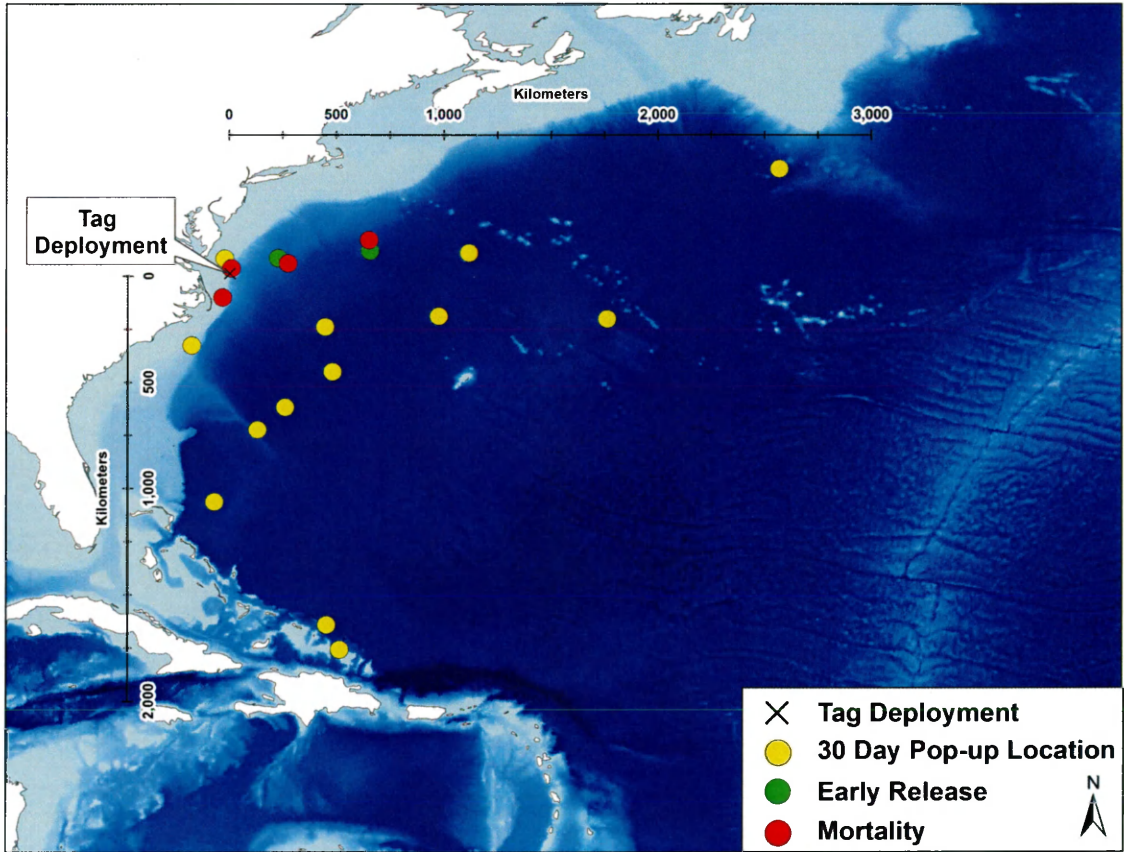


Figure 5. Temperature, depth, and light levels from White Marlin 120564. White Marlin 120564 was tagged with a 30-day PSAT between September 23 and October 24, 2012. During the tag deployment the fish migrated 1,951 straight-line km to the Caribbean.

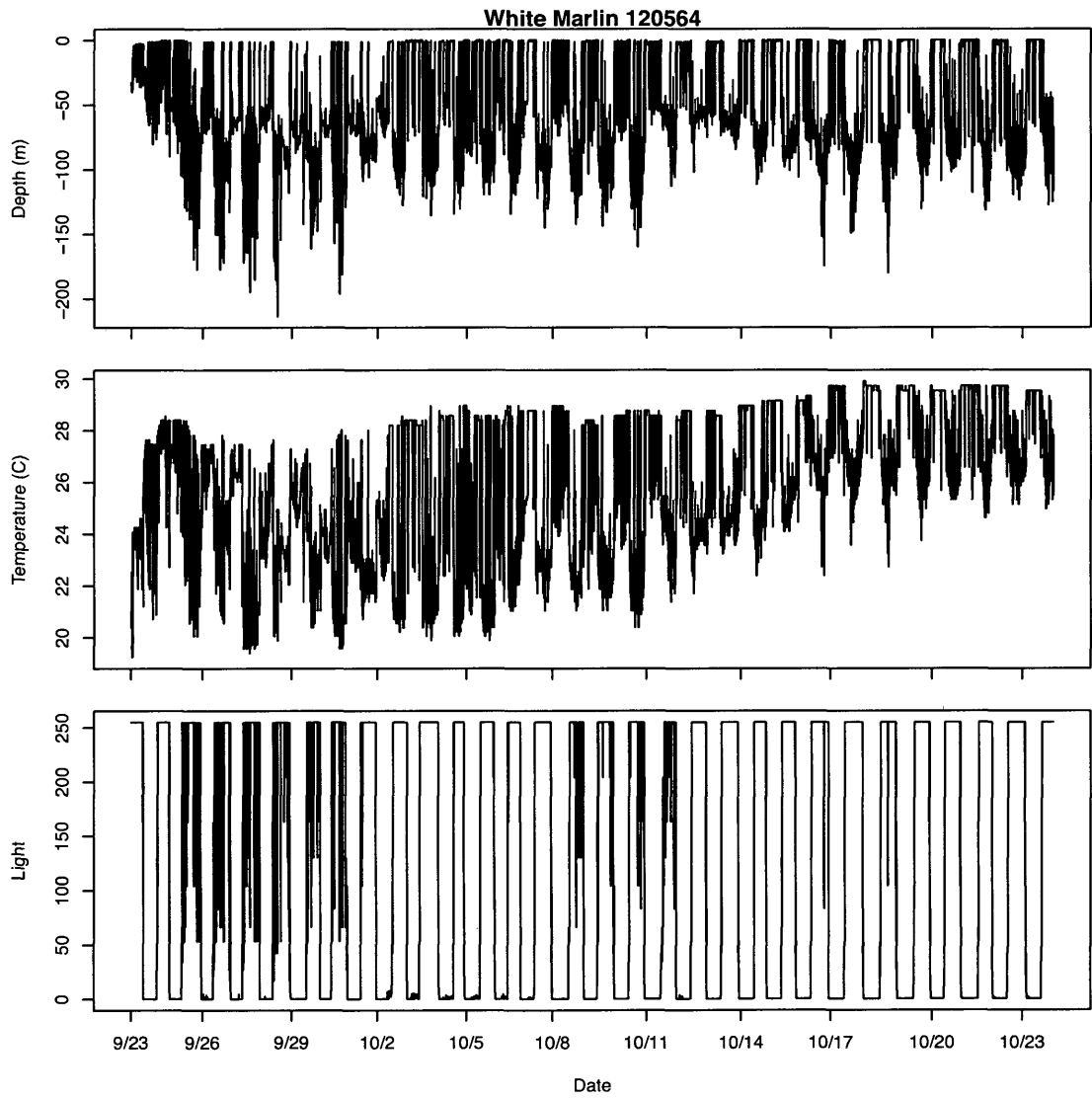


Figure 6. Temperature, depth, and light levels from White Marlin 120583 tagged with a thirty-day PSAT. White Marlin 120583 sank to the bottom and was scavenged by a predator following release.

