Vertical movement rates and habitat use of Atlantic tarpon

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ABSTRACT: We evaluated vertical depth and thermal habitat utilization of Atlantic tarpon *Megalops atlanticus* from high-resolution temporal data on 42 recovered pop-up archival transmitting (PAT) tags deployed and recovered from 2002 to 2010 to estimate vertical movement rates (swim speeds) during descents and ascents. All individuals strongly preferred shallow waters, spending >80 % of their time in water depths <10 m. Diel vertical distributions followed 4 patterns, but there was substantial variation within and among individuals. Vertical descent and ascent rates, defined as changes in depths extending ≥ 2 m over time, were estimated from tag data with 1 s sampling intervals. Descent rates ranged from 0.01 to 2.74 m s⁻¹, while ascent rates ranged from 0.01 to 4.5 m s⁻¹. Relatively uncommon deep diving behaviors might be associated with spawning activity. The most preferred water temperature was ~26°C, particularly during the spring and fall migratory periods. However, these reached >29°C in summer when tarpon were at their feeding grounds at the northern extreme of their range. Peaks of 'rolling and jumping' behaviors inferred from relative conductivity sensor data occurred with greatest frequency just after sunset and sunrise.

KEY WORDS: *Megalops atlanticus* · Satellite tracking · Thermal habitat · Rolling and jumping · Diel patterns

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INTRODUCTION

Vertical habitat use and movement rates of marine fishes are strongly influenced by their physiological requirements, foraging behaviors, and ambient environmental conditions (Evans 1993, Post et al. 1997, Brill & Lutcavage 2001, Prince & Goodyear 2006, Prince et al. 2010). Improved understanding of vertical habitat use and movement rates have great utility for fish ecology, fisheries resource management and species conservation (Pepperell & Davis 1999, Goodyear et al. 2008, Queiroz et al. 2010, Schaefer & Fuller 2010, Chiang et al. 2011, Hoolihan et al. 2011a). Knowledge of vertical movement rates provides the potential for a better understanding of how fish utilize vertical habitats and thermal structures in complex ocean environments to optimize their bioen-

ergetic potentials (Videler 1993, Jobling 1994, Hoolihan et al. 2009).

A number of acoustic telemetry tracking studies describe vertical movements of billfish and tuna, indicating that these fish frequently ascend and descend in the water column; however, they spend the majority of their time above the thermocline in the warm mixed surface layer (Jolley & Irby 1979, Block et al. 1992a, Hoolihan 2005, Hoolihan et al. 2009). These studies also suggest that billfishes spend the majority of their time swimming slowly (i.e. speeds <1 m s⁻¹). Notably, these estimates were made based on the position and horizontal travel of tracking vessels, and although informative, these estimates lack small-scale horizontal (zig-zag) and vertical movements. One exception is the study by Block et al. (1992b) in which instantaneous swimming speeds

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were obtained by attaching dedicated speed sensors to blue marlin *Makaira nigricans*. Typically, acoustic tracks of large pelagics are short in duration, usually not exceeding a few days. A major problem with inferences associated with short-term tracking is that the fish's post-release behavior may be anomalous, as fish may not have had sufficient time to recover to a 'normal' state (Hoolihan et al. 2011b).

Recent developments in electronic satellite-based pop-up archival transmitting (PAT) tagging technologies have greatly increased the number, deployment duration and information-gathering capacity for large pelagic fishes. PAT technologies provide a unique fisheries-independent method for acquiring and retrieving real-time environmental data relative to the animal's position in the ocean. This technology also allows accurate determination of the geolocation of a tag, an essential feature needed to ascertain the temporal and spatial movement characteristics of highly migratory 'rare event' species (Prince & Brown 1991, Block et al. 1998, Lutcavage et al. 1999).

An important coastal pelagic species suitable for use of these technologies is the Atlantic tarpon *Megalops atlanticus* (Ault 2008, Luo et al. 2008a,b). Perhaps one of the most storied sport fisheries, it contributes billions of dollars annually to regional USA economies—providing livelihoods to tens of thou-

sands of Americans from Texas to Florida to Virginia (Ault 2008, Mill et al. 2010). Florida waters are the seasonal centroid of the recreational fishery accounting for >75% of the tarpon world records (IGFA 2012). Although primarily a catch-and-release fishery in USA waters, tarpon fishery sustainability is under increasing regional threat from exploitation, loss of natal habitats from regional development, water management, and offshore impacts (Ault 2008, 2010, Ault et al. 2008, Barbieri et al. 2008). The Atlantic tarpon is a migratory species whose survival is dependent on the capability to range horizontally over large geographical areas and vertically over wide ranges of depths and seasonal temperatures (Ault et al. 2008, Luo et al. 2008b, Ault 2010).

PAT tag technologies are capable of recording accurate high-frequency measurements of ambient water temperature, depth (from pressure), light level, and salinity data that are monitored down to 1 s intervals throughout the period of deployment and stored in the instrument's non-volatile digital flash memory (Arnold & Dewar 2001, Luo et al. 2008a,b). When the tag has 'popped up' and been recovered, the non-volatile memory can be directly accessed and the entire database can be retrieved using an external power source (Luo et al. 2008a).

