FastTrack publication

BULLETIN OF MARINE SCIENCE, 84(3): 257–264, 2009

NOTE

VERTICAL MOVEMENT RATE ESTIMATES FOR ATLANTIC ISTIOPHORID BILLFISHES DERIVED FROM HIGH RESOLUTION POP-UP SATELLITE ARCHIVAL DATA

John P. Hoolihan, Jiangang Luo, David E. Richardson, Derke Snodgrass, Eric S. Orbesen, and Eric D. Prince

Development of pop-up satellite archival tag (PSAT) technology has greatly increased our knowledge of billfishes (Arnold and Dewar, 2001). The acquisition and subsequent fisheries-independent transmission of PSAT data via the Argos system has revealed behavioral traits of these comparatively rare species, whose survival depends on the ability to range over large geographical areas (Goodyear et al., 2008). While PSATs are capable of monitoring light level, depth, and temperature at relatively high resolution (i.e., ≤ 60 s intervals), battery power and data volume restrictions can limit data transmissions to summary information only. Occasionally, PSATs are recaptured with fishing gears or recovered after washing ashore (e.g., Gunn et al., 2003; Hoolihan and Luo, 2007). In these instances, the complete archived high resolution data are accessible from the PSAT memory. Analyzing these data for change in depth (over time) provides an opportunity to derive coarse estimates of vertical movement rates, in lieu of a dedicated speed sensor. Knowing these swimming rates provides the potential to better understand the vertical and thermal habitat use, and bioenergetic optimization of billfishes. Similar swimming capability may also be implied to horizontal movements, helping to elucidate home range and migration patterns. In addition, swimming speed information is a necessary component for building foraging models.

Methods

Six PSATs deployed between May and June 2003 on two blue marlin (BUM) *Makaira nigricans* (Lacépède, 1802) and two white marlin (WHM) *Tetrapturus albidus* (Poey, 1860), and during June 2005 on two sailfish (SAI) *Istiophorus platypterus* (Shaw, 1792) were recovered intact (Fig. 1). All were manufactured by Wildlife Computers (Redmond, Washington) and programmed to measure depth (± 0.5 m), temperature (± 0.05 °C), and ambient light level at 30- or 60-s intervals (Table 1).

From the archived data, we sub-sampled a 20 d series of data from each PSAT, beginning 11 d post-deployment, for the purpose of estimating descent and ascent rates (m s^{-1}). Rates were determined for individual vertical movement events, defined as a continuous and uni-directional vertical movement (i.e., depth change) extending ≥ 5 m. For example, representative vertical movement data from BUM-2 (Fig. 2) illustrates unpaired events for six descents (D1 to D6) and four ascents (A1 to A4). We calculated the average speed of each event by dividing the depth difference with the time interval, and grouped the events as descents or ascents. Prior to statistical analyses, descent speed samples were scrutinized for autocorrelation violations. For example, an autocorrelation plot of BUM-2's descent speeds (Fig. 3) showed only 1.86% of points outside the 95% confidence intervals (dashed lines), indicating a > 98% confidence that the events were independent random observations from a random variable.

