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David W. Kerstetter
Nova Southeastern University, kerstett@nova.edu

Eric S. Orbesen

S. Robert Snodgrass

Eric Prince

National Oceanic and Atmospheric Administration

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NOTE

MOVEMENTS AND HABITAT UTILIZATION OF TWO LONGBILL SPEARFISH *TETRAPTURUS PFLUEGERI* IN THE EASTERN TROPICAL SOUTH ATLANTIC OCEAN

David W. Kerstetter, Eric S. Orbesen, Derke Snodgrass, and Eric D. Prince

ABSTRACT

The longbill spearfish *Tetrapturus pfleugeri* Robins and de Sylva, 1963, is a small istiophorid billfish found in the Atlantic Ocean and adjacent seas that occurs as an infrequent by-catch in recreational and commercial pelagic fisheries. Although some data exist on diet and reproduction based on dead specimens, little is known of the species' habitat preferences or individual movement patterns. In 2004, two longbill spearfish were tagged with pop-up satellite archival tags (PSATs) near Ascencion Island in the South Atlantic for 11 d and 45 d. Individual movement tracks derived from light-based geolocation estimates suggested little relationship with sea surface temperature fronts, although both animals demonstrated a clear preference away from the West African subsurface hypoxic plume. Overall temperature at depth distributions for both fish were narrow; between 22–26 °C for 97% and 82% respectively of the total time at liberty durations. Almost all of the 8-h time-at-depth periods for both day and combined periods showed that these two fish remained within 150 m of the surface. However, time at depth utilization analyses suggest a slightly bimodal distribution, with the majority of the time at depths < 25 m and a secondary grouping at 50–100 m. Depth utilization data are consistent with the hypothesis that interactions between this species and deep-set pelagic longline fisheries for bigeye tuna in the eastern tropical South Atlantic occurs primarily at set and retrieval of the gear.

The longbill spearfish, *Tetrapturus pfluegeri* Robins and de Sylva, 1963, is a rare, comparatively petite istiophorid billfish with a broad distribution throughout the Atlantic Ocean and the Gulf of Mexico, ranging from Georges Bank in the North Atlantic to South Africa (Robins, 1974; Nakamura, 1985). The species is thought to have a more offshore orientation than the primarily coastal sailfish, *Istiophorus platypterus* (Shaw in Shaw and Nodder, 1792) (Wise and Davis, 1973), although catch records from the international pelagic longline fishery report considerable overlaps in spatial range for these two species (e.g., Japanese fleet data: Kikawa and Honma, 1983). The species is an uncommon by-catch or incidental catch throughout its geographic range, including captures in recreational rod-and-reel (RR; Witzell, 1989) and commercial pelagic longline (PLL; ICCAT, 2007) fisheries.

As with much of the species' overall biology, little is known about individual movements and overall habitat use by longbill spearfish. Only a few remote island groups (e.g., Azores and Canary Islands) maintain targeted seasonal fisheries for this species, although these fisheries appear to be dependent on the strength and location of variable currents, including the Gulf Stream. Total catch and landings data for longbill spearfish are reported annually to the International Commission for the Conservation of Atlantic Tunas (ICCAT), which has management jurisdiction for

the species. However, the vast majority of ICCAT-reported landings are from PLL fisheries for thunnid tunas and swordfish *Xiphias gladius* Linnaeus, 1758 (ICCAT, 2007). The similarity of dressed carcasses of spearfish and sailfish has confounded these reported catch and effort data to an unknown degree (ICCAT, 2007; Kikawa and Honma, 1983), and although ICCAT would be the entity to conduct the stock assessment of longbill spearfish, one has not yet been done.

The Cooperative Tagging Center (CTC) of the U.S. National Marine Fisheries Service and The Billfish Foundation (TBF) maintain two databases that are associated with the majority of the conventional tagging of pelagic teleosts in Atlantic waters. Based on historical conventional tagging activity (combined CTC and TBF) from both PLL and RR fisheries, there appears to be a peak in captures from late May through late August (Ortiz et al., 2003). Additionally, the past decade appears to show a shift in conventional tagging activities away from the PLL fishery and toward RR vessels for longbill spearfish in the remote island groups of the eastern and central Atlantic, as well as the Lesser Antilles. In general, fisheries interactions with longbill spearfish are rare, providing limited opportunities for conventional tag deployments. Ortiz et al. (2003) reported 753 releases with three recaptures for longbill spearfish in the combined CTC and TBF database through 2003. Although a data entry error in the TBF system inadvertently classified all spearfishes as longbill spearfish, removing misidentified releases still results in the actual recapture values for this species being among the lowest for all the istiophorids. Several fishery dependent and independent factors could cause such low recapture rates of tagged fish (see review in Ortiz et al., 2003). However, this suggests that tagging technologies that have fishery-independent mechanisms for data recovery may be a better option for studying movements and habitat utilization for longbill spearfish.