Our primary objectives were to evaluate vertical depth and thermal habitat utilization of Atlantic tar-

Fig. 1. *Megalops atlanticus*. Estimated daily geolocations of 158 PAT-tagged Atlantic tarpon (color coded by quarter of the year) in the western central Atlantic

Table 1. *Megalops atlanticus*. Details of recovered pop-up archival transmitting (PAT) tags (n = 42), and paired Student's *t*-tests of daily average depth (m) for day and night. ^aNight depth significantly greater. ^bDay depth significantly greater

Tag name	Fish weight (kg)	Deployment			Record interval (s)	Max. depth (m)	Days at liberty (d)	Depth (mean $\pm$ SD) (m)		<i>t</i> -statistic	p
		Date	Lat.	Long.				Day	Night		
T-03	36	21/09/02	31.70	-81.08	60	23	44	7.82 $\pm$ 3.94	10.81 $\pm$ 3.33	-3.98	0.0003 ^a
T-05	41	18/05/03	24.84	-80.77	60	14	79	3.11 $\pm$ 1.28	2.73 $\pm$ 1.32	2.40	0.0190 ^b
T-13	45	06/06/03	26.70	-82.27	60	11	29	2.37 $\pm$ 0.76	2.44 $\pm$ 0.69	-0.41	0.6827
T-15	90	11/05/04	19.37	-96.27	60	82	30	10.93 $\pm$ 7.22	11.91 $\pm$ 7.44	-0.78	0.4432
T-24	55	10/05/04	19.38	-96.29	60	48	120	7.12 $\pm$ 6.15	5.10 $\pm$ 4.26	3.81	0.0002 ^b
T-30	80	11/05/04	19.37	-96.27	60	109	27	8.12 $\pm$ 8.23	8.21 $\pm$ 5.47	-0.06	0.9502
T-42	62	28/05/06	19.34	-96.30	10	48	154	6.95 $\pm$ 3.94	6.55 $\pm$ 3.46	1.48	0.1417
8T-43	77	28/05/06	19.37	-96.29	10	105	161	11.79 $\pm$ 8.92	9.60 $\pm$ 4.98	3.29	0.0012 ^b
T-44	56	28/05/06	19.37	-96.30	10	41	106	5.28 $\pm$ 3.15	7.34 $\pm$ 3.47	-5.35	0.0000 ^a
T-48	54	10/09/06	28.41	-96.39	10	27	81	5.38 $\pm$ 6.17	4.39 $\pm$ 5.47	3.77	0.0003 ^b
T-52	64	16/10/06	27.16	-80.17	10	11	6	1.91 $\pm$ 0.93	1.84 $\pm$ 0.63	0.27	0.8070
T-53	47	11/06/07	24.84	-80.75	10	136	35	6.71 $\pm$ 12.04	5.57 $\pm$ 7.18	1.04	0.3056
T-54	51	16/10/06	27.20	-80.21	10	18	34	6.86 $\pm$ 3.86	6.38 $\pm$ 4.00	1.33	0.1935
T-56	49	21/05/07	24.84	-80.75	10	149	42	5.72 $\pm$ 2.64	6.94 $\pm$ 4.09	-3.44	0.0014 ^a
T-57	44	14/05/07	24.86	-80.75	10	7	11	3.47 $\pm$ 0.46	2.08 $\pm$ 0.35	6.52	0.0002 ^b
T-58	43	13/05/07	24.85	-80.75	10	9	12	2.15 $\pm$ 0.76	1.26 $\pm$ 0.72	2.62	0.0280 ^b
T-59	54	14/05/07	24.85	-80.75	10	7	36	2.87 $\pm$ 0.63	1.59 $\pm$ 1.18	6.67	0.0000 ^b
T-60	58	29/04/07	24.84	-80.75	1	134	65	2.36 $\pm$ 1.85	2.86 $\pm$ 6.49	-0.64	0.5271
T-61	35	29/04/07	24.84	-80.75	1	19	30	4.43 $\pm$ 3.30	3.34 $\pm$ 3.40	2.21	0.0358 ^b
T-65	46	23/07/07	27.17	-80.18	1	10	47	2.10 $\pm$ 0.52	2.55 $\pm$ 0.62	-4.90	0.0000 ^a
T-66	44	21/05/07	24.84	-80.77	1	9	52	0.58 $\pm$ 0.29	0.62 $\pm$ 0.24	-1.00	0.3201
T-69	75	30/05/07	19.38	-96.28	1	107	99	5.66 $\pm$ 6.58	6.12 $\pm$ 6.41	-0.96	0.3412
T-75	51	04/08/07	29.10	-94.99	1	32	57	7.54 $\pm$ 2.45	7.28 $\pm$ 2.44	0.66	0.5127
T-76	41	05/09/07	30.56	-87.98	1	47	89	11.52 $\pm$ 9.12	7.52 $\pm$ 5.48	5.50	0.0000 ^b
T-85	56	11/10/07	25.90	-81.64	1	9	12	2.61 $\pm$ 0.91	2.42 $\pm$ 1.05	0.66	0.5255
T-104	38	05/05/08	24.85	-80.75	10	5	30	1.79 $\pm$ 0.97	1.17 $\pm$ 0.73	5.58	0.0000 ^b
T-105	50	04/05/08	24.85	-80.75	10	22	128	3.57 $\pm$ 1.90	3.94 $\pm$ 2.90	-1.67	0.0982
T-106	54	05/05/08	24.85	-80.75	10	95	134	3.43 $\pm$ 3.03	3.08 $\pm$ 4.68	1.30	0.1960
T-107	39	05/05/08	24.85	-80.75	10	24	36	1.43 $\pm$ 0.82	1.07 $\pm$ 0.46	2.77	0.0091 ^b
T-116	46	12/05/08	24.85	-80.75	10	26	127	4.06 $\pm$ 2.66	4.42 $\pm$ 2.89	-1.75	0.0828
T-123	55	04/06/09	19.37	-96.29	30	27	17	5.93 $\pm$ 3.02	6.40 $\pm$ 3.95	-0.40	0.6950
T-124	40	20/08/09	27.17	-80.17	30	20	56	6.00 $\pm$ 3.10	6.33 $\pm$ 3.28	-1.01	0.3189
T-130	41	30/08/09	28.26	-96.52	30	24	71	8.09 $\pm$ 4.66	4.79 $\pm$ 3.52	6.22	0.0000 ^b
T-133	38	26/03/10	17.53	-88.23	30	8	6	3.70 $\pm$ 0.53	1.51 $\pm$ 0.85	3.82	0.0315 ^b
T-136	65	13/08/09	27.17	-80.17	30	7	5	1.57 $\pm$ 0.37	1.56 $\pm$ 0.58	0.02	0.9828
T-137	47	20/08/09	27.17	-80.18	30	5	23	0.79 $\pm$ 0.52	1.45 $\pm$ 0.67	-4.90	0.0001 ^a
T-140	57	10/04/10	25.29	-81.02	30	4	27	1.12 $\pm$ 0.58	1.21 $\pm$ 0.37	-0.85	0.4037
T-141	46	27/03/10	17.53	-88.23	30	14	17	5.07 $\pm$ 3.39	5.57 $\pm$ 3.30	-0.91	0.3773
T-142	58	12/04/10	25.29	-81.02	30	15	45	1.54 $\pm$ 1.16	2.63 $\pm$ 2.26	-3.75	0.0005 ^a
T-143	36	11/04/10	25.29	-81.02	30	6	40	1.01 $\pm$ 0.18	1.17 $\pm$ 0.33	-2.59	0.0136 ^a
T-150	43	09/06/10	24.84	-80.75	30	6	9	2.99 $\pm$ 0.73	1.43 $\pm$ 0.40	5.10	0.0022 ^b
T-164	53	18/09/10	33.18	-79.14	30	20	51	3.43 $\pm$ 1.76	6.02 $\pm$ 2.85	-7.12	0.0000 ^a

