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Horizontal movements of Atlantic blue marlin (*Makaira nigricans*) in the Gulf of Mexico

Richard T. Kraus · R. J. David Wells ·
Jay R. Rooker

Abstract We examined movements of Atlantic blue marlin (*Makaira nigricans*) from the Gulf of Mexico based upon 42 pop-up archival transmitting (PAT) tags. Long deployments (including one 334-day track) revealed diverse movement patterns within the Gulf of Mexico. North–south seasonal changes in blue marlin distribution showed strong correspondence with established seasonal patterns of sea surface temperature and primary production. During the summer spawning season, blue marlin utilized outer shelf and shelf edge waters in the northern Gulf of Mexico, and longer duration tracks indicated overwintering habitats in the Bay of Campeche. Egress occurred throughout the year and was difficult to determine because some tracks ended in the Straits of Florida ($n = 3$) while other tracks recorded movement through it or the Yucatan Channel ($n = 4$). Our results indicate that Atlantic blue marlin have a more restricted geographic range of habitats than previously recognized and that the Gulf of Mexico provides spatially dynamic suitable habitat that is utilized year-round through seasonal movements.

R. T. Kraus (✉)
Department of Environmental Science and Policy,
George Mason University, 4400 University Drive,
MS 5F2, Fairfax, VA 22030, USA
e-mail: rkraus@usgs.gov

R. J. D. Wells · J. R. Rooker
Department of Marine Biology, Texas A&M University
at Galveston, 5007 Avenue U, Galveston, TX 77551, USA

Present Address:
R. T. Kraus
US Geological Survey, Great Lakes Science Center,
Lake Erie Biological Station, 6100 Columbus Avenue,
Sandusky, OH 44870-8329, USA

Introduction

Tuna and billfish species are typically wide ranging, highly vagile, and support fisheries of significant value (Majkowski 2007). Mark–recapture and electronic tagging studies have demonstrated that many of these species make long-distance movements and in some cases regularly cross ocean basins (e.g., Adam et al. 2003; Ortiz et al. 2003; Block et al. 2005). Molecular markers indicate that such movements likely contribute to genetic homogeneity across large (e.g., hemisphere or ocean) spatial scales (Graves 1998; Buonaccorsi et al. 2001). Consequently, unit stock boundaries for these and similar oceanic fisheries are often defined to encompass long-range movements of individuals by including territorial waters of multiple nations.[1] This approach simply aims to equate the unit stock with the unit of production—a population—so that abundance and resiliency to exploitation can be accurately assessed. The underlying assumption of the large unit stock hypothesis is that the population of inter-breeding members produces offspring with similar movement trajectories and other life history characteristics.

Despite the assumption that individuals of a particular stock share life history characteristics, there is a growing body of research indicating that intra-population variability in movement patterns is widespread across disparate fish

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[1] Regional fishery management organizations such as the International Commission for the Conservation of Atlantic Tunas (ICCAT) are charged with assessment, monitoring, and management of these resources.

taxa (Secor and Kerr 2009). A classic example is the partial migration of many anadromous salmonid populations where precocious resident males represent an alternative to the ocean-type migratory life history (Jonsson and Jonsson 1993). Although the two forms are derived from the same population, migrant and resident subpopulations have contrasting growth, maturity, and mortality rates (Theriault et al. 2008). Similarly, divergent movement patterns are displayed by pelagic species including Atlantic bluefin tuna (*Thunnus thynnus*) with significant intra-population variability within and between eastern and western stocks (Rooker et al. 2007). Within each stock, subpopulation groups with divergent movements have been termed contingents (Secor 1999; Fromentin and Powers 2005). Because mortality risks (both fishing and natural) vary across the range of areas frequented by the different contingents, each group may contribute disproportionately to fishery landings and the overall dynamics of the population (Fromentin and Powers 2005). Intra-population variability in movement has clear importance in the context of managing highly migratory species at the ocean basin scale, and the development of meaningful, spatially explicit models will rely heavily on rates of exchange among different regions used by each contingent (Brill and Lutcavage 2001; Sibert and Hampton 2003). Unfortunately, for many oceanic species, our understanding of intra-population variability in movements is limited, compromising our ability to understand the significance of spatial variation in life history traits and fishery catches.

Atlantic blue marlin (*Makaira nigricans*) support highly valuable recreational and commercial fisheries throughout its range (Goodyear 1999; Luckhurst 2003; Brinson et al. 2006). Based upon approximately 50 years of mark–recapture data, Atlantic blue marlin exhibit some of the longest movements ever recorded for oceanic fishes (Ortiz et al. 2003), but the reported mean distance between release and recapture is 575 km with the majority of recaptures occurring within 1,000 km of the tagging locations from fish at large for less than 6 months (Orbesen et al. 2008). These data indicate that blue marlin may spend a high proportion of time within a single subregion of the stock boundaries. Recent catches of blue marlin reported by ICCAT[2] show three centers of catch production in the western North Atlantic Ocean; the Caribbean Sea (55.4%, primarily in the region near Venezuela), Gulf of Mexico (15.6%), and tropical North Atlantic Ocean west of the Antilles (13.4%) accounted for the majority of blue marlin catch (5,602.1 out of 6,631.6 tons total) between 1998 and

2007. ICCAT has also identified a potential catch reporting deficiency from fisheries in West Africa, which may represent a fourth center of catch production. Two of these areas (Caribbean Sea and Gulf of Mexico) are typified by a relatively high tendency for limited distance between release and recapture sites, with 92.9 and 78.3% of recaptures occurring within the tagging areas, respectively (Witzell and Scott 1990; Orbesen et al. 2008). The population connectivity of blue marlin from these areas is poorly understood, and seasonal and nomadic movements between release and recapture locations may result in a significant and unknown amount of time in other areas. Catch data and conventional tagging also indicate a north–south seasonal movement cycle in the western North Atlantic Ocean (Mather et al. 1972; Witzell and Scott 1990; Wilson et al. 1991; Orbesen et al. 2008). Unfortunately, both the catch data and the mark–recapture data are limited by a seasonally variable and spatially uneven distribution of fishing effort. Therefore, it is difficult to discern with these data whether the production centers should be viewed as ecologically independent subpopulations or simply as areas of high catch from a uniform population.

Only recently have new inferences from larval fish studies and electronic tagging provided further insights into blue marlin migration and population structure. Advances in molecular and morphological identification methods have led to the identification of putative larval nursery areas in the Gulf of Mexico, Straits of Florida, and Exuma Sound of the Bahamas (Serafy et al. 2003; Luthy et al. 2005; Richardson et al. 2007, 2009; Devine et al. 2008; Simms 2009, Appendix B). Unfortunately, much of the range in the Atlantic where blue marlin larvae are known to occur (Nishikawa et al. 1978) still has not been investigated to determine the relative importance of potential nursery areas. In addition, recent use of pop-up archival transmitting (PAT) tags to examine hooking mortality and vertical habitat utilization (Graves et al. 2002; Kerstetter et al. 2003; Prince and Goodyear 2006; Goodyear et al. 2008) has also begun to provide information on horizontal movements that complements previous telemetry results (Holland et al. 1990; Block et al. 1992). Although PAT tags have a significant advantage over conventional tags by providing daily location estimates and ending locations via satellite, knowledge of population connectivity between subregions is still limited because most deployments to date have been short-term (<90 days) and typically programmed to end after 30 days.

To better understand intra-population variability in movements, we have been deploying PAT tags on blue marlin in the Gulf of Mexico since 2003. Due to the significance of this region to fishery catches and efforts to estimate spawning population size from larval collections (Richardson et al. 2009), more information on movements

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[2] ICCAT reported estimates of catch in tons from the western North Atlantic based upon spatially aggregated (5-degree intervals of latitude and longitude) data from all gear types. See Task II CATDIS data for tunas and tuna-like species posted at: http://www.iccat.int/en/accesingdb.htm.

and habitat use of adult fish from the Gulf of Mexico is needed to support improved stock assessment and fishery management of blue marlin. Further, the Gulf of Mexico provides a unique opportunity to examine blue marlin in a semi-enclosed marginal sea of the Atlantic Ocean. Only two relatively narrow passages to the Gulf of Mexico exist (Straits of Florida, Yucatan Channel) through which the western boundary current of the North Atlantic passes (Sturges and Blaha 1976; Sturges 1993). Within the Gulf of Mexico, this portion of the current can extend north to 28°N latitude and west to 88°W longitude and is called the Loop Current. A combination of nutrient inputs from the Mississippi River and upwelling fronts along the edge of the Loop Current (Walsh et al. 1989; Muller-Karger et al. 1991) supports high primary production in pelagic habitats as well as high catches of tropical and subtropical fishery species (Chesney et al. 2000; Dagg and Breed 2003). Interestingly, the Orinoco and Amazon River plumes likely have analogous effects, respectively, in the Caribbean Sea and tropical North Atlantic Ocean west of the Antilles (Dagg et al. 2004) where catches of blue marlin are also concentrated. Our work responds to reports from the recreational fishery in the northern Gulf of Mexico that blue marlin size range and seasonal movements vary independently from adjacent areas of the western North Atlantic Ocean. Here, we examined results from PAT tags deployed on blue marlin over a 6-year period to characterize horizontal movement patterns, describe seasonal distribution changes, and gain insight into the population connectivity between the Gulf of Mexico and adjacent regions. In addition, we examined factors that may be used to refine future application of PAT tags for this purpose.

