Gulf and Caribbean Research Vol 19(2), 89–97, 2007 Manuscript received November 17, 2006; accepted January 1, 2007

PATTERNS OF VERTICAL HABITAT USE BY ATLANTIC BLUE MARLIN (*MAKAIRA NIGRICANS*) IN THE GULF OF MEXICO

Richard T. Kraus[1] and Jay R. Rooker[2]
[1]*George Mason University, 4400 University Drive, MSN 5F2, Fairfax, VA 22030 USA, E-mail rkraus1@gmu.edu*
[2]*Texas A&M University, 5007 Avenue U, Galveston, Texas 77551 USA*

ABSTRACT We examined data from pop-up archival transmitting (PAT) tags ($n = 18$) to characterize aspects of vertical habitat use by blue marlin (*Makaira nigricans*) from the Gulf of Mexico (GOM). Two of these tags were recovered and provided fine-scale information about diving patterns and the relationship between time at depth and temperature. Similar to previous studies, blue marlin in the GOM spent most of their time at the surface and at temperatures within 3º C of surface temperatures. Time at depth was multimodal and the magnitude of the smaller modes was dependent upon the strength and depth of the thermocline. Importantly, time at depth was a complex function of the temperature change relative to the surface, time of day, lunar phase, and water column structure. Temperature change with depth between the western and eastern GOM and the adjacent western Atlantic Ocean was also examined. The depth range (maximum depths varied between 68 and 388 m) varied widely between fish and did not appear to correspond with any particular magnitude of temperature change relative to the surface. Although these data may help to improve stock assessments that are based upon habitat standardizations of CPUE, progress will be limited until the distribution of feeding activity with depth and other aspects of blue marlin behavior in relation to capture probability are elucidated.

RESUMEN Examinamos los datos de marcas archivo por satellite (PAT) ($n = 18$) para caracterizar los aspectos del uso vertical del hábitat por el aguja azul (*Makaira nigricans*) del Golfo de México (GOM). Dos de estas marcas fueron recuperadas y proporcionadron información a la escala fina acerca de los patrónes de zambullir y la relación entre tiempo en la profundidad y la temperatura. Semejante a estudios previos, el aguja azul en el GOM gastó la mayor parte de su tiempo en la superficie y en zonas dentro de 3°C de temperaturas en la superficie. El tiempo en la profundidad fue multimodal y la magnitud de los modos más pequeños fueron dependientes sobre la fuerza y la profundidad del termoclino. Importantemente, el tiempo en la profundidad fue una función compleja referente al cambio de la temperatura a la superficie, el tiempo de día, de la fase lunar, y de la estructura de la columna de agua. El cambio de la temperatura con la profundidad entre el GOM occidental y oriental y el Océano Atlántico occidental adyacente fue examinado también. La gama de la profundidad (las profundidades máximas variaron entre 68 y 388m) varió extensamente entre pez y no apareció corresponder con ninguna magnitud particular del pariente del cambio de la temperatura a la superficie. Aunque estos datos puedan ayudar a mejorar las evaluaciones de acciones que son basadas sobre estandardizaciones de hábitat de CPUE, el progreso será limitado hasta que la distribución de actividades alimentarios con la profundidad y otros aspectos de la conducta de la aguja azul en la relación a la probabilidad de captura es aclarada.

INTRODUCTION

Atlantic blue marlin (*Makaira nigricans*) have been exploited extensively for recreation and by commercial longline fisheries, and current assessments indicate that the stock is overfished and biomass is well below the level that would support a maximum sustained yield (ICCAT 2006). More importantly, assessments indicate that fishing mortality may be fluctuating around the level that would allow year-to-year replacement of biomass lost to fishing (ICCAT 2006). Since fishery-independent data upon which to base assessments of blue marlin are limited, catch per unit effort (CPUE) indices from commercial longline fisheries are a key input for population models. Thus, important efforts have been directed at understanding the relationship between habitat use and the probability of capture on longline gear (Suzuki et al. 1977, Suzuki 1989, Hinton and Nakano 1996, Goodyear 1999, Luo et al. 2006).

One widely applied concept is that CPUE indices can be standardized using environmental data and information about behavior of species such as blue marlin. Goodyear et al. (2003) pointed out that this habitat standardization approach to refining CPUE indices is fraught with problems, most of which reflect an inadequate knowledge of the biology and ecology of fishes caught on longlines. One of the many research needs identified by Goodyear et al. (2003) was a better understanding of vertical habitat use based upon temperature and depth (two of the most commonly measured habitat variables). Brill and Lutcavage (2001) postulated that differences in temperatures experienced by billfish from different locations would not reflect varying temperature preferences but rather selection of the warmest temperatures available, which usually occur at the surface. Saito et al. (2004) presented support for this hypothesis with electronic tag data from the tropical Atlantic. In addition, Graves et al. (2002, 2003) reported that the distribution of time at temperature and depth was multi-modal for blue marlin with high proportions of time spent in the warmer surface mixed layer. Smaller but pronounced peaks of time spent at depth were observed and were assumed to represent important feeding zones. The multi-modal distribution of time at depth (and temperature) was also substantiated by earlier telemetry studies from the tropical Pacific (Holland et al. 1990, Block et al. 1992). Finally, other restrictions to vertical habitat use, such as dissolved oxygen concentration in the oxygen minimum layer, may limit the depth distribution of blue marlin, albeit dissolved oxygen is probably not a limitation in the western Atlantic Ocean (see Prince and Goodyear 2006).