pon from high-resolution temporal data on 42 recovered PAT tags deployed and recovered from 2002 to 2010. These data were used to estimate vertical movement rates (swim speeds) during descents and ascents based on the changes in depth over time. In addition, based on relative conductivity sensor (RCS) data stored by the PAT tags, we critically examined the times of day when the tarpon displayed their characteristic surface 'rolling and jumping' behaviors indicative of foraging.

MATERIALS AND METHODS

From 2002 to 2010, 158 PAT tags manufactured by Wildlife Computers¹ were deployed on Atlantic tarpon in the central western Atlantic, Gulf of Mexico, and Caribbean Sea (Fig. 1). Of these, 64 were subsequently physically recovered using an ARGOS locator (Table 1). In this paper we focus our analyses

¹References to commercial products do not imply endorsement by the authors

on 42 of these tags that had deployment periods longer than 5 d. During the course of this research we varied the tag's sampling frequency for 4 physical parameters (depth, water temperature, light level, and relative conductivity) from 1 to 60 s, principally to determine the optimal setup balance between the amount of data collected and the required battery power needed for transmission to the ARGOS satellite network.

During normal operation of a PAT tag, at a user-defined time, a 100 pound test stainless steel wire link connecting the tethered fish to the PAT tag dissolved via electrolysis, enabling the tag to detach from the fish and float to the surface. At the ocean surface, the PAT tag transmitted summarized archived sensor data to the ARGOS satellite network. These data were subsequently forwarded to a public company authorized by NOAA, and then on to the researcher without the need of physical recovery of the tag.

However, a limitation of the technology is that uplink time for a PAT tag is constrained to when the orbiting satellite network is overhead, and the duration of transmissions is constrained by the internal battery capacity of the PAT tag, which greatly restricts the quantity of data that can be successfully transmitted. This problem is particularly acute with large archived datasets generated when sensor data are recorded at short time intervals for relatively lengthy periods of monitoring. To contend with this problem, prior to transmission, data are internally compressed by averaging observations into 12 user-defined bins. This process provides a limited representation of the animal's actual activities, and may exclude significant temporal blocks of data when transmission events fail or are otherwise corrupted.

Fortunately, the nearshore coastal distribution of tarpon (Fig. 1) facilitated physical recovery of 64 of 158 of our deployed tags (~41%), either by use of a handheld Argos AL-1 PTT Locator System (Communications Specialists, www.com-spec.com) or by recovery by beach-goers who subsequently returned tags to us. With recovery of the PAT tag the entire archived database can be downloaded from the non-volatile memory to provide high-resolution datasets on depth, temperature, light-level, and wet-dry sensor values (RCS data, used to determine wet or dry status of

the tag, and to estimate an approximate salinity following Luo et al. 2008a). Ambient light intensity data recorded by PAT tags were first processed using software provided by the manufacturer (Hill & Braun 2001) to derive the initial estimates of geoposition (geographical location) of the tagged tarpon. We then applied a sea-surface temperature-corrected Kalman filter (Nielsen et al. 2006, Lam et al. 2008) and a custom bathymetry filter to refine the final movement track, based on 2×2 grid ETOP02 bathymetry data and the daily maximum depth recorded by the tag (Hoolihan & Luo 2007). Because of the inherent magnitude of geoposition errors in the algorithms (i.e. the root-mean-squared RMS error is $\sim 0.5^\circ$ for longitude and 1.2° for latitude, following Lam et al. 2008), associating vertical movement rate behaviors to particular oceanographic features would be unreliable.