Ascencion Island is located at 7°S latitude in the equatorial South Atlantic Ocean, about 1600 km west of the African coast (Fig. 1). The island has a slowly growing recreational fishery for istiophorid billfish due to catches of large blue marlin *Makaira nigricans* Lacépède, 1802, but this part of the South Atlantic has also been noted as a location with frequent recreational fishery interactions with longbill spearfish (e.g., Giangio, 1999). We describe here 56 total monitored days of movement and habitat utilization data from two pop-up satellite archival tags (PSATs) deployed on longbill spearfish off Ascencion Island in late 2004. These two datasets are the only documented use of this technology on longbill spearfish and thus represent the only high resolution habitat utilization data currently available for this species.

Materials and Methods

The PAT4 model pop-off satellite archival tag (PatHost software v. 4.01.0010, hardware v. 2.03; Wildlife Computers, Redmond, WA, USA) was used. The tags were rigged with a 1.8 mm monofilament tether and a double barb nylon anchor using the basic attachment method described in Graves et al. (2002). A pressure-activated guillotine (RD-1800; Wildlife Computers), designed to sever the tether prior to descent below tag crush depth ($\it ca.$ 2000 m), was also included in the tether construction. The tags were programmed to automatically release from the animal if the ambient depth stayed within a range of \le 5 m for 24 hrs.

This tag model allowed the end user to pre-program sampling intervals, as well as the overall deployment duration. User-defined programming for this tag recorded ambient environmental data (temperature, pressure, and light level) every 30 s, which was then binned into each of the three daily histograms for transmission through the ARGOS satellite system. The

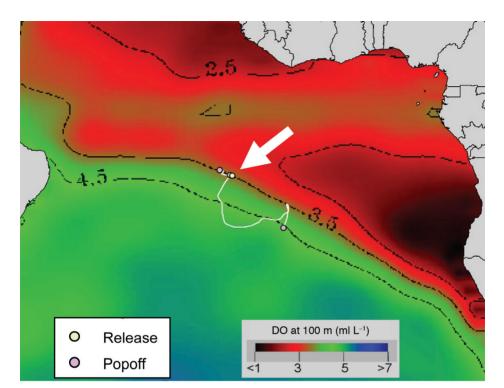


Figure 1. Track movement of two longbill spearfish attached with pop-up archival tags off Ascension Island, UK overlaid on isopleths of dissolved oxygen (DO) concentration (ml L^{-1}) at 100 m depth from the World Ocean Atlas. White arrow points to location of Ascencion Island in the South Atlantic Ocean; fish 2004-03 is the shorter track to the northwest of the island and fish 2004-06 is the longer track to the southeast.

PAT4 software segregated the sampled data into 12 intervals for both depth (–1, 25, 50, 75, 100, 125, 150, 175, 200, 225, 250, and 1000 m; \leq 4 m resolution at < 300 m depth) and temperature (12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, and 60 °C; 0.15 °C resolution). The programming then summarized these archived data further into three discrete 8-hr periods: 0000–0800, 0800–1600, and 1600–0000 UTC (also local time for Ascension Island). In addition to summary histograms, each tag also generated "pressure-depth-temperature" (PDT) profile data. This supplemental dataset provides summary data in which the depths and temperatures encountered by the tag are split into eight approximately equally-sized bins, as well as providing minimum and maximum depth and temperature for each 8-hr binning period.

Tag 2004-03 was programmed to detach from the fish on 17 January, a user defined 90-d monitoring period, while tag 2004-06 was programmed to detach on 2 January, a user defined 45-d monitoring period.