Here, we contribute to efforts to characterize the vertical habitat use of Atlantic blue marlin, presenting data from 18 pop-up archival transmitting (PAT) tags deployed in the GOM between 2003 and 2005. Regional differences in time at depth and time at temperature were examined using all tags. Two of these tags were recovered, providing fine-scale information (1 min intervals) on temperature and depth histories of blue marlin from regions within and outside the Loop Current. Archival data from recovered tags were also used to examine effects of day and lunar period on vertical patterns of habitat use.

MATERIALS AND METHODS

Blue marlin (size range: 45–81 kg, mean = 93.4 kg) were caught on sport fishing gear, and PAT tags were deployed in a manner similar to Squire (1987) and Chaprales et al. (1998), using either a titanium chevron anchor provided by the tag manufacturer or the nylon anchor described in Domeier et al. (2005). Tags were PAT3 and PAT4 models (Wildlife Computers, Inc., Redmond, Washington). Tags were deployed opportunistically between May and August in 2003 ($n = 3$), 2004 ($n = 9$), and 2005 ($n = 9$) in the northern GOM (within the U.S. exclusive economic zone), and programmed deployment durations were 30 ($n = 5$), 90 ($n = 4$), and 180 d ($n = 12$). Seven of the tags detached prematurely and transmitted data (durations ranged from 12 to 109 d), and 3 additional tags never transmitted (programmed durations were 180 d). Out of 1482 deployment days (excluding tags that did not transmit), 713 d (representing 18 tags) of summarized data were transmitted via satellite, had contemporaneous temperature, depth and light level measurements, and were used for this analysis.

Short-term changes in vertical movements in the recovered tags were examined by plotting depth as a function of time. The temperature time-series from the recovered tags were smoothed and overlaid on the depth data to view water column structure, and diel patterns were assessed by determining day and night from the light level measurements. Lunar phase was determined from published almanacs based upon date. Longer-term (seasonal) patterns were explored with the satellite-transmitted data; however, patterns (if present) were too variable to discern, and thus not addressed here.

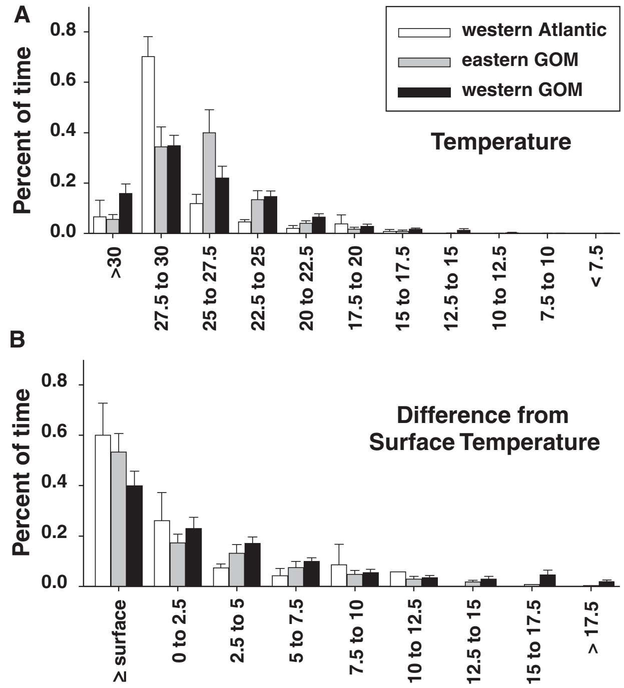

Figure 1. Percent of time as a function of temperature (A) and temperature relative to the surface temperature (B) for Atlantic blue marlin ($n = 18$). Plots were constructed with summarized data transmitted via satellite from pop-archival transmitting (PAT) tags, and standard error bars show variability between individual fish. Sub-regions are described in the text.

To understand how both depth and temperature delineate blue marlin habitat, recovered tag data were used to calculate the percent of time as a function of both depth and change in temperature relative to the surface temperature. Temperature change was calculated as the difference between the temperature at depth and the most recently adjacent surface (< 2 m) temperature in the series (this approach accommodated for changes in surface temperature throughout the day on each dive). For the satellite-transmitted data, time-at-temperature summaries were based upon 2.5 degree bins, and the percent of time was calculated as a function of both temperature and change in temperature at depth. In addition, we also plotted the change in temperature (relative to the surface, < 2 m) with depth based upon daily surface temperature means.