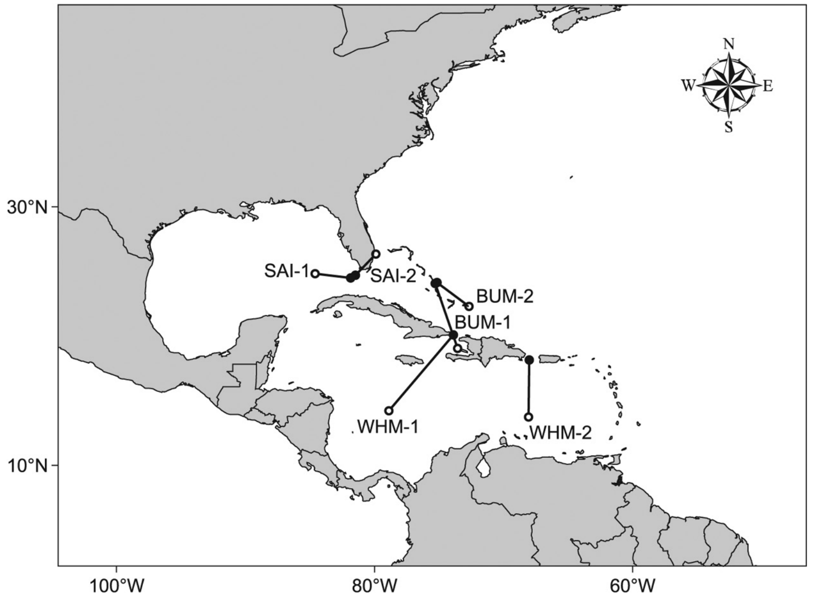

Figure 1. Pop up satellite deployment locations in western North Atlantic for two blue marlin (BUM), two white marlin (WHM), and two sailfish (SAI). Lines depict linear displacement from points of release (solid circles) to pop-up locations (open circles).

Data were log transformed to fit testing criteria for normality and equal variances. Since the sample number of individuals was small, no statistical comparisons or inferences were made between individuals or species. Differences between the mean rate of movement for descent and ascent events were compared using the *z* test. In turn, group comparisons between day, night, and crepuscular unidirectional movements (ascents or descents) were analyzed with Welch's ANOVA, a robust technique that is sympathetic to variance heterogeneity and unequal sample sizes (Lix et al., 1996).

Results and Discussion

The total number of descent events ranged from 1802 (WHM-2) to 3925 (SAI-1), while the number of ascent events ranged from 1763 (WHM-2) to 3767 (SAI-1, Table 2). In general, the vertical distances moved during descent and ascent events were small, with the highest frequencies occurring in the 5–20 m range (data not shown). Maximum distance for descent events ranged from 184 m (BUM-1) to 452 m (BUM-

Table 1. Summary details of PSAT releases and archival data analyses from deployments (n = 6) on blue marlin *Makaira nigricans* (BUM), white marlin *Tetrapturus albidus* (WHM), and sailfish *Istiophorus platypterus* (SAI) in the Atlantic Ocean.

Specimen	Tag model*	Date deployed	Deployment location	Days at liberty	Period analyzed	Recording interval
BUM-1	PAT3	4 June 2003	24°06′N 75°17′W	82	14 June–4 July	30 s
BUM-2	PAT3	7 June 2003	24°06′N 75°15′W	61	17 June–7 July	30 s
WHM-1	PAT3	15 May 2003	18°36′N 68°17′W	37	26 May–15 June	60 s
WHM-2	PAT2	12 June 2003	20°07′N 73°51′W	60	22 June–12 July	30 s
SAI-1	PAT4	10 May 2005	24°27′N 81°42′W	120	21 May–10 June	30 s
SAI-2	PAT4	11 May 2005	24°29′N 81°32′W	135	20 May–9 June	30 s

