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RESEARCH ARTICLE

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Movements of bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags

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Abstract Pop-up satellite archival tags were implanted into 68 Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus), ranging in size from 91 to 295 kg, in the southern Gulf of Maine ($n=67$) and off the coast of North Carolina ($n=1$) between July 2002 and January 2003. Individuals tagged in the Gulf of Maine left that area in late fall and overwintered in northern shelf waters, off the coasts of Virginia and North Carolina, or in offshore waters of the northwestern Atlantic Ocean. In spring, the fish moved either northwards towards the Gulf of Maine or offshore. None of the fish crossed the 45°W management line (separating eastern and western management units) and none traveled towards the Gulf of Mexico or the Straits of Florida (known western Atlantic spawning grounds). The greatest depth recorded was 672 m and the fish experienced temperatures ranging from 3.4 to 28.7°C. Swimming depth was significantly correlated with location, season, size class, time of day, and moon phase. There was also evidence of synchronous vertical behavior and changes in depth distribution in relation to oceanographic features.

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Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) are widely distributed throughout the northern Atlantic Ocean, ranging from Norway to Africa in the east and from Newfoundland to Brazil in the west. The species is considered to be overexploited (NRC 1994) and is currently managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) as two distinct populations, an eastern stock and a western stock separated by 45°W longitude. The two groups are believed to have markedly different reproductive patterns, with eastern fish spawning at a smaller size (15–45 kg vs 135+ kg) and younger age (3–5 years vs 6–10 years) than those in the western Atlantic Ocean (Rodriguez-Roda 1967; Baglin 1982; NRC 1994; Nemerson et al. 2000). The eastern stock reproduces between June and August in the Mediterranean Sea while the western stock spawns between April and June in two known areas, the Gulf of Mexico and the Straits of Florida (Roule 1924; Rivas 1954; Richards 1976).

For decades, stock assessments have indicated that the putative western population is more depleted than the eastern population (Sissenwine et al. 1998). Consequently, catch quotas and size limits in the two management areas have been different (NRC 1994). However, there is some evidence that Atlantic bluefin tuna could comprise a single stock. These include conventional tag returns, similarity in growth rates, synchronous long-term catch trends in the east and west, and a seamless trans-Atlantic distribution of longline catches (ICCAT 2001). Reviews of conventional tag returns provide mixing rate estimates ranging from 1–10% (e.g. NRC 1994; Mather et al. 1995). Recent findings from electronic tagging studies (Lutcavage et al. 1999; Block et al. 2001a), however, suggest that transfer rates may be significantly higher in some years and possibly warrant management of Atlantic bluefin tuna as a single stock.

An improved understanding of bluefin tuna migration patterns, spawning locations and stock structure is clearly necessary for fishery management regulations to be equitable and for rebuilding efforts to have maximal effect. Additionally, knowledge of the depth distribution of bluefin tuna and the physiological limitations and environmental conditions controlling vertical behavior are crucial to the development of habitat-based stock assessments (e.g. Hinton and Nakano 1996; Bigelow et al. 2002; Graves et al. 2003). Until recently, researchers interested in addressing such issues had few options available to them: (1) analysis of catch statistics; (2) conventional tag-recapture studies; or (3) acoustic tracking studies (Boustany et al. 2001). Unfortunately, these techniques are either biased by spatial and temporal patterns in fishing effort or limited to short time scales. Recent technological advances, however, provide us with new, fishery-independent telemetry techniques that can track the movements of fish for periods ranging from months to several years (Block et al. 1998). In the present study, we used pop-up satellite archival tags (PSATs) to examine the horizontal and vertical movements of the Atlantic bluefin tuna seasonally inhabiting the Gulf of Maine.

Materials and methods

Tagging

PSATs (model PTT-100, Microwave Telemetry, Columbia, MD, USA) were deployed on 68 Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus): 67 in the southern Gulf of Maine and one off North Carolina. In addition to recording ambient light levels (used to provide geolocation estimates), these tags recorded depth (into 5.38-m bins) and temperature (resolution ±0.17°C) data at 1-h intervals. Monofilament tethers were used to attach the PSATs to flat metal darts, constructed of either stainless-steel or titanium (Wildlife Computers, Redmond, WA, USA). The metal darts were implanted in the dorsal musculature of the fish using a modified harpoon tagging pole (Chaprales et al. 1998). PSATs were programmed to detach from the fish and transmit their archived light-level, depth, and temperature data through the Argos data collection and location service (DCLS) on 1 June 2003. A fail-safe mechanism in each tag initiates release and data transmission if the tag approaches its depth limit (approx. 1,200 m) or remains at a constant depth for 4 days (e.g., if the fish is dead on the bottom or the tag has prematurely detached and is floating at the surface).

In the southern Gulf of Maine, bluefin tuna schools were captured by the purse seiner "White Dove Too" between mid-July and late September 2002. Some members of each school were allowed to escape and were tagged as they left the net ($n=65$ fish). Temperature profiles of the water column were recorded using expendable bathythermographs (XBTs) (Sippican, Marion, MA, USA) after all purse seine tag deployments. Two tags were also deployed on fish caught in the southern Gulf of Maine on rod and reel from the sport-fishing vessel "Cookie Too" in early October 2002 using methods previously described (Lutcavage et al. 1999). The North Carolina fish was caught on rod and reel from the sport-fishing vessel "Striker" on 14 January 2003.

Horizontal movements

Geolocation estimates were computed from recovered light-level data using a proprietary algorithm (Microwave Telemetry) derived from US Naval Observatory data. These estimates are based on daily records of the time of sunrise and sunset, taking into account prevailing conditions measured by the light, pressure, and temperature sensors, and data from the preceding days. A state-space Kalman filter model (Sibert and Fournier 2001; Sibert et al. 2003) was then applied to estimate movement parameters and provide a "most probable" trackline for each fish. Residency periods in two seasonal habitats, the Gulf of Maine and coastal waters off Virginia and North Carolina, were calculated by determining the mean dates of arrival and departure for all fish that entered these areas. For this analysis, the Gulf of Maine was defined as waters north of 40°N latitude and west of 65°W longitude (these boundaries include Georges Bank in the Gulf of Maine habitat area). Virginia and North Carolina waters were bounded to the north by 38°N latitude and to the east by 73°W longitude. Only permanent movements into or away from these areas were considered (i.e. brief excursions inside or beyond these boundaries were ignored).

Fixed kernel utilization distribution contours (Worton 1989) representing 50% (core areas of distribution) and 95% (overall range of distribution) of the pooled daily geolocation estimates were created for seasonal subsets of the data to examine temporal patterns in horizontal distributions. These were derived using the animal movement analysis extension (Hooge and Eichenlaub 1997) and the ArcView Geographic Information System (version 3.2, Environmental Systems Research Institute, Redlands, CA, USA). Contour smoothing parameters were calculated using least-squares cross-validation (Silverman 1986).

Vertical movements

We used generalized estimating equations (GEEs) (Liang and Zeger 1986) to examine the effects of the following variables: location (inshore, offshore, indeterminate), season (July–October, November–February, March–May), size class (≤ 136 kg, >136 kg), time of day (dawn, day, dusk, night), and moon phase (full moon, new moon, intermediate moon) on vertical distribution, as repeated observations of depth are correlated. If autocorrelation is ignored, multiple measurements of a single sampling unit are treated as single measurements from multiple sampling units. Such pseudoreplication erroneously increases the sample size and inflates the power of the statistical analysis, leading to the description of phenomena that the data may not actually support.

Locations were determined by examining the filtered tracklines and depth records of each fish. Indeterminate locations were those where it was not possible to assign an inshore or offshore locality with any certainty. The smaller size class presumably contained immature (i.e. non-spawning) fish, if western bluefin tuna are fully mature at a weight of approximately 136 kg (Baglin 1982; NRC 1994). The larger size class was presumed to represent entirely adult fish. Dawn, day, dusk, and night were defined as 0500–0600 hours, 0700–1600 hours, 1700–1800 hours, and 1900–0400 hours, respectively (Eastern Standard Time). No adjustments were made to account for the effects of longitudinal movements or seasonal change on the time of sunrise and sunset. Full and new moons refer to the day of each full or new moon and the two days preceding and following it.