Methods

Pop-up archival transmitting tags have been widely applied to study movements in many large pelagic species, and the details of the technology are well described in other papers (e.g., Lutcavage et al. 1999; Teo et al. 2004). We deployed PAT tags opportunistically from sport fishing vessels following the methods of Squire (1987) and Chaprales et al. (1998). The vertical movement data gathered from 2003 to 2005 have been analyzed previously (Kraus and Rooker 2007), and here, we focus on the light-based daily geo-locations derived from PAT tag data. Through 2004, programmed deployments were 30 ($n = 5$), 90 ($n = 5$), or 180 days ($n = 2$). We subsequently established programmed durations of 180 days through 2007 ($n = 22$) and increased the duration to 365 days in 2008 ($n = 8$) for a total of 42 tags used in this analysis.

Although accuracy of deployment (GPS based) and pop-up locations (ARGOS® satellite transmission based) is relatively high, light-based geo-locations from the rest of the tracks are known to be highly uncertain, especially in the latitude dimension surrounding equinox periods (Welch and Eveson 1999; Hill and Braun 2001; Musyl et al. 2001). Therefore, we used state-space models that implement the Kalman filter algorithm to estimate the most probable tracks from light-based location data (Kalman 1960; Sibert et al. 2003; Nielsen et al. 2006; Lam et al. 2008). These models explicitly account for stochasticity in both measurement (uncertainty in location) and process (fish movement) and further refine movement tracks according to sea surface temperature by comparing tag observations with historical remote sensing data. Initially, light-based geo-locations were estimated using software provided by the tag manufacturer (Global Position Estimator©, Wildlife Computers, Inc., Redmond, Washington, USA). Reduced state-space models for each tag were developed interactively from the light-based locations by removing nonsignificant parameters as measured by likelihood ratio tests and by considering erroneous locations on land. In cases where the number of observations was small and the pop-up location was relatively close to the deployment location, we used a model with uniform variance structure lacking sea surface temperature parameters and/or advection parameters to estimate a reasonable track solution. Otherwise, the full model often provided the most reasonable solution (see Appendix).

We used refined daily location estimates from the reduced state-space models to examine horizontal movements, seasonal distributions, and duration of time in the Gulf of Mexico. Movements were assessed by plotting tracks and calculating displacement (distance between deployment and pop-up), displacement rate (displacement divided by deployment duration), daily speed (based upon refined daily location estimates), and directional components of movement using GIS (from refined daily locations). Seasonal and daily characteristics of movement were heavily influenced by short duration tracks and limited movements of fish within the first month after tagging. This effect disproportionately weighted results toward short duration tracks; therefore, we did not use the first 30 days of deployment of each track to assess seasonal distribution patterns with the kernel density analysis. This approach did not affect comparisons of displacement with other published studies, which were made without excluding any data.

For analysis of fish size effect on speed, short duration tracks were incorporated. We evaluated fish size effects on speed using linear regression and correlation. Speed data were log-transformed to satisfy assumptions of normality.

Seasonal distributions were characterized by examining plots of the empirical kernel density distributions using the daily geo-location estimates (Worton 1989). We

categorized data into 2-month intervals that provided sufficient sample sizes for detecting differences between intervals. Kernel densities were estimated using the spatial analyst extension of ArcView 3.2 (ESRI), and the distributions were visualized with volume contours of 25, 50, 75, and 100% occupancy. Further, we examined speed of travel between days by decomposing speed and direction into north–south and east–west components for fish with long-term deployments (defined here as ≥90 days). Values were averaged for individual fish for analysis, and reported means and errors characterize variability among individuals rather than variability among days.

We quantified duration of time in the Gulf of Mexico using event analysis (i.e., survival analysis) with the Kaplan–Meier estimator (Castro-Santos and Haro 2003; Schroepfer and Szedlmayer 2006). This approach accommodates right-censored data, or tracks in which the tag came off of the fish before an egress event could be observed. In addition, event analysis has the advantage of properly handling tracks of varying programmed durations such that the estimates are not disproportionately influenced by short duration tracks (Castro-Santos and Haro 2003). Mean duration was estimated by calculating the area under the survivorship function, following Hosmer and Lemeshow (1999). In our data, the longest track (334 days) did not end with egress; therefore, we included the area under the survivorship curve between the last observed egress event and the longest track (Hosmer and Lemeshow 1999). This effectively treated the longest track as ending with egress; therefore, inferences from the mean duration are conditioned on a 334-day period.

Some tracks ended within the Straits of Florida (defined here as the region between 80°W and 82°W longitude that is north of Cuba and south of the Florida Keys); therefore, we estimated the average duration two ways: by classifying these fish as (a) having egressed and (b) remaining within the Gulf of Mexico. No such ambiguity was observed in the Yucatan Channel; therefore, egress there was defined as southward movement crossing 21.5°N latitude.

To evaluate the importance of premature tag release on time spent in the Gulf of Mexico, we conducted additional event analyses to determine the rate of premature tag release for the pooled data and for data grouped by tag anchor type (metal chevron, nylon barb, modified nylon barb). Anchor types were compared with log-rank tests that were adjusted for multiple comparisons (Cox and Oakes 1984). Statistical significance of all performed tests was assessed at alpha = 0.05.

Results

All of the tags were deployed from May to August (2003 to 2008) in the northern Gulf of Mexico in continental slope waters off of Texas and Louisiana (Fig. 1; Table 1). Mean weight of tagged blue marlin (approximated by experienced fishermen to the nearest 10 kg) was 100 kg (range: 30–250 kg), indicating that these individuals were primarily average size mature males or young mature females (Erdman 1968; de Sylva and Breder 1997). Although eight of the tags were recovered, we obtained most of our data via

Fig. 1 Tag deployment (*dots*) and pop-up locations (*triangles*) for 42 Atlantic blue marlin in the Gulf of Mexico. *Lines* connect end points for individual fish. *Lightly shaded* region represents the continental margin to a depth of 1,000 m
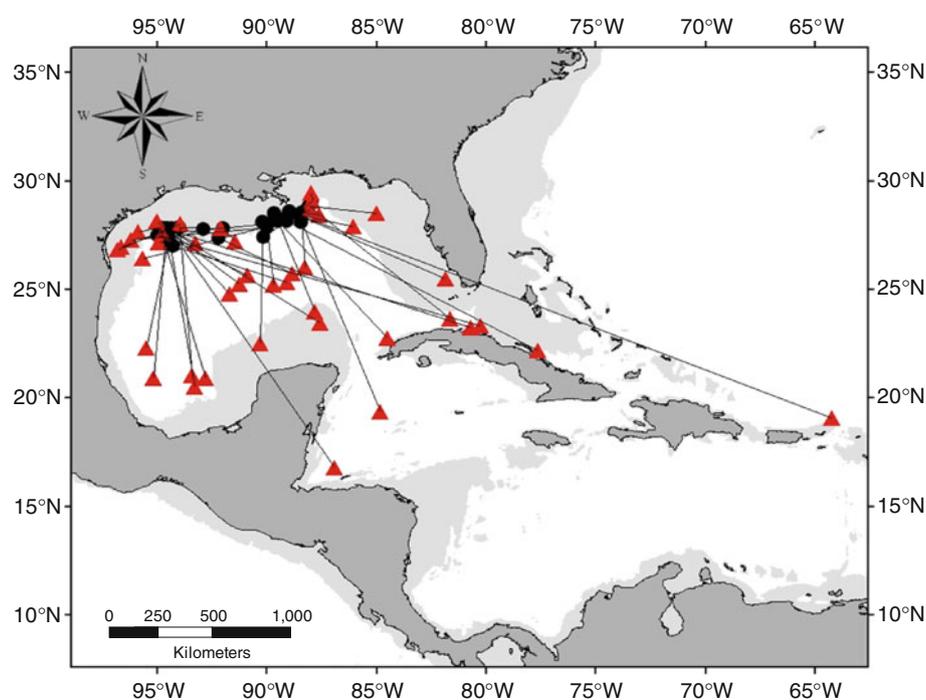
satellite where factors such as meteorological condition, sea condition, and/or battery life usually prevented complete transmission of data. Consequently, a significant fraction of the deployment days lacked sea surface temperature and/or complete dawn and dusk light-level curves for daily geo-location estimates. Out of a total of 3468 deployment days, 2011 days were available for state-space modeling. Missing periods from the tracks totaled 475, and these gaps were modally 1 day long with a mean of three missing days per gap. In each case, parsimonious interpretations of gaps never included egress from and return to the Gulf of Mexico. This situation mainly affected fish ID 16 (Table 1) where egress occurred during a 19-day data gap. In this case, we used the calendar midpoint to mark the timing of egress. We compared pop-up locations with refined light-based geo-locations 1 day prior to the pop-up date and found variations that were on average 0.6° (SE = 0.10) for longitude and 0.4° (SE = 0.09) for latitude. Based upon potential uncertainty of geo-location estimates and the geography of the basin, classification of positions as occurring either inside or outside of the Gulf of Mexico was unambiguous.

