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1-2005

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

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Recommended Citation

Horodysky, AZ and Graves, John, "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" (2005). VIMS Articles. 1760. [https://scholarworks.wm.edu/vimsarticles/1760](https://scholarworks.wm.edu/vimsarticles/1760?utm_source=scholarworks.wm.edu%2Fvimsarticles%2F1760&utm_medium=PDF&utm_campaign=PDFCoverPages)

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Abstract— Short-duration (5- or 10 day) deployments of pop-up satellite archival tags were used to estimate survival of white marlin (*Tetrapturus albidus*) released from the western North Atlantic recreational fishery. Forty-one tags, each recording temperature, pressure, and light level readings approximately every two minutes for 5-day tags (*n*=5) or four minutes for 10-day tags (*n*=36), were attached to white marlin caught with dead baits rigged on straight-shank ("J") hooks (*n*=21) or circle hooks $(n=20)$ in offshore waters of the U.S. Mid-Atlantic region, the Dominican Republic, Mexico, and Venezuela. Forty tags (97.8%) transmitted data to the satellites of the Argos system, and 33 tags (82.5%) transmitted data consistent with survival of tagged animals over the deployment duration. Approximately 61% (range: 19−95%) of all archived data were successfully recovered from each tag. Survival was significantly (*P*<0.01) higher for white marlin caught on circle hooks (100%) than for those caught on straightshank ("J") hooks (65%). Time-todeath ranged from 10 minutes to 64 hours following release for the seven documented mortalities, and five animals died within the first six hours after release. These results indicate that a simple change in hook type can significantly increase the survival of white marlin released from recreational fishing gear.

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*

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Atlantic white marlin (*Tetrapturus albidus* Poey, 1860) are targeted by a directed recreational fishery and occur as incidental bycatch in commercial fisheries throughout the warm pelagic waters of the Atlantic Ocean. Total reported recreational and commercial landings of white marlin peaked at 4911 metric tons (t) in the mid-1960s, declined steadily during the next 15 years, and have since fluctuated without trend between 1000 and 2000 t despite substantial increases in fishing effort (ICCAT, 2003). Recent population assessments conducted by the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) indicate that the Atlantic-wide white marlin stock is currently at historically low levels and has been severely overexploited for over three decades (ICCAT, 2003). In the 2002 white marlin assessment, the 2001 biomass was estimated to be less than 12% of that required for maximum sustainable yield (MSY) under the continuity case (ICCAT, 2003). Current harvest is estimated to be more than eight times the replacement yield (ICCAT, 2003).

In response to the overfished status of white marlin, ICCAT has adopted binding international recommendations to decrease overall Atlantic landings of this species by 67% from 1996 or 1999 levels (whichever is greater) through the release of all live white marlin from commercial pelagic longline and purse-seine gears (ICCAT, 2001). How-

ever, even these dramatic reductions may be ineffective in rebuilding the white marlin stock. Goodyear (2000) estimated that a 60% decrease from 1999 fishing mortality levels would be required to halt the reduction of Atlantic blue marlin (*Makaira nigricans*). Because white marlin experience higher levels of fishing-induced mortality, it is expected that the reduction in mortality required to stabilize this stock will be even greater.

Management measures within the United States, established by the Atlantic Billfish Fishery Management Plan (FMP) (NMFS, 1988) and subsequent Amendment 1 (NMFS, 1999), have also been implemented to reduce white marlin fishing mortality. U.S. commercial fishermen have been prohibited from landing or possessing all Atlantic istiophorids since 1988. Dead discards of white marlin from the U.S. commercial pelagic longline fishery peaked at 107 t in 1989, and have decreased to 40−60 t over the last several years (White Marlin Status Review Team¹). Management

Manuscript submitted 20 January 2004 to the Scientific Editor's Office.

Manuscript approved for publication 2 August 2004 by the Scientific Editor. Fish. Bull. 103:84–96 (2005).