We assumed that observations were distributed as gamma random variables and that correlation between depth observations could be modeled as an autoregressive process with lag one. This allowed us to account for the fact that all data were bounded at zero (depths of zero or greater were set to -0.1 m) and assume that correlation between observations decreased exponentially as the time between observations increased. A powerful advantage of GEEs over more traditional mixed effect models is that GEEs treat the correlation coefficients as nuisance parameters, and therefore the statistical tests are robust to mis-specification of the correlation structure (Diggle et al. 1994).

The analysis was implemented in SAS (version 8.02, SAS Institute, Cary, NC, USA) using the PROC GENMOD procedure. Significance tests are based on type III Wald statistics, which are chi-square distributed, with an alpha level of 0.05 for main effects and 0.10 for interaction effects (Sokal and Rohlf 1981). Type III test statistics are "marginal statistics" in that they report the significance of a given variable after taking into account the other variables in the model. If a main effect is involved in a significant interaction, the main effect is retained in the model regardless of its significance (McCullagh and Nelder 1989). Differences between levels of the categorical variables were analyzed using Wald chi-square tests based on population marginal means (Searle et al. 1980), and adjusted for multiple comparisons using Bonferroni adjustments (adjusted P-value = estimated P-value multiplied by the number of comparisons). Marginal population means are the predicted means of the dependent variable (depth) associated with each level of an independent variable (e.g. location) when all other variables in the model are set to their estimated mean values.

Results

Data were received from 60 of the 68 tags, three of which remained attached until the programmed pop-up date. One fish died immediately after release, leaving 59 tags for inclusion in the dataset. A summary of the dates and locations of the start and end of each tag deployment, fish weights, days at liberty, and distance traveled is provided in Table 1.

Horizontal movements

Sufficient geolocation data were available to estimate the horizontal movements of 50 bluefin tuna. The maximum distance traveled was 5820 km in 304 d, with average daily movements ranging from 1.6–71.6 km day^{-1} (mean ± SE 16.18 ± 1.95 km day^{-1}) (Table 1). Of the 50 fish, 23 remained in northern coastal waters between Maryland and Nova Scotia (many of these tags detached after only short periods at liberty). The fish tagged off North Carolina (03–01) stayed in that area for the duration of tag attachment. Of the remaining 26 fish, 13 traveled southwest to coastal waters off Virginia and North Carolina after leaving the Gulf of Maine (Fig. 1A). Nine moved offshore (i.e. beyond the shelf break) into the northwestern Atlantic Ocean (Fig. 1B). Four fish traveled to more than one defined locality: two fish (02–13 and 02–17) first moved offshore and then into coastal waters off Nova Scotia; one individual (02–25) spent time off the Virginia coast before moving offshore into the Atlantic Ocean; and another (02–34) traveled to Nova Scotia waters, then to areas off Virginia and then back to Nova Scotia waters before returning to the Gulf of Maine.

Fish tagged in the Gulf of Maine left that area in late October (mean ± SE 25 Oct 2002 ± 16.26 days) (n = 34 fish). Of those that entered coastal waters off Virginia and North Carolina, the mean dates of arrival and departure were 24 Nov 2002 ± 11.90 days (n = 16 fish) and 4 Feb 2003 ± 10.84 days (n = 3 fish), respectively. As a result of tag shedding and the 1 June 2003 programmed pop-up date, only three records of fish returning to the Gulf of Maine were obtained. The mean date of arrival was 5 May 2003 ± 12.47 days, but this is likely biased towards early returning fish.

Temporal patterns in the distribution of bluefin tuna are shown in the seasonal distribution contours presented in Fig. 2A–C. In summer/fall (July-October), the 50% and 95% probability contours are centered around the tagging location in the southern Gulf of Maine (Fig. 2A). Over the winter months (November–February), the core area of distribution (50% probability contour) shifted southwards to coastal waters off Virginia and North Carolina (Fig. 2B). The overall range

Table 1 Dates and locations of the start and end of each tag deployment on bluefin tuna (*Thunnus thynnus*). Reporting date/location refers to the point at which the tag transmitted its data to the satellite. Locations are provided in decimal degrees. Fish weights were initially estimated to the nearest 50 lb and then converted to kg. Days at liberty is the period for which the tag remained attached to the fish. Distance traveled is along the "most probable" trackline

Fish ID	Weight (kg)	Tagging date	Tagging location		Reporting date	Reporting location		Days at liberty	Distance traveled (km)	Distance traveled (km) d^{-1}
			Latitude	Longitude		Latitude	Longitude			
2–1	136	17 Jul 02	41.97°N	69.39°W	4 Aug 02	41.65°N	69.06°W	18	535	29.7
2–2	181	17 Jul 02	41.97°N	69.39°W	27 Jul 02	41.81°N	69.46°W	10	19	1.9
2–3	204	17 Jul 02	41.97°N	69.39°W	18 Sep 02	39.99°N	69.36°W	63	354	5.6
2–4	136	17 Jul 02	41.97°N	69.39°W	22 Jan 03	36.31°N	73.74°W	189	-	-
2–5	204	17 Jul 02	41.97°N	69.39°W	18 Sep 02	44.79°N	60.87°W	63	1912	30.3
2–6	181	17 Jul 02	41.97°N	69.39°W	29 Jul 02	41.88°N	69.43°W	12	19	1.6
2–7	136	17 Jul 02	41.97°N	69.39°W	18 Mar 03	36.83°N	73.45°W	244	1476	6.0
2–8	136	17 Jul 02	41.99°N	69.40°W	20 Feb 03	35.82°N	60.45°W	218	2995	13.7
2–9	159	17 Jul 02	41.99°N	69.40°W	16 Sep 02	42.10°N	67.76°W	61	391	6.4
2–10	113	17 Jul 02	41.99°N	69.40°W	17 Mar 03	38.93°N	65.53°W	243	4535	18.7
2–11	136	1 Aug 02	42.02°N	69.02°W	9 Dec 02	34.16°N	77.12°W	130	1445	11.1
2–12	136	1 Aug 02	42.02°N	69.02°W	25 Jan 03	36.22°N	63.05°W	177	2216	12.5
2–13	159	1 Aug 02	42.02°N	69.02°W	1 Jun 03	41.15°N	66.90°W	304	2050	6.7
2–14	181	1 Aug 02	42.02°N	69.02°W	7 Apr 03	39.12°N	71.65°W	249	2870	11.5
2–15	159	1 Aug 02	42.02°N	69.02°W	7 Mar 03	40.10°N	55.43°W	218	2486	11.4
2–16	204	1 Aug 02	42.02°N	69.02°W	22 Jan 03	39.55°N	63.22°W	174	1458	8.4
2–17	181	1 Aug 02	42.02°N	69.02°W	7 Feb 03	42.89°N	62.21°W	190	3512	18.5
2–18	136	1 Aug 02	42.02°N	69.02°W	7 May 03	40.42°N	68.71°W	279	2302	8.3
2–19	136	1 Aug 02	42.02°N	69.02°W	5 Oct 02	40.47°N	68.56°W	65	-	-
2–20	181	1 Aug 02	42.02°N	69.02°W	29 Dec 02	38.31°N	72.72°W	150	2217	14.8
2–21	136	1 Aug 02	42.02°N	69.02°W	20 Feb 03	43.24°N	60.49°W	203	2245	11.1
2–22	181	1 Aug 02	42.02°N	69.02°W	14 Dec 02	34.46°N	75.15°W	135	1462	10.8
2–23	136	1 Aug 02	42.02°N	69.02°W	30 Jan 03	33.99°N	76.36°W	182	1578	8.7
2–24	181	1 Aug 02	42.02°N	69.02°W	13 Dec 02	39.06°N	68.45°W	134	1525	11.4
2–25	181	1 Aug 02	42.02°N	69.02°W	1 Jun 03	40.66°N	52.55°W	304	5820	19.1
2–26	136	1 Aug 02	42.11°N	69.07°W	15 Sep 02	42.08°N	67.50°W	45	240	5.3
2–27	113	1 Aug 02	42.11°N	69.07°W	19 Oct 02	42.95°N	68.57°W	79	555	7.0
2–28	113	1 Aug 02	42.11°N	69.07°W	29 Oct 02	37.17°N	74.96°W	89	1274	14.3
2–29	91	1 Aug 02	42.11°N	69.07°W	6 Nov 02	40.69°N	69.10°W	97	1869	19.3
2–30	136	1 Aug 02	42.11°N	69.07°W	27 Nov 02	37.12°N	74.44°W	118	1303	11.0
2–31	91	1 Aug 02	42.11°N	69.07°W	2 Jan 03	38.62°N	72.77°W	154	858	5.6
2–32	136	8 Aug 02	41.88°N	68.84°W	16 Feb 03	36.75°N	75.17°W	192	1947	10.1
2–33	136	8 Aug 02	41.88°N	68.84°W	22 Feb 03	43.38°N	61.96°W	198	1623	8.2
2–34	113	8 Aug 02	41.88°N	68.84°W	1 Jun 03	40.26°N	68.14°W	297	5764	19.4
2–35	136	8 Aug 02	41.88°N	68.84°W	11 Dec 02	41.05°N	64.82°W	125	1743	13.9
2–36	159	8 Aug 02	41.88°N	68.84°W	18 Aug 02	41.76°N	67.98°W	10	221	22.1
2–37	91	8 Aug 02	41.88°N	68.84°W	21 Aug 02	39.93°N	72.74°W	13	931	71.6
2–38	136	8 Aug 02	41.88°N	68.84°W	19 Sep 02	41.74°N	66.41°W	42	775	18.5
2–39	159	8 Aug 02	41.88°N	68.84°W	24 Sep 02	40.63°N	71.54°W	47	655	13.9
2–40	159	8 Aug 02	41.88°N	68.84°W	15 Dec 02	33.59°N	77.32°W	129	1565	12.1
2–41	136	8 Aug 02	41.88°N	68.84°W	31 Aug 02	41.83°N	69.34°W	23	622	27.0
2–42	159	8 Aug 02	41.88°N	68.84°W	26 Oct 02	41.94°N	66.72°W	79	396	5.0
2–43	136	8 Aug 02	41.88°N	68.84°W	18 Aug 02	41.90°N	67.72°W	10	186	18.6
2–44	91	8 Aug 02	41.88°N	68.84°W	7 Mar 03	41.19°N	61.28°W	211	3263	15.5
2–45	136	8 Aug 02	41.88°N	68.84°W	4 Nov 02	42.50°N	66.93°W	88	1154	13.1
2–46	147	8 Aug 02	41.88°N	68.84°W	19 Dec 02	41.88°N	62.89°W	133	1173	8.8
2–47	113	17 Aug 02	41.88°N	68.72°W	1 Mar 03	37.85°N	50.77°W	196	4147	21.2
2–48	204	6 Sep 02	41.30°N	69.17°W	25 Sep 02	39.41°N	72.12°W	19	-	-
2–49	204	30 Sep 02	41.43°N	68.98°W	24 Oct 02	39.88°N	70.75°W	24	-	-
2–50	227	30 Sep 02	41.43°N	68.98°W	1 Feb 03	36.00°N	73.18°W	124	948	7.6
2–51	204	30 Sep 02	41.43°N	68.98°W	1 Nov 02	33.87°N	75.17°W	32	1461	45.7
2–52	295	30 Sep 02	41.43°N	68.98°W	12 Oct 02	41.76°N	68.78°W	12	-	-
2–53	272	30 Sep 02	41.43°N	68.98°W	16 Oct 02	33.61°N	71.22°W	16	995	62.2
2–54	249	30 Sep 02	41.43°N	68.98°W	6 Oct 02	39.79°N	69.72°W	6	-	-
2–55	227	30 Sep 02	41.43°N	68.98°W	6 Oct 02	41.84°N	68.06°W	6	-	-
2–56	181	30 Sep 02	41.43°N	68.98°W	8 Oct 02	41.59°N	69.02°W	8	-	-
2–57	181	10 Oct 02	41.35°N	69.20°W	16 Oct 02	40.36°N	71.38°W	6	-	-
2–58	272	10 Oct 02	41.35°N	69.20°W	9 Nov 02	33.89°N	76.63°W	30	1298	43.3
3–1	125	14 Jan 03	34.38°N	76.52°W	11 May 03	38.24°N	72.91°W	117	1229	10.5