Of the 64 recovered PAT tags, 42 of these were deployed for at least 5 d (mean $\pm$ SD = 54 ± 43 d, range = 5 to 161 d) (Table 1). To minimize the potential influence of anomalous post-release behaviors of the tarpon (Hoolihan et al. 2011b), we used these 42 tag datasets to analyze the vertical depth-thermal habitats, and vertical movement rates (swimming speeds). Frequency distributions of average daily depth and temperature were tabulated for daylight and night-time periods. We used the 8 tags with 1 s sampling intervals to estimate tarpon descent and ascent rates (m s^{-1}) based on changes in individual depth over time. Descent and ascent events were defined as vertical movements (i.e. depth changes) of ≥ 2 m, assuming continuous and uni-directional lines of travel (e.g. Fig. 2). Vertical movement rates were

Fig. 2. *Megalops atlanticus*. Event identification diagram derived from T-69 data. D1 to D4: descent events; A1 to A8: ascent events

Fig. 3. *Megalops atlanticus*. Example of relative conductivity sensor (RCS) data for T-60 in May 2007 indicating apparent surface 'rolling and jumping' by tarpon as illustrated in the insets

derived from the average speed over individual ascent or descent events. We used 'movement rates' instead of 'swimming speeds' because the speed could be much higher if we have the angles of the ascent and decent. We used RCS values from the eight 1 s tags to analyze the surface oriented 'rolling and jumping' behaviors of tarpon. When a tarpon rolls or jumps, the tethered PAT tag can hit the surface or come completely out of the water. In such events, the RCS would record substantially higher values in air compared to the baseline values gathered while the tag remained submerged (Fig. 3). Air-exposed values were confirmed in laboratory tests where the tag was repeatedly taken in and out of water quickly (<1 s). We combined all these 'dry events' for individuals and tabulated these by hour to show the times of day when the rolling behaviors occurred.

Statistical differences in daily day and night average depths were evaluated using paired Student's *t*-tests (Sokal & Rohlf 1995). Differences in mean movement rates for individual descent and ascent events were statistically compared (z-test) using log-transformed data (Zar 1999). Pairwise probability comparisons of unidirectional vertical movement rates (ascents or descents) were conducted between day-night, day-crepuscular, and night-crepuscular periods using ANOVA (Montgomery 2001). Further, we compared ascent and descent rates within each of these periods. Unless otherwise stated, all statistical tests were performed at the $\alpha = 0.05$ level of significance.

RESULTS

A summary of the details of 42 recovered satellite-based PAT-tagged tarpon covering 2198 d of deployment is given in Table 1, and the overall seasonal spatial distribution of all 158 tags is shown in Fig. 1. In general, migrating tarpon schools enter USA waters in late spring (April–June) in Florida and the Bay of Campeche, in the southern Gulf of Mexico, to feed and spawn. The tarpon that reach Florida then travel northward in late May and early June along the Gulf and Atlantic coasts to ultimately reach the rich estuarine and coastal ocean environments of the Mississippi River in the upper Gulf of Mexico, and the Chesapeake Bay along the central Atlantic coast, to rebuild their gonads and soma (body) by voraciously

feeding on abundant menhaden, crabs and shrimp during the summer (July–September). As coastal ocean waters cool in the fall, the enormous schools of tarpon then reverse course and begin the southward component of their seasonal migration, moving through Florida and Texas waters from late September through early December. Observed tarpon migration and movement patterns covered the entire Gulf of Mexico, Florida and the southeastern USA (Fig. 1).

Maximum depths ranged from 5 to 149 m (mean $\pm$ SD = 36.7 ± 41.1 ; Table 1). The cumulative frequency distribution of all tags indicated that, on average, tarpon spent >80% of the time in waters <10 m deep during both day and night (Fig. 4, dashed lines). While the overall distribution was symmetric, individual mean daily depths ranged from 0.58 to 11.79 m in the daytime, and 0.62 to 11.91 m during nighttime (Table 1). Day and night depth distributions varied among individual tarpon: (1) 14 of 42 stayed significantly deeper during the day than at night; (2) 8 of 42 stayed significantly shallower during the day than at night; and (3) the remaining 20 tarpon had no significant day-night depth differences. The pooled depth frequency distribution from all tags indicated no significant day-night depth differences (Fig. 4). However, there was substantial individual variation. Fig. 5a–e shows the depth frequency distributions of 5 individuals that stayed deeper during the day than at night. Fig. 5f–j shows the depth frequency distributions of 5 ind. that stayed shallower during the day than at night.

Fig. 4. *Megalops atlanticus*. Day (light bars) and night (dark bars) depth frequency distribution for data from all tarpon tags combined. Dashed lines: cumulative frequency distributions

Close examination of diel depth distributions revealed great variations in the observed patterns, which can be summarized into 4 basic types: (1) a clear diel pattern of deep at night and shallow during the day (Fig. 6a); (2) inverse Type 1, i.e. tarpon remained deep during the day and occupied shallow water at night (Fig. 6b); (3) an irregular interval of deep and shallow distribution during the day and night (Fig. 6c); and (4) random up and down movements throughout the day and night (Fig. 6d). Beside the 4 basic types, many variations of diel vertical distributions can be described as a combination of either Types 1 and 4 (Fig. 6e), Types 2 and 4 (Fig. 6f), or Types 3 and 4 (Fig. 6g). However, for the duration of each tag deployment period, each tarpon usually utilized different types of vertical distribution patterns on different days; see for example tarpon T-03 (Fig. 6a,d) and tarpon T-24 (Fig. 6c,f,g). Thus, to some extent, the average statistics (Table 1, Fig. 4) do not tell the full story of the observed tarpon diel vertical depth distributions.