The geographic range of movements of blue marlin encompassed areas as far away as oceanic habitats near Belize in the Caribbean Sea and the U.S. Virgin Islands in the North Atlantic Ocean, but the majority of geo-locations and tag pop-up locations were within the Gulf of Mexico (Fig. 1). Mean displacement ranged between ∼300 and 1,200 km across years, with an overall mean of 588 km (±80.9 SE). Inter-annual variability in displacement was significant (ANOVA: displacement, $F_{5,36} = 3.38$, $P = 0.013$). This result was driven by significantly larger displacements observed in 2005 relative to 2004, 2006, and 2008 (Tukey–Kramer adjusted P values for multiple comparisons were <0.03): other years were not significantly different from each other. Displacement rates (based upon straight line distances between tagging and pop-up locations) were on average 11.7 km per day for all tags combined. Average daily speed was 31.3 km/day, and movement paths were significantly more complex than what could be inferred solely from deployment and pop-up locations (or mark–recapture data). Daily speed estimates were not significantly different among years (ANOVA: speed, $F_{5,36} = 1.06$, $P = 0.398$).

Tracks from the longest deployment durations revealed highly variable patterns of movement, regardless of tagging location, season of release, or egress status (Fig. 2). Linear regression analysis showed no significant relationship between the estimated fish weight and the average daily speed ($r^2 = 0.003$, $P = 0.746$).

Seasonal changes in distribution emphasized a north–south cyclical pattern within the Gulf of Mexico, but small sample sizes limited inferences for winter and spring. During May to June, blue marlin ($n = 6$) primarily utilized an expansive shelf edge area that spanned the northern Gulf of Mexico from Florida to Texas and south from Texas to the U.S.–Mexico border into the central region of the Bay of Campeche (Fig. 3). In July and August, the distribution shifted away from the continental shelf into open ocean habitats ($n = 17$), but was still primarily concentrated in the northern Gulf of Mexico, especially in the offshore region of Texas and Louisiana (Fig. 3). In September and October, the distribution ($n = 23$) was primarily in slope and open ocean areas off the U.S.–Mexico border and the central part of the Bay of Campeche with a smaller area of habitat utilization in the northeastern Gulf of Mexico in the region of the Loop Current. Although the number of fish at large was much smaller ($n = 9$) in November and December, the distribution was similar to September and October with a southerly shift away from the northern Gulf of Mexico. In January and February, these regions of primary habitat utilization ($n = 7$) shifted farther south and were concentrated in the Bay of Campeche and near the western end of Cuba (Fig. 3). The March and April distribution pattern was based upon a single fish that spent all of its time in the western Gulf of Mexico at the U.S.–Mexico border. Unfortunately, no tagged fish were at large from the eastern Gulf of Mexico and adjacent areas during March and April.

Across seasons, finer-scale patterns of long-term movement showed some directional biases that varied among fish that egressed (including tracks that ended in the Straits of Florida) versus those that remained in the Gulf of Mexico for the duration of the tracks. From September to December, daily speeds were slow and exhibited no significant directional biases or differences between groups (Fig. 4). Fish that egressed tended to show faster daily speeds with a strong southeast bias from May to August and from January to February (Fig. 4). This result was consistent with movement into or through the Straits of Florida ($n = 5$). By comparison, the group of fish that did not egress showed a pattern of change in direction of movement that reinforced the same annual cycle observed in the kernel density distribution analysis. These fish tended to move west during May and June and south during July and August (Fig. 4). Although movements were slow and without prominent directionality during September through February, the single fish available during March to April showed net movement northwest out of the Bay of Campeche. This northwest movement direction resulted in a 101-km difference between the July 2008 deployment and June 2009 pop-up locations and suggests that some individuals return to the same regions in which they were tagged during the previous year.

Although the majority of blue marlin remained within the Gulf of Mexico for the durations of the PAT tag deployments, up to 1 year (see Table 1 for the following), deployment durations varied greatly with most (69%)

Table 1 Summary information from PAT tags deployed on Atlantic blue marlin from the Gulf of Mexico

ID	Weight (kg)	Deployment date	Deployment location	Pop-off date	Pop-off location	Programmed duration	Actual duration	Days for geo-location	Speed (km/day)	Displacement (km)	Displacement rate (km/day)
1	182	7/19/2003	27.37 N, 94.47 W	8/18/2003	25.65 N, 90.89 W	30	30	30	31.7	405	13.5
2	91	7/27/2003	27.87 N, 93.99 W	10/25/2003	21.04 N, 93.40 W	90	90	83	44.9	763	8.5
3*	91	8/2/2003	27.78 N, 92.91 W	8/22/2003	27.18 N, 94.95 W	30	20	20	10.6	212	10.6
4	91	5/21/2004	29.11 N, 87.94 W	8/25/2004	29.48 N, 88.00 W	180	96	91	55.6	42	0.5
5	102	5/23/2004	28.04 N, 90.02 W	7/4/2004	27.57 N, 94.79 W	90	42	41	33.7	473	11.2
6	91	5/23/2004	28.04 N, 90.02 W	8/22/2004	25.22 N, 89.69 W	90	91	64	48.3	316	3.8
7	80	5/28/2004	28.86 N, 88.06 W	6/28/2004	28.52 N, 85.02 W	30	31	23	19.4	299	9.6
8	68	7/2/2004	27.41 N, 90.16 W	8/1/2004	29.08 N, 87.95 W	30	30	30	33.6	286	9.5
9	68	7/3/2004	28.86 N, 88.06 W	9/30/2004	23.65 N, 81.67 W	90	89 (88)	70	57.2	862	9.8
10	159	7/24/2004	27.50 N, 94.97 W	10/5/2004	23.33 N, 80.26 W	90	73 (57)	58	47.7	1,549	20.7
11	91	8/5/2004	27.87 N, 90.00 W	9/4/2004	27.31 N, 96.22 W	30	30	30	32.2	617	20.6
12	91	8/9/2004	27.83 N, 94.67 W	8/19/2004	28.14 N, 95.01 W	180	10	8	4.8	48	4.8
13*	57	5/22/2005	28.60 N, 88.98 W	6/7/2005	25.50 N, 81.86 W	180	16	15	58.1	785	48.8
14	45	6/3/2005	28.62 N, 88.98 W	9/20/2005	19.09 N, 64.25 W	180	109 (16)	51	38.5	2,725	25.1
15	91	7/31/2005	27.80 N, 94.50 W	1/30/2006	24.78 N, 91.72 W	180	183	50	21.2	436	2.5
16	114	7/31/2005	27.80 N, 94.50 W	1/27/2006	23.25 N, 80.73 W	180	180 (179)	9	13.0	1,472	7.9
17	182	8/3/2005	27.80 N, 94.50 W	1/28/2006	16.78 N, 86.94 W	180	178 (162)	40	27.8	1,452	8.4
18	91	8/3/2005	27.80 N, 94.50 W	1/31/2006	23.47 N, 87.56 W	180	181	55	17.0	847	4.5
19	136	6/11/2006	27.87 N, 93.99 W	7/1/2006	27.84 N, 92.13 W	180	20	10	9.1	183	9.1
20	102	6/24/2006	27.84 N, 91.99 W	7/1/2006	27.20 N, 91.47 W	180	7	6	12.5	88	12.5
21	136	7/9/2006	27.86 N, 94.88 W	9/12/2006	20.93 N, 92.79 W	180	65	17	23.0	800	12.2
22	114	7/23/2006	27.83 N, 94.55 W	8/1/2006	27.11 N, 93.24 W	180	9	9	16.8	152	16.8
23*	68	7/30/2006	27.84 N, 94.63 W	10/8/2006	25.24 N, 91.27 W	180	70	60	39.0	442	6.4
24	125	7/30/2006	27.83 N, 94.55 W	9/2/2006	28.03 N, 93.97 W	180	34	24	23.2	61	1.7
25	159	8/6/2006	27.38 N, 94.47 W	1/1/2007	22.32 N, 95.50 W	180	148	53	18.3	573	3.8
26	114	8/20/2006	27.36 N, 94.64 W	10/18/2006	20.92 N, 95.20 W	180	59	21	40.8	719	12.9
27	91	6/5/2007	28.23 N, 89.27 W	10/23/2007	22.19 N, 77.64 W	180	140 (26)	74	29.1	1,349	9.7
28	91	6/22/2007	28.12 N, 88.45 W	6/27/2007	26.04 N, 88.28 W	180	5	5	39.4	232	39.4
29*	80	6/30/2007	28.58 N, 88.38 W	7/6/2007	28.42 N, 87.60 W	180	6	4	11.3	78	11.2
30	159	7/2/2007	28.12 N, 88.45 W	9/18/2007	19.36 N, 84.83 W	180	78 (51)	55	59.1	1,042	13.3
31*	114	7/3/2007	28.44 N, 88.50 W	7/7/2007	27.89 N, 86.05 W	180	4	4	35.3	248	35.3
32	114	8/2/2007	27.00 N, 94.30 W	10/14/2007	25.34 N, 89.09 W	180	73	25	22.7	552	8.0
33	136	8/10/2007	27.39 N, 92.19 W	12/4/2007	25.75 N, 88.84 W	180	116	74	35.8	380	3.6
34	250	9/2/2007	28.14 N, 89.49 W	1/26/2008	22.75 N, 84.51 W	180	146	80	26.4	781	5.1