^{*} Contribution 2610 from the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062.

¹ White Marlin Status Review Team. 2002. Atlantic white marlin status review document, 49 p. Report to the National Marine Fisheries Service. Southeast Regional Office, September 3, 2002. www.nmfs.gov/ prot_res/readingrm/Candidate_Plus/ white_marlin/whm_status_review.pdf

measures for U.S. recreational anglers include a minimum size of 66 inches lower jaw fork length (NMFS, 1999) and mandatory reporting of landed billfishes (NMFS, 2003). White marlin landings by U.S. recreational anglers ranged between 40 and 110 t from 1960 to the mid-1980s (Goodyear and Prince, 2003) and have decreased to about 2 t in recent years. At present, over 99% of the 4000−8000 white marlin estimated to be caught annually by U.S. recreational fishermen are released (Goodyear and Prince, 2003).

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

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

Survival estimates for other istiophorid species released from recreational fishing gear may not be applicable to white marlin. One reason may involve body size: recreationally caught blue marlin and striped marlin are generally larger than white marlin. Interand intra-specific differences in body size may affect feeding behavior, fight time, handling time, as well as postrelease recovery (Kieffer, 2000). Another reason may involve the different angling techniques used to catch certain istiophorid species. Blue marlin often hook themselves in the mouth and head while aggressively pursuing high speed trolled lures (Graves et al., 2002). In contrast, as white and striped marlin approach a specific baitfish in the trolling spread, many anglers free-spool (i.e., "drop-back") rigged natural baits to feeding marlin to imitate stunned baitfish (Mather et al., 1975). This process increases the probability that straight-shank ("J") hooks rigged with natural baits will damage vital internal areas such as the gills, esophagus, and stomach (Prince et al., 2002a). Recently, several studies have documented a reduction in hookinduced trauma associated with the use of circle hooks in fisheries targeting estuarine and pelagic fishes (Lucy and Studholme, 2002). However, there is little research specifically comparing levels of postrelease survival of pelagic fishes caught on circle and straight-shank ("J") hooks. Prince et al. (2002a) and Skomal et al. (2002) examined hooking locations and injuries in sailfish and bluefin tuna caught on both hook types but lacked postrelease survival data from study animals. Domeier et al. (2003) did not detect a significant difference between striped marlin caught on circle and straightshank ("J") hooks, although the authors did observe significantly decreased rates of deep-hooking and tissue trauma with circle hooks compared to straight-shank $('J")$ hooks.

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

Methods

Tags

The Microwave Telemetry, Inc. (Columbia, MD) PTT-100 HR model PSAT tag was used in our study. This tag is slightly buoyant, measures 35 cm by 4 cm, and weighs <70 grams. The body of the tag contains a lithium composite battery, a microprocessor, a pressure sensor, a temperature gauge, and a transmitter, all housed within a black resin-filled carbon fiber tube. Flotation is provided by a spherical resin bulb embedded with buoyant glass beads. This tag model is programmed to record and archive a continuous series of temperature,

light, and pressure (depth) measurements, and can withstand pressure equivalent to a depth of 3000 m. Tags programmed to disengage after five days $(n=5)$ recorded measurements approximately every two minutes, whereas tags programmed to disengage after ten days (*n*=35) recorded measurements about every four minutes. Additionally, both 5-day and 10-day tag models transmitted archived and real-time surface temperature, pressure, and light level readings to orbiting satellites of the Argos system for 7−10 days following release from the study animals.