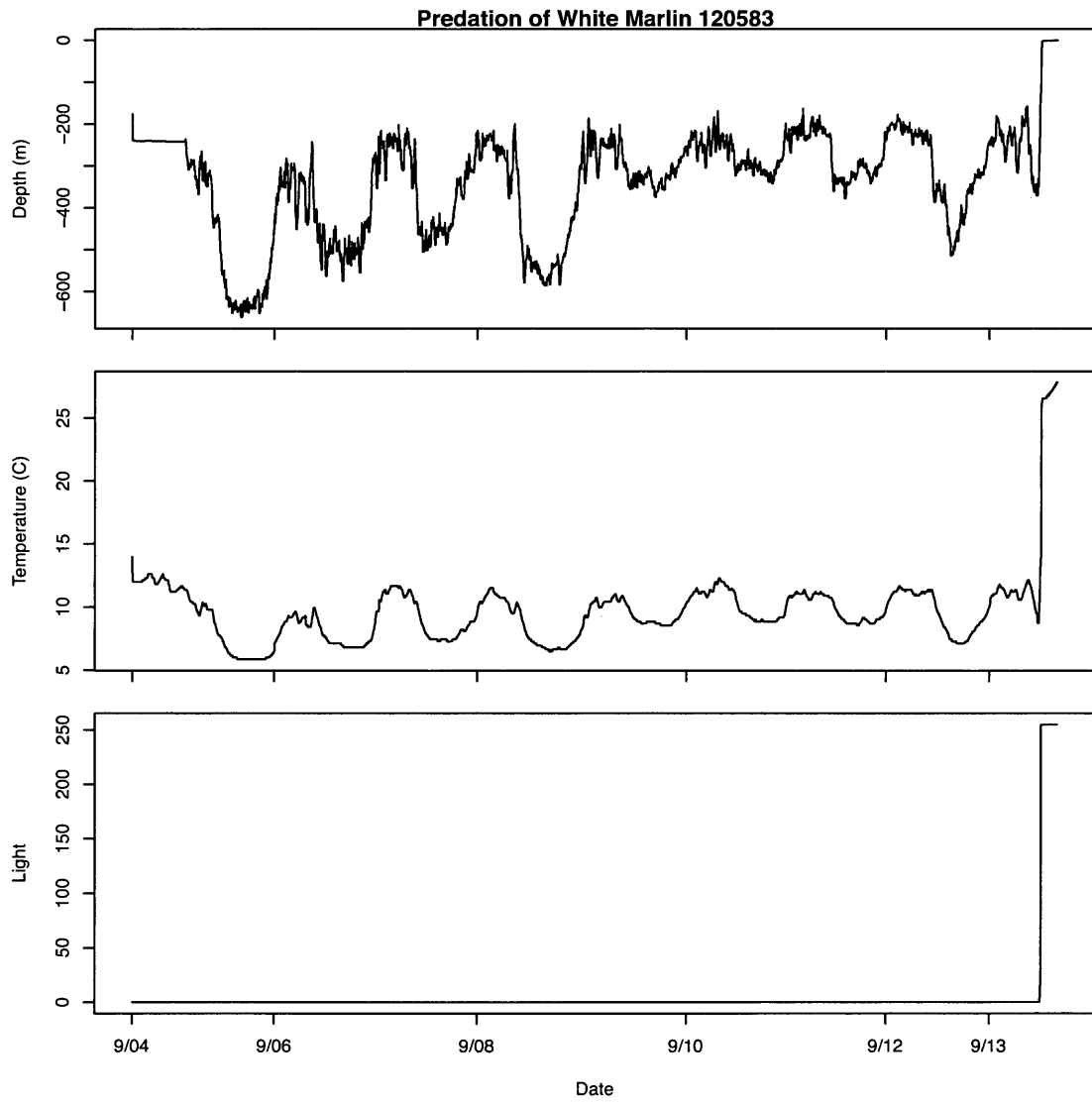


Figure 7. Temperature, depth, and light levels from White Marlin 110289 tagged with a thirty-day PSAT. White Marlin 110289 sank to the bottom and was scavenged by a predator following release.

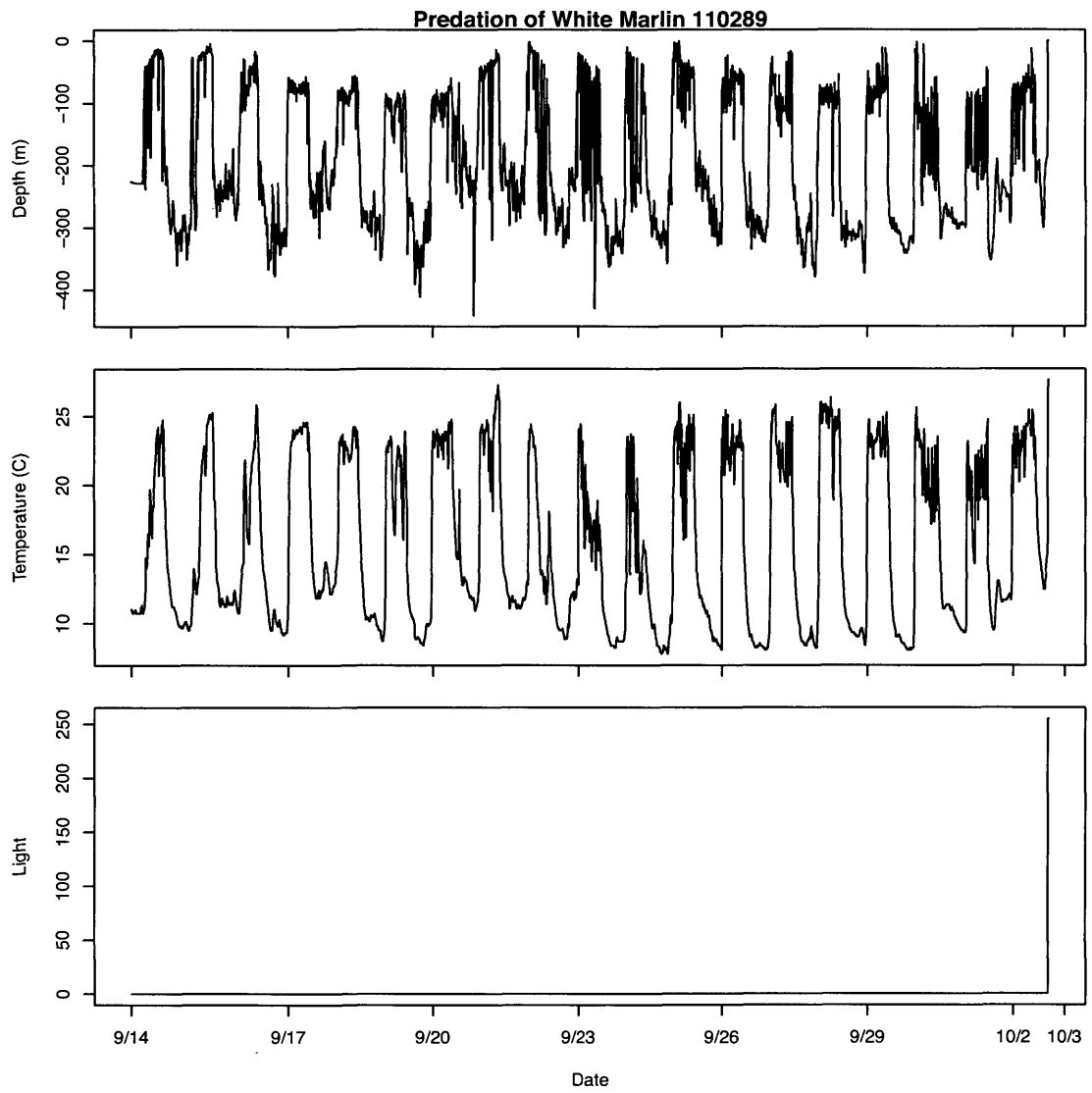


Figure 8. Temperature, depth, and light levels from White Marlin 120577 tagged with a thirty-day PSAT. White Marlin 120577 died and sank to the bottom following release.