Tagging Event and Individual Animal Description.—Both tags were deployed on fish caught by sportfishing gear. On 20 October 2004, the fish that was to carry tag 2004-03 was caught using a size 11/0 circle hook lodged in the bill. Total fight time was about 20 min, and despite the minor bleeding evident at boatside, the fish was very active upon release. The estimated length was 205 cm lower jaw-fork length (LJFL) and the fish was estimated to weigh 32 kg. Fish 2004-06 was caught on 18 November 2004, with a size 11/0 J-style hook also lodged in the bill. The total fight time was about 5 min and the fish appeared in excellent condition at release. Estimated length for the second fish was 150 cm LJFL and estimated weight was 18 kg.

Both spearfish were manually leadered to the vessel gunwale and retained in the water during the tagging procedure. The PSAT was inserted into the anterior dorsal musculature,

with the nylon anchor of the tether placed on the distal side of the pterygiophores, but short of penetrating the other side of the fish. After each tag was attached, the hook was removed and the fish released. Neither animal was resuscitated prior to release. A GPS-based position of the vessel and sea surface temperature at the time of release (2004-03: 7.9°S, 14.2°W and 25.0 °C; 2004-06: 7.9°S, 14.4°W and 25.3 °C) was recorded from the on-board vessel electronics.

Analyses.—Moon phase and local times for sunrise, sunset, and nautical twilight were obtained from the U.S. Naval Observatory (USNO; http://aa.usno.navy.mil). Based on the USNO data, local sunrise and sunset occurred between 0628 and 1845 throughout the duration of both tag time at large durations. The bin period between 0800–1600 was therefore considered the "day" period. However, the two remaining bin periods from 0000–0800 and 1600–2400, contained a large percentage of daylight and crepuscular time (ca. 25%) in addition to the night photoperiod, thus prohibiting an unambiguous diel analysis. Because the first and last 8-hr binning periods of the time at liberty were incomplete for each tag, these two bins were excluded from time-at-depth analyses for each fish. The time-at-depth data from fish 2004-03 are presented, but may be affected by a presumed mortality event. Time at depth distributions for both fish were tested for bimodality using the "dip test" per Hartigan and Hartigan (1985) in the R programming language (R Development Core Team, 2005). Statistical tests were evaluated with an α -level of $P \le 0.05$.

Initial processing of the light-level based geolocation data used the global positioning software WC-AMP (Wildlife Computers). Aqua-MODIS sea surface temperature (SST) data were obtained from NASA (http://oceancolor.gsfc.nasa.gov/cgi/level3.pl). A SST-corrected Kalman filter (Nielsen et al., 2006) was then applied to the light-level-derived locations. Using ArcGIS 9 (ArcGIS v. 9.2; ESRI, Inc., Redlands, CA, USA), track movements were overlaid on SST values and isopleths of dissolved oxygen (DO) at 100 m obtained from the World Ocean Atlas (http://www.nodc.noaa.gov). ArcGIS was also used to plot the distribution of conventional tag deployments to analyze releases in relation to the 200 m isopleth.

RESULTS

Tag 2004-03 prematurely released from the fish after 11 d at liberty, with the first transmission to the ARGOS system occurring at 7.29°S, 15.59°W (ARGOS estimated location error > 1000 m). A full 100% of the archived 8-hr summary histograms were recovered from tag 2004-03 through ARGOS transmissions. Tag 2004-06 released from the animal after 45 d at liberty, with the first transmission occurring at 13.78°S, 8.35°W (ARGOS estimated location error between 350–1000 m). A total of 89.9% of the archived 8-hr summary histograms were recovered from tag 2004-06. A total of 56 aggregate monitoring days were recorded and transmitted for these two fish.

A total of 12 geolocations were derived for fish 2004-03 (including the geolocation from the first period following tag release), and 31 geolocations were derived for fish 2004-06. Estimated errors for these positions were 1° latitude and 1° longitude. Both fish were released near the 3.5 ml L^{-1} dissolved oxygen (DO) isopleth (Fig. 1). Fish 2004-03 moved in a general west-northwest direction following the edge of the 3.5 ml L^{-1} DO isopleth. Fish 2004-06 initially moved in a southerly direction away from the 3.5 ml L^{-1} DO isopleth. After 17 d, the fish began traveling in a easterly direction until it again encountered the edge of the 3.5 ml L^{-1} (DO) isopleth, where the fish resumed a pattern of southerly movement for the remainder of the track. Neither corrected track approached any major bathymetric features.