* Wildlife Computers hardware versions

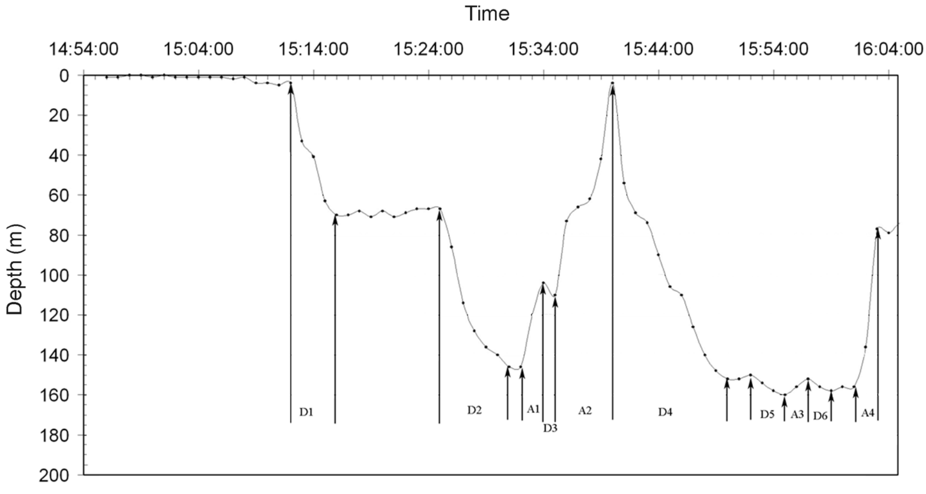

Figure 2. Event identification diagram derived from blue marlin pop up satellite data (BUM-2). D1–D6 illustrates descent events, while A1-A4 illustrates ascent events.

2), while maximum distances for ascents ranged from 180 m (SAI-1) to 532 m (BUM-2, Table 2).

The mean descent rate per event ranged from 0.02 (WHM-1) to 3.76 m s^{-1} (BUM-2), while ascents ranged from 0.02 (WHM-2) to 3.40 m s^{-1} (BUM-1, Table 2). The maximum rate of movement recorded for a single time interval within an event was 7.20 m s^{-1} achieved by BUM-2 during descent. For most individuals, the mean movement rate for ascents was significantly higher than descents (Table 3). The exception was WHM-2, which exhibited the opposite (Table 3, Fig. 4). Ascent rates for all individuals were significantly lower at night, when compared to day (Table 3). The two sailfish showed similar behavior for descent events, but the blue marlin and white marlin exhibited no difference between day and night for descent speed (Table 3).

Among individuals, the proportion of total monitoring time engaged in vertical movement events ranged from 29.4% (WHM-2) to 54.4% (WHM-1, Fig. 5). For all individuals, the greatest percentage of total vertical movement events occurred during daylight hours (data not shown). This may be explained by the fact that because istiophorids are active sight feeders, more movement associated with foraging would be expected during daylight. The maximum durations of descent and ascent events are shown in Table 2.

The vertical movement rates presented here represent minimum estimates of swimming speeds, since the horizontal components were unknown. Because our methods did not directly measure swimming speed, several behavioral assumptions were necessary. First, descent and ascent events were assumed to be absolutely vertical, which in most cases is improbable. Therefore, actual distances moved are most likely underestimated, as are movement rates. Second, direction of movement was assumed to be straight and continuous. In actual fact our billfish had sufficient opportunity between monitoring intervals (30 s or 60 s) to engage in horizontal movement, stop and start, or reverse vertical direction, which suggests the mean vertical movement rate estimates ($\leq$ 0.36 m s^{-1}, Table 2) were probably below the actual rates. In comparison, Block et al. (1992) monitored the speed of three blue marlin, using

Table 2. Total number of descent and ascent events for six PSAT monitored blue marlin (BUM), white marlin (WHM), and sailfish (SAI). Events are defined as continuous, uni-directional vertical movement (i.e., depth change) extending 5 m or greater.

