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Tracking adult North Atlantic bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry

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Abstract Ultrasonic, depth-sensitive transmitters were used to track the horizontal and vertical movements, for up to 48 h, of 11 adult (136 to 340 kg estimated body mass) North Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus). Fish were tracked in October 1995, September and October 1996, and August and September 1997 in the Gulf of Maine, northwestern Atlantic. The objective was to document the behavior of these fish and their schools in order to provide the spatial, temporal, and environmental information required for direct (i.e. fishery-independent) assessment of adult bluefin tuna abundance using aerial surveys. Transmitters were attached to free-swimming fish using a harpoon attachment technique, and all fish remained within the Gulf of Maine while being followed. Most of the bluefin tuna tagged on Stellwagen Bank or in Cape Cod Bay (and followed for at least 30 h) held a predominately easterly course with net horizontal displacements of up to 76 km d^{-1}. Mean ($\pm$SD) swimming depth for all fish was 14 $\pm$ 4.7 m and maximum depth for individuals ranged from 22 to 215 m. All but one fish made their deepest excursions, often single descents, at dawn and dusk. In general, adult bluefin tuna spent $<8\%$ of their time at the surface (0 to 1 m), $<19\%$ in the top 4 m, but $>90\%$ in the uppermost 30 m. Mean ($\pm$SD) speed over ground was 5.9 km h^{-1}, but for brief periods surpassed 20 to 31 km h^{-1}. Sea surface temperatures during tracking were 11.5 to 22.0 °C, and minimum temperatures encountered by the fish ranged from 6.0 to 9.0 °C. Tagged bluefin tuna and their schools frequented ocean fronts marked by mixed vertebrate feeding assemblages, which included sea birds, baleen whales, basking sharks, and other bluefin schools.

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Supplementary material Figures showing the horizontal movements of Fish 9601, 9702 and 9705 (*Thunnus thynnus*) superimposed on sea surface temperature from Advanced High Resolution Radiometry (AVHRR) images (NOAA Coastal Ocean Program Coast Watch Active Access System, NCASS) are available in electronic form on Springer-Verlag's server under http://link.springer.de/link/service/journals/00227/tocs.htm

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Introduction

From late May through November, schools of North Atlantic bluefin tuna (*Thunnus thynnus*) are present in the western North Atlantic over the New England and Canadian continental shelf (i.e. in the Gulf of Maine) (Fig. 1). Bluefin schools typically consist of tens to hundreds of individuals (Crane 1936; Bigelow and Schroeder 1953; Mather 1962), but surface feeding aggregations of $>5{,}000$ fish have been recorded (Lutcavage and Kraus 1995). The seasonal assemblage consists primarily of the large size classes known collectively as "giants" [these include the fishery management classes "large" giant ≥196 cm standard fork length (SFL) and