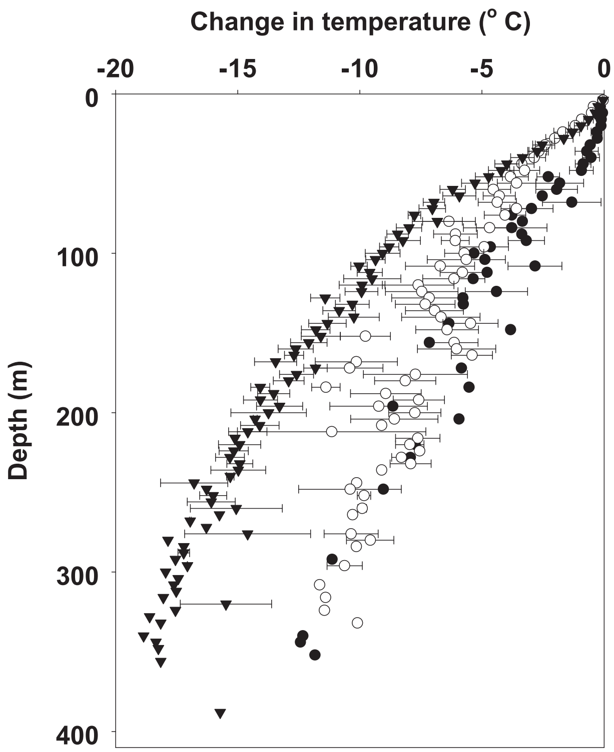

Figure 2. Change in temperature with depth for Atlantic blue marlin (*n* = 18) in the western GOM (filled triangles), eastern GOM (open circles) and adjacent western Atlantic (filled circles). Standard error bars show variability between individual fish. Some combinations of change in temperature and depth were only observed for one blue marlin, thus some points have no error bars (mostly at depths > 150 m). Sub-regions are described in the text.

Finally, to understand large-scale spatial patterns, we divided data based upon sub-regions with longitude values that were estimated using standard algorithms (see Hill 1994, Welch and Eveson 1999) and refined using the Kalman filter tools developed by Sibert et al. (2003) and Nielsen et al. (2006). Sub-regions were arbitrarily chosen to divide the GOM roughly in half at 90°W longitude. We also accounted for locations in the western Atlantic (only one fish showed movement into the Atlantic through the Straits of Florida) by defining a third category for longitudes < 81°W. Uncertainty in longitude estimates from light-sensor data is typically < 1° (Musyl et al. 2001); therefore, it is important to note that locations west of 90°W are definitively within the GOM, those between 90°W and 81°W are not differentiated between the GOM and the Caribbean Sea, and those east of 81°W are generically in the western Atlantic. The estimated latitudes and the inferred horizontal movement patterns are the subject of a separate manuscript (Kraus and Rooker, in preparation).

Results

Summarized data transmitted by satellite reflected the distinct water column structures found within the three sub-regions: western GOM and eastern GOM and the western Atlantic. The data were classified according to the 2.5° C time-at-temperature bins, and in terms of the absolute temperature, the mean varied by sub-region (Figure 1). In the western GOM and in the western Atlantic, the highest percent of time was spent at temperatures between 27.5° and 30° C (Figure 1a). By comparison, blue marlin in the eastern GOM spent more time at cooler temperat ures from 25° to 27.5° C (Figure 1a). These sub-regional differences were not evident when the temperatures were expressed relative to the surface temperature, indicating that blue marlin spent most of their time at the highest temperatures available (i.e., at the surface or within 2.5° C of the surface temperature, Figure 1b). The satellite-transmitted data also demonstrated sub-regional differences in the relationship between depth and change in temperature with depth (Figure 2). West of 90°W longitude, temperature declined rapidly with depth as compared to locations east of 81°W longitude. Intermediate values of change in temperature with depth were observed in the eastern GOM between 81° and 90°W longitudes. As this intermediate area also contains the Loop Current (intrusion of the North Atlantic western boundary current; see Sturges 1993), the water column structure is more variable. Thus, the values recorded by PAT tags showed larger standard errors than in the other sub-regions (Figure 2). It is not clear that either change in temperature or depth presented limitations to blue marlin habitat when comparing sub-regions. Maximum depths ranged between 68 and 388 m between individual fish, and associated temperature changes (relative to the surface) increased linearly with depth, ranging from 5.5° to 18.1° C and showing no apparent limitation with temperature. Finally, there were wide variations between individual fish in the functions of percent of time at depth (Figure 3). Overall, blue marlin spent at least 57% of time at depths < 50 m and at least 78% of time at depths < 100 m, but the high variability indicates that depth alone is a poor predictor of how much time blue marlin will spend in a given water column stratum.

More detailed short-term changes in diving behavior observed from recovered tags were remarkably different between individuals tagged in the western versus the eastern GOM (refer to Figures 4 and 5 for this paragraph). For the fish released in 2004 in the western GOM, there were prominent diel differences in diving behavior with repeated dives and extended periods spent between 30 and 60 m during the day (Figure 4). This range of depths coin-