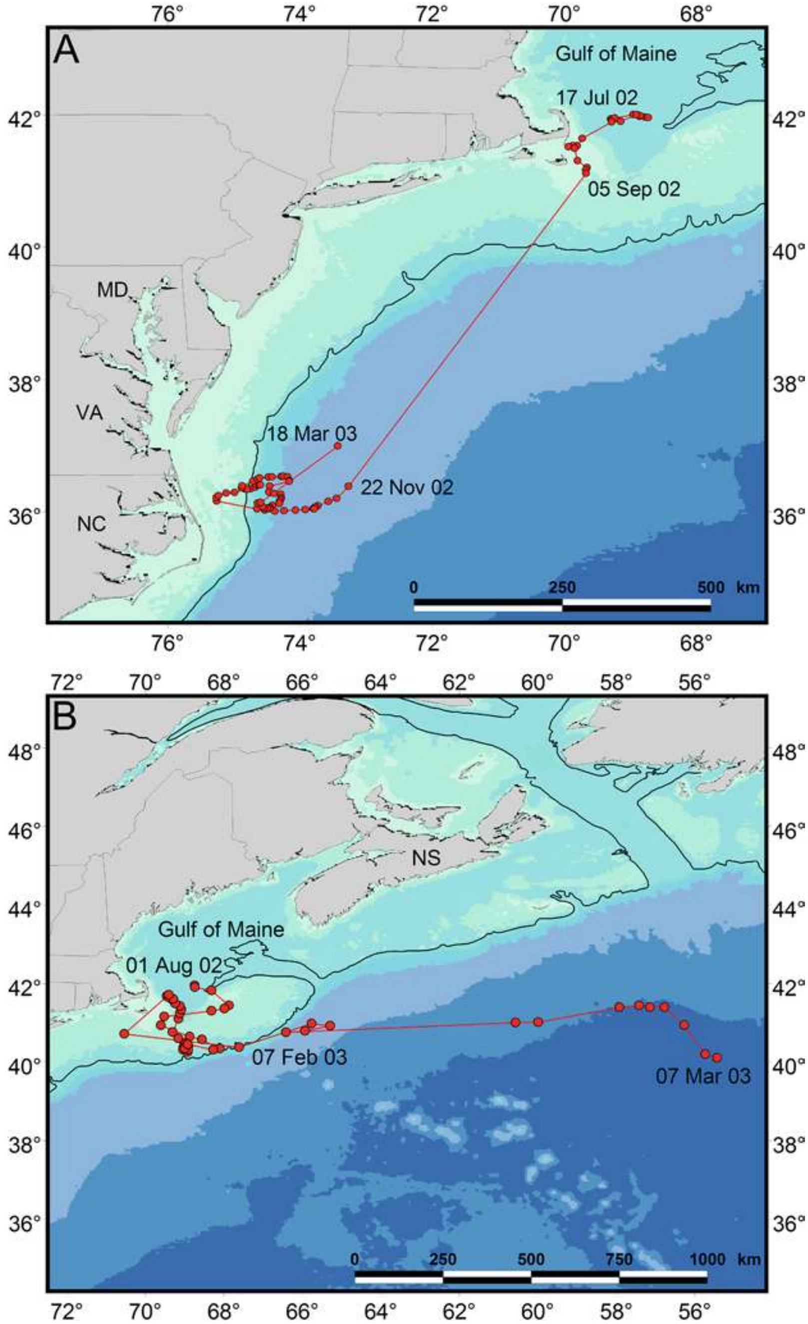

Fig. 1 Exemplary Kalman filtered tracks of bluefin tuna (*Thunnus thynnus*): **A** fish 02–07 and **B** fish 02–15. The 200-m isobath (*black line*) indicates approximate position of the shelf break. *NS* Nova Scotia, *MD* Maryland, *VA* Virginia, *NC* North Carolina

(95% probability contour) extended northwards to Nova Scotia waters and offshore as far as 60°W longitude. In the spring months (March–May), the core area of distribution remained in coastal waters off Virginia and North Carolina while the overall range extended offshore as far as 50°W longitude (Fig. 2C).