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

Deployment

White marlin were tagged in the offshore waters of the U.S. Mid-Atlantic Bight, the Dominican Republic, Mexico, and Venezuela (Table 1). These locations were chosen for vessel availability and seasonal concentrations of white marlin. All tagging operations were conducted on private or charter recreational fishing vessels targeting billfishes and tunas. White marlin were caught on 20−40 lb class sportfishing tackle and fought in a manner consistent with typical recreational fishing practice $(G.$ Harvey, personal commun.²). The first 41 white marlin caught and successfully positioned boatside were tagged. Fish were not brought to the boat until they were sufficiently quiet to facilitate optimal tag placement. When possible, crew members positioned white marlin for tagging by holding them by the bill and dorsal fin in the water alongside the boat, a technique often used when controlling a billfish to remove hooks. On boats with high gunwhales that prohibited holding the captured fish by the bill, the marlin were "leadered" to the boat's side and moved into position for tagging when calm. Six hooked white marlin escaped prior to tagging because frayed leaders broke or hooks slipped during this process. Hooks were removed when feasible;

² Harvey, G. 2002. Personal commun. Guy Harvey Enterprises. 4350 Oakes Rd. Suite 518. Davie, FL 33314.

otherwise, they were left in the fish and the leader was cut as close to the animal as possible prior to release. Both practices are common in the recreational billfish fishery. After capture and positioning alongside tagging vessels, six white marlin were observed to have lost color, and were lethargic and unable to maintain vertical position in the water. These fish were resuscitated alongside the moving boat for 1−5 minutes prior to release — also a common practice in the recreational fishery.

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

Hooking locations were pooled into two categories: jaw, externally visible (including all lip-hooked, foulhooked, and bill-entangled white marlin) and deep, not externally visible (including all white marlin hooked in the palate, gills, esophagus, and everted stomachs). Bleeding was recorded as present or absent, and the

general location of bleeding was recorded when it was possible to identify the source.

Data analysis

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

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

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

Results

Forty-one white marlin were tagged in four geographic locations during 2002−2003 (Table 1). Information for each fish is summarized in Table 2. Fight times were fairly typical for this fishery (mean: 15.8 min, range: 3−83 min), although two animals required more than 30 minutes before they were sufficiently calm at boatside for tag placement. Overall, forty tags (97.6%) transmitted data to the satellites of the Argos system and of these, thirty-seven tags remained attached to study animals for the full five- or tenday duration. One five-day tag was released prematurely from a surviving white marlin after 2.5 days, presumably because it had not been attached securely. This individual showed behavior similar to other surviving white marlin while the tag was attached and was presumed to have survived for the purposes of our study. Additionally, two 10 day tags attached to moribund white marlin disengaged from the carcasses prior to the expected date after an extended amount of time at a constant depth and temperature on the seafloor. Approximately 61% of data (range: 19−95%) were successfully transmitted from reporting tags.

Overall, 33 of 40 tags (82.5%) returned data that indicated the survival of tagged animals throughout the duration of tag deployment. Surviving white marlin exhibited daily variations in water temperature and depth data while carrying PSATs (Fig. 2A). The net movement of surviving animals could not be explained by the speed or direction of current patterns alone over the course of the tag deployment (Table 2, Fig 3A). In contrast, moribund white marlin (Fig. 2B) sank to the seafloor (237−1307

m) and to constant water temperatures (3.7−12.5°C), where they remained until the tags disengaged and floated to the surface not far from the initial tagging location (Fig 3B). Five of the seven moribund white marlin died within the first six hours of release;

four of these five animals died within the first hour (Table 2).

The two white marlin that experienced the longest fight times (46 and 83 min) died more than 24 hours following their release. White marlin VZ03-11 had a

Table 2

Summary information for tagged white marlin (*Tetrapturus albidus*) released from recreational fishing gear in the western North Atlantic Ocean. Total fight time is defined as the interval between the time that the fish was hooked and the time that it was brought to the side of the boat prior to tagging. Handling time included tagging and resuscitation, where applicable. "D/N" refers to deep, not externally visible hooking locations, "foul" refers to a white marlin hooked in the dorsal musculature. Tailwrapped fish are denoted with the symbol "*T*", resuscitated marlin are denoted with the symbol "*R*".