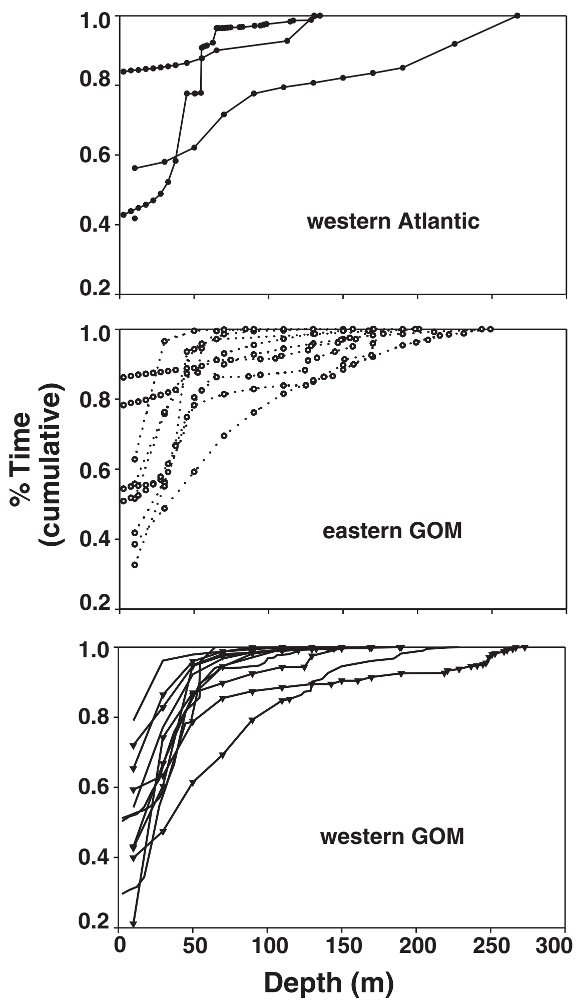

Figure 3. Cumulative percent of time as a function of depth for individual Atlantic blue marlin in different sub-regions (defined in the key) as observed from satellite-transmitted PAT tag data.

cided with a strong thermocline marked by a temperature decline from 28° to 22° C. During the first week at large, the thermocline was more diffuse than in the latter part of the track (the 22° C isotherm occurred between 70 and 80 m during the first 4 d), and the character of the diving pattern was different with slower dives to greater depths early in the track. The first 48 hr of the track should be considered with caution, as this period may represent behavior associated with recovery from tagging and not typical blue marlin diving behavior. Although most of the time in the latter part of the track was spent at or above the thermocline, there were infrequent, short dives below the thermocline. In addition, the diel patterns of diving showed correspondence with lunar phase, in which there was increased diving activity on the night of the full moon and the preceding night. Night-time diving activity was less frequent on the nights prior to and following this period. By comparison, the fish released in the eastern GOM in 2005 experienced a broad vertical temperature gradient (i.e., the temperature changed from 28° to 22° C between the surface and 300m) and exhibited different diving behavior (Figure 5). The range of depths utilized by this fish was twice that of the fish in the western GOM, and diel changes in diving behavior (if present) were evident only for specific instances (e.g., between the day and night on June 5th). Otherwise, there was little evidence of a diel or lunar pattern, and dives tended to by slower and to greater depths than for the fish in the eastern GOM.

In terms of the percent of time spent as a function of depth and the change in temperature, both of the recovered tags demonstrated that the greatest amount of time was spent at the warmest temperatures available. The top 2 m of the water column and temperatures within 0.5 degrees of the surface represented 62.3% and 88.5% of the total track time for the tags in the eastern and western GOM, respectively. The pattern with depth was also multimodal, especially for the individual tracked in the western GOM. The percent of time spent at depths between 30 and 60 m, and temperatures within 3 degrees of the surface temperature represented 15.9% of the total track time for the tag in the western GOM, whereas this range of values accounted for only 1.8% of the total track time in the eastern GOM. For both of the recovered tags, the remaining proportions of time were spread out over depths up to 150 and 310 m in the eastern and western GOM, respectively in 2004 and 2005 (Figure 6). Temperature differences (relative to the surface) were similar between these fish and no significant amount of time was spent at temperatures > 12 degrees less than the surface temperature (Figure 6).

DISCUSSION

The PAT tags deployed in this study have provided some important insights to the variability in vertical habitat use by blue marlin from a previously overlooked region of the North Atlantic, the GOM. Using temperature and depth as variables that partially describe the habitat of blue marlin, our results further substantiate that the percentage of time spent at depth is closely linked to the temperature change relative to the surface (Brill and Lutcavage 2001, Saito et al. 2004), with the vast majority of time spent at temperatures within 3° C of the surface temperature. There is no reason to expect that size of blue marlin would influence this pattern (the so-called thermal-inertia hypothesis). Because the heart receives blood directly from the gills (where blood rapidly cools to ambient temperature), its temperature (and hence swimming performance) will be nearly identical to the water and will vary independently of