Our data also revealed some uncommon deep diving behaviors of the Atlantic tarpon that, to our knowledge, have never previously been reported (Fig. 6h). On May 14th, in the morning, tarpon T-60 started in shallow waters where the temperature was 26.5°C (Fig. 6h, grey line). By afternoon, it had moved out to warmer waters and started deep diving. As the hours progressed, it dove deeper and deeper. The deepest depth (136 m) occurred at sunset and continued until just before midnight, when the surface water temperature was 27.6°C and the bottom temperature was

Fig. 5. *Megalops atlanticus*. Tarpon day (light bars) and night (dark bars) depth frequency distributions for 10 ind. (a to j)

Fig. 6. *Megalops atlanticus*. Diel depth distribution of 8 ind. Dark horizontal bars = night hours. Note the different depth scales on y-axes. A second y-axis for temperature (gray line) is added in (h)

23°C. After midnight, the tarpon gradually reduced its diving depth, with just a few deep dives before sunrise. The deep diving completely stopped after sunrise and the tarpon moved to an area where the surface water temperature was 26°C. We speculate that this deep diving behavior was possibly related to spawning. There were 6 tarpon that had dives deeper than 100 m (Table 1), and all these deep dives occurred around either the new or full moon phases.

The daily average water temperatures recorded by all tags over all months ranged from 20 to 32°C (Fig. 7). The mode of the pooled temperature frequency distribution of all months was 28°C. The daily average and monthly frequency distributions indicated clear patterns in water temperature use: 26°C (April and May); 28°C (June and July); 30°C (August); 29°C (September); 25–27°C (October); and 22°C (November). Despite the large range of temperature use during the year, tarpon used a specific temperature of 26°C as a cue for migrations (Fig. 8).

Eight recovered tags with sampling frequencies of 1 s were used to estimate vertical movement rates. The high sampling frequency obviated the need for interpolation. Vertical movement rates were estimated for both descent and ascent events (cf. Fig. 2). The total number of descents by individual tarpon ranged from 291 (T-66) to 31037 (T-69). Maximum vertical distance moved for descent events ranged from 3 m (T-66) to 87 m (T-60) (Table 2). For ascents, maximum vertical movement ranged from 3 m (T-66) to 57 m (T-60). The mean descent rate per event ranged from 0.1 to 2.74 m s⁻¹, while ascents ranged from 0.1 to 4.5 m s⁻¹ (Table 2). The maximum rate of movement recorded for a single time interval within an event was over 5.0 m s⁻¹ (Fig. 9), and most of the fastest rates occurred near the surface. The mean rates of movement for ascents and descents were similar for all individuals (Table 2); however, due to the large number of events for some individuals, these were significantly different. During the day, 5 ind.

Fig. 7. *Megalops atlanticus*. Daily average water temperatures (•) and associated monthly frequency distribution (gray bars)

Fig. 8. Movement track of T-116 over sea surface temperature (SST) at 4 dates: (A) May 28, 2008; (B) June 5, 2008; (C) July 3, 2008; and (D) July 27, 2008. SST values are indicated by the color scale in (A), and the 26°C isotherm is specifically marked in the scale-bar with an orange-colored line. In each panel, the blue dots are the tarpon daily locations, and the purple dot is the end location for each date specified

Table 2. *Megalops atlanticus*. Total number of descent and ascent events for 8 ind. Events are defined as continuous, uni-directional vertical movement (i.e. depth change) ≥ 2 m, including a subset of those starting or ending near the surface (≤ 1 m depth). ^aRefers to distance traveled during vertical movement event-not actual depth in the water column. ^bDerived from average speed over individual events. Means $\pm$ SD in ()

Specimen	No. days	Depth range (m)	Temp. range (°C)	Total descents	Total ascents	Descending range ^a		Ascending range ^a		Speed range ^b (m s ⁻¹)	
						(m)	(s)	(m)	(s)	Descent	Ascent
T-60	60	0-134 (2.7 ± 6.32)	18.2-31.5 (27.6 ± 1.77)	3565	3114	2-87 (4.1 ± 3.92)	3-207 (13.6 ± 9.75)	2-57 (4.5 ± 4.42)	2-142 (15.8 ± 11.54)	0.1-2.74 (0.35 ± 0.17)	0.1-2.0 (0.31 ± 0.13)
T-61	28	0-19 (4.0 ± 3.82)	24.6-30.0 (26.9 ± 1.43)	2460	2475	2-17 (3.9 ± 2.15)	3-42 (13.2 ± 6.08)	2-16 (3.7 ± 1.90)	2-45 (13.4 ± 5.80)	0.10-1.46 (0.34 ± 0.17)	0.10-3.75 (0.34 ± 0.30)
T-65	46	0-9.5 (2.2 ± 1.03)	27.3-32.4 (30.7 ± 0.89)	677	750	2-5 (2.3 ± 0.44)	5-20 (11.0 ± 2.70)	2-5 (2.3 ± 0.46)	3-26 (10.3 ± 3.11)	0.1-0.53 (0.24 ± 0.061)	0.1-0.83 (0.26 ± 0.083)
T-66	47	0-5.5 (1.5 ± 0.64)	25.0-32.3 (29.4 ± 2.37)	141	150	2-3 (2.2 ± 0.22)	3-18 (8.3 ± 2.81)	2-3.0 (2.2 ± 0.21)	6-16 (9.8 ± 2.08)	0.1-0.94 (0.32 ± 0.12)	0.1-0.39 (0.25 ± 0.048)
T-69	95	0-107.5 (5.8 ± 7.42)	20.4-32.5 (29.0 ± 2.24)	15538	15499	2-58 (4.3 ± 3.03)	3-120 (16.4 ± 8.65)	2-34 (4.0 ± 2.67)	2-118 (15.8 ± 7.93)	0.1-2.6 (0.28 ± 0.12)	0.1-2.3 (0.27 ± 0.11)
T-75	55	0-17 (7.4 ± 3.51)	26.8-32.8 (29.6 ± 0.82)	3983	4458	2-15 (4.7 ± 2.55)	3-48 (16.1 ± 6.88)	2-14 (4.5 ± 2.43)	2-53 (15.2 ± 6.51)	0.1-2.03 (0.33 ± 0.16)	0.1-4.5 (0.33 ± 0.17)
T-76	85	0-47 (9.5 ± 8.61)	20.1-31.7 (25.6 ± 2.97)	14306	13550	2-33 (4.1 ± 2.74)	3-84 (14.7 ± 7.84)	2-37 (4.0 ± 2.55)	2-84 (14.5 ± 7.54)	0.1-1.98 (0.33 ± 0.20)	0.1-2.67 (0.33 ± 0.22)
T-85	11	0-7.5 (2.6 ± 0.74)	25.2-30.1 (28.4 ± 0.71)	377	396	2-5.5 (2.4 ± 0.51)	4-20 (8.2 ± 2.68)	2-5.5 (2.4 ± 0.53)	3-22 (8.1 ± 3.14)	0.1-0.71 (0.35 ± 0.10)	0.1-0.78 (0.34 ± 0.10)