Specimen	No. days	Depth (m) range (mean ± SD)	Temp (°C) range (mean ± SD)	Total descent events ≥ 5 m	Total ascent events ≥ 5 m	Meters descending range* (mean ± SD)	Minutes descending range (mean ± SD)	Meters ascending range* (mean ± SD)	Minutes ascending range (mean ± SD)	Descent rate (m s^{-1}) range** (mean ± SD)	Ascent rate (m s^{-1}) range** (mean ± SD)
BUM-1	20	0–196 (28.6 ± 32.6)	21.1–30.0 (27.7 ± 1.1)	3,373	3,244	5–184 (24.1 ± 21.4)	0.5–8.5 (1.87 ± 1.18)	5–192 (25.2 ± 23.0)	0.5–10.5 (1.27 ± 0.85)	0.03–1.43 (0.22 ± 0.15)	0.04–3.40 (0.36 ± 0.30)
BUM-2	20	0–660 (32.8 ± 32.8)	11.1–30.6 (27.8 ± 1.0)	3,550	3,358	5–452 (24.6 ± 22.8)	0.5–11.5 (1.95 ± 1.16)	5–532 (26.1 ± 24.4)	0.5–16.5 (1.30 ± 0.97)	0.03–3.76 (0.22 ± 0.18)	0.03–1.73 (0.36 ± 0.26)
WHM-1	20	0–188 (33.2 ± 33.5)	17.7–28.2 (26.9 ± 1.1)	3,131	2,977	5–188 (33.1 ± 24.4)	1.0–13.0 (2.97 ± 1.82)	5–188 (34.8 ± 25.7)	1.0–23.0 (2.13 ± 1.78)	0.02–1.36 (0.20 ± 0.13)	0.02–1.85 (0.32 ± 0.25
WHM-2	20	0–260 (74.6 ± 67.7)	19.4–30.3 (27.0 ± 2.2)	1,802	1,763	5–260 (24.0 ± 34.6)	0.5–10.5 (1.58 ± 1.54)	5–222 (21.4 ± 31.2)	0.5–23.5 (2.40 ± 2.47)	0.04–1.40 (0.23 ± 0.16)	0.03–1.33 (0.14 ± 0.11)
SAI-1	20	0–244 (14.8 ± 19.8)	13.5–30.8 (25.1 ± 2.0)	3,925	3,767	5–244 (22.1 ± 17.5)	0.5–13.5 (1.50 ± 1.00)	5–180 (23.0 ± 18.3)	0.5–15.0 (1.32 ± 1.06)	0.04–1.62 (0.26 ± 0.16)	0.03–1.66 (0.34 ± 0.23)
SAI-2	20	0–232 (14.5 ± 25.6)	15.3–29.0 (26.4 ± 1.8)	3,405	3,459	5–190 (24.2 ± 21.2)	0.5–7.5 (1.60 ± 0.95)	5–232 (23.8 ± 20.7)	0.5–8.5 (1.36 ± 0.91)	0.03–3.40 (0.26 ± 0.18)	0.04–2.13 (0.32 ± 0.21)

* refers to distance traveled during vertical movement event–not actual depth in the water column
** derived from average speed over individual events

Table 3. Mean movement rate (± SD) for descent and ascent events during day, night, and crepuscular periods for six Atlantic billfish. Upper values represent descent events, while those in parentheses represent ascent events. Asterisks denote significance levels for movement rate differences between descent and ascent events within each period.

	Day rate (m s^{-1})	Night rate (m s^{-1})	Crepuscular rate (m s^{-1})
BUM-1	0.22 ± 0.15**	0.20 ± 0.12 n.s.	0.26 ± 0.16**
	(0.36 ± 0.30)	(0.18 ± 0.13)	(0.36 ± 0.28)
BUM-2	0.22 ± 0.18**	0.21 ± 0.18 n.s.	0.23 ± 0.16**
	(0.36 ± 0.26)	(0.19 ± 0.13)	(0.36 ± 0.25)
WHM-1	0.20 ± 0.13**	0.20 ± 0.14**	0.18 ± 0.11*
	(0.36 ± 0.26)	(0.14 ± 0.06)	(0.22 ± 0.17)
WHM-2	0.23 ± 0.15**	0.23 ± 0.14**	0.26 ± 0.20**
	(0.15 ± 0.11)	(0.10 ± 0.06)	(0.18 ± 0.18)
SAI-1	0.28 ± 0.16**	0.14 ± 0.13*	0.27 ± 0.18*
	(0.37 ± 0.23)	(0.14 ± 0.12)	(0.32 ± 0.22)
SAI-2	0.29 ± 0.19**	0.15 ± 0.11*	0.26 ± 0.17 n.s.
	(0.36 ± 0.22)	(0.16 ± 0.10)	(0.26 ± 0.17)

n.s. not significant ; * $P < 0.05$; ** $P < 0.001$

direct speed sensors, during short-term acoustic tracking studies; and reported that 97% of time traveled was at < 1.20 m s^{-1}.