Vertical movements

Depth and temperature data, recorded at one-hour intervals, were recovered from all 59 tags in the dataset. Figure 3A shows the percentage time-at-depth (10-m intervals) in darkness and during the day. The fish spent >25% of their time in the top 10 m of the water column (night = 27.5%, day = 29.8%) and >50% of their time at depths of ≤20 m (night = 57.0%, day = 51.0%). The maximum depth recorded by any fish was 672 m. Most deep descents (to depths of >200 m) were made during the day. Figure 3B shows the percentage time-at-temperature (2°C intervals) for night and day combined. The fish spent >50% of their time in water of 15–23°C and encountered ambient temperatures of 3.4–28.7°C. Temperature changes of up to 19°C were experienced in a single day, with most fish encountering differentials of 15–17°C (Fig. 4). A weak correlation was found between

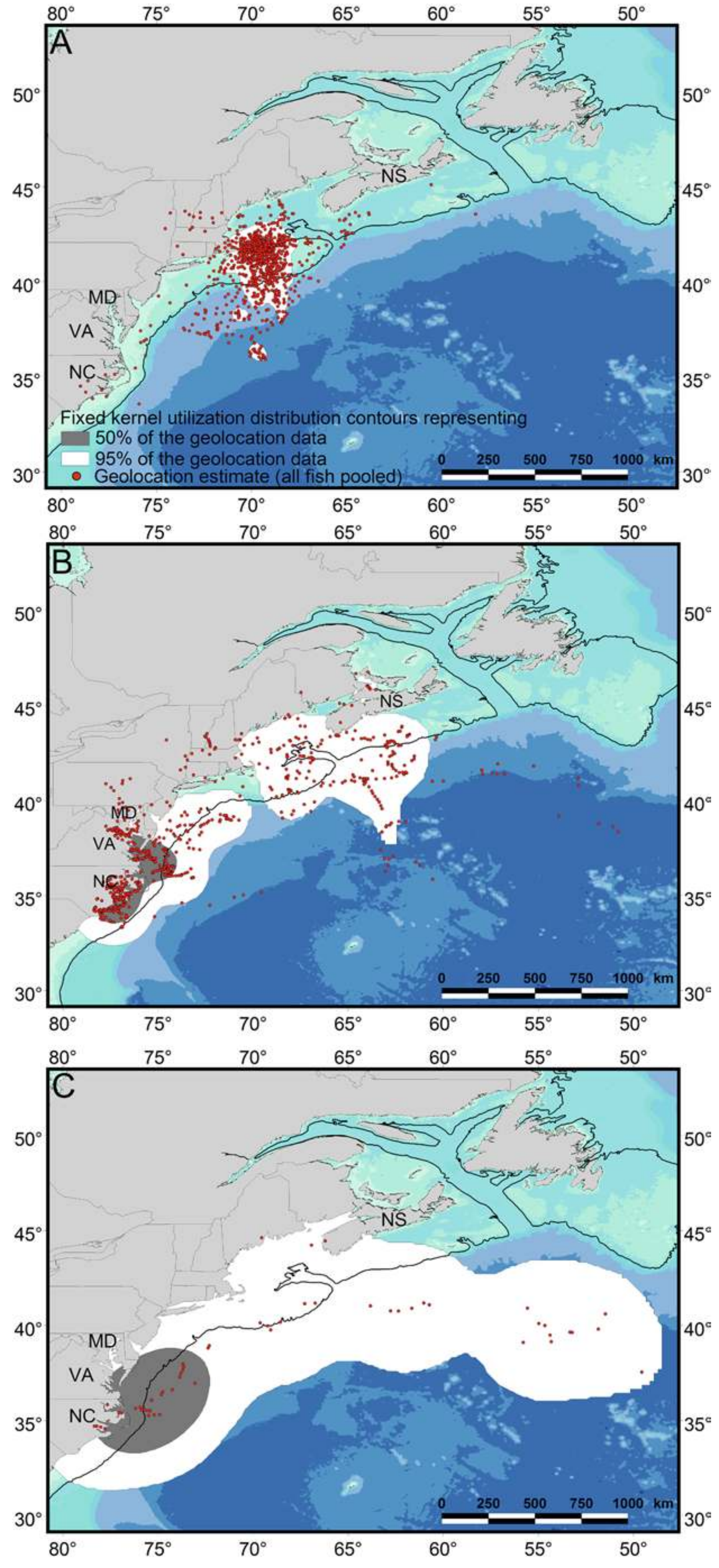

Fig. 2A–C Distribution contours comprising 50% and 95% of the pooled geolocation data. **A** July–October ($n = 50$ fish), **B** November–February ($n = 33$ fish), and **C** March–May ($n = 11$ fish). The 200-m isobath (*black line*) indicates approximate position of the shelf break. *NS* Nova Scotia, *MD* Maryland, *VA* Virginia, *NC* North Carolina

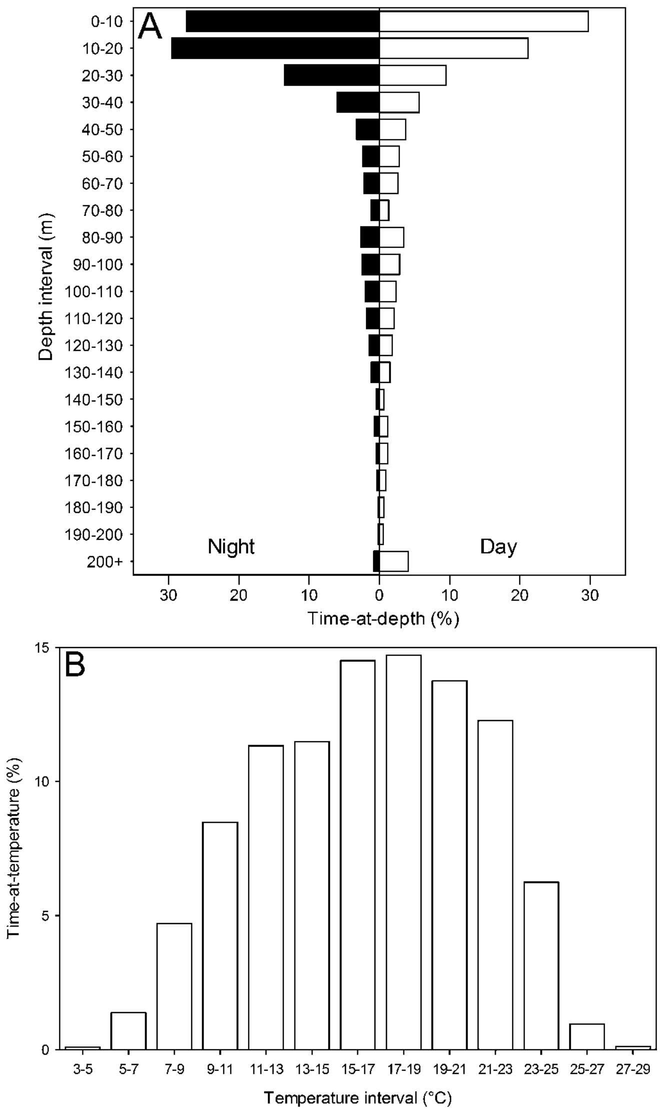

Fig. 3 Histograms showing percentage **A** time-at-depth (night = 2000–0500 hours, day = 0600–1900 hours) and **B** time-at-temperature. Data from all fish in dataset pooled ($n = 59$ fish)

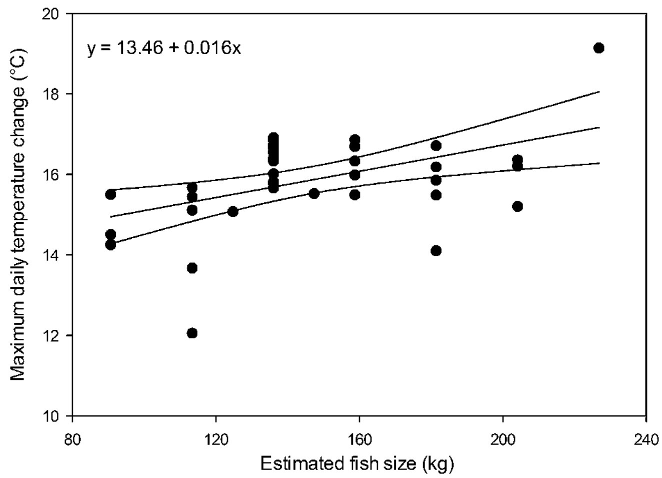

Fig. 4 Scatterplot of estimated fish size versus maximum daily temperature change ($n = 38$). Fish with depth records of < 30 days were excluded from this analysis. Linear regression line and 95% confidence intervals are included

fish size and maximum daily temperature change (linear regression: $r^2 = 0.218$, $P < 0.05$), with larger fish experiencing larger daily temperature changes than smaller fish.