Almost all of the 8-hr time-at-depth periods for both day and combined periods showed that these two fish remained within 150 m of the surface (Fig. 2A,B). Both individuals exhibited an apparent bimodal distribution of depth utilization: a large

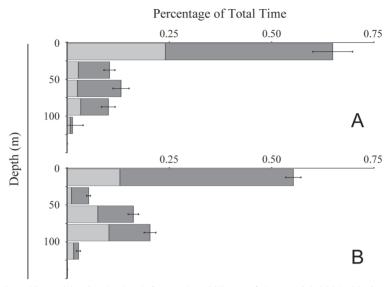


Figure 2. Habitat utilization by depth for two longbill spearfish [(A) Fish 2004–03, October 2004; (B) Fish 2004–06, November 2004] with attached pop-up satellite archival tags off Ascencion Island, UK. Light gray bars are the one 8-hr day period bins (per 24-hr period) while the dark gray bars are the remaining two 8-hr bins (per 24-hr period; includes a combination of night, crepuscular, and daylight time). Error bars represent \pm SE for the total 24-hr period.

peak for the portion of time in depths < 25 m and another, smaller peak centered on 75–100 m. However, results of the dip test analysis found only one significant peak in each time-at-depth distribution (P > 0.25).

Immediately following tagging, fish 2004-03 descended to depth and remained between 75–125 m during the partial first period (1 hr). The fish subsequently moved between the surface and 160 m depth for the remainder of the PSAT deployment until 8 d later, when the fish began to exhibit unusual habitat utilization patterns of wide depth variations. On the eleventh day, the fish rapidly descended to depths approaching 980 m where the tag detached, floated to the surface, and transmitted; we attribute this uncharacteristic movement to such extreme depth as an undefined mortality event. Tag 2004-06 also had a partial first period (4 hrs), although the depths for this fish ranged from 25–100 m. Minimum-maximum depth ranges and interpolated ambient isotherms were generated for each fish (Fig. 3A,B).

Overall temperature ranges experienced by both fish were narrow during the monitored time-at-liberty durations. Sea surface temperatures ranged between 23.2–25.2 °C. For fish 2004-03, 97% of total time at temperature was within 22–26 °C, while fish 2004-06 was within this range for 82% of total time (99% of total time within 20–26 °C). For the daytime 8-hr bin periods, fish 2004-03 had an average temperature range of 3.10 °C (SE = 0.581), while the ranges of fish 2004-06 during the daytime periods were 3.17 °C (SE = 0.204).

Discussion

Although the biology of billfishes in general is only moderately understood (reviewed in Prince and Brown, 1991; also see Pepperell, 2003 and Holland et al., 2006), even less is known of the longbill spearfish. Habitat utilization data indicate that

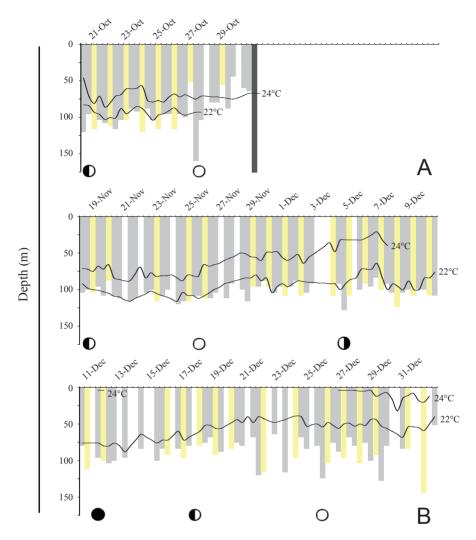


Figure 3. Depth range of two longbill spearfish tagged with pop-up satellite archival tags off Ascencion Island, UK, by 8-hr summary bins. (A) Fish 2004-03, 11-d deployment beginning October 2004, and (B) Fish 2004-06, 45-d deployment beginning November 2004. Gray bars indicate combined nighttime and crepuscular binning periods, while yellow bars indicate daytime periods. The fish did not descend to depths > 5 m during 28 and 30 October. Black bar in panel A indicates 8-hr bin with presumed mortality (depths > 200 m not shown). Isotherms along the 24 °C and 22 °C gradients were generated from a combination of transmitted and interpolated PDT data and are shown by the superimposed horizontal lines. Moonphase is depicted below each corresponding calendar day by circular symbols (open circle is full moon).