Other studies, using acoustic tracking methods, also reported that istiophorids engage in slow sustained swimming most of the time (Yuen et al., 1972; Jolley and Irby, 1979; Holland et al., 1990; Holts and Bedford, 1990; Brill et al., 1993; Pepperell and Davis, 1999; Hoolihan, 2005). Notably, these studies relied on vessel speed and position to define the movement of the tracked fish, resulting in estimates probably below true swimming speed.

The higher movement rates achieved by billfish in the present study are more likely to reflect burst swimming events, rather than sustained swimming speeds (Table 2). Burst swimming speed can be generally characterized as a high-speed, short-duration (< 20 s) event, often associated with foraging activities or avoidance of predators

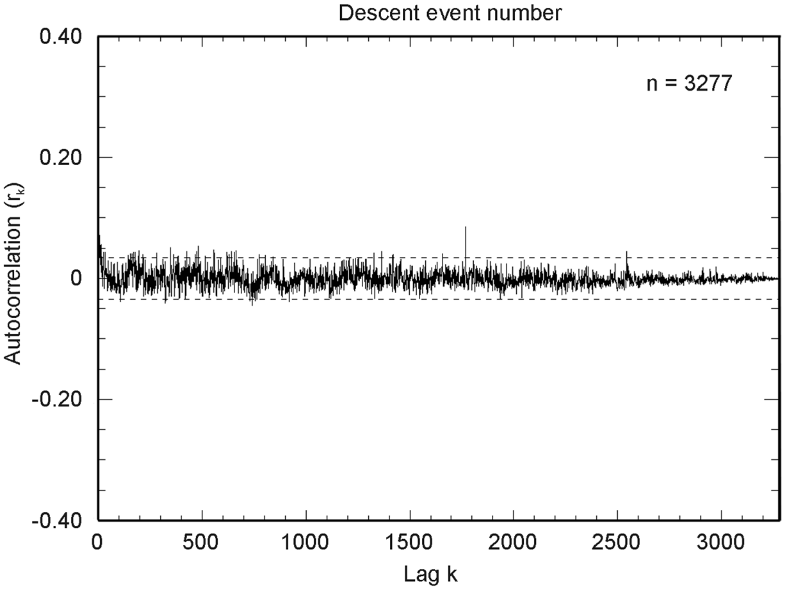

Figure 3. Autocorrelogram example of descent speeds for a blue marlin (BUM-2), for descents represented in Figure 2. Dashed lines indicate 95% confidence intervals.