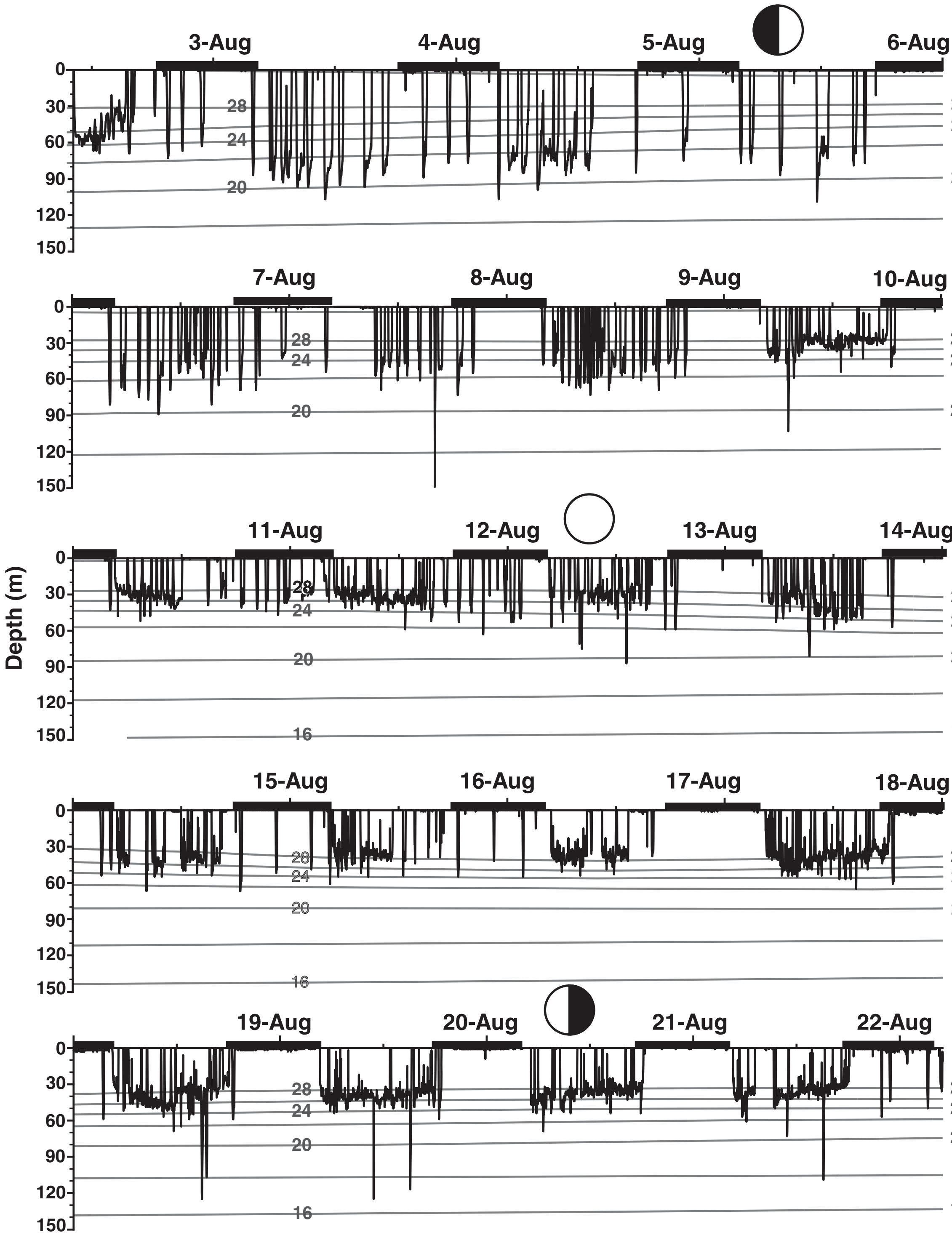

Figure 4. Time series of depth recorded by an electronic tag attached to a blue marlin in the northern Gulf of Mexico during 2004. The deployment, pop-off, and intermediate locations were in the western Gulf of Mexico (west of 90°W longitude). Measurements of depth, temperature and light level were recorded every minute, and the temperature contours were interpolated from the tag data. The black bars on the time axis indicate night, and lunar phase is indicated graphically next to the date. Note that the temperature gradient (in gray) is smoothed and actual temperatures for some of the measurements at the greatest depths are colder than indicated.