GEE analysis indicated that swimming depth was significantly correlated with location, season, size class, time of day, and moon phase (Tables 2, 3). The effect of season differed by location and the effect of size class differed by season. Time of day and moon phase effects differed by both location and season. Swimming depths at inshore locations were shallower than those at offshore and indeterminate locations ($X_1^2 = 51.47$, adjusted $P < 0.001$; $X_1^2 = 75.98$, adjusted $P < 0.001$), but depths at offshore and indeterminate locations did not differ ($X_1^2 = 2.48$, adjusted $P = 0.35$).

Swimming depths during the winter months (November-February) were deeper than those during the summer/fall (July-October) and spring (March-May)

Table 2 Wald statistics for type III analyses

Variable	*df*	Chi-square	*P*-value
Location	2	76.25	< 0.001
Season	2	53.89	< 0.001
Season × location	4	54.12	< 0.001
Size class	1	3.25	0.072
Size class × season	2	7.16	0.028
Time of day	3	70.47	< 0.001
Time of day × location	6	77.89	< 0.001
Time of day × season	6	79.77	< 0.001
Time of day × location × season	12	462.04	< 0.001
Moon phase	2	16.07	< 0.001
Moon phase × location	4	4.43	0.350
Moon phase × season	4	20.03	< 0.001
Moon phase × location × season	8	53.01	< 0.001

Table 3 Mean depths (m) of variable categories

Variable	Category	Mean depth (m)
Location	Inshore	22.17*
	Offshore	45.45
	Indeterminate	53.19
Season	July–October	29.15
	November–February	54.95*
	March–May	29.85
Size class	≤ 136 kg	32.36
	> 136 kg	38.02
Time of day	Dawn	33.78
	Day	40.82*
	Dusk	34.25
	Night	32.05
Moon phase	Full moon	36.90*
	New moon	33.56
	Intermediate moon	34.48

* significantly different from other categories of the same variable

($X_1^2 = 36.46$, adjusted $P < 0.001$; $X_1^2 = 45.36$, adjusted $P < 0.001$), but were similar during summer/fall and spring ($X_1^2 = 0.12$, adjusted $P = 2.19$). However, there were exceptions: depths during the winter were similar to those during the spring at indeterminate locations; and depths during the summer/fall were shallower than those during the spring at indeterminate locations.

The main effect of size class was not significant ($X_1^2 = 3.25$, $P = 0.072$) (i.e. the swimming depths of the two size classes, overall, were similar). There was, however, a significant interaction between size class and season ($X_1^2 = 7.16$, $P = 0.028$), with smaller fish swimming at shallower depths than larger fish during the summer/fall ($X_1^2 = 6.36$, adjusted $P = 0.035$). In contrast, the two size classes had similar swimming depths during the winter and spring months ($X_1^2 = 0$, adjusted $P = 1.0$; $X_1^2 = 0.1$, adjusted $P = 1.0$).

Daytime swimming depths were deeper than those at dusk, night, and dawn ($X_1^2 = 38.87$, adjusted $P < 0.001$; $X_1^2 = 25.62$, adjusted $P < 0.001$; and $X_1^2 = 25.17$, adjusted $P < 0.001$), while depths at dusk, night, and dawn were all similar. However, there were exceptions: depths during the day were not different from those at night at inshore locations; depths during the day were not different from those at dusk at indeterminate locations; depths during the day were not different from those at dusk, night, and dawn at offshore locations; depths at dusk were different from those at dawn at inshore locations; depths at dusk were different from those at night at indeterminate locations; day and dawn depths were similar during the summer/fall; and depths during the day were similar to those at dusk, night, and dawn during the winter.

During full moons, the fish were deeper than during intermediate or new moons ($X_1^2 = 13.58$, adjusted $P < 0.001$; $X_1^2 = 9{,}60$, adjusted $P = 0.006$) and depths during intermediate and new moons were similar ($X_1^2 = 0.95$, adjusted $P = 0.99$). However, there were exceptions: depths during full moons were similar to those during intermediate and new moons at offshore and indeterminate locations; depths during full moons were similar to those during new and intermediate moons in the summer/fall; depths during full moons were similar to those during new moons in the winter; depths during full moons were similar to those during intermediate moons in the spring; and depths during intermediate moons were deeper than those during new moons in the spring.

Figure 5A,B shows simultaneously recorded depth and temperature data from four fish located in the Gulf of Maine (16–22 August 2002). These individuals were tagged at three different locations over a 7-day period, suggesting that similarities in their profiles indicate synchronous behavior patterns rather than evidence that they regrouped into a single school. Evident in these profiles are deep descents made at times of light transition (i.e. at dusk and dawn), with the dusk descent usually to greater depths than the dawn descent. These vertical movements at the beginning and end of each day were sporadic, and usually absent when fish were in waters off the Virginia and North Carolina coasts and beyond the edge of the continental shelf (Fig. 6A–C).

Hourly depth records are plotted over contoured hourly temperature data in Fig. 7A,B. Fish 02–12 appears to have spent its first three weeks at liberty in coastal waters, descending to a maximum depth of 75 m during that period (Fig. 7A). The warm temperature signature of the Gulf Stream (or associated eddies and filaments) is evident in weeks 3–7, with only shallow descents (to a maximum depth of 129 m) made while swimming in this water mass. A change in the vertical behavior of this individual occurred after emerging from the Gulf Stream, with deeper (to a maximum depth of 237 m) and more frequent descents being made. Fish 02–35 entered the Gulf Stream twice between weeks 3–6 and 8–10, with its depth patterns becoming shallower each time (Fig. 7B). Periods spent in cooler waters were again characterized by deeper (to a maximum depth of 344 m) and more frequent dives. Similar patterns were observed in other fish spending extended periods offshore.

Discussion and conclusions

Of the 68 tags deployed in this study, only three remained attached until the programmed pop-up date. Possible causes of premature tag release include: (1) dart shedding/ tissue rejection (resulting from dart design, suboptimal placement, etc.); and (2) failure of the tether or the tag's nosecone pin (resulting from material wear/ fatigue, corrosion, predation events, rubbing against the seafloor, etc.). Estimated average daily displacements (1.6–71.6 km day^{-1}) were consistent with results from a previous acoustic tracking study in the Gulf of Maine (Lutcavage et al. 2000). All the fish remained west of the 45°W management line for the period that the tags remained attached. In contrast, 29% of the single-point PSATs deployed in 1997 by Lutcavage et al. (1999) in the Gulf of Maine reported from locations east of the 45°W management line. However, the fish tagged in the present study were significantly smaller than those in the previous study (mean estimated fork length 201 cm vs 224 cm) and bluefin tuna dispersal patterns are known to vary with size and environmental conditions (Mather et al. 1995). Block et al. (2001a) found that 31% of recovered implantable archival tags and 3% of reporting PSATs deployed primarily during the winter in North Carolina waters were east of the 45°W management line.