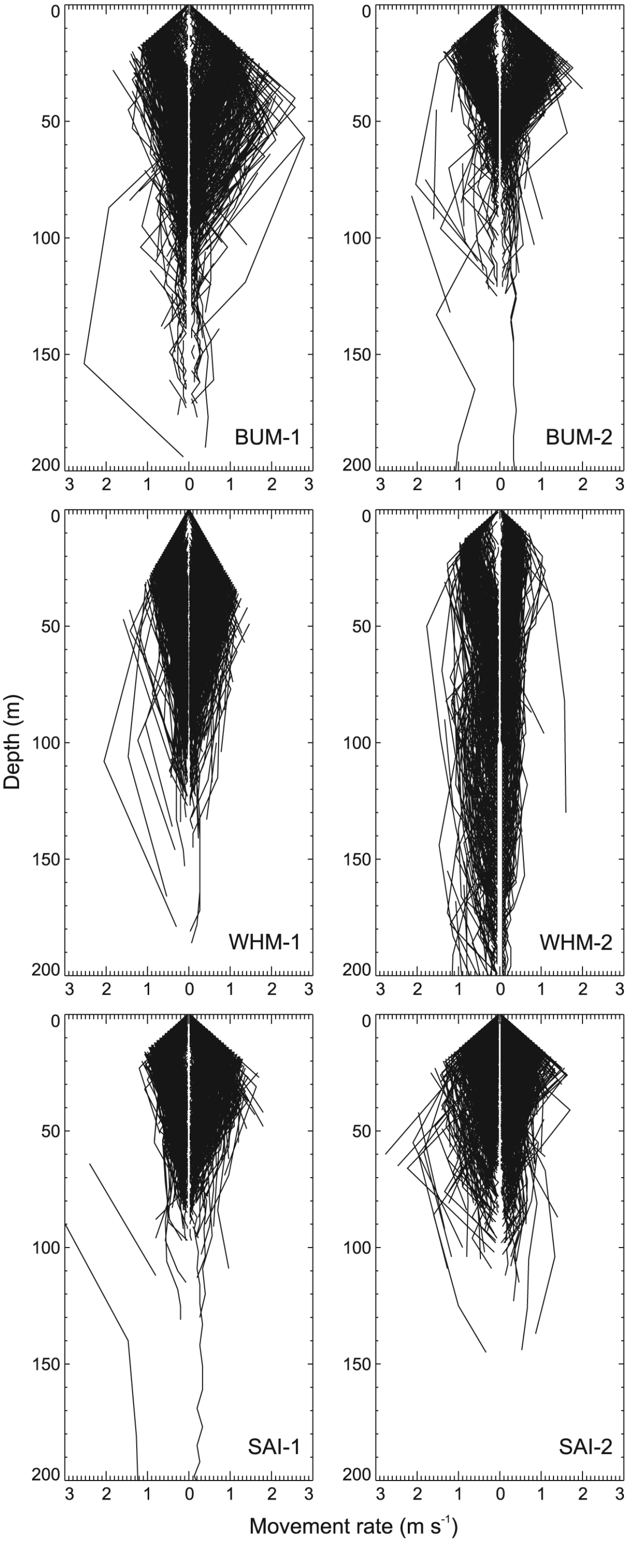

Figure 4. Mean rate of vertical movement (m s^{-1}) as a function of depth during ascent and descent events for two blue marlin (BUM), two white marlin (WHM), and two sailfish (SAI). Descents are plotted to left of zero on x-axis, ascents to the right.

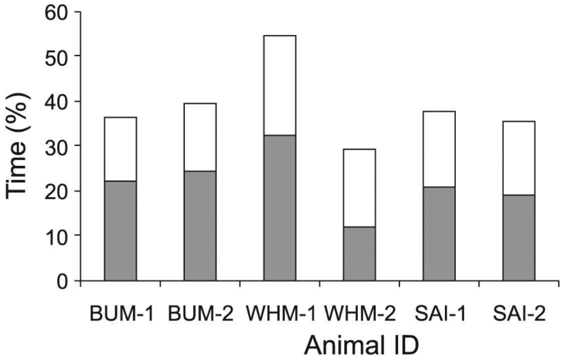

Figure 5. Percentage of total monitoring time engaged in descent (shaded) and ascent (unshaded) event activities for two blue marlin (BUM), two white marlin (WHM), and two sailfish (SAI) monitored with pop-up archival satellite tags. An event was defined as continuous, uni-directional vertical movement (i.e., depth change) extending ≥ 5 m.

(Beamish, 1978). Block et al. (1992) reported burst speed events exceeding 2.00 m s^{-1}, and lasting 10 to 30 s, during direct-speed monitoring of blue marlin. Underwater observations confirm that billfishes use rapid acceleration, speed, and turning in pursuit of prey (G. Harvey, Davie, Florida, pers. comm.). The 30 s to 60 s monitoring intervals used in our study prevented us from detecting most short-burst events with any certainty.

Despite shortfalls, our results provide a step forward in understanding Atlantic billfish behavior by presenting the first detailed information on vertical movement rates extending over a lengthy period. These estimates could be improved by shortening sampling intervals to < 30 s, a certain possibility using newer version PSATs with larger memory and battery capacities. However, retrieval of PSAT archival data from billfishes is an uncommon occurrence. Further, using change in depth over time as a method to estimate speed is less than optimal, for the reasons mentioned above. Using a direct speed sensor would eliminate the errors generated by the unaccounted vertical and horizontal movements in the present study. The development and integration of a dedicated speed sensor for the PSAT would represent a considerable advancement in our ability to understand billfish movement characteristics.