Minimum straight line distances traveled by a surviving white marlin (*Tetrapturus albidus*) (solid line) (**A**) and the drifting track of a transmitting tag (dotted line) in offshore waters of the U.S. Mid-Atlantic Bight. The cross (**B**) denotes a moribund white marlin that sank to the seafloor shortly after it was released, illustrating that dead fish did not travel far from the initial tagging coordinates.

fight time of 46 minutes and died 27 hours after tagging, and DR02-04 had a fight time of 83 minutes and died 64 hours after tagging (Fig. 4). There was no significant difference in fight time (*Z*=0.4996, *P*=0.62) between surviving and moribund white marlin, largely due to the large range of fight times for moribund animals. Handling times ranged from 1 to 5 minutes per fish.

Hook type had a highly significant effect on the postrelease survival of white marlin (Fig. 5). Fish caught on circle hooks experienced significantly higher survival (20 of 20; 100%) than those caught on straightshank ("J") hooks (13 of 20; 65%) (Yates's corrected CMH χ^2 =7.386, *P*<0.007). There were also highly significant differences in hooking locations and hook-induced trauma between hook types (Fig. 5). Odds ratios revealed that white marlin caught on straight-shank ("J") hooks were 41 times more likely to be hooked deeply (Yates's corrected CMH χ^2 =11.48, P<0.001) and over 15 times more likely to sustain hook-induced tissue trauma resulting in bleeding (CMH χ^2 =8.3, *P*<0.005) than fish caught on circle hooks. Of the white marlin caught on straight-shank ("J") hooks, half were hooked in deep locations, and 70% of these fish were bleeding. Four of the seven observed mortalities were those of deep-hooked and bleeding fish. Overall, 56% of bleeding, 40% of deep-hooked, and 57% of deep-hooked and bleeding white marlin perished following release. In contrast, all white marlin caught on circle hooks were hooked in the jaw, and bleeding was evident only in a single animal in which the hook point exited the edge of the eye socket but did not damage the eye. Additionally, 20% (8 of 40) of the white marlin in our study became entangled in the line during the fight and were "leadered" to the boat tail-first, a condition known as "tailwrapped" (Holts and Bedford, 1990). This phenomenon was equally distributed with respect to hook type. Five tailwrapped white marlin required resuscitation, and two tailwrapped white marlin hooked in the jaw with straight-shank ("J") hooks died.

With the model developed by Goodyear (2002), the results of 10,000 simulated experiments at an underlying true mortality rate of 35% indicated that approximate 95% confidence intervals for mortality estimates for an experiment deploying 20 tags on white marlin caught on straight-shank ("J") hooks range from 15% to 59% in the absence of confounding factors. A dramatic increase in sample size would be required to improve the precision of mortality estimates (Fig 6). Doubling the sample size $(n=40)$ would decrease the 95% confidence intervals to about $\pm 15\%$ of the true value and quadrupling the number of tags (*n*=80 PSATs) would reduce confidence intervals to about $\pm 10\%$ of the true value. More than 200 PSATs would have to be deployed to lower the confidence intervals to $\pm 5\%$ of the true value.

The net displacement of released white marlin was variable among individuals and across locations and was used as an independent line of evidence to assess survival. Surviving white marlin demonstrated movement patterns that cannot be explained by surface currents alone. Distances and directions of displacement are summarized in Table 2. White marlin tagged with

10-day PSATs moved an average of 101 (± 84) nautical miles (nmi) or 188 km (± 155) and those tagged with 5-day PSATs moved an average of 38.8 nmi (±15.6) or 72 km (±29).

Discussion

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

The survival rate observed for white marlin caught on straight-shank ("J") hooks in our study (65%) is slightly lower than that reported for other istiophorid species (blue marlin 89%, Graves et al., 2002; striped marlin 71%, Domeier et al., 2003) caught on this type of hook. Differences in the recreational fishing practices for these species may account for the variation in levels of istiophorid postrelease survival. In recreational fisheries that target striped marlin and white marlin, longer drop-back durations with natural baits rigged on "J" hooks increase the probability of deep-hooking and internal damage, which influence mortality. The postrelease mortality rates of white marlin and striped

Effects of circle and straight-shank ("J") hooks on hooking location, trauma, and fate. Ext. = externally. $n/a =$ not applicable.

marlin from drop-back fisheries are similar and are notably higher than that of blue marlin caught on highspeed trolled baits.