Most of the fish tagged in the southern Gulf of Maine in late summer/early fall remained in that area until late October, consistent with previous studies (Mather et al. 1995; Lutcavage et al. 1999). Of the 33 fish with PSATs remaining attached over the winter months, 14 remained in northern shelf waters (between Maryland and Nova Scotia), 14 moved south to waters off the coasts of Virginia and North Carolina, and 5 were in offshore waters of the northwestern Atlantic Ocean. In spring, 6 of the 11 fish with tags remaining either stayed in

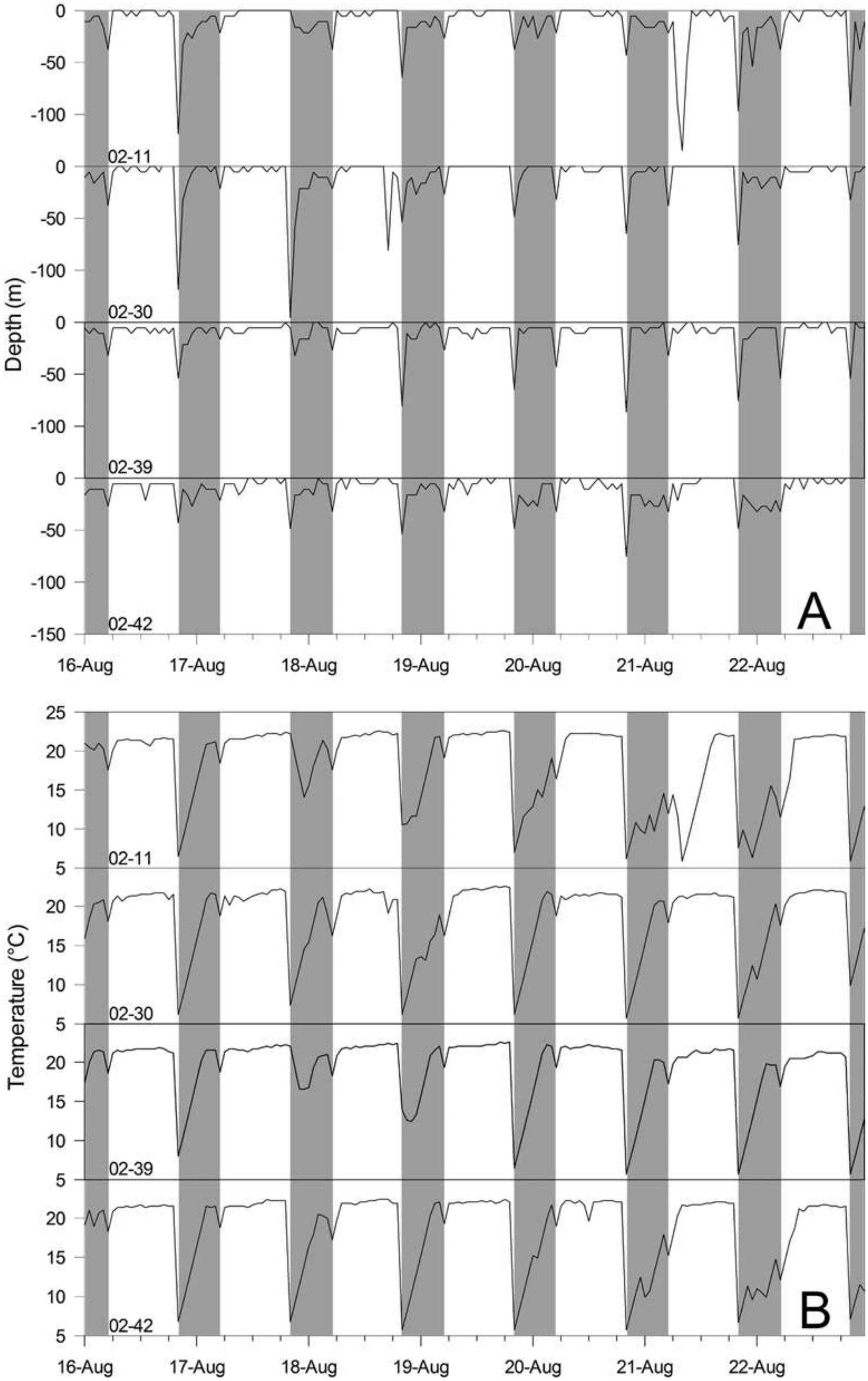

Fig. 5 Hourly **A** depth and **B** temperature data from two fish (02–11 and 02–30) tagged on 1 August 2002 and two fish (02–39 and 02–42) tagged on 8 August 2002 for a 7-day period (16–22 August 2002). *Shaded areas* indicate nighttime

northern waters or moved to that area from Virginia and North Carolina waters and the other five fish moved offshore into the mid-Atlantic Ocean. Similar seasonal movement patterns were displayed by individuals tagged in coastal waters off North Carolina (Block et al. 2001a, 2001b; Gunn and Block 2001). During the winter months, these fish remained either on the Carolina shelf or in offshore waters of the northwestern Atlantic Ocean and moved offshore along the path of the Gulf Stream in spring. By summer, many were in northern shelf waters.

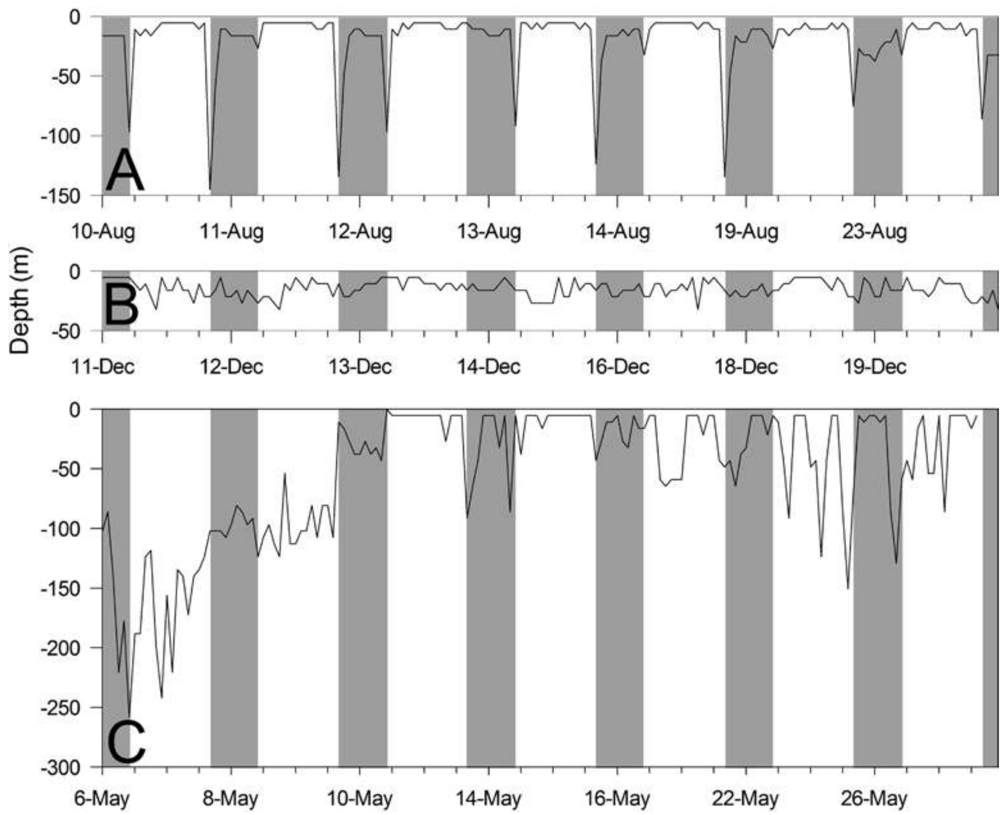

Fig. 6 Hourly depth data from fish 02–25 for three 7-day periods when located in **A** the Gulf of Maine, **B** coastal waters off Virginia and North Carolina, and **C** offshore waters. Note that days are not necessarily consecutive due to incomplete data transmission. *Shaded areas* indicate nighttime

The residency periods calculated for the Gulf of Maine and coastal waters off Virginia and North Carolina temporally coincide with commercial and recreational fisheries targeting bluefin tuna in these habitats.