Table 1 continued

ID	Weight (kg)	Deployment date	Deployment location	Pop-off date	Pop-off location	Programmed duration	Actual duration	Days for geo-location	Speed (km/day)	Displacement (km)	Displacement rate (km/day)
35*	45	5/27/2008	28.15 N, 89.10 W	9/2/2008	26.43 N, 95.68 W	365	98	83	34.7	678	6.7
36*	102	6/12/2008	28.10 N, 90.20 W	10/1/2008	28.70 N, 88.01 W	365	111	70	45.5	225	1.9
37	114	6/17/2008	28.52 N, 89.65 W	10/12/2008	24.00 N, 87.82 W	365	117	86	39.3	535	4.5
38	68	6/30/2008	27.37 N, 94.47 W	10/16/2008	20.50 N, 93.29 W	365	108	75	30.7	774	5.4
39	125	7/2/2008	28.12 N, 90.18 W	8/31/2008	22.50 N, 90.30 W	365	60	9	16.3	626	10.6
40*	80	7/31/2008	27.86 N, 94.88 W	6/30/2009	27.67 N, 95.88 W	365	334	278	66.1	101	0.4
41	68	7/31/2008	27.82 N, 94.32 W	10/14/2008	26.97 N, 96.67 W	365	75	39	34.3	251	5.1
42	34	7/31/2008	27.83 N, 94.55 W	11/14/2008	26.84 N, 96.83 W	365	106	82	32.4	251	2.0

Due to premature releases and variations in tag operation, actual deployment durations were frequently shorter or (in a few cases) slightly longer than the programmed duration. For those individuals that egressed, time in the Gulf of Mexico is given in parentheses. Durations are in days

* Recovered tag

lasting between 30 and 183 days. Excluding both short (<31 days) and long durations (>185), 23 out of 30 individuals remained in the Gulf of Mexico during tag deployments. Seven fish exhibited movement into the Straits of Florida ($n = 3$) or clearly left the Gulf of Mexico ($n = 4$). The timing of movements into or through the Yucatan Channel and the Straits of Florida was highly variable, occurring from June to January, but still provided information for estimating the mean time to egress from PAT tag data (Fig. 5). Estimates were not significantly different whether tracks ending in the Straits of Florida were classified as showing egress (mean duration = 223 days, SE = 34.8) or classified as remaining within the Gulf of Mexico (mean duration = 264 days, SE = 36.4). Thus, based upon an 11-month (334 days) observation period, adult blue marlin tagged in the Gulf of Mexico remained there on average for a minimum of 7 to 8 months.

Premature release of tags due to unknown causes affected a large fraction of our deployments ($n = 31$). Although seven tags prematurely released within 20 days, eleven tags remained attached for the programmed durations up to 180 days (Fig. 5; one track was 334 days, but no tags with programmed durations of 365 days remained attached until the programmed release date). The mean time to premature release of tags was estimated to be 115 days (SE = 18.0). The three types of tag anchors used over the course of this study were metal chevron style (supplied by the manufacturer) from 2003 to 2004, nylon barb (Domeier et al. 2005) from 2005 to 2006, and a modified nylon barb from 2007 to 2008. Comparisons of premature release rates between tag anchor types revealed no significant differences (Bonferonni corrected P values were >0.50 for all log-rank tests comparing time to release), indicating that tag anchor type was not a factor leading to premature tag release.

Discussion

Application of PAT tags on Atlantic blue marlin from the Gulf of Mexico revealed horizontal movement patterns within an area of relatively high larval production and catches of adults (Diaz and Ortiz 2006; Wilson et al. 2007). At the coarsest spatial scale, displacement between tag deployment and pop-up (mean = 588 km) was very similar to that obtained with conventional tagging (575 km; Orbesen et al. 2008). Mean displacement distance emphasized that most pop-up locations were observed within the Gulf of Mexico. Although mean displacement was consistent across most years, larger displacements were observed during 2005—a year characterized by high sea surface temperature and strong hurricane activity in the
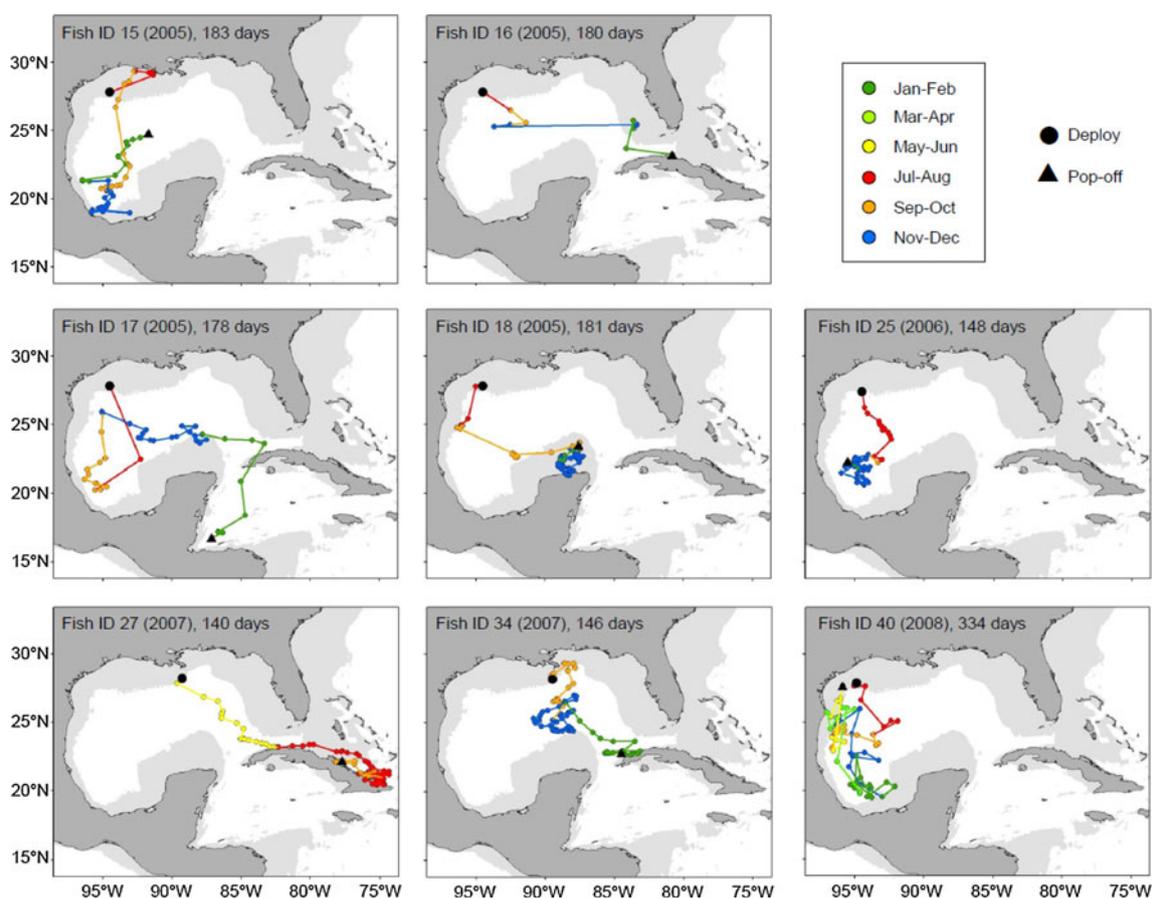
Fig. 2 Tracks of blue marlin with deployment durations ≥140 days. *Symbols* and *line shades* are coded by 2-month intervals. To reduce clutter, geo-location estimates of fish ID 40 are displayed with 5-day increments

Gulf of Mexico (Kafatos et al. 2006). Similar inter-annual variability has also been observed for Atlantic bluefin tuna in the Gulf of Maine where regional climate was strongly associated with horizontal movement patterns (Sibert et al. 2006). Average displacement rate of blue marlin in the Gulf of Mexico (11.7 km/day) was less than half of the speed estimate obtained from state-space modeling of daily location tracks (31.3 km/day), emphasizing that tracks were nonlinear. Though our displacement rate estimate was lower than that reported for blue marlin in adjacent areas of the North Atlantic Ocean by Graves et al. (33 km/day; 2002) and Kerstetter et al. (28–72 km/day; 2003), our tracks were typically 2–5 months longer, and movements may have been constrained by the geography and circulation patterns in the Gulf of Mexico. Especially in the western Gulf of Mexico, Loop Current eddies (Sturges and Leben 2000) may influence the magnitude and direction of horizontal movements either passively (by advection) and/or indirectly (by affecting prey distribution). Further, the idea that geography may constrain movements of blue marlin in this region is supported by faster daily speeds

exhibited by individuals that moved into or through the Straits of Florida or the Yucatan Channel.