(T-60, T-66, T-69, T-76, and T-85) had significantly faster descent than ascent speeds (Table 3). During the night, 3 ind. (T-60, T-65, and T-76) had significantly faster ascent than descent speeds, and 2 ind. were opposite. During the crepuscular period, only 1 ind. (T-60) had significantly faster descent than ascent speeds.

The eight 1 s sampling tags captured 3827 'rolling and jumping' events over a total of 427 d for an average of ~ 9 rolls ind.⁻¹ d⁻¹. Examination of the full distribution of rolling events showed that tarpon rolled during all hours of the day (Fig. 10). However, there were some apparent diel patterns in rolling behavior. In general, higher frequency rolling occurred during the night than during the day. There were apparently 3 distinct peaks: (1) before sunrise (03:00-05:00 h); (2) after sunrise (08:00-10:00 h); and (3) after sunset (21:00-23:00 h).

DISCUSSION

This research presented extensive results on vertical habitat use and swim speeds of the Atlantic tarpon based on archival data from 42 recovered PAT tags. The time spent at depth by individual tarpon in the present study corroborates other reports demonstrating tarpon's preference for surface waters; this fact is well-known to serious anglers, and is the general reason why tarpon are thought of as shallow water 'flats' fish (Ault 2008, 2010). The proportion of time spent in waters < 10 m by tarpon in the present study exceeded 80 % (Fig. 4), which corresponds well with their essential habitats that include bays, estuaries, rivers, and the surface waters across the continental shelf (Fig. 1).

While there are no similar studies on Atlantic tarpon vertical distributions for comparison, studies on other large pelagic and coastal pelagic fishes show similar results. For example, Marcinek et al. (2001) reported that Pacific bluefin tuna *Thunnus orientalis* spent > 80 % of their time in the top 40 m of the water column. Schaefer & Fuller (2010) showed that bigeye tuna *T. obesus* spent 72 and 98 % of their time during day and night, respectively, above thermocline depths of 60 m. Pepperell & Davis (1999) found that black marlin *Makaira indica* spent most of their time within 10 m of the surface during both day and night. Horodysky et al. (2007) stated that white marlin *Tetrapturus albidus* spent nearly half of their time associated with warm near-surface waters < 10 m deep. Goodyear et al. (2008) reported that Atlantic blue marlin *M. nigricans* spent > 58 and 85 % of their

Fig. 9. *Megalops atlanticus*. Vertical movement rates (m s^{-1}) as a function of depth during descent (negative on x-axis) and ascent (positive) events for 8 individuals

time during the day and night, respectively, in the surface mixed layer (i.e. layer of the ocean surface where temperature change $[\Delta T]$ is $<1^\circ\text{C}$). Hoolihan et al. (2011a), in a similar study on Atlantic sailfish *Istiophorus platypterus*, showed that sailfish spent >82 and 93% of their time during the day and night, respectively, in the surface mixed layer where $\Delta T < 1^\circ\text{C}$; while Chiang et al. (2011) showed that sailfish in western Pacific spent 88% of their time in the upper uniform mixed layer of 50 m . Abecassis et al. (2012) revealed that swordfish *Xiphias gladius* spent 97% of their time at depths $<100\text{ m}$ during the night, 37% of which is spent near the surface ($<5\text{ m}$). Sepulveda et al. (2004) reported that mako sharks *Isurus oxyrinchus* spent 80% of their time at depths $<12\text{ m}$. In

general, these shallow surface waters are characterized by a relatively high oxygen tension, and of course, are the primary location of their food sources.