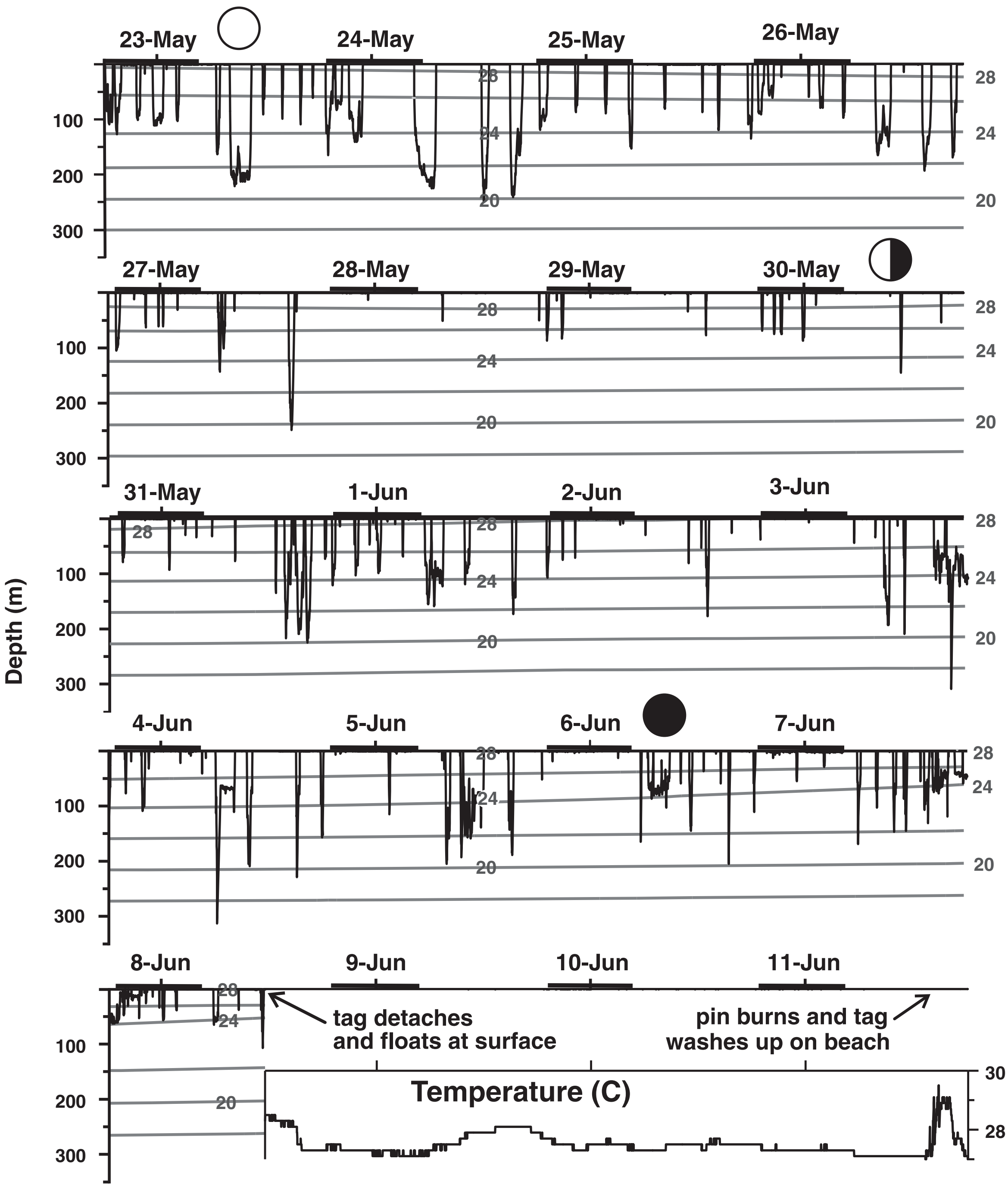

Figure 5. Time series of depth recorded by an electronic tag attached to a blue marlin in the northern Gulf of Mexico during 2005. The deployment, pop-off, and intermediate locations were in the eastern Gulf of Mexico (between 81° and 90°W longitude). Measurements of depth, temperature and light level were recorded every minute, and the temperature contours were interpolated from the tag data. The black bars on the time axis indicate night, and lunar phase is indicated graphically next to the date. Note that the temperature gradient (in gray) is smoothed and actual temperatures for some of the measurements at the greatest depths are colder than indicated.

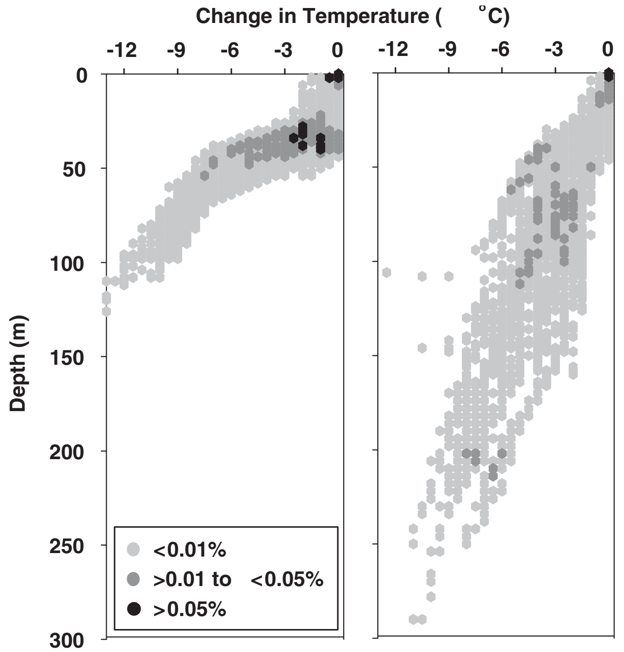

Figure 6. Percent of time as a function of depth and change in temperature relative to the surface (at < 2 m) for 2 blue marlin: one tagged in 2004 in the northwestern Gulf of Mexico (left panel) and one in 2005 in the northeastern Gulf of Mexico (right panel). Areas without any shading represent combinations of depth and temperature change that were not observed, and intervals are inclusive of the upper bound defined in the key.

body size (Brill et al. 1998). In addition, the diving behavior of blue marlin is dependent upon water column structure, and in areas with a well defined shallow thermocline (such as in the western GOM), time-at-depth and time-at-temperature distributions may show additional modes related to time spent in the thermocline. Such bivariate-bimodal patterns are well known from the Pacific (Holland et al. 1990, Block et al. 1992) and the Atlantic (Graves et al. 2002, 2003, Kerstetter et al. 2003), and may vary sharply between day and night with more time at depth during the day. Caution is advised for interpreting diel changes in depth patterns, as distributions of time with depth that pool across days will not be reflective of any particular day. A consistent pattern that varied by lunar phase was equivocal with correspondence to lunar phase in the track from the western GOM in 2004 and no apparent correspondence in the eastern GOM in 2005. Dives to depths >300 m were observed in all three sub-regions and were associated with changes in temperature up to –18° C relative to the surface. Therefore, to address a primary question raised by Goodyear et al. (2003), our results show clearly that the percent of time at any particular depth is not simply a function of the difference in temperature relative to the surface. Instead, it is also dependent upon time of day, lunar phase, and most importantly the nature of the thermocline, which can vary greatly between sub-regions of the North Atlantic (as demonstrated by the tag data presented here).