None of the 11 fish (6 of which were of mature size i.e. ≥136 kg) at liberty between March and May moved towards a known western Atlantic spawning ground. There are, however, conventional tag records of fish tagged in the Gulf of Maine being recaptured in the Gulf of Mexico during the spawning season (Mather et al. 1995). Individuals tagged off North Carolina have also traveled to the Gulf of Mexico and were presumed to have spawned there (Block et al. 2001a; Gunn and Block 2001). Atlantic bluefin tuna are believed to spawn in sea surface temperatures of 24°C and higher (Richards 1976; NRC 1994; Mather et al. 1995; Schaefer 2001), yet none of our temperature records of 24°C and higher were collected during the spring spawning period. Our data, therefore, imply either that: (1) mature fish do not spawn each year (Lutcavage et al. 1999); or (2) they spawn at other locations in waters cooler than 24°C, such as off the Carolinas, along the edge of the Gulf Stream, in the Caribbean Sea, or in the central Atlantic Ocean. These areas have been proposed as possible spawning grounds (Mather 1974; Baglin 1976; Suzuki and Ishizuka 1990; Lutcavage et al. 1999; Block et al. 2001a; Secor et al. 2002). Bluefin tuna larvae have been collected along the shelf break off North Carolina, but these were thought to have been advected northwards in the Gulf Stream from known spawning grounds (McGowan and Richards 1989). As a number of individuals moved into the mid-Atlantic Ocean in the spring, we cannot discount the possibility that some fish may have moved to the Mediterranean or other spawning areas after either tag detachment or the programmed 1 June 2003 pop-up date. Records obtained from implanted archival tags have shown such movements (Block et al. 2001a; Gunn and Block 2001). Recently, we verified that data reception from current PSATs by Argos DCLS receivers is poor to nonexistent in the central and western Mediterranean (Lutcavage et al., unpublished data). Bluefin of mature size have historically been captured throughout the central Atlantic Ocean and in the Caribbean Sea (Bullis and Captiva 1955; Wilson and Bartlett 1967), where they are still encountered by pelagic longliners. These areas do not include known feeding or spawning grounds and the reproductive status of these fish is not known (Richards 1976; Mather et al. 1995; Lutcavage and Luckhurst 2002).

Archival tags utilize light-level data to estimate latitude (from day length) and longitude (from time of local noon). Several factors can influence the accuracy of these estimates, including equinoxes, light attenuation, water clarity, resolution of the light sensor, and vertical behavior of the fish (Arnold and Dewar 2001; Musyl et al. 2001). A detailed analysis of the accuracy of the geolocation estimates presented here will be provided in a subsequent paper (Sibert et al., in preparation).

Our data show that Atlantic bluefin tuna spend the majority of their time in the top 20 m of the water

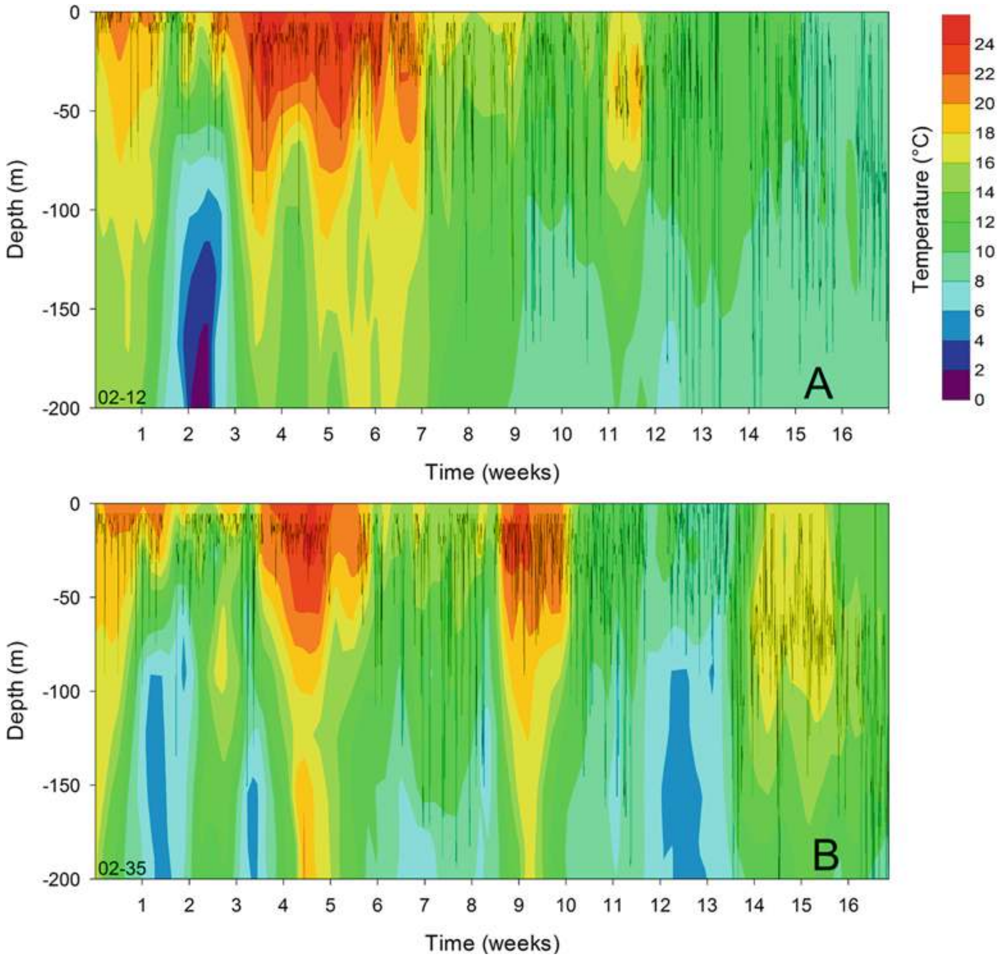

Fig. 7 Hourly depth data from **A** fish 02–12 and **B** fish 02–35 plotted over contoured hourly temperature data

column, descending occasionally to depths in excess of 500 m. The wide range of environmental temperatures experienced (3.4–28.7°C) by the fish was similar to that previously reported for this species in the northwestern Atlantic Ocean (Carey and Lawson 1973; Lutcavage et al. 2000; Block et al. 2001a, 2001b; Brill et al. 2002). Daily temperature changes of up to 19°C were recorded and a weak relationship was noted between fish size and maximum daily temperature change. Brill and Lutcavage (2001) suggested that bluefin tuna tolerate maximum changes of 14°C and that this is independent of fish size, as in other tuna species (e.g. yellowfin tuna, *Thunnus albacares*, Brill et al. 1999).

The vertical behavior of bluefin tuna differed among locations, with shallower swimming depths occurring when fish were in inshore waters. It seems unlikely that this reflects bathymetric constraints, as mean swimming depths at offshore and indeterminate locations were shallower than the seafloor in inshore habitats. Rather, these distributions may reflect shallower prey depths in coastal waters. Alternatively, these visual predators may be distributed closer to the surface due to reduced light penetration in turbid inshore waters. Atlantic bluefin tuna inhabiting the Gulf of Maine during the summer months are known to have a predominantly piscivorous diet, with sandlance (*Ammodytes americanus*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), and unidentified squid species the most common prey items (Crane 1936; Lutcavage et al. 2000; Chase 2002; Estrada et al., submitted). In contrast, stomach contents of individuals captured in the winter fishery off North Carolina contain mostly Atlantic menhaden (*Brevoortia tyrannus*) and unidentified portunid crabs (J.A. Buckel, North Carolina State University, personal communication). In offshore waters, bluefin tuna sampled during pelagic longline cruises had mostly mesopelagic fishes and squid in their stomachs (Matthews et al. 1977), indicating very different feeding regimes. Fish arriving in the Gulf of Maine in early summer are often quite emaciated, and stable isotope analysis of their tissues suggests that they feed on prey items from lower trophic levels in the months preceding their arrival (Estrada et al., submitted). Similarly, Young et al. (1997) found that juvenile southern bluefin tuna (*Thunnus maccoyii*) have a diet composed mainly of fish when on the continental shelf and squid and planktonic crustaceans when in offshore waters.

We found that swimming depths varied among seasons, with fish distributed significantly deeper during the winter months, despite many fish being located in shallow coastal waters off the coasts of Virginia and North Carolina at that time of year. Kitagawa et al. (2000) also noted seasonal differences in the vertical distributions of small Pacific bluefin tuna (*Thunnus orientalis*), with deeper distributions occurring during the winter months in association with a mixed water column. During the summer, they found that fish were limited to mostly surface waters by strong thermal gradients. Similarly, strong thermoclines develop in the Gulf of Maine during the summer and fall months, evident in the XBT profile presented in Fig. 8. It is not surprising, therefore, that most of the maximum daily temperature changes presented in Fig. 4 were recorded during this period. In contrast, shelf waters off North Carolina are known to be only weakly stratified during the winter months due to storm mixing and cooling (Werner et al. 1999). Furthermore, temperature data recorded by our tags during the winter often revealed a relatively homogenous water column.