We found that tarpon used a combination of 4 basic diel vertical movement patterns (Fig. 6). Differences in diel vertical movement patterns observed by us might have resulted from necessarily different feeding strategies for various key prey species encountered in specific ocean environments (e.g. rivers, bays, coastal, and offshore waters) as tarpon foraged along their seasonal migration routes. Similarly, days in which no clear diel vertical movement patterns were observed may signal a feeding strategy for prey with no diel changes in distribution patterns. Schaefer & Fuller (2010) found similar variations in vertical habitat utilization among bigeye tuna *Thunnus obesus* based on archival tag data. While there is limited scientific literature on the diet of adult Atlantic tarpon *per se* (Ault et al. 2008), knowledge of their diet came indirectly from sport anglers who specified what they used to catch them. Adult tarpon feed on a variety of prey species including polychaetes, shrimps, blue crabs *Callinectes sapidus*, mullet *Mugil cephalus*, mollies and killifishes (Poeciliidae), silversides (Atherinidae), menhaden *Brevoortia* spp., ladyfish *Elops saurus*, marine catfish *Bagre marinus*, and ribbonfish *Trichiurus lepturus* (Ault 2010). For example, in

the spring, anglers in the tidal passes of the Florida Keys and Boca Grande, Florida, (i.e. the same area where tarpon were tagged), drift live crabs at the surface at night to catch tarpon, which matched perfectly with one of the diel vertical distribution patterns observed by us: shallow at night and deep during the day (Fig. 6b). The striped or black mullet *Mugil cephalus* is a diurnal species that usually schools and feeds at the surface during the day (Sogard et al. 1989). This behavioral pattern matches another diel vertical distribution pattern observed in

Table 3. *Megalops atlanticus*. Mean movement rate $\pm$ SD for descent and ascent events during day, night, and crepuscular periods for 8 ind., including ANOVA pairwise p-values comparing descent and ascent during day, night, and crepuscular periods. Upper values: descent events, values in (): ascent events. ns: not significant; *p < 0.05, **p < 0.001

Specimen	Mean movement rate $\pm$ SD (m s ⁻¹)		
	Day	Night	Crepuscular
T-60	0.35 $\pm$ 0.17** (0.31 $\pm$ 0.14)	0.25 $\pm$ 0.18** (0.31 $\pm$ 0.13)	0.32 $\pm$ 0.17* (0.30 $\pm$ 0.13)
T-61	0.33 $\pm$ 0.16 ^{ns} (0.33 $\pm$ 0.32)	0.36 $\pm$ 0.17 ^{ns} (0.35 $\pm$ 0.22)	0.35 $\pm$ 0.17 ^{ns} (0.36 $\pm$ 0.37)
T-65	0.24 $\pm$ 0.074 ^{ns} (0.25 $\pm$ 0.071)	0.23 $\pm$ 0.051** (0.27 $\pm$ 0.099)	0.25 $\pm$ 0.065 ^{ns} (0.26 $\pm$ 0.075)
T-66	0.31 $\pm$ 0.13** (0.25 $\pm$ 0.049)	0.33 $\pm$ 0.11** (0.25 $\pm$ 0.047)	0.31 $\pm$ 0.12 ^{ns} (0.19 $\pm$ 0.031)
T-69	0.29 $\pm$ 0.13** (0.27 $\pm$ 0.11)	0.27 $\pm$ 0.10** (0.26 $\pm$ 0.10)	0.27 $\pm$ 0.11 ^{ns} (0.28 $\pm$ 0.11)
T-75	0.32 $\pm$ 0.17 ^{ns} (0.32 $\pm$ 0.17)	0.33 $\pm$ 0.15 ^{ns} (0.34 $\pm$ 0.19)	0.32 $\pm$ 0.18 ^{ns} (0.31 $\pm$ 0.13)
T-76	0.35 $\pm$ 0.22** (0.33 $\pm$ 0.22)	0.30 $\pm$ 0.16** (0.33 $\pm$ 0.21)	0.33 $\pm$ 0.21 ^{ns} (0.33 $\pm$ 0.22)
T-85	0.35 $\pm$ 0.10** (0.31 $\pm$ 0.09)	0.37 $\pm$ 0.10 ^{ns} (0.38 $\pm$ 0.10)	0.34 $\pm$ 0.11 ^{ns} (0.36 $\pm$ 0.10)

Fig. 10. *Megalops atlanticus*. Frequency distribution of tarpon 'rolling and jumping' as a function of hour of day. Bars: black = night, light gray = day, dark gray = crepuscular period. Black line: 24 h averaged frequency (4.17%). EST: eastern standard time

our tagged tarpon: shallow during the day and deep at night (Fig. 6a).

The relatively deep diving behaviors (>100 m) of 6 tarpon observed in our study (Table 1, Fig. 6h) were likely related to spawning activity because they occurred a few days around the new and full moon phases. For example, deep diving for T-60 occurred on May 14th, 2 d before the new moon (May 16th). Based on early-stage tarpon larval distributions, Smith (1980), Crabtree (1995) and Crabtree et al. (1997) suggested the west Florida shelf and the entire east coast of Florida shelf as potential spawning areas. Baldwin & Snodgrass (2008) reported on observations of courtship and pre-spawning behaviors of tarpon they observed on the ocean side of the mid-Florida Keys, 2 d before the new moon of June 2002. J. M. Shenker (pers. comm.) found newly hatched tarpon larvae at the new moon during larval tows in the Straits of Florida that indicated tarpon spawning had occurred a few days before.

Tarpon have adapted morphological, physiological, and behavioral characteristics for conserving energy that allow them to meet their energetic requirements (Clark et al. 2007, Ault 2010). Our data suggest that Atlantic tarpon have a relatively plastic range of thermal use (22 to 30°C) that corresponds with their seasonal migratory needs. However, 26°C seems to be the triggering water temperature that drives migratory behaviors (Ault et al. 2008, Ault 2010). Slow swimming speeds minimize energy consumed by tarpon over lengthy periods and great distances in search of prey, and higher ram speeds allow them to strike prey in an instant (Tran et al. 2010). Unique osmoregulatory capabilities allow them to forage over a wide range of environmental conditions. The large mouth and powerful jaw of the tarpon (creating massive suction) make it a formidable predator (Tran et al. 2010).