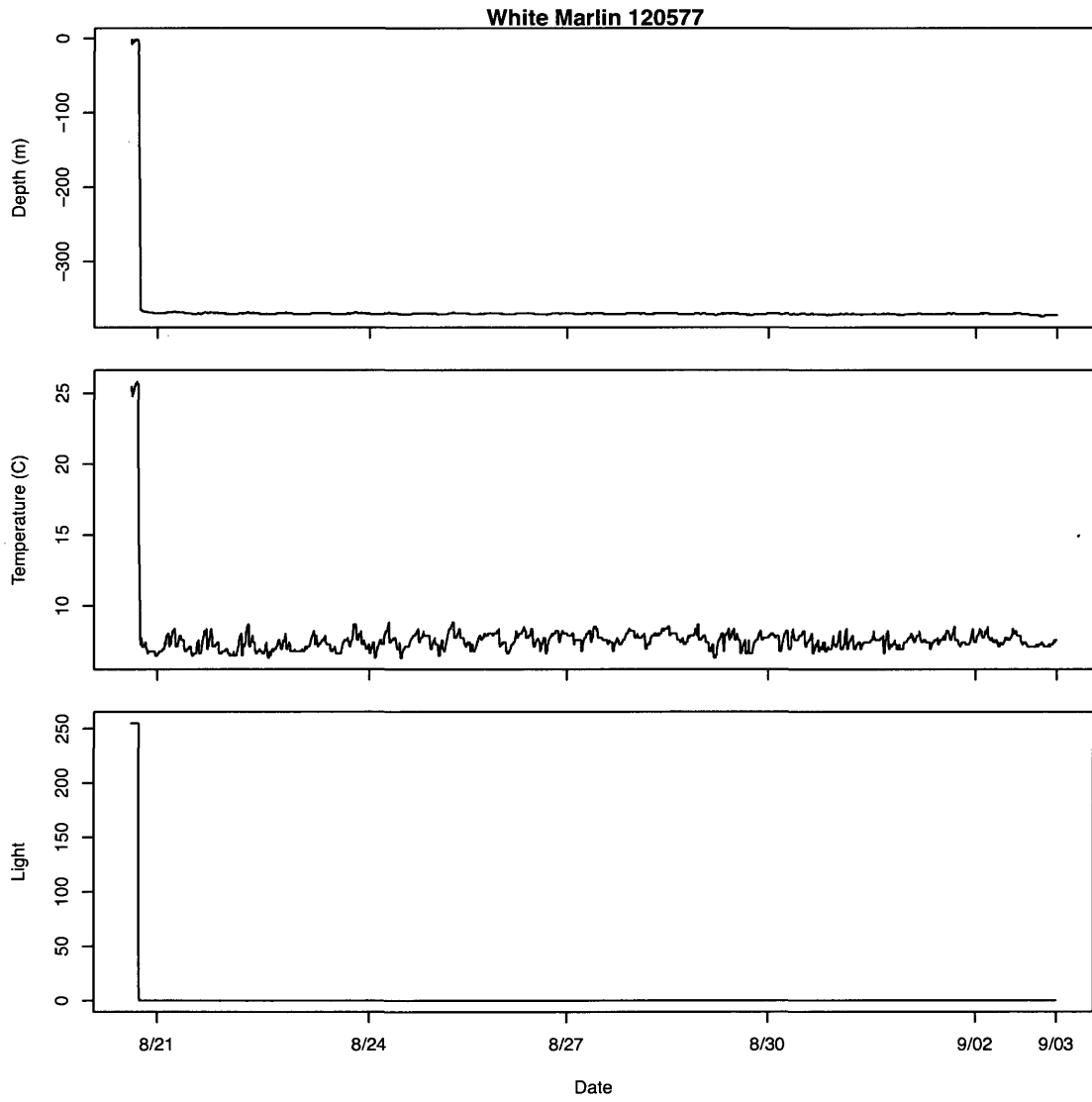


Figure 9. Generalized linear models using a Gaussian distribution for plasma sodium, potassium, chloride, and glucose. The solid line depicts model prediction and dashed lines denote 95% prediction intervals.

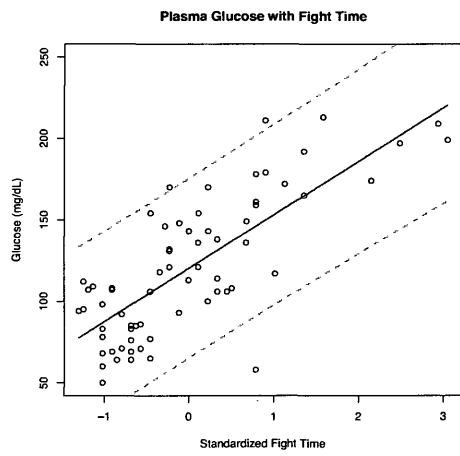
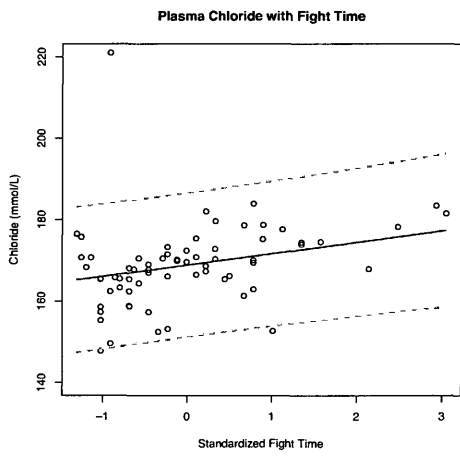
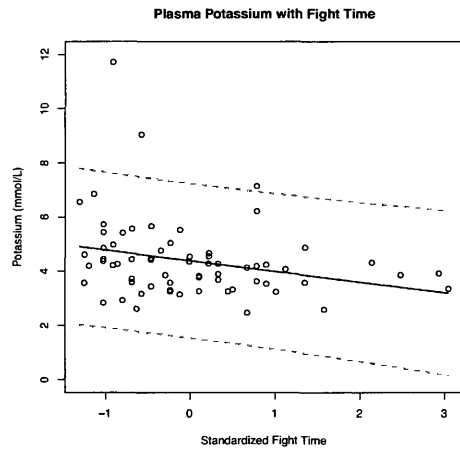
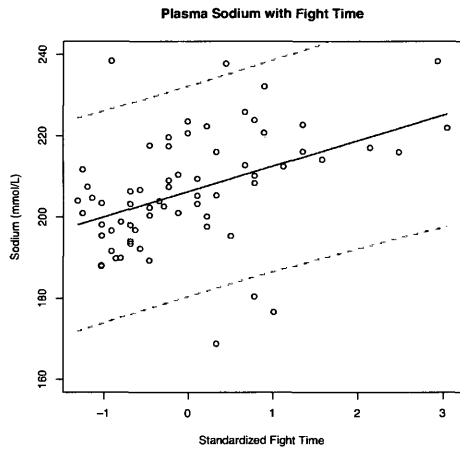
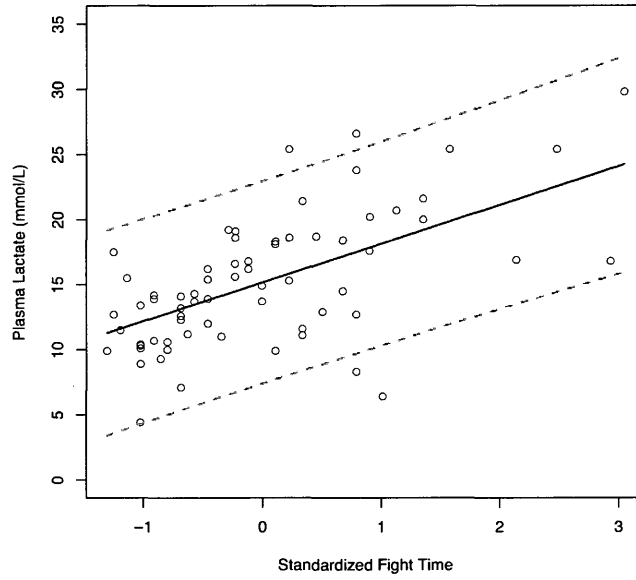