Some of the variation in vertical habitat use of the blue marlin in this study can be explained by light level. Blue marlin and other billfish species have specially adapted vision that allows them to forage in low light conditions (Block and Finnerty 1994, Fritsches et al. 2005), thus explaining increased diving behavior at night during a full moon and maximum recorded depths that appear to be independent of temperature change. The greatest depths observed in the PAT tag data represent the limit of light penetration in the GOM, but the maximum depths varied as much as 320 m between individual fish. As the amount of light at depth is dependent upon turbidity and cloud cover, it would be desirable to utilize ancillary meterological and water quality data to investigate this idea. Yet even with the best available ancillary data, resolution of geolocations from PAT tags is too coarse to match specific tag measurements with environmental conditions, and additional telemetry studies would be necessary. In addition, depths between 300 and 400 m also correspond to the oxygen minimum layer in the GOM (McLellan and Nowland 1963, Morrison et al. 1983); therefore, both low light intensity and limiting oxygen levels (Brill 1994, Prince and Goodyear 2006) likely combine to define the range of depths utilized by Atlantic blue marlin in this study.

It has long been appreciated that habitat standardization of CPUE indices are inadequate due to a paucity of knowledge concerning the behavior of both the longline gear and the fish (Venizelos et al. 2001, Goodyear et al. 2003, Yokawa et al. 2003). The range of diving behaviors of blue marlin that we described here show that more complex models of vertical habitat use (that account for sub-regional differences in water column structure) may improve assessments that rely on longline CPUE indices (see Brill and Lutcavage 2001). Still, it is difficult to determine the position of a longline hook in the water column (e.g., Bigelow 2002, Bigelow et al. 2006), and it may be even more complex to predict the movements and behavior of a large pelagic fish in response to a baited hook. Aspects of fish behavior that relate probability of capture to how the longline gear is set and retrieved have important consequences (Boggs 1992) that cannot be addressed with PAT tags. More importantly, although the time at depths >30 m may represent a very small percentage, it is likely that this part of the habitat has a disproportionately high level of importance as a feeding zone based upon diet analysis for blue marlin (Strasburg 1970, Harvey 1989). Thus, the portion of the habitat in which blue marlin spend the least amount of time may equate to the zone of highest probability of capture. Although more detailed studies on the behaviors of blue marlin (e.g., Holland et al. 1990) and longline fishing gear (e.g., Boggs 1992) have been short-term and sporadic, there appears to be a great deal of active work that should provide a much improved understanding of the relationship between blue marlin habitat use and catch rates in pelagic longline fisheries in the near future.

ACKNOWLEDGMENTS

We are grateful for the participation of the captains and crew of the sport fishing vessels in the PAT tagging work, especially B. Lyons, M. Lyons, J. Cochrane, and B. Falterman. The PAT tagging research was funded by awards to J.R.R. from the McDaniel Charitable Foundation. R.T.K. was supported in part by a Texas Institute of Oceanography Postdoctoral Research Fellowship.

LITERATURE CITED

Bigelow, K., J. Hampton, and N. Miyabe. 2002. Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). Fisheries Oceanography 11:143–155.

Bigelow, K., M.K. Musyl, F. Poisson, and P. Kleiber. 2006. Pelagic longline gear depth and shoaling. Fisheries Research 77:173–183.

Block, B.A., D.T. Booth, and F.G. Carey. 1992. Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. Marine Biology 114:175–183.

Block, B.A. and J.R. Finnerty. 1994. Endothermy in fishes: a phylogenetic analysis of constraints, predispositions and selection pressures. Environmental Biology of Fishes 40:283–302.

Boggs, C.H. 1992. Depth, capture time, and hooked longevity of longline-caught pelagic fish: timing bites of fish with chips. Fishery Bulletin 166:267–284.

Brill, R.W. 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. Fisheries Oceanography 3:204–216.

Brill, R.W., T.E. Lowe, and K.L. Cousins. 1999. How water temperature really limits the vertical movements of tunas and billfishes—it's the heart stupid. In: Gamperl, K., A. Farrell, and D. MacKinlay, eds. Fish Cardiovascular Function: Control Mechanisms and Environmental Influences. Symposium proceedings of the International Congress on the Biology of Fish, July 27–30. Towson University, Baltimore, MD, USA, p. 57–62.

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. American Fisheries Society Symposium 25:179–198.

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

Domeier, M.L., D. Kiefer, N. Nasby-Lucas, A. Wagschal, and F. O'Brien. 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. Fishery Bulletin 103:292–306.

Fritsches, K.A., R.W. Brill, and E.J. Warrant. 2005. Warm eyes provide superior vision in swordfishes. Current Biology 15:55–58.

Graves, J.E., B.E. Luckhurst, and E. Prince. 2002. An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. Fishery Bulletin 100:134–142.

Graves, J.E., D.W. Kerstetter, B.E. Luckhurst, and E.D. Prince. 2003. Habitat preferences of istiophorid billfishes in the western north Atlantic: applicability of archival tag data to habitat based stock assessment methodologies. SCRS/2002/071, ICCAT Collected Volume of Scientific Papers 55:594–602.