Within the Gulf of Mexico, estimates of daily locations between tag deployment and pop-up provided a more detailed characterization of seasonal distribution changes of blue marlin. The most prominent pattern was that blue marlin tended to remain in the western Gulf of Mexico (west of longitude 88°W) and shifted their distribution seasonally between three distinct areas: (1) the shelf edge of the Texas coastline and adjacent offshore area during summer, (2) the central region of the Bay of Campeche during winter, and (3) shelf edge and adjacent offshore area at the U.S.–Mexico border during spring and fall. Individual tracks, movement direction analysis, and aggregate kernel density analysis supported this pattern of north–south movement among three primary habitats in the western Gulf of Mexico (Figs. 2, 3, 4). Centers of distribution in the eastern Gulf of Mexico showed a similar north–south seasonal change, but the smaller number of fish and geo-locations made this pattern more difficult to characterize.
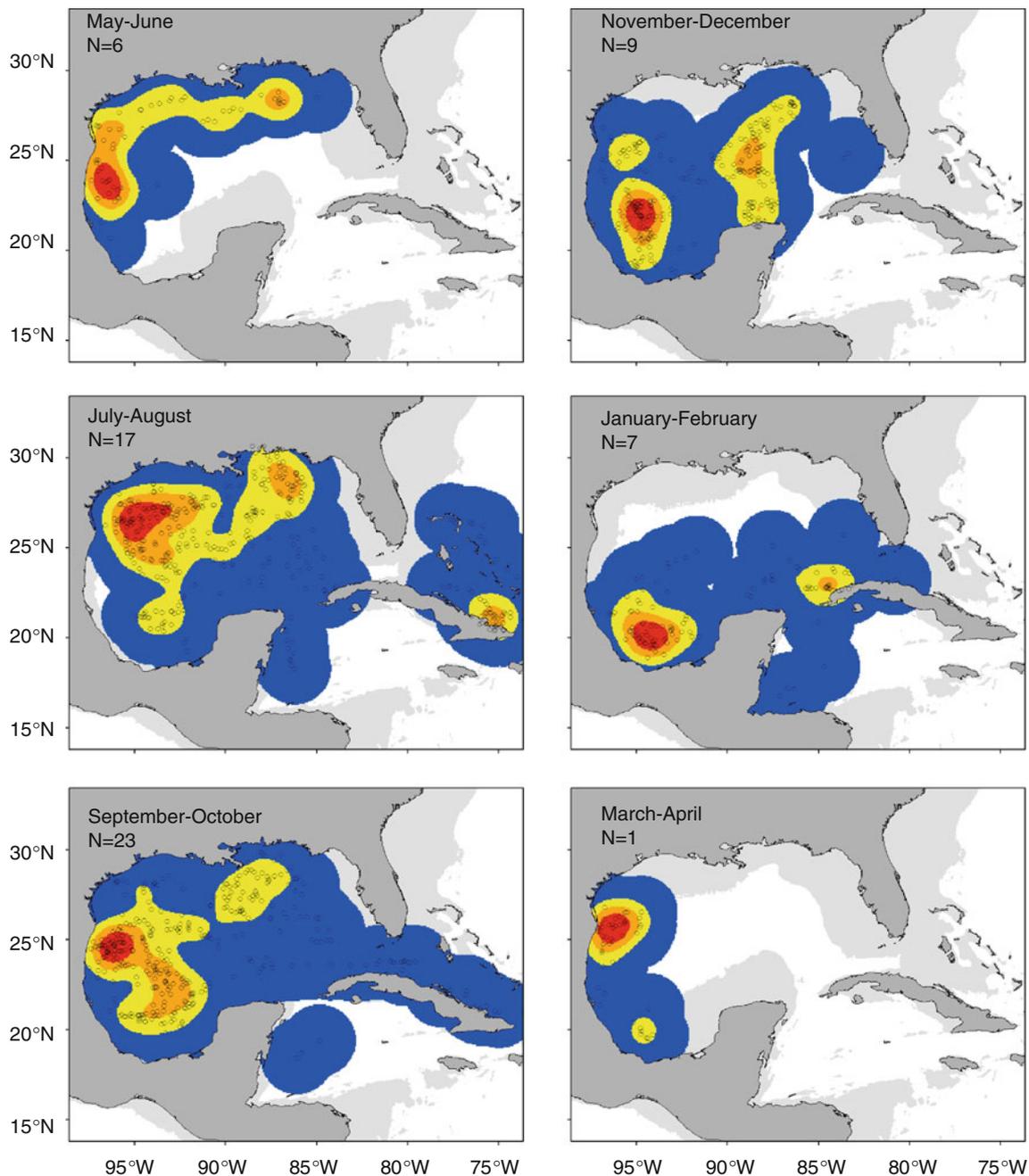
Fig. 3 Seasonal distributions of Atlantic blue marlin geo-locations derived from PAT tag data. The first 30 days of each track were not used for kernel density estimation (see explanation in "Methods"); therefore, these results are based upon a total of 30 individuals. *Shaded* areas demarcate 25, 50, 75, and 100% of the distribution. Individual locations used to estimate the distribution are shown as *circles*

Our findings emphasize that most blue marlin remain in the northern Gulf of Mexico throughout the spawning season, which occurs from May to September based upon gonad development (Erdman 1968; de Sylva and Breder 1997), larval occurrence (Serafy et al. 2003; Luthy et al. 2005; Devine et al. 2008; Richardson et al. 2009; Simms 2009, Appendix B), and back-calculation of hatch-dates from otoliths (Prince et al. 1991). While this complements larval surveys that have identified the Gulf of Mexico as an important geographic area for reproduction, a minority of individuals moved into the Straits of Florida, the North Atlantic Ocean, or the Caribbean Sea, and these could potentially contribute to spawning in both the Gulf of Mexico and adjacent regions. This type of population connectivity helps to explain why genetic markers are homogeneous across the western North Atlantic Ocean
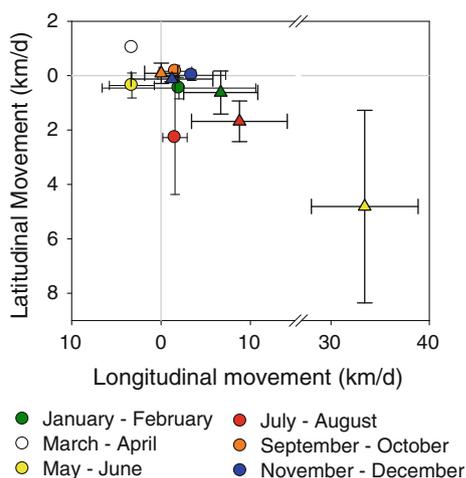
Fig. 4 Average longitudinal and latitudinal movement (speed in km/day, based upon state-space modeling of tracks) of blue marlin with deployment durations ≥90 days. *Symbols* denote fish that egressed (*triangles*) versus those that remained in the Gulf of Mexico for the duration of tag deployments (*circles*). *Error bars* represent 1 standard error, and some error bar intervals are small such that the *symbols* overlap. The *symbol* for the March to April interval represents only one fish and has no error bars

Fig. 5 Empirical functions of track duration within the Gulf of Mexico (**a**) and premature tag release (**b**) for tagged Atlantic blue marlin. Egress from the Gulf of Mexico or tag loss events are indicated by 'stair-step' inflections in the *black lines*. Here, tracks ending in the Straits of Florida are treated as exhibiting egress (see text). *Circles mark* when tracks ended before an event could be observed (right-censored data). Although the displayed time dimension is truncated to 200 days, the period of inference extends to 334 days (the longest track duration)

(Buonaccorsi et al. 2001). On ecological time scales relevant to fisheries management, estimation of time spent in a putative spawning area supports more accurate assessment of spawning stock biomass based upon larval surveys—a key research frontier for blue marlin and related species (Hunter and Lo 1993; Richardson et al. 2009). Our period of observation (limited to 11 months) indicated blue marlin stay in the Gulf of Mexico, including the Straits of Florida, for an average of at least 8 months.