We have also found that Atlantic bluefin tuna tagged in the Mediterranean Sea (DeMetrio et al., unpublished data), where warm isotherms extend to depths of hundreds of meters in certain locations, have deeper distributions and are more vertically active than those in the present study. This suggests that strong thermal gradients limit the vertical movements of Atlantic bluefin tuna. This is illustrated in the vertical profiles of fish 02–25 over the different seasons (Fig. 6A–C). The location of prey in the different habitats occupied by the fish at different times of the year may also contribute to seasonal changes in vertical behavior (Nakamura 1965; Mather et al. 1995; Marcinek et al. 2001).

Overall, no significant difference was found between the depths of the two size classes. The relatively large size (91–136 kg) of the smaller size class in this study may account for this (i.e. fish in the smaller size class may have exhibited adult depth patterns). Previous studies have noted that the depth distributions of juvenile Atlantic bluefin tuna (Roffer 1987; Brill et al. 2002) and Pacific bluefin tuna (Marcinek et al. 2001; Itoh et al

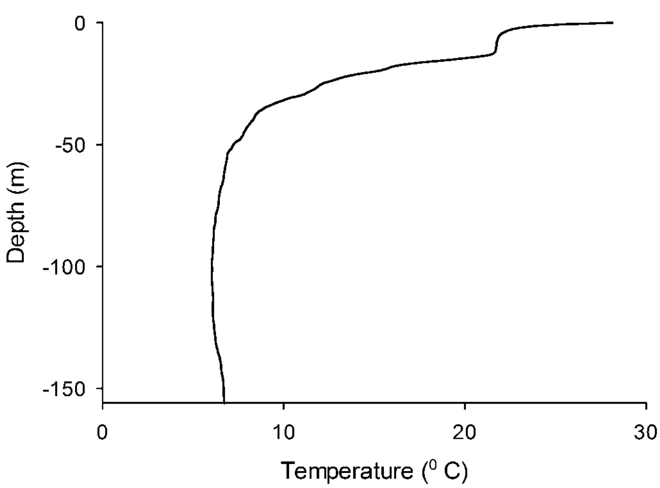

Fig. 8 Vertical profile of water temperature recorded with an XBT in the southern Gulf of Maine on 17 August 2002. Note the strong summer thermocline

2003) are restricted to the mixed surface layer, with only brief excursions made to significant depths. As body mass is known to affect the rate of change in muscle temperature following a change in ambient temperature (Neill and Stevens 1974; Neill et al. 1976; Brill et al. 1994), small fish may need to spend most of their time in surface waters in order to maintain optimal body temperatures. Similarly, Brill and Lutcavage (2001) report that small bigeye tuna (*Thunnus obesus*) have shallower daytime depths than larger individuals. Holland et al. (1992) and Dagorn et al. (2000) suggested that small bigeye tuna make frequent daytime excursions into surface waters in order to increase their body temperatures and repay oxygen debt. We did find, however, that the depths of smaller fish were shallower than those of larger fish during the summer/fall. Although there was no difference between the temperature changes routinely experienced by acoustically tracked juvenile and adult Atlantic bluefin tuna (Brill and Lutcavage 2001), our data imply that the strong summer thermoclines that develop in the Gulf of Maine may constrain the vertical movements of smaller fish to a greater extent than those of larger individuals. This is corroborated by the weak correlation identified between fish size and maximum daily temperature change.

Daytime depths were significantly deeper than those at dusk, night, and dawn. Clear day-night differences have been identified in the vertical distributions of many large pelagic fishes, including tunas (e.g. Yuen 1970; Holland et al. 1992; Josse et al. 1998; Dagorn et al. 2000; Kitagawa et al. 2000; Schaefer and Fuller 2002; Itoh et al. 2003; Musyl et al. 2003), billfishes (e.g. Carey and Robison 1981; Carey 1990; Holland et al. 1990), and sharks (e.g. Carey and Scharold 1990; Nelson et al. 1997; West and Stevens 2001). In each of these studies, daytime distributions were deeper than those occurring during the night. Such depth patterns might be expected if the fish were following certain isolumes/light levels (Blaxter and Parrish 1965; Boden and Kampa 1967; Carey and Robison 1981) or diurnal vertical migrations of the deep scattering layer (DSL) and associated prey (e.g. Carey 1990; Josse et al. 1998; Dagorn et al. 2000; Marcinek et al. 2001).

The majority of deep descents (to depths of >200 m) occurred during daytime. They likely represent foraging excursions (Holland et al. 1992; Kitagawa et al. 2000; Schaefer and Fuller 2002). In other studies, such descents appear to be associated with an increase in the frequency of vertical excursions, but this is difficult to ascertain with our data given the hourly depth-sampling interval. Hypotheses proposed to account for such regular up-and-down movements in the water column include: (1) fish swim up and glide down to conserve energy (Weihs 1973); (2) it is a form of behavioral thermoregulation (Carey and Scharold 1990); (3) the movements represent a search pattern used to detect odors in different strata of the water column and thus guide foraging or migratory movements (Westerberg 1984; Carey and Scharold 1990; Gunn et al. 1999); and

(4) the descents are made to detect magnetic fields in the seafloor and thus aid in navigation (Klimley et al. 2002).

We also noted dramatic depth changes at dawn and dusk, a recurring feature in the vertical behavior of large pelagic fishes, including bluefin tuna (Lutcavage et al. 2000; Marcinek et al. 2001), other tunas (e.g. Block et al. 1997), billfishes (Carey and Robison 1981), and sharks (Nelson et al. 1997). While certainly related to changing light levels, their function remains unknown. A number of hypotheses have been suggested, however, including: (1) the descents represent the day's first and last opportunities to visually locate the DSL and associated prey (Davis and Stanley 2001); (2) fish are avoiding certain light levels at which predators would have a visual advantage (Itoh et al. 2003); and (3) the descents represent a shift between behavioral modes (Newlands et al. 2004). In the present study, consistent dawn and dusk descents occurred only when fish were located in the Gulf of Maine, but similar patterns have been detected in fish tagged in North Carolina (Gunn and Block 2001). Lutcavage et al. (2000) suggested that bluefin tuna dive at times of light transition in the Gulf of Maine to prey upon sandlance rising up off the bottom. In other locations, it may be that this behavior is not always beneficial and, therefore, not always exhibited.

Swimming depths were found to be significantly deeper around full moons. A number of other studies have found relationships between the vertical distribution of large pelagic fishes and moon phase, with deeper nighttime distributions found in bigeye tuna (Schaefer and Fuller 2002; Musyl et al. 2003), school sharks (*Galeorhinus galeus*) (West and Stevens 2001), and swordfish (*Xiphias gladius*) (Carey and Robison 1981) during full moons. It seems likely that these vertical changes reflect shifts in the depth distribution of prey in response to increased lunar illumination.

Depth records from fish tagged on different days and in different areas of the Gulf of Maine were remarkably similar. Such synchronized behavior is well known among fishermen targeting bluefin tuna in these waters, with large numbers appearing almost simultaneously at the surface over large areas on so-called "show days" (Lutcavage and Kraus 1995). Upon entering the Gulf Stream, the swimming depth of fish noticeably shoaled and extensive vertical movements ceased (Fig. 7A,B). This behavioral change may again be related to the strong thermal gradients associated with the warm water mass and the cooler waters it flows over. After emerging from the Gulf Stream into cooler and relatively homogenous waters along the edge of the current, regular descents to significant depths resumed. This finding contrasts with a report of bluefin tuna diving to depths of 1,000 m in the Gulf Stream (Gunn and Block 2001).

While the present study has revealed new insights into the horizontal and vertical movements of Atlantic bluefin tuna, many important questions still remain. Although many of the fish exhibited similar movement patterns, they were different from those detected for larger fish in previous years (Lutcavage et al. 1999) and from individuals tagged in North Carolina waters (Block et al. 2001a, 2001b; Gunn and Block 2001). The area occupied by fish in our study represents only a small portion of the northwestern Atlantic Ocean known to be occupied by adult bluefin tuna at the same time of year (e.g. Tiews 1963; Nakamura 1965; Wilson and Bartlett 1967; Mather et al. 1995). Although PSATs are fishery-independent, as opposed to implanted archival tags that must be recovered (Arnold and Dewar 2001), current models do not provide data records of sufficient duration to identify possible spawning and alternative foraging areas, and data reception problems remain. This highlights the need for improved tag technologies, expanded deployments throughout the bluefin tuna's range, and incorporation of movement patterns into operational models to support stock assessment and biomass estimation.

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