longbill spearfish are predominantly epipelagic fishes. Available feeding and diet (gut-content) studies further reinforce this perspective. Recreational fishery data suggest that longbill spearfish feed predominantly during daylight hours (Witzell, 1989), and this is also supported by time-at-hooking data from pelagic longline research (Yokawa and Saito, 2004). Prior diet studies have shown that longbill spearfish feed broadly on a variety of epipelagic organisms (Nakamura, 1985; Júnior et al., 2004), and a gut-content study specific to the central South Atlantic (Cherel et al.,

2007) found a high percentage of epipelagic glassy flying squid, *Hyaloteutis pelagica* (Bosc, 1802). However, the depth distributions for both tagged longbill spearfish in this study suggest a weak (but nonsignificant) bimodal distribution similar to that seen in other billfishes (e.g., blue marlin: Kerstetter et al., 2003), possibly related to foraging behavior at depth (Goodyear et al., 2008). A diet study in the western Atlantic (Júnior et al., 2004) also found that many mesopelagic gempylids (e.g., snake mackerel, *Gempylus serpens* Cuvier, 1829) and pomfrets (Bramidae) were ingested by longbill spearfish, a finding reinforced by an eastern Atlantic study that showed the top four dietary components as exocetids (flyingfishes), gempylids, scombrids, and bramids (Satoh et al., 2004).

Given the available depth data from these two tagged longbill spearfish, individuals may feed opportunistically on mesopelagic organisms as they ascend during nighttime hours with the mixed layer. Alternatively, the low ambient DO could similarly restrict the available habitat of the prey to within the approximate depth ranges seen in these two datasets. For example, descriptions of Japanese pelagic longline sets targeting bigeye tuna, *Thunnus obesus* (Lowe, 1839), in this geographic area are deeper than sets targeting swordfish, yet are shallower than similar operations elsewhere in the Atlantic (e.g., Matsumoto et al., 2004). Although some thunnid tunas can tolerate lower DO levels than istiophorids (e.g., bigeye tuna in Lowe et al., 2000; scombroids reviewed in Prince and Goodyear, 2006), a compressed oxycline would presumably affect prey and targeted species similarly. Longer duration monitoring of spearfishes in a variety of oceanographic conditions would allow a more detailed description of the species' use of the water column and allow for potential comparisons between istiophorid species.

Habitat compression conditions are characterized by relatively shallow thermoclines with cold hypoxic conditions below (Prince and Goodyear, 2006). The timeat-temperature distributions for these two spearfish show a limited range of utilized temperatures, which may be reflective of these compressed habitat conditions. Additionally, Block (1986) found that the eye-brain heater organ, which serves to elevate temperatures in these core areas above ambient water, is less developed in the spearfishes, perhaps reflecting an inability to effectively forage at colder depths such as observed for blue marlin (Goodyear et al., 2008). However, the temperature ranges are also far narrower than the range of 8 °C noted by Brill and Lutcavage (2001) for short duration movements in large scombroid fishes. In this geographic region, DO levels at depth may have a stronger influence than temperature strata. As reviewed by Prince and Goodyear (2006), DO levels ≤ 3.5 ml L⁻¹ induce symptoms of stress for high oxygen consumption species such as tunas and istiophorid billfish, and the proximity of Ascension Island to the 3.5 ml L⁻¹ isopleth may restrict deep diving behavior in this region. Based on the geolocation position estimates, fish 2004–06 apparently left the edge of the hypoxic plume on 19 Nov 2008 and moved south before returning near the edge of the hypoxic plume again 38 d later on 27 Dec 2008.

Longbill spearfish are an infrequent by-catch in pelagic fisheries throughout the North and South Atlantic Oceans that are fishing at various depths, times of day, and oceanographic areas. In particular, the oceanic spatial distribution of longbill spearfish remains poorly known. From 1967 through 2007 there have been only 751 longbill spearfish tagged by CTC and TBF constituent-based tagging programs. Billfish angler surveys in the U.S. recreational fishery have noted that longbill spearfish were caught throughout the year in the tropics, but only seasonally in more temperate

waters, suggesting that the species preferred warmer offshore waters (Witzell, 1989). Pelagic longline catch records appear to show a slightly higher percentage of long-bill spearfish in offshore waters (Kikawa and Honma, 1983; Uozumi, 1998), although there remain problems with species identification with many of these fisheries data.