Remote sensing and physical oceanographic research predicts that suitable habitats for blue marlin are available year-round in the Gulf of Mexico, but the location of these habitats changes throughout the year. Seasonal movements that we observed appear to respond to these dynamic changes in habitat, particularly with respect to temperature and primary production. Patterns of vertical habitat use have demonstrated that blue marlin spend most of their time in the upper mixed layer of the water column at the warmest temperatures available and rarely occupy water temperatures <19°C (Kraus and Rooker 2007; Goodyear et al. 2008). Sea surface temperatures in shelf edge habitats in the northwestern Gulf of Mexico typically decline in winter to 18–19°C (Rezak et al. 1985); therefore, thermal habitat preferences may play an important role in the timing of southerly movements during fall and winter. Circulation patterns and nutrient fluxes in the Gulf of Mexico are quite complex, and the most important processes contributing to primary production are freshwater flows from the Mississippi River and upwelling along the outer edge of the Loop Current. The latter process has been
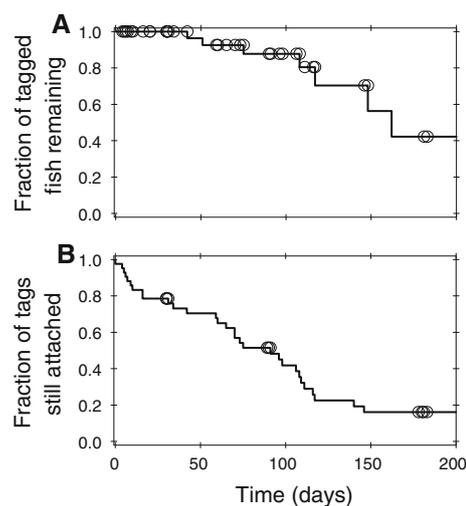
estimated to contribute three times more nitrogen to the euphotic zone than the Mississippi River (Walsh et al. 1989), and the smaller number of tagged blue marlin in the eastern Gulf of Mexico provided some evidence of utilizing habitats along the western edge of the Loop Current as well as areas seaward of the shelf at the Mississippi River delta (Fig. 5). On a seasonal basis, chlorophyll pigment concentration (determined from satellite remote sensing) throughout the Gulf of Mexico appears to change synchronously and monotonically, rising from 0.06 mg m^{-3} during May to July and peaking at >0.18 mg m^{-3} from December to February in habitats seaward of the shelf edge (Muller-Karger et al. 1991). Based upon observed thermal habitat use by blue marlin, declining sea surface temperatures in winter probably inhibit use of otherwise highly productive habitats along the northern shelf edge of the Gulf of Mexico. Fall movements to more southern regions such as the Bay of Campeche and the shelf edge of the Yucatan Peninsula provide a more suitable thermal regime during a time of seasonally increasing primary production. The high concentrations of geo-locations near the U.S.–Mexico border during spring and fall and surrounding the Texas–Louisiana shelf edge during summer are more difficult to understand but may be related to other persistent oceanographic processes. For example, net direction of prevailing currents on the Texas–Louisiana shelf is west, while seaward of this shelf edge, the net current direction is east. This situation combined with periodic movements of Loop Current eddies across the shelf edge generates

upwelling conditions that contribute significantly to primary production in this region, especially during summer (Lohrenz et al. 1999). Eddies that form from the Loop Current travel relatively slowly into the western Gulf of Mexico, typically reaching the shelf edge near the U.S.–Mexico border where they gradually disintegrate through loss of momentum (Sturges and Leben 2000). Although more research is still needed, eddies in this area may interact with the shelf edge (Ohlmann et al. 2001) or other eddies (Toner et al. 2003) to enhance primary production in habitats that appear to be important for blue marlin.

While correlations between spatial distribution patterns and seasonal changes in temperature and primary production seem to provide a useful explanation for understanding movements within the Gulf of Mexico, our observation period represents a small fraction of time in the life of a species that may live for 20 years (Wilson et al. 1991), and an outstanding question is whether or how often individuals return to the Gulf of Mexico. Evidence indicates limited population connectivity between the Gulf of Mexico and other regions of the North Atlantic Ocean. Otolith stable isotope markers suggested limited movement of blue marlin within the Gulf of Mexico relative to other regions (Wells et al. 2010). Recapture rates of conventional tags suggest an asymmetrical exchange of individuals: 0.18% (13 out of 7,084 releases) of blue marlin tagged in the Gulf of Mexico were recaptured in other areas of the North Atlantic Ocean (west of 60°W longitude), whereas only 0.047% (19 out of 39,825 releases) of recaptures indicated movement in the opposite direction (Orbesen et al. 2008). Likewise, other PAT tagging studies have not yet documented movement into the Gulf of Mexico from areas in the adjacent North Atlantic Ocean (Graves et al. 2002; Kerstetter et al. 2003; Prince et al. 2005; Prince and Goodyear 2006; Goodyear et al. 2008), but inferences from these studies are limited by low sample sizes and short tag deployments. Similarly, our results demonstrate a relatively low rate of movement into the Straits of Florida and out of the Gulf of Mexico of at least 16.6% of tagged fish per 11 months, but premature tag releases indicate that this could be an underestimate. One intriguing possible explanation for this limited connectivity is that fish overwinter in the southern Gulf of Mexico to gain a reproductive advantage through early arrival to the spawning area in the northern Gulf of Mexico. Studies of partial migration in birds have established that residency or limited migration can provide this type of priority effect and represents an important life history tactic of territorial species that may offset growth and/or survival disadvantages of not migrating (Kaitala et al. 1993; Berthold 2001). Comparative information on the growth and survival of blue marlin with respect to movement distance is lacking and would be difficult to obtain; therefore, the early arrival advantage

hypothesis is not easily tested. Still, future efforts to understand the relationship between movement patterns and physiological condition (e.g., lipid content of biopsy samples obtained at tagging) might provide insight into this problem.

More detailed investigations into habitat associations and longer studies of blue marlin movements with PAT tags have important limitations, some of which may be overcome with modifications to study design and application of additional technologies. Interpretation of fine spatial scale patterns of movement from our results was limited by the precision of daily location estimates. Through comparison of pop-up location with last geo-location for Atlantic bluefin tuna, errors in daily geo-locations from PAT tags have been estimated to be 0.6°–0.9° in longitude and 1.2°–1.5° in latitude (Teo et al. 2004). Double-tagging experiments on pelagic sharks yielded similar error values (Teo et al. 2004). Although our estimated errors were smaller, we still could not determine associations with smaller spatial scale features such as oil and gas platforms, seamounts, frontal current boundaries, and eddies. Fast GPS transmitter technologies are now being engineered into electronic tags for pelagic fishes (e.g., www.wildlifecomputers.com). Although these technologies could provide a wealth of high-resolution geo-location data for analyzing habitat associations, more work is needed to develop successful tag attachment methods that ensure the safety of the fish as well as the tagger. In addition, premature tag release is a common issue for billfishes and other pelagic fishes (Gunn and Block 2001). Our results indicated that tag anchor type was not a significant factor leading to premature tag release. More importantly, the mean time to premature release was about half of the mean time that blue marlin spent in the Gulf of Mexico. Better tag attachment methods would improve this situation, but we note that longer-term inferences on movements would also be possible through complementary tag deployments in other regions and seasons (for example in winter in the southern Gulf of Mexico).

In summary, our results support a new perspective of blue marlin in which the Gulf of Mexico provides dynamic suitable habitat that is utilized year-round through seasonal movements of a subset of the Atlantic population. Future insights are needed from ichthyoplankton surveys, age and growth work, electronic tagging and population genetics to clarify the dynamics and population structure of Atlantic blue marlin. From this emerging perspective, it becomes important to recognize that the divergent use of semi-isolated habitats throughout ontogeny may be essential to a robust population or meta-population (Kraus and Secor 2004; Secor and Kerr 2009). Of foremost concern is spatial variation in fishing effort and/or selective fishing practices that could disproportionately alter the abundance and

reproductive contributions of those fish that spend time in the Gulf of Mexico. This type of spatially varying mortality risk applies to many highly migratory pelagic species for which conservation status may be in question (Die 2006; Rooker et al. 2008). Thus, our ability to meet future challenges of fisheries management and conservation for billfishes and other wide ranging oceanic species will depend upon our knowledge of the evolutionary significance of intra-population variability in movement patterns.

Appendix

See Table 2.

Table 2 State-space model parameters for tracks of Atlantic blue marlin from the Gulf of Mexico