Figure 10. Generalized linear models using a Gaussian distribution for plasma lactate and cortisol. The solid line depicts model prediction and dashed lines denote 95% prediction intervals.

Plasma Lactate with Fight Time



Plasma Cortisol with Fight Time

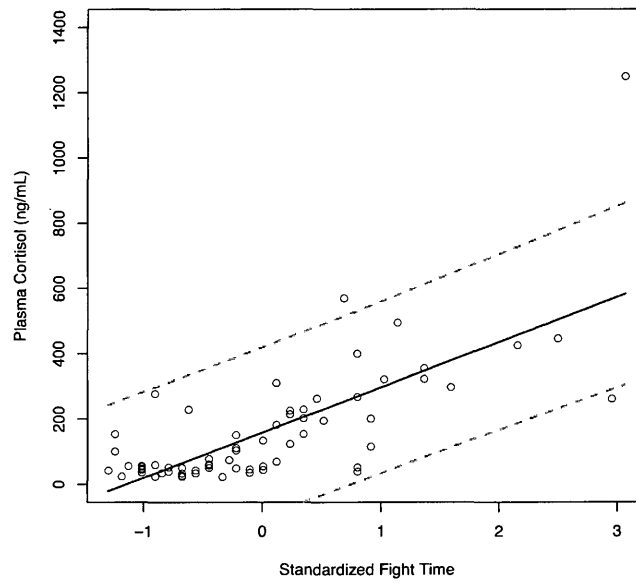


Figure 11. Generalized linear models using a Gaussian distribution for plasma calcium, magnesium, and whole blood hematocrit. The solid line depicts model prediction and dashed lines denote 95% prediction intervals.

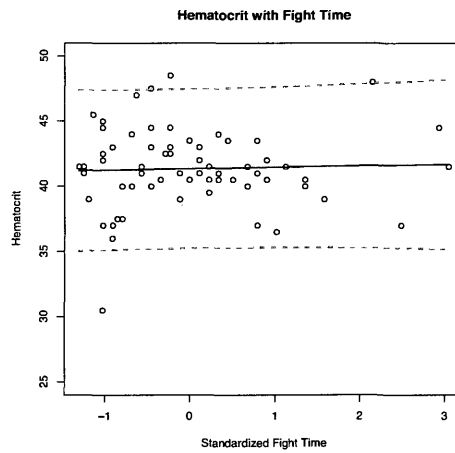
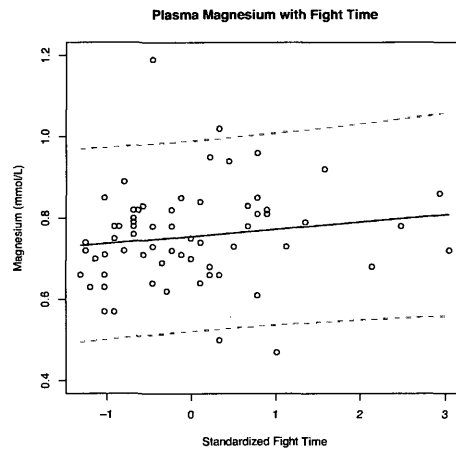
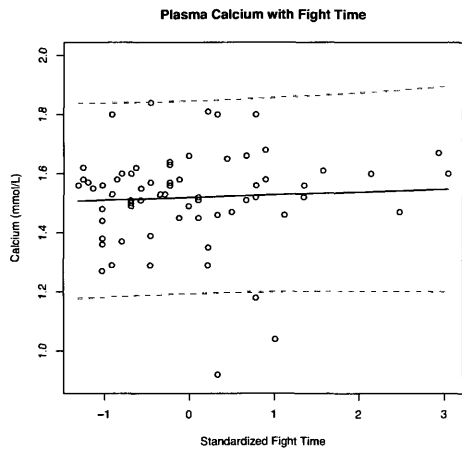


Figure 12. Generalized linear model with a Gaussian distribution predicting median temperature in the first four hours following release. The solid line depicts model prediction and dashed lines denote 95% prediction intervals. Median Temperature \sim Plasma calcium + LJFL, $p= 0.055$ for plasma calcium and $p=0.121$ for LJFL.