Acknowledgments

We acknowledge the captains, anglers, and other constituents of the Adopt-A-Billfish program for making the PSAT deployments possible. The Billfish Foundation was instrumental in PSAT project funding and support. The views expressed herein are those of the authors, and do not necessarily reflect the views of NOAA or any of its sub-agencies.

Literature Cited

Arnold, G. and H. Dewar. 2001. Electronic tags in marine fisheries research. Pages 7–64 *in* J. R. Sibert and J. L. Nielsen, eds. Proc. Symp. Tagging and tracking marine fish with electronic devices, February 7–11, 2000, East-West Center, University of Hawaii. Kluwer Academic, Dordrecht. 468 p.

Beamish, F. W. H. 1978. Swimming capacity: locomotion. Pages 101–111 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, Vol VII. Academic Press, New York. 576 p.

Block, B. A., D. T. Booth, and F. G. Carey. 1992. Direct measurement of swimming speeds and depth of blue marlin. J. Exp. Biol. 166: 267–284.

Brill, R. W., D. B. Holts, R. K. C. Chang, S. Sullivan, H. Dewar, and F. G. Carey. 1993. Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. Mar. Biol. 117: 567–574.

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 (*Makaira nigricans*): insights into interaction with pelagic longline gear. Mar. Ecol. Prog. Ser. 365: 233–245.

Gunn, J. S., T. A. Patterson, and J. G. Pepperell. 2003. Short-term movement and behaviour of black marlin *Makaira indica* in the Coral Sea as determined through a pop-up satellite archival tagging experiment. Mar. Freshw. Res. 54: 515–525.

Holland, K., R. W. Brill, and R. K. C. Chang. 1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. Fish. Bull. 88: 397–402.

Holts, D. and D. Bedford. 1990. Activity patterns of striped marlin in the southern California Bight. Pages 81–93 *in* R. H. Stroud, ed. Proc. Second Int. Billfish Symp. National Coalition for Marine Conservation, Inc. Savannah, Georgia. 321 p.

Hoolihan, J. P. 2005. Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging. Mar. Biol. 146: 1015–1029.

____________ and J. Luo. 2007. Determining summer residence status and vertical habitat use of sailfish (*Istiophorus platypterus*) in the Arabian Gulf. ICES J. Mar. Sci. 64: 1791–1799.

Jolley, J. W., Jr. and E. W. Irby, Jr. 1979. Survival of tagged and released Atlantic sailfish (*Istiophorus platypterus*: Istiophoridae) determined with acoustical telemetry. Bull. Mar. Sci. 29: 155–169.

Lix, L. M., J. C. Keselman, and H. J. Keselman. 1996. Consequences of assumption violations revisited: a quantitative review of alternatives to the one-way analysis of variance *F* test. Rev. Edu. Res. 66: 579–619.

Pepperell, J. G. and T. L. O. Davis. 1999. Post-release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. Mar. Biol. 135: 369–380.

Yuen, H. S. H., A. E. Dizon, and J. H. Uchiyama. 1972. Notes on the tracking of the Pacific blue marlin, *Makaira nigricans*. Pages 265–268 *in* R. S. Shomura and F. Williams, eds. Proc. Int. Billfish Symp. Kailua-Kona, Hawaii, 9–12 August 1972 Part 2. NOAA Tech. Rep. NMFS SSRF-675, Seattle. 335 p.

Date Submitted: 10 October, 2008.
Date Accepted: 23 January, 2009.
Available Online: 10 March, 2009.

Addresses: (J.P.H., D.S., E.S.O., E.D.P.) *NOAA Fisheries, Southeast Fisheries Science Center, Miami, Florida 33149.* (J.L.) *Rosenstiel School of Marine & Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149.* (D.E.) *NOAA Fisheries, Northeast Fisheries Science Center, 28 Tarzwell Drive, Narragansett, Rhode Island 02882.* Corresponding Author: (J.P.H.) *Telephone: 305-365-4116, Fax: 305-361-4562, E-mail: <john.hoolihan@noaa.gov>.*