Tag	u	v	D	b_x	b_y	b_t	s_x	s_y	s_t	a_0	b_0	$-\log L$
1	−6.52	−2.95	252.78	0.07	−0.65	0.11	0.23	0.88	0.31	0.07	−38.88	89.50
2	0.66	−9.06	617.61	−0.70	0.82	0.08	0.06	0.91	0.19	0.26	58.48	145.45
3	−5.43	−1.80	40.15		−0.24		0.34	0.21		<0.01	−39.63	49.62
4	0.01	−0.61	674.55	0.49	2.37	0.04	0.23	0.64	0.41	0.10	58.13	137.40
5	6.04	−0.70	169.96	−0.62	−0.57	−0.25	0.09	0.54	0.34	<0.01	24.20	79.96
6	−0.41	−1.79	581.34	−0.17	−0.97	0.06	0.00	1.04	0.43	<0.01	11.49	231.32
7	−5.12	−0.62	119.84	−0.37	−0.51	−0.09	0.18	0.58	0.43	<0.01	41.88	56.09
8	−3.93	4.13	268.76	−0.40	1.23	−0.18	0.31	0.77	0.32	<0.01	−80.00	85.83
9	−3.42	−3.46	778.85	0.82	2.83	0.15	0.00	1.10	0.29	<0.01	21.01	245.02
10	−9.70	−2.08	589.81	0.87	−1.73	0.14	0.48	1.69	0.27	<0.01	−21.12	240.62
11	10.97	−1.15	289.78	−1.36	−3.41	0.30	0.40	0.27	0.49	<0.01	19.90	112.05
12			14.18		−4.13		0.26	0.09		<0.01	−35.77	15.86
13	23.65	−11.56	358.76	0.83	−2.20		0.19	1.07				35.57
14	−12.21	−5.55	623.38	−0.56	3.08	0.36	0.32	1.88	0.32	1.02	51.76	195.55
15	−0.89	−1.08	423.41	−0.13	−0.75		0.32	1.86	0.10	0.06	27.31	205.33
16	4.21	−0.98	615.41		−0.72		0.13	0.77		<0.01	−80.00	37.79
17	−0.55	−3.59	543.69	−0.89	1.82	0.55	0.00	1.39	0.34	0.07	37.24	164.60
18	−2.14	−2.08	232.48	−0.28	−0.50	−0.07	0.39	1.04	0.55	0.04	17.83	226.04
19	4.93	−0.09	62.24		−0.67		0.27	0.36		0.08	−80.00	17.24
20			69.56		−0.23		0.00	0.03		0.01	80.00	0.30
21	−1.47	−7.88	384.36	−0.60	1.71	0.09	0.58	3.69	0.19	3.29	−80.00	57.05
22			131.93		−1.28		0.34	0.73		<0.01	80.00	17.28
23	−2.87	0.87	283.37	−0.27	0.47	−0.08	0.00	1.80	0.21	0.03	15.99	197.57
24	−0.64	−0.12	200.60	−0.06	2.34	−0.25	0.19	1.04	0.46	0.03	38.23	68.92
25	−0.82	−0.82	306.16	−0.93	2.40	0.13	0.18	3.32	0.25	2.13	80.00	177.30
26	0.19	−7.65	703.90	−0.07	−1.28	0.12	0.00	1.43	0.35	0.48	−9.92	83.31
27	−4.62	−3.18	343.06	−0.02	−0.63	−0.30	0.14	1.60	0.49	0.01	−17.92	288.41
28			261.64		−0.34		<0.01	0.25		<0.01	80.00	11.91
29			47.25		0.09		<0.01	0.23		<0.01	80.00	2.18
30	−3.88	−5.39	836.55	−0.60	0.07	0.06	0.21	0.25	0.32	0.01	27.18	177.97
31			230.25		0.33		0.39	<0.01		<0.01	−74.52	11.26
32	−4.01	−1.47	295.49	0.29	−0.05	−0.04	<0.01	0.17	0.24	0.03	19.56	58.30
33	−1.87	−0.76	411.58	−0.18	1.51	0.18	0.25	2.74	0.35	0.03	−1.25	350.69
34	−1.84	−2.09	326.82	0.06	−2.45	−0.08	0.21	2.07	0.46	0.21	−17.67	335.26

Table 2 continued

Tag	u	v	D	b_x	b_y	b_t	s_x	s_y	s_t	a_0	b_0	$-\log L$
35	3.60	−1.76	269.27	−0.29	−1.05	0.12	<0.01	1.71	0.29	0.23	−37.34	238.40
36	−0.75	0.67	534.73	−0.27	−1.08	0.09	0.09	1.11	0.49	0.70	44.38	236.35
37	−0.99	−2.54	385.31	0.47	−0.37	0.01	0.00	0.51	0.59	0.18	7.26	275.28
38	−0.81	−1.57	275.44	−0.63	−0.65	0.07	0.13	0.96	0.31	0.01	16.22	227.53
39	1.30	−5.69	313.60	−1.18	−2.40	0.02	<0.01	0.53	0.11	<0.01	−80.00	22.76
40	0.04	0.06	190.49	−1.28	−0.30	0.27	0.84	2.84	0.34	0.29	7.61	1134.62
41	3.55	−0.96	411.97	−0.11	0.80	−0.17	0.20	3.85	0.37	50.00	80.00	104.83
42	1.16	−0.08	313.07	−0.42	0.06	0.30	0.09	0.97	0.26	0.01	−16.66	267.24

Fish movement (process error) was modeled as a diffusion process with parameters for the mean rate of displacement in the x and y directions (u and v in nautical miles (nm) per day, respectively) and a diffusion parameter (D, in nm^2 day^{-1}) for the rate at which uncertainty in position increases with time. The model parameters dealing with measurement error include raw error in longitude, latitude, and sea surface temperature (b_x, b_y, b_t in degrees, respectively) and standard deviations of those errors (s_x, s_y, and s_t in degrees, respectively). Latitude estimation error was modeled as either uniform variance function or a solstice function defined by the number of days before/after the equinox when variance is maximal (b_0 in days) and an upper bound to the variance (a_0 in degrees). For a detailed explanation of the state-space model and maximum likelihood estimation, refer to Sibert et al. (2003), Nielsen et al. (2006), and Lam et al. (2008)

References

Adam MS, Sibert J, Itano D, Holland K (2003) Dynamics of bigeye (*Thunnus obesus*) and yellowfin (*T. albacares*) tuna in Hawaii's pelagic fisheries: analysis of tagging data with a bulk transfer model incorporating size-specific attrition. Fish Bull 101:215–228

Berthold P (2001) Bird migration: a general survey. Oxford University Press, Oxford

Block BA, Booth D, Carey FG (1992) Direct measurement of swimming speeds and depth of blue marlin. J Exp Biol 166:267–284

Block BA, Teo SLH, Walli A, Boustany A, Stokesbury MJW, Farwell CJ, Weng KC, Dewar H, Williams TD (2005) Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:1121–1127

Brill RW, Lutcavage ME (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

Brinson AA, Alcala A, Die DJ, Shivlani M (2006) Contrasting socioeconomic indicators for two fisheries that target Atlantic billfish: Southeast Florida recreational charter boats and Venezuelan artisanal gill-netters. Bull Mar Sci 79:635–645

Buonaccorsi VP, McDowell JR, Graves JE (2001) Reconciling patterns of inter-ocean molecular variance from four classes of molecular markers in blue marlin (*Makaira nigricans*). Mol Ecol 10:1179–1196

Castro-Santos T, Haro A (2003) Quantifying migratory delay: a new application of survival analysis methods. Can J Fish Aquat Sci 60:986–996

Chaprales W, Lutcavage M, Brill R, Chase B, Skomal G (1998) Harpoon method for attaching ultrasonic and "popup" satellite tags to giant bluefin tuna and large pelagic fishes. Marine Technol Soc J 32:104–105

Chesney EJ, Baltz DM, Thomas RG (2000) Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. Ecol Appl 10:350–366

Cox DR, Oakes D (1984) Analysis of survival data. Chapman and Hall, New York

Dagg MJ, Breed GA (2003) Biological effects of Mississippi River nitrogen on the northern gulf of Mexico—a review and synthesis. J Mar Syst 43:133–152

Dagg M, Benner R, Lohrenz S, Lawrence D (2004) Transformation of dissolved and particulate materials on continental shelves influenced by large rivers: plume processes. Cont Shelf Res 24:833–858

de Sylva DP, Breder PR (1997) Reproduction, gonad histology, and spawning cycles of North Atlantic billfishes (Istiophoridae). Bull Mar Sci 60:668–697

Devine B, Simms J, Holt S, Rooker J (2008) Age and growth of larval blue marlin (*Makaira nigricans*) from the northern Gulf of Mexico. Proc Gulf Caribb Fish Inst 60:638

Diaz GA, Ortiz M (2006) Updated white marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) catch rates from the U.S. recreational tournament fishery in the northwest Atlantic and the U.S. Gulf of Mexico 1973–2004. ICCAT Coll Vol Sci Paps 59:182–195

Die DJ (2006) Are Atlantic marlins overfished or endangered? Some reasons why we may not be able to tell. Bull Mar Sci 79:529–543

Domeier ML, Kiefer D, Nasby-Lucas N, Wagschal A, O'Brien F (2005) Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. Fish Bull 103:292–306

Erdman DS (1968) Spawning cycle sex ratio and weights of blue marlin off Puerto Rico and Virgin islands. Trans Am Fish Soc 97:131–137

Fromentin JM, Powers JE (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish Fish 6:281–306

Goodyear CP (1999) An analysis of the possible utility of time-area closures to minimize billfish bycatch by US pelagic longlines. Fish Bull 97:243–255

Goodyear CP, Luo JG, Prince ED, Hoolihan JP, Snodgrass D, Orbesen ES, Serafy JE (2008) Vertical habitat use of Atlantic blue marlin, *Makaira nigricans*: interaction with pelagic longline gear. Mar Ecol Prog Ser 365:233–245

Graves JE (1998) Molecular insights into the population structures of cosmopolitan marine fishes. J Hered 89:427–437

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

Gunn JS, Block BA (2001) Advances in acoustic, archival, and satellite tagging of tunas. In: Block BA, Stevens ED (eds) Tuna: physiology, ecology and evolution. Academic Press, San Francisco

Hill RD, Braun MJ (2001) Geolocation by light levels—the next step latitude. In: Sibert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Boston, pp 315–330

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

Hosmer DW, Lemeshow S (1999) Applied survival analysis: regression modeling of time to even data. John Wiley & Sons, Inc., New York

Hunter JR, Lo NCH (1993) Ichthyoplankton methods for estimating fish biomass introduction and terminology. Bull Mar Sci 53:723–727