Median temperature in the first 4 hours following release

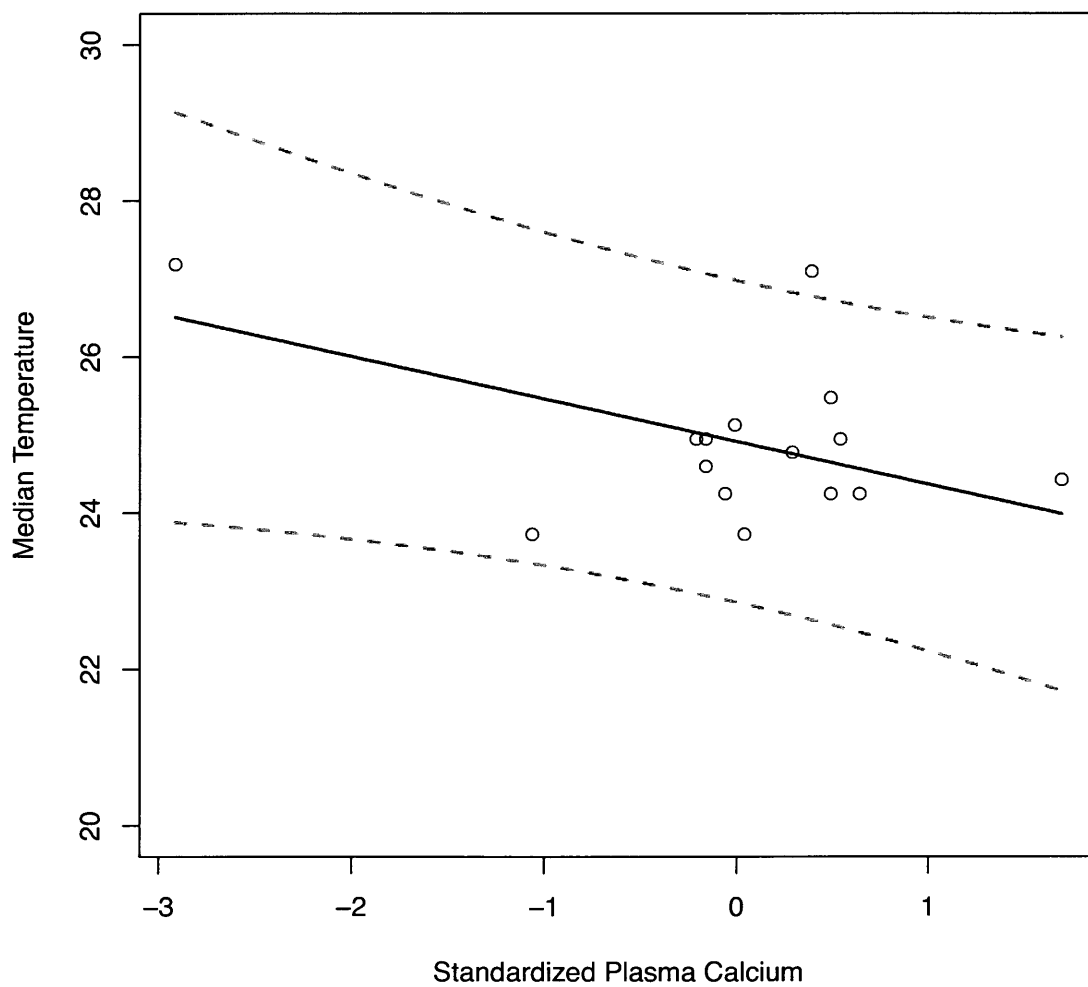


Figure 13. Generalized linear model predicting mortality (Mortality ~ Plasma potassium) using a binomial distribution and five mortalities ($p=0.0509$). Vertical dashed line denotes the point of 50% mortality at 4.57 mmol/L plasma potassium.

Mortality Model using K+ as a Predictor for Mortality

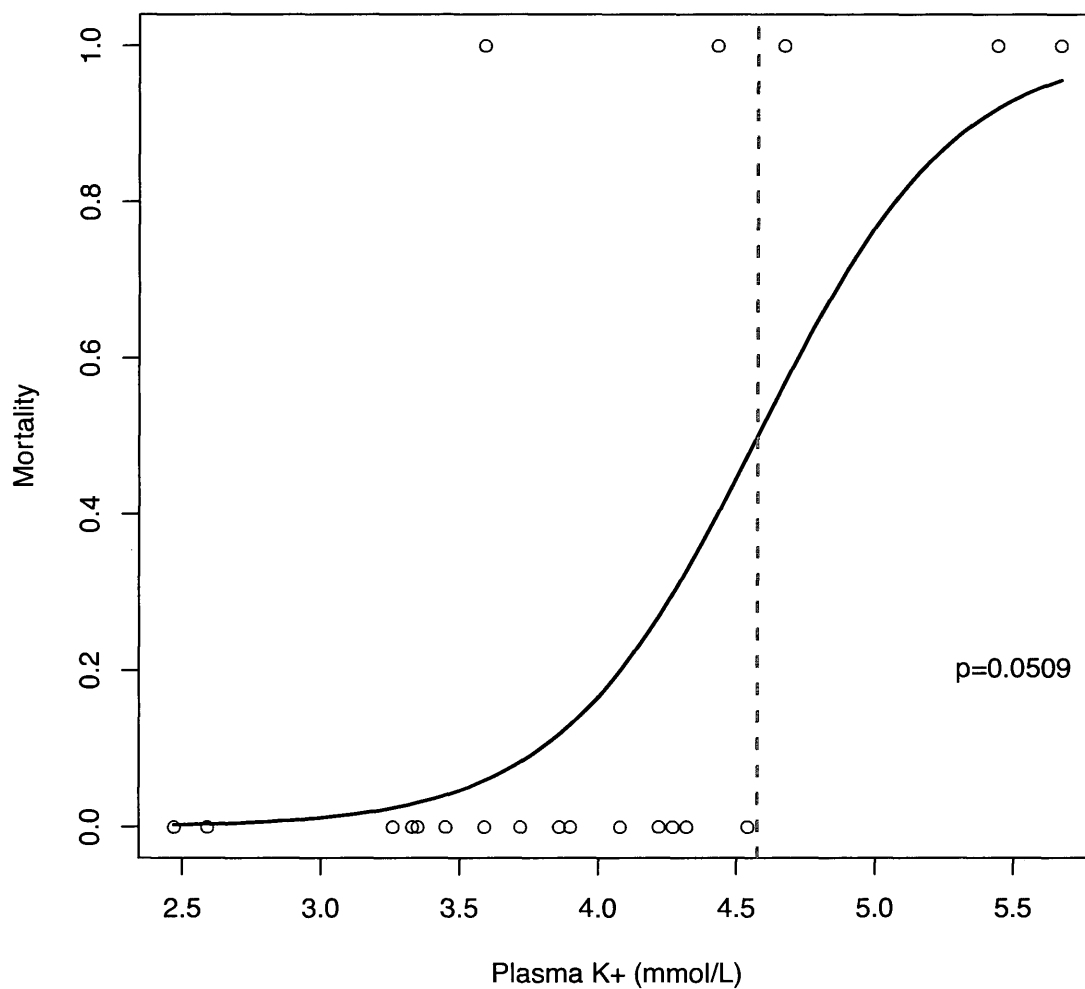
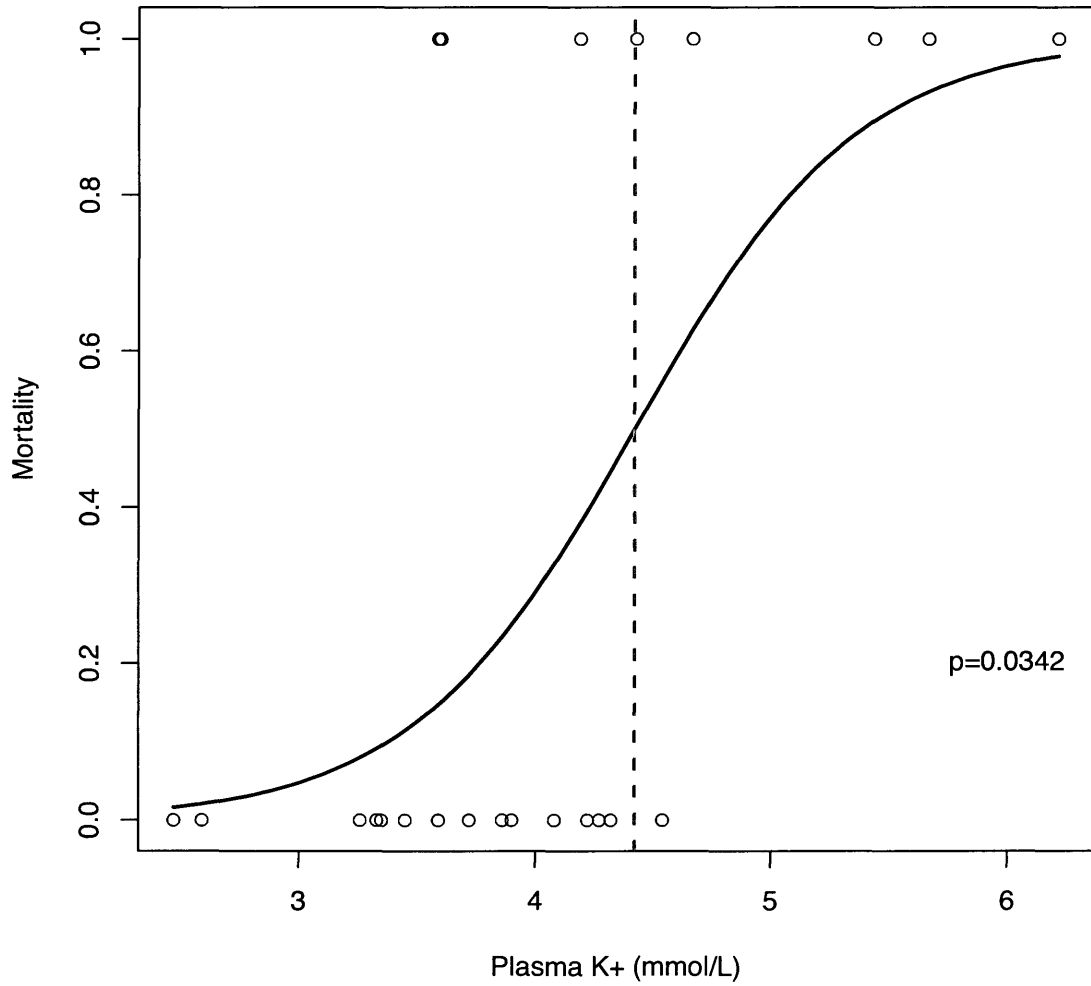