The data from both tags indicate vertical movements to depths > 175 m did not occur, unlike larger istiophorids such as blue marlin, which are known to undertake short duration vertical movements to depths > 800 m (Goodyear et al., 2008). Although the summarized data from the PAT tag that is transmitted through Argos does not allow the re-creation of individual movements to depth ("dives"), the combined analysis of both the PDT-recorded maximum depths and time-at-depth histograms provides insight on whether the animal made short-duration movements to depths greater than those seen in the histogram alone. In the cases of these two tagged fish, it does not appear that there were any short duration movements to deeper depths. However, additional research will be required to assess whether this species exhibits patterns of vertical movements similar to that seen in other bill-fishes, particularly over longer deployment durations.

One possible explanation for the rarity of this species in catches by pelagic longline vessels targeting bigeye tuna is that the majority of the effective fishing depths for this fishery may be below the depths frequented by longbill spearfish. This is supported by pelagic longline research activities in the central South Atlantic that found significantly lower CPUEs for this species on "deep-set" gear vs "shallow-set" configurations (Yokawa and Saito, 2004). Although data from only two individuals are examined here, the apparent depth segregation between longbill spearfish and deep-set pelagic longline gear targeting bigeye tuna might provide an opportunity for by-catch reduction efforts. As PSAT technology and memory capacity improves over time, the tagging of additional longbill spearfish with shorter bin durations (e.g., 1-hr instead of 6-hrs or 8-hrs) and longer monitoring periods would provide greater insight into the species' behavior, including details regarding potential short-duration movements to depth or possible bimodal depth distributions.

Little is known of the ecological role of longbill spearfish, as well as what impact increasing fishing effort may have on the Atlantic stock of this species. Stock assessments for the species have not yet been attempted, nor have indices of abundance or catch trends been generated from the available pelagic longline records (ICCAT, 2007). Increasing effort in the international pelagic longline fishery over time may have detrimental effects on by-catch species, such as the spearfishes and marlins, although post-release survival studies of smaller istiophorids have shown that live release can have benefits to overfished stocks (e.g., Kerstetter and Graves, 2006, 2008). Additional study of this billfish species in other geographic locations within its range, as well as longer monitoring durations, will improve our understanding of the mix of behaviors exhibited by istiophorids in various environmental and resource availability conditions.

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LITERATURE CITED

- Block, B. A. 1986. Structure of the brain and eye heater tissue in marlins, sailfish, and spearfishes. J. Morphol. 190: 169–190.
- Brill, R. W. and M. E. Lutcavage. 2001. Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. Am. Fish. Soc. Symp. 25: 179–198.
- Cherel, Y., R. Sabatié, M. Potier, F. Marsac, and F. Ménard. 2007. New information from fish diets on the importance of glassy flying squid (*Hyaloteuthis pelagica*) (Teuthoidea: Ommastrephidae) in the epipelagic community of the tropical Atlantic Ocean. Fish. Bull. 105: 147–152.
- Giangio, A. 1999. The facts of swords and spears. Marlin Magazine 100: 134–142. Available from: http://www.marlinmag.com/species/swords-spears/the-facts-on-swords-and-spears-16527. http://www.marlinmag.com/species/swords-spears/the-facts-on-swords-and-spears-16527. http://www.marlinmag.com/species/swords-spears/the-facts-on-swords-and-spears-16527. http://www.marlinmag.com/species/swords-spears/the-facts-on-swords-and-spears-16527. http://www.marlinmag.com/species/swords-spears/the-facts-on-swords-and-spears-16527. http://www.marlinmag.com/spears-16527. https://www.marlinmag.com/spears-16527. <a href="https
- Graves, J. E., B. E. Luckhurst, and E. D. Prince. 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
- Goodyear, C. P., J. Luo, E. D. Prince, J. P. Hoolihan, D. Snodgrass, E. S. Orbesen, and J. E. Serafy. 2008. Vertical habitat use of Atlantic blue marlin: insights into interaction with pelagic longline gear. Mar. Ecol. Prog. Ser. 365: 233–245.
- Holland, K. H., M. L. Domeier, D. B. Holts, J. E. Graves, and J. G. Pepperell (eds). 2006. Proc. Fourth Int. Billfish Symp., Avalon, CA, 31 October–3 November 2005. Bull. Mar. Sci. 79: 429–874.
- Hartigan, J. A. and P. M. Hartigan. 1985. The dip test of unimodality. Ann. Stat. 13: 70–84.
- International Commission for the Conservation of Atlantic Tunas (ICCAT). 2007. Report of the Standing Committee for Research and Statistics (SCRS). ICCAT: Madrid, Spain. 213 p.
- Júnior, T. V., C. M. Vooren, and R. P. Lessa. 2004. Feeding habits of four species of Istiophoridae (Pisces: Perciformes) from northeastern Brazil. Environ. Biol. Fishes 70: 293–304.
- _______, B. E. Luckhurst, E. D. Prince, and J. E. Graves. 2003. Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear Fish. Bull. 101: 939–948.
- Kikawa, S. and M. Honma. 1983. Trends in the Japanese sailfish/spearfish catches in the Atlantic Ocean as apportioned into separate species. Collect. Vol. Sci. Pap. ICCAT 18: 645–649.
- Lowe, T. E., R. W. Brill, and K. L. Cousins. 2000. Blood oxygen-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient oxygen. Mar. Biol. 136: 1087–1098.
- Matsumoto, T., H. Saito, and N. Mīyabe. 2004. Report of the observer program for the Japanese tuna longline fishery in the Atlantic Ocean from September 2002 to January 2003. Collect. Vol. Sci. Pap. ICCAT 56: 254–281.
- Nakamura, I. 1985. FAO species catalogue, Vol. 5. Billfishes of the world. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes, and swordfishes known to date. FAO Fisheries Synopsis No. 125. Vol. 5, 65 p.
- Nielsen, A., K. A. Bigelow, M. K. Musyl, and J. R. Sibert. 2006. Improving light-based geolocation by including sea surface temperature. Fish. Oceanogr. 15: 314–325.