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

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

Resuscitation of exhausted istiophorids is a common practice in the recreational fishery. Five white marlin that were tailwrapped and unable to ram-ventilate during the fight were resuscitated in our study. For example, white marlin MX03-03 was tailwrapped for the final seven minutes of the 21-minute fight and appeared to be severely exhausted at boatside. This fish was unable to regulate its position in the water when the PSAT was implanted, and required the longest resuscitation of any white marlin in this study (~5 min.). After release, a diver confirmed that this marlin regained color and actively swam away upon reaching cooler water at a depth of about 20 m $(G.$ Harvey²). Depth and temperature data showed that this fish survived for the entire 10-day tag deployment duration. Failure

to revive any of the exhausted or tailwrapped white marlin in this study would have biased the mortality estimate upwards if any of these animals perished as a result of exhaustion.

It is unlikely that trauma induced by boatside handling or tagging contributed to the difference between the mortality of white marlin caught on circle hooks and those caught on "J" hooks. Holts and Bedford (1990) and Domeier et al. (2003) suggested that striped marlin in their studies may have died as a result of striking the tagging vessel rather than from hook-induced injury. We observed only one white marlin (DR02-01) strike the side of a tagging vessel; this fish survived and exhibited behavior similar to other healthy white marlin for the full five-day tag deployment duration.

The implications for stomach eversion on billfish survival are unclear because of fairly few observations in studies assessing survival. Stomach eversion appears to be a natural behavioral mechanism by which undesired food items and remnants may be expelled, and stomachs quickly retracted (Holts and Bedford, 1990). In addition, the generally weakened condition of some marlin with everted stomachs indicates that this condition may occur in response to stress (Holts and Bedford, 1990; Pepperell and Davis, 1999). A striped marlin with an everted stomach tracked by Holts and Bedford (1990) survived, whereas a black marlin with an everted stomach tracked by Pepperell and Davis (1999) and a white marlin in this condition tagged by Kerstetter et al. (2004) were both attacked by sharks and died. In the present study, two white marlin (DR02-03 and MA01) everted their stomachs during the fight. White marlin DR02-03 showed behavior consistent with survival until the tag was prematurely released after 2.5 days. In contrast, white marlin MA01 was hooked in its everted stomach and bled profusely during the fight. Depth data recovered from the PSAT attached to this animal indicated that it died less than 10 minutes after release. The survival of some istiophorids with everted stomachs supports the release of fish in this condition; however, without further observations of animals in this condition, the relevance of stomach eversion in predicting mortality of released billfishes remains uncertain.

The majority of mortalities observed in our study occurred within the first six hours of release; however two mortalities (DR02-04 and VZ03-13) occurred more than 24 hours after tagging. Insights into the behavior of VZ03-13 prior to mortality are compromised by large sections of missing data; however, it should be noted that the final four hours prior to death were associated with surface waters. Likewise, white marlin DR02-04 (Fig. 3A) spent the majority of the first day almost entirely within nearsurface waters following release. Similar prolonged surface associations have been documented in blue marlin (Block et al., 1992) and striped marlin (Brill et al., 1993)—a behavioral pattern that has been attributed to that of a badly injured fish (Brill et al., 1993). White marlin DR02-04 resumed diving behavior similar to that observed in healthy tagged fish (Fig. 3B) after 20 hours, indicating possible recovery from catch-and-release procedures. This white marlin again returned to the surface for four hours prior to its death 64 hours after release.