Figure 14. Generalized linear model predicting mortality (Mortality ~ Plasma potassium) using a binomial distribution and eight mortalities ($p=0.0342$). Model includes five mortalities shown in Fig. 13 plus one non-reporting tag and two tags that detached within hours of being deployed that are assumed to be mortalities in this model scenario. Vertical dashed line denotes the point of 50% mortality at 4.42 mmol/L plasma potassium.

Mortality Model using K+ as a Predictor for Mortality



LITERATURE CITED

- Arocha F, Bárríos, A (2009) Sex ratios, spawning seasonality, sexual maturity, and fecundity of white marlin (*Tetrapturus albidus*) from the western central Atlantic. *Fish Res* 95:98-111.
- Arends RJ, Mancera JM, Muñoz JL, Wendelaar Bonga SE, Flik, G (1999). The stress response of the gilthead sea bream (*Sparus aurata* L.) to air exposure and confinement. *J Endocrinol* 163: 149-157.
- Bartholomew A, Bohnsack JA (2005) A review of catch-and-release angling mortality with implications for no-take reserves. *Rev Fish Biol Fisher* 15: 129-154.
- Barton BA (2002) Stress in fishes: A diversity of responses with a particular reference to changes in circulating corticosteroids. *Integr Comp Biol* 42: 517-525.
- Barton BA, Iwama GK (1991) Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annu Rev Fish Dis* 1: 3-26.
- Black EC (1958) Hyperactivity as a lethal activity in fish. *J Fish Res Board Can* 15: 573-586.
- Block BA, Booth DT, Carey FG (1992) Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Mar Biol* 114: 175-183.
- Beerkircher L, Arrocha F, Barse A, Prince E, Restrepo V, Serafy J, Shivji M (2009) Effects of species misidentification on population assessment of overfished white marlin *Tetrapturus albidus* and roundscale spearfish *T. georgii*. *Endanger Species Res* 9: 81-90.
- Brill RW, Holts DB, Chang RKC, Sullivan S, Dewar H, Carey FG (1993) Vertical and horizontal movements of striped marlin (*Tetrapterus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurements of oceanic currents. *Mar Biol* 117: 567-574.
- Brill RW, Lutcavage ME (2001) Understanding the environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. *Am Fish S S* 25: 179-198.

- Brill RW, Block BA, Boggs CH, Bigelow KA, Freund EV, Marcinek DJ (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Mar Biol* 133: 395-408.
- Brooks EJ, Mandelman JW, Slowman KA, Liss S, Danylchuk AJ, Cooke SJ, Skomal GB, Philipp DP, Sims DW, Suski CD (2012) The physiological response of the Caribbean reef shark (*Carcharhinus perezi*) to longline capture. *Comp Biochem Phys A* 162: 94-100.
- Carey JB, McCormick SD (1998) Atlantic salmon smolts are more responsive to handling and confinement stress than parr. *Aquaculture* 168: 237-253.
- Cicia AM, Schlenker LS, Sulikowski JA, Mandelman JW (2012) Seasonal variations in the physiological stress response to discrete bouts of aerial exposure in the little skate, *Leucoraja erinacea*. *Comp Biochem Phys A* 162: 130-138.
- Cliff G, Thurman GD (1984) Pathological effects of stress during capture and transport in the juvenile dusky shark, *Carcharhinus obscurus*. *Comp Biochem Phys A* 78: 167-173.
- Collette BB, McDowell JR, Graves JE (2006) Phylogeny of recent billfishes (Xiphoidei). *B Mar Sci* 79(3): 455-468.
- Cooke SJ, Ostrand KG, Bunt CM, Schreer JF, Wahl DH, Philipp DP (2003) Cardiovascular responses of largemouth bass to exhaustive exercise and brief air exposure over a range of temperatures. *T Am Fish Soc* 132: 1154-1165.
- Cooke SJ, Philipp DP (2004) Behavior and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. *Biol Conserv* 118(5): 599-607.
- Cooke SJ, Schreer JF, Dunmall KM, Philipp DP (2002) Strategies for quantifying sub-lethal effects of marine catch-and-release angling: insights from novel freshwater applications. In: Lucy JA, Studholme AL, eds. Catch and release in marine recreational fisheries, American Fisheries Society, Symposium 30, Bethesda, MD, pp 121-134.
- Cooke SJ, Raby GD, Donaldson MR, Hinch SG, O'Connor CM, Arlinghaus R, Danylchuk AJ, Hanson KC, Clark TD, Patterson DA (2012) The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. *Fisheries Manag Ecol* 20(2-3): 268-287.
- Cooper AR, Morris S (1998) The blood respiratory, haematological, acid-base and ionic status of the Port Jackson shark, *Heterodontus portusjacksoni*, during recovery from anaesthesia and surgery: a comparison with sampling by direct caudal puncture. *Comp Biochem Phys A* 119: 895-903.