- Ortiz, M., E. D. Prince, J. E. Serafy, D. B. Holts, K. B. Davy, J. G. Pepperell, M. B. Lowry, and J. C. Holdsworth. 2003. Global overview of the major constituent-based billfish tagging programs and their results since 1954. Mar. Freshw. Res. 54: 489–507.
- Pepperell, J. G. (ed) 2003. Proc. Third Int. Billfish Symp. 19–23 August 2001, Cairns, Australia. Mar. Freshw. Res. 54: 287–584.
- Prince, E. D. and B. E. Brown. 1991. Coordination of the ICCAT enhanced research program for billfish. Am. Fish. Soc. Symp. 12: 13–18.
 - and C. P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fish. Oceanogr. 15: 451–464.
- R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org.
- Robins, C. R. 1974. Synopsis of biological data on the longbill spearfish, *Tetrapturus pfleugeri* Robins and de Sylva. Pages 28–38 *in* R. S. Shomura and F. Williams, eds. Proc. Int. Billfish Symp. Kailua-Kona, Hawaii. Part 2. Review and contributed papers, NOAA Tech. Rep. NMFS SSRF-675.
- Satoh, K., K. Yokawa, H. Saito, H. Matsunaga, H. Okamoto, and Y. Uozumi. 2004. Preliminary stomach contents analysis of pelagic fish collected by Shoyo-Maru 2002 research cruise in the Atlantic Ocean. Collect. Vol. Sci. Pap. ICCAT 56: 1096–1114.
- Uozumi, Y. 1998. Distribution of sailfish and longbill spearfish in the Atlantic Ocean during 1994-1996 based on the logbook database of the Japanese longline fishery. Collect. Vol. Sci. Pap. ICCAT 48: 246–248.
- Wise, J. P. and C. W. Davis. 1973. Seasonal distribution of tunas and billfishes in the Atlantic. NOAA Tech. Rep. NMFS SSRF-2.
- Witzell, W. N. 1989. Longbill spearfish, *Tetrapturus pfleugeri*, incidentally caught by recreational billfishermen in the western North Atlantic Ocean, 1974-86. Fish. Bull. 87: 982–984.
- Yokawa, K. and H. Saito. 2004. Results of comparison of catch ratio between shallow and deep setting obtained from 2002 Shoyo-Maru survey in the tropical Atlantic. Collect. Vol. Sci. Pap. ICCAT 56: 195–200.

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Addresses: (D.W.K.) Nova Southeastern University Oceanographic Center, 8000 North Ocean Drive, Dania Beach, Florida 33004. (E.S.O., D.S., E.D.P.) Southeast Fisheries Science Center, NOAA National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 37375. Corresponding Author: (E.D.P.) E-mail: <eric.prince@noaa.gov>.