Jonsson B, Jonsson N (1993) Partial migration—niche shift versus sexual-maturation in fishes. Rev Fish Biol Fish 3:348–365

Kafatos M, Sun D, Gautam R, Boybeyi Z, Yang R, Cervone G (2006) Role of anomalous warm gulf waters in the intensification of Hurricane Katrina. Geophys Res Lett 33:L17802

Kaitala A, Kaitala V, Lundberg P (1993) A theory of partial migration. Am Nat 142:59–81

Kalman RE (1960) A new approach to linear filtering and prediction problems. Transactions of the American Society of Mechanical Engineers. J Basic Eng 82(Series D):35–45

Kerstetter DW, Luckhurst BE, Prince ED, Graves JE (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

Kraus RT, Rooker JR (2007) Patterns of vertical habitat use by Atlantic blue marlin (*Makaira nigricans*) in the Gulf of Mexico. Gulf Caribb Res 19:89–97

Kraus RT, Secor DH (2004) Dynamics of white perch Morone americana population contingents in the Patuxent River estuary, Maryland, USA. Mar Ecol Prog Ser 279:247–259

Lam CH, Nielsen A, Sibert JR (2008) Improving light and temperature based geolocation by unscented Kalman filtering. Fish Res 91:15–25

Lohrenz SE, Wiesenburg DA, Arnone RA, Chen X (1999) What controls primary production in the Gulf of Mexico? In: Kumpf H, Steidinger K, Sherman K (eds) The Gulf of Mexico large marine ecosystem: assessment, sustainability, and management. Blackwell Science, Inc., Massachusetts, pp 151–170

Luckhurst BE (2003) Historical development of recreational billfishing in Bermuda and the significance of catches of large blue marlin (*Makaira nigricans*). Mar Freshw Res 54:459–462

Lutcavage ME, Brill RW, Skomal GB, Chase BC, Howey PW (1999) Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? Can J Fish Aquat Sci 56:173–177

Luthy SA, Cowen RK, Serafy JE, McDowell JR (2005) Toward identification of larval sailfish (*Istiophorus platypterus*), white marlin (*Tetrapturus albidus*), and blue marlin (*Makaira nigricans*) in the western North Atlantic Ocean. Fish Bull 103:588–600

Majkowski J (2007) Global fishery resources of tuna and tuna-like species. FAO, Rome

Mather FJ, Beardsle Gl, Jones AC (1972) Migration and distribution of white marlin and blue marlin in Atlantic Ocean. Fish Bull 70:283–298

Muller-Karger FE, Walsh JJ, Evans RH, Meyers MB (1991) On the seasonal phytoplankton concentration and sea-surface temperature cycles of the Gulf of Mexico as determined by satellites. J Geophys Res Oceans 96:12645–12665

Musyl MK, Brill RW, Curran DS, Gunn JS, Hartog JR, Hill RD, Welch DW, Eveson JP, Boggs CH, Brainard RE (2001) Ability of electronic archival tags to provide estimates of geographical position based on light intensity. In: Sibert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Boston, pp 315–330

Nielsen A, Bigelow KA, Musyl MK, Sibert JR (2006) Improving light-based geolocation by including sea surface temperature. Fish Oceanogr 15:314–325

Nishikawa Y, Kikawa S, Honma M, Ueyanagi S (1978) Distribution atlas of larval tunas, billfishes, and related species—results of larval surveys by R/V *Shunyo Maru* and *Shoyo Maru* 1956-1975. Far Seas Fisheries Research Laboratory S Series 9:1–99 (in Japanese, English summary)

Ohlmann JC, Niiler PP, Fox CA, Leben RR (2001) Eddy energy and shelf interactions in the Gulf of Mexico. J Geophys Res Oceans 106:2605–2620

Orbesen ES, Hoolihan JP, Serafy JE, Snodgrass D, Peel EM, Prince ED (2008) Transboundary Movement of Atlantic istiophorid billfishes among international and U.S. domestic management areas inferred from markrecapture studies. Mar Fish Rev 70:14–23

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. Mar Freshw Res 54:489–507

Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. Fish Oceanogr 15:451–464

Prince ED, Lee DW, Zweifel JR, Brothers EB (1991) Estimating age and growth of young atlantic blue marlin, *Makaira nigricans*, from otolith microstructure. Fish Bull 89:441–459

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

Rezak R, Bright TJ, McGrail DW (1985) Reefs and banks of the northwestern Gulf of Mexico—their geological, biological, and physical dynamics. Wiley, New York

Richardson DE, Vanwye JD, Exum AM, Cowen RK, Crawford DL (2007) High-throughput species identification: from DNA isolation to bioinformatics. Mol Ecol Notes 7:199–207

Richardson DE, Cowen RK, Prince ED, Sponaugle S (2009) Importance of the Straits of Florida spawning ground to Atlantic sailfish (*Istiophorus platypterus*) and blue marlin (*Makaira nigricans*). Fish Oceanogr 18:402–418

Rooker JR, Bremer JRA, Block BA, Dewar H, de Metrio G, Corriero A, Kraus RT, Prince ED, Rodríguez-Marín E, Secor DH (2007) Life history and stock structure of Atlantic Bluefin Tuna (*Thunnus thynnus*). Rev Fish Sci 15:265–310

Rooker JR, Secor DH, De Metrio G, Schloesser R, Block BA, Neilson JD (2008) Natal homing and connectivity in Atlantic Bluefin Tuna populations. Science 322:742–744

Schroepfer RL, Szedlmayer ST (2006) Estimates of residence and site fidelity for red snapper Lutjanus campechanhus on artificial reefs in the northeastern Gulf of Mexico. Bull Mar Sci 78:93–101

Secor DH (1999) Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish Res 43:13–34

Secor DH, Kerr LA (2009) Lexicon of life cycle diversity in diadromous and other fishes. Am Fish Soc Symp 69:537–556

Serafy JE, Cowen RK, Paris CB, Capo TR, Luthy SA (2003) Evidence of blue marlin, *Makaira nigricans*, spawning in the

vicinity of Exuma Sound, Bahamas. Mar Freshw Res 54:299–306

Sibert J, Hampton J (2003) Mobility of tropical tunas and the implications for fisheries management. Marine Policy 27:87–95

Sibert JR, Musyl MK, Brill RW (2003) Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. Fish Oceanogr 12:141–151

Sibert JR, Lutcavage ME, Nielsen A, Brill RW, Wilson SG (2006) Interannual variation in large-scale movement of Atlantic bluefin tuna (*Thunnus thynnus*) determined from pop-up satellite archival tags. Can J Fish Aquat Sci 63:2154–2166

Simms JR (2009) Early life ecology of sailfish, *Istiophorus platypterus*, in the northern Gulf of Mexico. M.Sc. Thesis. Texas A&M University, College Station

Squire JL (1987) Striped marlin, *Tetrapturus audax*, migration patterns and rates in the Northeast Pacific Ocean as determined by a cooperative tagging program: its relation to resource management. Mar Fish Rev 49:26–43

Sturges W (1993) The annual cycle of the western boundary current in the Gulf-of-Mexico. J Geophys Res Oceans 98:18053–18068

Sturges W, Blaha JP (1976) A western boundary current in the Gulf of Mexico. Science 92:367–369

Sturges W, Leben R (2000) Frequency of ring separations from the loop current in the Gulf of Mexico: a revised estimate. J Phys Oceanogr 30:1814–1819

Teo SLH, Boustany A, Blackwell S, Walli A, Weng KC, Block BA (2004) Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Mar Ecol Prog Ser 283:81–98

Theriault V, Dunlop ES, Dieckmann U, Bernatchez L, Dodson JJ (2008) The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evol Appl 1:409–423

Toner M, Kirwan AD, Poje AC, Kantha LH, Muller-Karger FE, Jones C (2003) Chlorophyll dispersal by eddy-eddy interactions in the Gulf of Mexico. J Geophys Res Oceans 108:3105

Walsh JJ, Dieterle DA, Meyers MB, Mullerkarger FE (1989) Nitrogen exchange at the continental margin—a numerical study of the Gulf of Mexico. Prog Oceanogr 23:245–301

Welch DW, Eveson JP (1999) An assessment of light-based geoposition estimates from archival tags. Can J Fish Aquat Sci 56:1317–1327

Wells RJD, Rooker JR, Prince ED (2010) Regional variation in the otolith chemistry of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) from the western North Atlantic Ocean. Fish Res 106:430–435

Wilson CA, Dean JM, Prince ED, Lee DW (1991) An examination of sexual dimorphism in Atlantic and Pacific blue marlin using body-weight, sagittae weight, and age estimates. J Exp Mar Biol Ecol 151:209–225

Wilson J, Rilling C, Defosse J, Brewster-Geisz K (2007) Temporal and spatial analyses of pelagic longline time/area closures in the Gulf of Mexico to reduce discards of bluefin tuna. ICCAT Coll Vol Sci Paps 60:1179–1236

Witzell WN, Scott EL (1990) Blue marlin, *Makaira nigricans*, movements in the western North Atlantic ocean: results of a cooperative game fish tagging program, 1954–88. Mar Fish Rev 52:12–17

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168