- Cramer J (2004) Life After Catch and Release. *Mar Fish Rev* 66(1): 27-30.
- Curie S, Tufts BL, Moyes CD (1999) Influence of bioenergetics stress on heat shock protein gene expression in nucleated red blood cells of fish. *Am J Physiol* 276: R990-R996.
- Danylchuck AJ, Cooke SJ, Goldberg TL, Koppelman J, Phillip DP (2007) Effects of recreational angling on the post-release Behavior and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. *J Exp Mar Biol Ecol* 346: 127-133.
- Davies JH, Bortone SA (1976) Partial food list of three species of istiophoridae (pisces) from the northeastern Gulf of Mexico. *J Biol Sci* 4.
- Davis MW, Parker SJ (2004) Fish size and exposure to air: potential effects on behavioral impairment and mortality rates in discarded sablefish. *N Am J Fish Manage* 24(2): 518-524.
- Davis MW, Schreck CB (2005) Responses by Pacific halibut to air exposure: lack of correspondence among plasma constituents and mortality. *T Am Fish Soc* 134: 991-998.
- De Sylva DP, Davis WP (1963) White marlin, *Tetrapturus albidus*, in the middle Atlantic Bight, with observations on the hydrography of the fishing grounds. *Copeia* 1.
- Die DJ, Drew K (2008) An Atlantic-wide study of age and growth of Atlantic marlins. Proceedings from the Atlantic billfish research program symposium. Gulf States Marine Fisheries Commission Spring Meeting. Galveston, Texas.
- Dobson GP, Wood SC, Daxboeck C, Perry SF (1986) Intracellular buffering and oxygen transport in the pacific blue marlin (*Makaira nigricans*): adaptations to high speed swimming. *Physiol Zool* 59: 150-156.
- Drew K, Die D, Arocha F (2006) Current efforts to develop and age and growth model of Blue Marlin (*Makaira Nigricans*) and White Marlin (*Tetrapturus albidus*). *Collect. Vol. Sci. Pap. ICCAT* 59(1): 274-281.
- Frick LH, Walker TI, Reina LD (2010) Trawl capture of Port Jackson sharks, *Heterodontus portusjacksoni*, and gummy sharks, *Mustelus antarcticus*, in a controlled setting: effects of tow duration, air exposure and crowding. *Fish Res* 106: 344-350.
- Fritsches KA, Brill RW, Warrant EJ (2005) Warm eyes can provide superior vision in swordfish. *Curr Biol* 15: 55-58.
- Ferguson RA, Tufts BL (1992) Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for “catch-and-release” fisheries. *Can J Fish Aquat Sci* 49: 1157-1162.

- Gallagher AJ, Serafy JE, Cooke SJ, Hammerschlag N (2014) Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Mar Ecol-Prog Ser* 496: 207-218.
- Gingerich AJ, Cooke SJ, Hanson KC, Donaldson MR, Hasler CT, Suski C.D, Arlinghaus R (2007) Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. *Fish Res* 86: 169-178.
- Goodyear CP (2002) Factors affecting robust estimates of the catch-and-release mortality using pop-off tag technology. In: Lucy JA, Studholme AL, eds. Catch and release in marine recreational fisheries, American Fisheries Society, Symposium 30, Bethesda, MD, pp 172-179.
- Goodyear CP, Prince ED (2003) U.S. Recreational harvest of white marlin. *Collect. Vol. Sci. Pap. ICCAT* 55(2): 624-632.
- Graves JE, Luckhurst BE, Prince ED (2002) An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fish Bull* 100: 134-142.
- Graves JE, McDowell JR (2006) Genetic analysis of White Marlin (*Tetrapterus albidus*) stock structure. *B Mar Sci* 79(3): 469-482.
- Graves JE, Horodysky AZ (2008) Does hook choice matter? Effects of three circle hook models on postrelease survival of white marlin. *N Am J Fish Manage* 28: 471-480.
- Graves JE, Horodysky AZ (2010) Asymmetric conservation benefits of circle hooks in multispecies billfish recreational fisheries: a synthesis of hook performance and analysis of blue marlin post-release survival. *Fish Bull* 108: 433-441.
- Gunn JS, Patterson TA, Pepperell JG (2003) Short-term movement and behavior of black marlin *Makaira indica* in the Coral Sea as determined through a pop-up satellite archival tagging experiment. *Mar Freshwater Res* 54: 515-525.
- Heberer C, Aalbers SA, Bernal D, Kohin S, DiFiore B, Sevulpeda CA (2010) Insights into catch-and-release survivorship and stress-induced blood biochemistry of common thresher sharks (*Alopias vulpinus*) captured in the southern California fishery. *Fish Res* 106: 495-500.
- Holland K, Brill R, Chang RKC (1990) Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fish Bull* 88: 397-402.
- Hoolihan JP, Luo J, Goodyear CP, Orbesen ES, Prince, ED (2011) Vertical habitat use of sailfish (*Istiophorus platypterus*) in the Atlantic and eastern Pacific, derived from pop-up satellite archival tag data. *Fish Oceanogr* 20(3): 192-205.

Hoolihan JP, Luo J, Prince ED (2012) Preliminary analysis of time spent at temperature relative to the surface temperature for white marlin monitored with pop-up satellite archival tags. *Collect. Vol. Sci. Pap. ICCAT* 68:1585-1589.

Horodysky AZ, Graves JE (2005) 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. *Fish Bull* 103: 84-96.

Horodysky AZ, Kerstetter DW, Latour RJ, Graves JE. 2007. Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: Inferences from short duration pop-up archival satellite tags. *Fish Oceanogr* 16 (3): 240-256.

Hur JW, Park IS, Chang YI (2007) Physiological responses of the olive flounder *Paralichthys olivaceus*, to a series stress during the transportation process. *Ichthyol Res* 54: 32-37.

ICCAT (2012) Report of the Standing Committee on Research and Statistics (SCRS). October 1-5, 2012. Madrid, Spain.

Iwama GK, Afonso LOB, Vijayan MM (2006) Stress in fish. In: Evans DH, Claiborne JB, eds. *The Physiology of Fishes*, 3rd Edition. CRC Press, Boca Raton, pp 319-335.

Jackson TL, Farber MI (1998) Summary of the at-sea sampling of the western Atlantic Ocean, 1987-1995, by industrial longline vessels fishing out of the port of Cumana, Venezuela: ICCAT enhanced research program for billfish. *Col. Vol. Sci. Pap. ICCAT* 47: 203-228.

Juan-Jordá MJ, Mosqueira I, Cooper AB, Freire J, Dulvy NK (2011) Global population trajectories of tunas and their relatives. *PNAS*. doi: 10.1073/pnas.1107743108.

Júnior TV, Vooren CM, Lessa RP (2004) Feeding Habits of four species of Istiophoridae (Pisces: Perciformes) from northeastern Brazil. *Environ Biol Fish* 70: 293-304.

Kerstetter DW Graves JE (2008) Postrelease survival of sailfish caught by commercial pelagic longline gear in the southern Gulf of Mexico. *N Am J Fish Manage* 28:1578-1586.

Kerstetter DW, Polovina JJ, Graves JE (2004) Evidence of shark predation and scavenging on fishes equipped with pop-up satellite archival tags. *Fish Bull* 102: 750-756.

Kieffer JD, Kubacki MR, Phelan FJS, Philipp DP, Tufts BL (1995) Effects of catch-and-release angling on nesting male smallmouth bass. *T Am Fish Soc* 124(1): 70-76.

Landkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *J Exp Biol* 209: 1035-1043.

Lenarz WH, Nakamura EL (1972) Analysis of length and weight data on three species of billfish from the western Atlantic Ocean. In: Shomura RS, Williams F, eds. Proceedings of International Billfish Symposium: Species Synopses, 9-12 Aug. 1972. Kailua-Kona, Hawaii: NOAA Technical Report NMFS, pp121-125.

Lupes SC, Davis MW, Olla BL, Schreck CB (2006) Capture-related stressors impair immune system function in sablefish. *T Am Fish Soc* 135: 129-138.