The vertical movement rate data presented here represent minimum swimming speed estimates, since the horizontal components are relatively unknown. Our methods did not allow direct measurement of swimming speeds. We assumed that descent and ascent events were purely vertical, which in most cases is in fact unlikely. As a result, actual distances moved were most likely underestimated, as were movement rates. Hoolihan et al. (2009) used a similar methodology to estimate the vertical movement rates of Atlantic istiophorid billfishes. Despite the deeper distribution of billfish (maximum depths ranged from 188 to 660 m, as compared to 5 to 136 m for tarpon), the mean descent and ascent rates (range: 0.14 to 0.36 m s⁻¹) from Hoolihan

et al. (2009) were similar to our results (0.24 to 0.38 m s⁻¹). While no study has yet directly monitored tarpon swimming speeds in the ocean, Block et al. (1992b) monitored speeds of 3 blue marlin using direct speed sensors during short-term acoustic tracking studies. They reported that 97 % of the time, billfish speeds were <1.20 m s⁻¹. Other acoustic tracking studies report that istiophorids typically engage in slow sustained swimming most of the time (Yuen et al. 1972, Jolley & Irby 1979, Holland et al. 1990, Holts & Bedford 1990, Brill et al. 1993, Hoolihan 2005).

The greater estimated vertical movement rates achieved by tarpon in the present study (>2 m s⁻¹) (Table 2, Fig. 9) most likely reflect burst swimming events, presumably in the attack and capture of prey, rather than a sustained swimming speed *per se*. Burst swimming speeds can generally be characterized by high-speed, short-duration (<20 s) events, often associated with foraging activities or avoidance of predators (Beamish 1978). Tran et al. (2010), based on their laboratory experiments, reported ram speeds of juvenile (13–14 cm standard length) Indo-Pacific tarpon *Megalops cyprinoides* as high as 1.38 m s⁻¹ during predation events, which is equivalent to 8.5 body lengths s⁻¹.

The instantaneous movement rate versus depth (Fig. 9) indicates some different patterns of descent and ascent by tarpon. Both descents and ascents started slowly because of physical laws such as Newton's laws of motion. However, maximum speeds were mostly reached at middle depths on descents, but near the surface on ascents. Malte et al. (2007) showed that maximum speeds for bigeye tuna descents and ascents were reached at mid-depths, and Hoolihan et al. (2009) reported the same for billfish. We believe that the differences are the result of the particular feeding behavior of tarpon. The Atlantic tarpon typically attacks prey from underneath since it has a super-terminal mouth (Guigand & Turingan 2002, Jud et al. 2011). The high instantaneous ascent speeds observed near the surface are most likely the result of attacking near-surface prey.

Our results show that there were diel differences in vertical swim speeds (Table 3). During the day, 5 of the 8 ind. had faster descent speeds than ascent, while there were no differences in the other 3. But during the night, only 2 of the 8 ind. had faster descent than ascent speeds, and 3 ind. had faster ascent than descent speeds. The faster ascent speeds at night are consistent with the observation of more frequent rolling and jumping at night. Hoolihan et al. (2009) reported opposite results for billfish, in that most individuals had faster ascent than descent

speeds during the day, and during the night had faster descent than ascent speeds.

While we do not report detailed horizontal movements here, our results from the first detailed analysis of vertical movement rates extending over a fairly lengthy period provide better understanding of Atlantic tarpon vertical movement behaviors. However, in the future, use of a direct speed sensor would potentially eliminate the errors generated by the unaccounted vertical and horizontal movements in the present study. To this end, a dedicated speed sensor integrated into the PAT tag technology would represent a considerable advancement and help to improve understanding of tarpon movement characteristics.

The RCS data from 1 s sampling tags produced very interesting results of tarpon 'rolling and jumping' frequency. But the number of rolling events recorded by the RCS might be lower than the actual number, because the tag might not come completely out of the water during low rolls due to the length of the tether that attached the tag to the fish. However, this is the first time that anyone has reported such results. The peaks of observed rolls occurred at night and just after sunrise, and are supported by the laudatory tales and spectacular stories of tarpon fishers (Ault 2010). It is not entirely clear why tarpon 'roll' or 'free-jump'. However, Atlantic and Pacific tarpon are the only elopomorph teleosts that have a facultative capacity to breathe air (Graham 1997), and possess a rudimentary lung-capillary system. As facultative air breathers, they surface periodically to gulp air as an alternative to passing water over the gills. Of course, to breathe air, tarpon have to be at the air-sea interface; therefore, rolling may be a mechanism to facilitate air-breathing. Clark et al. (2007) reported that Pacific tarpon under normoxic exercise (swimming at about 1.1 body length s⁻¹) increased air-breathing frequency 8-fold compared to routine air-breathing. Therefore, rolling can be used as an index of activity for tarpons. The higher frequency of rolling at night corresponded well with the faster ascent speeds at night. The peaks of rolling that occurred after sunset and before sunrise are possibly associated with feeding on nocturnal species, while the peak of rolling after sunrise may be associated with feeding on diurnal species after they change habitats during the twilight period (Hobson 1973, Helfman 1978, Sale 1980, Robblee & Ziemen 1984). Improved knowledge of these critical scientific and conservation issues will help to improve our understanding of tarpon ocean habitat use, the interrelationships between predator and prey, the quality

of angling, and inform fishery management on issues that are central to the sustainability of this species, the *Silver King*.

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