Goodyear, C.P. 1999. An analysis of the possible utility of time-area closures to minimize billfish bycatch by US pelagic longlines. Fishery Bulletin 97:243–255.

Goodyear, C.P., D. Die, D.W. Kerstetter, D. B.Olson, E. Prince, and G.P. Scott. 2003. Habitat standardization of CPUE indices: Research needs. SCRS/2002/073, ICCAT Collected Volumes of Scientific Papers 55:613–623.

Harvey, G.C.M. 1989. An historical review of recreational and artisanal fisheries for billfish in Jamaica, 1976-1988. SCRS/88/057, ICCAT Collected Volume of Scientific Papers 30:440–450.

Hill, R.D. 1994. Theory of geolocation by light levels. *In* Elephant Seals: Population Ecology, Behavior, and Physiology. Edited by B.J. Le Boeuf and R.M. Laws University of California Press, Berkeley, CA, USA, p. 227–236.

Hinton, M.G. and H. Nakano. 1996. Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with and application to blue marlin (*Makaira nigricans*) catch and effort data from the Japanese longline fisheries in the Pacific. Bulletin of the Inter-American Tropical Tuna Commission 21:171–200.

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

ICCAT (International Commission for the Conservation of Atlantic Tunas). 2006. Blue Marlin and White Marlin. ICCAT Report 2006–2007. URL: http://www.iccat.es/Documents/SCRS/ExecSum/BUM-WHM%20EN.pdf, p. 68–77.

Kerstetter, D.W., 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. Fishery Bulletin 101:939–948.

Luo, J.G., E.D. Prince, C.P. Goodyear, B.E. Luckhurst, and J.E. Serafy. 2006. Vertical habitat utilization by large pelagic animals: a quantitative framework and numerical method for use with pop-up satellite tag data. Fisheries Oceanography 15:208–229.

McLellan, H.J. and W.D. Nowlin, Jr. 1963. Some features of the deep water in the Gulf of Mexico. Journal of Marine Research 21:233–245

Morrison, J.M., W.J. Merrell, Jr., R.M. Key, and T.C. Key 1983. Property distributions and deep chemical measurements within the western Gulf of Mexico. Journal of Geophysical Research 88(C4): 2601–2608

Musyl, M.K., R.W. Brill, D.S. Curran, J.S. Gunn, J.R. Hartog, R.D. Hill, D.W. Welch, J P. Eveson, C.H. Boggs, and R.E. Brainard. 2001. Ability of electronic archival tags to provide estimates of geographical position based on light intensity. In: J. R. Sibert and J. L. Nielsen Kluwer, eds. Electronic tagging and tracking in marine fisheries. Academic Publishers, Boston, MA, USA, p. 315–330.

Neilsen, A., K.A. Bigelow, M.K. Musyl, and J.R. Sibert. 2006. Improving light-based geolocation by including sea surface temperature. Fisheries Oceanography 15:314–325

Prince, E.D. and C.P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fisheries Oceanography 15:451–464.

Saito, H., Y. Takeuchi, and K. Yokawa. 2004. Vertical distribution of Atlantic blue marlin obtained from pop-up archival tags in the tropical Atlantic Ocean. SCRS/2003/037, ICCAT Collected Volumes of Scientific Papers 56:201–211.

Sibert, J.R., M.K. Musyl, and R.W. Brill. 2003. Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. Fisheries Oceanography 12:141–151.

Squire, J.L. 1987. Striped marlin migration patterns and rates in the northeast Pacific Ocean as determined by a cooperative tagging program: Its relation to resource management. Marine Fisheries Review 49:26–43.

Strasburg, D.W. 1970. A report on the billfishes of the central Pacific Ocean. Bulletin of Marine Science 20:575–604.

Sturges, W. 1993. The annual cycle of the western boundary current in the Gulf-of-Mexico. Journal of Geophysical Research-Oceans 98:18053–18068.

Suzuki, Z. 1989. Catch and fishing effort relationships for striped marlin, blue marlin, and black marlin in the Pacific Ocean, 1952 to 1985. In: R.H. Stroud, ed. Planning the future of billfishes: Research and management in the 90s and beyond. National Coalition for Marine Conservation, Inc., Savannah, GA, USA, p. 165–177.

Suzuki, Z., Y. Warashina, and M. Kishida, 1977. The comparison of catches by regular and deep tuna longline gears in the western and central equatorial Pacific. Bulletin of the Far Seas Fishery Research Laboratory 25:73–144.

Venizelo, A., M.I. Farber, D.D. Benetii. 2001. An evaluation of assumptions associated with blue marlin depth distribution towards the possible incorporation into the standardization of catch and effort statistics for use in stock assessment. SCRS/2000/061, ICCAT Collected Volumes of Scientific Papers 53:258–262.

Welch, D.W. and J.P. Eveson. 1999. An assessment of light-based geoposition estimates from archival tags. Canadian Journal of Fisheries and Aquatic Sciences 56:1317–1327.

Yokawa, K., H. Saito, and H. Shono. 2003. Preliminary result of vertical distribution patterns between Atlantic blue marlin and its CPUE. 16th Meeting of the Standing Committee on Tuna and Billfish, Mooloolaba, Queensland, Australia, July 2003. SCTB16 Working Paper BBRG-13, 10 p.