Manire C, Hueter R, Hull E, Spieler R (2001) Serological changes associated with gill-net capture and restraint in three species of sharks. *T Am Fish Soc* 130: 1038-1048.

Mandelman JW, Farrington MA (2007) The physiological status and mortality associated with otter-trawl capture, transport, and captivity of an exploited elasmobranch, *Squalus acanthias*. *ICES J Mar Sci* 64: 122-130.

Marshall H, Field L, Afiadata A, Sepulveda C, Skomal G, Bernal D (2012) Hematological indicators of stress in longline-captured sharks. *Comp Biochem Phys A* 162: 121-129.

Mazeaud MM, Mazeaud F, Donaldson EM (1977) Primary and secondary effects of stress in fish: some new data with a general review. *T Am Fish Soc* 106 (3): 201-212.

McDonald DG, Milligan CL (1992) Chemical properties of the blood. In: Hoar WS, Randall DJ, Farrell AP, eds. Fish Physiology, Volume XII, Part B, The Cardiovascular System. Academic Press, California, pp 56-133.

Mellergaard S, Nielsen E (1995) Impact of oxygen deficiency on the disease status of the common dab *Limanda limanda*. *Dis Aquat Organ* 22: 101-114.

Milligan CL (1996) Metabolic recovery from exhaustive exercise in rainbow trout. *Comp Biochem Phys A* 113: 51-60.

Milligan CL (2003) A regulatory role for cortisol in muscle glycogen metabolism in rainbow trout *Oncorhynchus mykiss* Walbaum. *J Exp Biol* 206: 3167-3173.

Milston RH, Davis MW, Parker SJ, Olla BL (2006) Characterization of the physiological stress response in lingcod. *T Am Fish Soc* 135: 1154-1174.

Mommsen TP, Vijayan MM, Moon TW (1999) Cortisol in teleosts: dynamics, mechanisms of action, and metabolic regulation. *Rev Fish Biol Fisher* 9: 211-268.

- Moyes CD, Fragoso N, Musyl MK, Brill RW (2006) Predicting postrelease survival in large pelagic fish. *T Am Fish Soc* 135: 1389-1397.
- Musyl MK, Domeier ML, Nasby-Lucas N, Brill RW, McNaughton LM, Swimmer JY, Lutcavage MS, Wilson SG, Galuardi B, Liddle JB (2011) Performance of pop-up satellite archival tags. *Mar Ecol-Prog Ser* 433:1-28.
- Nakamura I (1983) Systematics of the billfishes (Xiphiidae and Istiophoridae). *Publ Seto Mar Biol Lab* 28(5-6): 255-396.
- Oliveira IM, Hazin FHV, Travassos P, Pinheiro PB, Hazin HG (2007) Preliminary results on the reproductive biology of the white marlin, *Tetrapterus albidus* Poey 1960, in the western equatorial Atlantic Ocean. *Col. Vol. Sci. Pap. ICCAT* 60(5): 1738-1745.
- Ortiz M, Prince ED, Serafy JE, Holts DB, Davy KB, Pepperell JG, Lowry MB, Holdsworth JC (2003) Global overview of the major constituent-based billfish tagging programs and their results since 1954. *Marine Freshwater Res* 54: 489-507.
- Pagnotta A, Brooks L, Milligan L (1994) The potential regulatory roles of cortisol in recovery from exhaustive exercise in rainbow trout. *C J Zoolog* 72: 2136-2146.
- Pepperell JG, Davis TLO (1999) Post-release behavior of black marlin (*Makaira indica*) caught and released using sportfishing gear off the Great Barrier Reef (Australia). *Mar Biol* 135: 369-380.
- Prince ED, Cowen RK, Orbesen ES, Luthy SA, Llopiz JK, Richardson DE, Serafy JE (2005) Movements and spawning of white marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) off Punta Cana, Dominican Republic. *Fish Bull* 103: 659-669.
- R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rapp T, Hallermann J, Cooke SJ, Hetz SK, Wuertz S, Arlinghaus R (2012) Physiological and behavioural consequences of capture and retention in carp sacks on common carp (*Cyprinus carpio* L.) with implications for catch-and-release recreational fishing. *Fish Res* 125-126: 57-68.
- Randall DJ, Perry SF (1992) Catecholamines. *Fish Physiol* 12B: 255-300.
- Shivji MS, Magnussen JE, Beerkircher LR, Hinteregger G, Lee DW, Serafy JE, Prince ED (2006) Validity, identification, and distribution of the roundscale spearfish, *Tetrapturus georgii* (Teleostei: Istiophoridae): Morphological and molecular evidence. *Bull Mar Sci* 79(3): 483-491.

Skomal GB (2006) The physiological effects of capture stress on post-release survivorship of sharks, tunas, and marlin. Dissertation. Boston University Graduate School of Arts and Sciences.

Skomal GB (2007) Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. *Fisheries Manage Ecol* 14: 81-89.

Skomal G, Bernal D (2010) Physiological response to stress in sharks. In: Carrier JC, Musick JA, Heithaus MR, eds. *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology and Conservation*, First Edition. CRC Press, Boca Raton, pp. 459-490.

Skomal GB, Mandelman JW (2012) The physiological response to anthropogenic stressors in marine elasmobranch fishes: A review with a focus on the secondary response. *Comp Biochem Phys A* 162: 146-155.

Suski CD, Killen SS, Kieffer JD, Tufts BL (2006) The influence of environmental temperature and oxygen concentration on the recovery of largemouth bass from exercise: implications for live-release angling tournaments. *J Fish Biol* 68: 120-136.

Suski CD, Cooke SJ, Danylchuck AJ, O'Connor CM, Gravel MA, Redpath T, Hanson KC, Gingerich AJ, Murchie KJ, Danylchuck SE, et al. (2007) Physiological disturbances and recovery dynamics of bonefish (*Albula vulpes*), a tropical marine fish, in response to variable exercise and exposure to air. *Comp Biochem Phys A* 148: 664-673.

Thompson LA, Donaldson MR, Hanson KC, Arlinghaus R, Cooke SJ (2008) Physiology, behavior, and survival of angled and air exposed largemouth bass. *N Am J Fish Manage* 28: 1059-1068.

Voss M, Shutler D, Werner J (2010) A hard look at blood sampling of birds. *The Auk* 127(3): 704-708.

Waring CP, Stagg RM, Poxton MG (1996) Physiological responses to handling in the turbot. *J Fish Biol* 48: 161-173.

Wells RMG, Davie PS (1985) Oxygen binding by the blood and hematological effects of capture stress in two big gamefish: mako shark and striped marlin. *Comp Biochem Phys A* 81: 643-646.

Wells RMG, McIntyre RH, Morgan AK, Davie PS (1986) Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. *Comp Biochem Phys A* 84(3): 565-571.

Wendelaar Bonga SE (1997) The stress response in fish. *Physiol Rev* 77: 591-625.

White Marlin Biological Review Team (2007) Atlantic White Marlin Status Review. Report to National Marine Fisheries Service, Southeast Regional Office, December 10, 2007, pp 88.

Wood CM (1991) Acid-base and ion balance, metabolism, and their interactions after exhaustive exercise in fish. *J Exp Biol* 160: 285-308.

Wood CM, Turner JD, Graham MS (1983) Why do fish die after severe exercise? *J Fish Biol* 22: 189-201.

VITA

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