The two white marlin that had the longest fight times in our study, DR02-04 and VZ03-11 (83 and 46 min, respectively), may have experienced delayed postrelease mortality associated with physiological stress, such as intracellular acidosis following exhaustive exercise (Wood et al., 1983) or haemodilution (Bourke et al., 1987). These mortalities appear to have occurred too soon to have been caused by infection (Bourke et al., 1987) and too late to have been caused by lactic acidosis. Postexertion recovery in istiophorid billfishes is poorly studied, but Skomal and Chase (2002) reported significant perturbations in blood chemistry, including elevation in blood cortisol levels in bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), and white marlin exposed to prolonged angling bouts (mean=46 min). Acoustic tracks of these animals revealed recovery periods characterized by limited diving behavior for two hours or less after release. The death of white marlin DR02-04 after apparent recovery (Fig. 3C) may be the result of natural mortality, another capture event, or delayed mortality associated with release from recreational fishing gear. Mortality associated with the trauma induced by retained fishing hooks need not be immediate. Blue sharks with fishing hooks embedded in the esophagus or perforating the gastric wall have been found to experience systemic debilitating disease that may affect survival over longer time intervals (Borucinska et al., 2001, 2002).

We also cannot discount predation as a possible cause of mortality for any of the white marlin that died in our study. Acoustic tagging studies have described predation on tagged and released sailfish (Jolley and Irby, 1979), blue marlin (Block et al., 1992) and black marlin (Pepperell and Davis, 1999) by sharks. Recently, Kerstetter et al. (2004) observed results consistent with scavenging and predation on PSAT-tagged white marlin and opah (*Lampris guttatus*) by sharks. Both Block et al. (1992) and Kerstetter et al. (2004) documented attacks on tagged marlin that exhibited prolonged surface associations— the same pattern shown by DR02-04 immediately following its release and prior to mortality.

One tag (MA04) in our study failed to transmit data and was eliminated from all analyses. In previous PSAT studies demonstrating billfish survival, mortalities of tagged istiophorids were not directly observed (Graves et al., 2002; Kerstetter et al., 2003), and the authors conservatively regarded nonreporting tags to be evidence of mortality. The early tag models used in these studies may have failed to transmit data because moribund animals were located at depths that exceeded the tolerance limit (650 m) of the tags or because of other factors, including tag malfunction, mechanical damage (Graves et al., 2002; Kerstetter et al., 2003) or tag ingestion (Kerstetter et al., 2004), or a combination of these factors. Other authors, using newer models of PSATs rated to withstand pressure equivalent to a depth of 3000 m, have clearly documented several mortalities and have chosen to eliminate nonreporting tags from their analyses (Domeier et al, 2003, present study). Treating nonreporting tags as mortalities will bias mortality estimates upwards if tags fail to report for reasons other than catch-and-release–induced mortality (Goodyear, 2002).

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

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

Acknowledgments

The authors would like to thank Captains Mike Adkins (*South Jersey Champion*), O. B. O'Bryan (*Sea-D*), Jimmy Grant (*Vintage*), Gene Hawn (*Ocean Fifty Seven*), Ryan Higgins (*Caliente*), Ken Neill (*Healthy Grin*), Steve Richardson (*Backlash*), Rod Ryan (*White Witch*), and Rom Whittaker (*Release*), as well as their crews, for their skill in finding white marlin and for their patience with us as we deployed PSATs. We thank Phil Goodyear for kindly providing the bootstrapping software for simulations, Eric Prince (NMFS) for suggestions regarding bait rigging techniques, Paul Howey and Lissa Werbos (Microwave Telemetry, Inc) for technical assistance with the tags, Lorraine Brasseur (VIMS) for assistance with MATLAB programming, Robert Diaz (VIMS) for advice with statistical methods, and David Kerstetter (VIMS) for helpful comments on this manuscript. We gratefully acknowledge the logistical support of Guy Harvey, Dick Weber, and John Wendkos. This project was funded by the National Marine Fisheries Service and Marine Ventures, Inc.

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