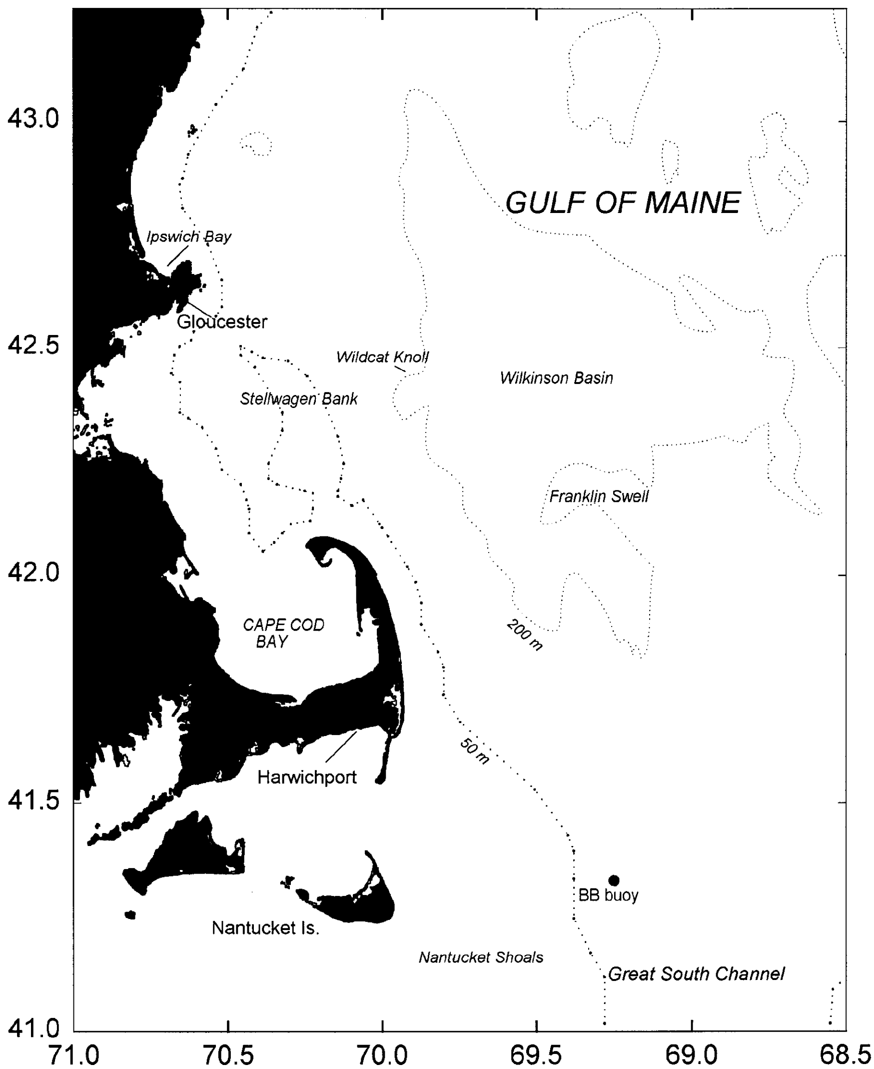


Fig. 1 Map of Gulf of Maine including bathymetry (50 and 200 m depth contours). Scale in all map figures is given longitude: 1degree = 111.2 km

≥141 kg, and "large medium" 178 to 195 cm SFL and 107 to ≤141 kg body mass]. Separate bluefin assemblages are believed to enter the Gulf of Maine over the season as the muscle fat content and body shape of landed fish change on a weekly and sometimes daily basis (Crane 1936; Bigelow and Schroeder 1953). Although little is known about residency patterns or the degree of interchange of schools from one area of the Gulf of Maine to another, distinct assemblages of fish of similar size, shape, and behavior have been reported to reoccur over a number of years in specific areas such as Cape Cod Bay, Ipswich Bay, and southwest of Nova Scotia (Fig. 1) (Porter and Hogans 1991).

The species has a history of over-exploitation and is currently considered highly over-fished. Fishery based catch per unit effort (CPUE) data, the principal input for population assessments, have been questioned (e.g. National Research Council 1994) because with highly mobile schooling fishes, the relationship between CPUE and real abundance is usually not known with any certainty (Sharp 1978; Clark and Mangel 1979; Hillborn and Walters 1992; Brill et al. 1994; Djama and Pitcher 1997). Moreover, development of robust, fishery-independent abundance estimates, such as using direct aerial surveys, has been called crucial for the management of this long-living, highly migratory species (National Research Council 1994).

Understanding the behavior and movements of bluefin tuna, particularly their depth distribution, surfacing frequency, travel speeds, and residency patterns is critical for developing accurate population assessments based on aerial surveys. Specifically, there is a need to establish the probability of detecting schools either within the surface layer or at depth visually, photographically, or with new remote sensing technologies such as Laser Imaging Detection and Ranging (LIDAR; Oliver et al. 1994; Hunter and Churnside 1995; Lutcavage and Newlands in press) and Synthetic Aperture Radar (SAR). An aerial survey program from 1993 to 1996 examined the distribution and behavior of adult North Atlantic bluefin tuna in the Gulf of Maine as they aggregated in surface schools, and demonstrated the feasibility of obtaining direct fishery-independent estimates of abundance (Lutcavage and Kraus 1995; Lutcavage et al. 1997a, b).

We therefore undertook a study of the horizontal and vertical movements of adult North Atlantic bluefin tuna in three distinct oceanographic subregions that are traditional fishing areas: Stellwagen Bank, the Great South Channel east of Nantucket Shoals, and Cape Cod Bay (Fig. 1). By following the movements of fish carrying ultrasonic, depth-sensitive transmitters we obtained continuous information on behavior, movements, and their association with environmental features.

Materials and methods

Fish tagging and tracking operations

A light aircraft flown by an experienced commercial tuna spotter pilot located bluefin tuna (*Thunnus thynnus* Linnaeus) schools, directed the tagging vessel onto the school, and estimated the sizes and total number of individuals within the school. To place an ultrasonic transmitter (34 or 50 kHz, Vemco Inc., Shad Bay, Nova Scotia, Canada) onto a free-swimming fish, we used a harpooning technique traditionally utilized to capture giant bluefin tuna in New England waters. The transmitter was attached to a medical grade nylon tag head with monofilament line and mounted on a modified harpoon pole (Chaprales et al. 1998). Employing a free-throw technique, a commercial fishermen with over 25 years of experience harpooned a tag head (with an ultrasonic transmitter attached) into the dorsal musculature of a fish, and estimated the size of the tagged individual. Once the tag was in place, the spotter pilot continued to report on the behavior of the school. During daylight, other professional tuna spotter pilots remained in radio contact with the tracking vessel and provided additional information on school movements, behaviors, and number of individuals within the school.

To evaluate the feasibility of the harpoon tagging technique in 1995, a single bluefin track (9501) was conducted from an 8 m research vessel. For the remaining ten tracks, we chartered a 12 m commercial fishing vessel equipped with a small vessel tracking system similar to that described by Holland et al. (1985). A single direction hydrophone (Model V-10 or V-11, Vemco Inc.) was mounted on an aluminum pipe which, in turn, was mounted in a steel bracket that was clamped to the hull. The pipe could be turned to detect the relative bearing to the transmitter, and we could detect the transmitter's signal from ~1.7 km. With the exception of the 1995 track and the first track of 1996, data on the fish's swimming depth (encoded by the interval between the transmitter's pulsed signal) was continuously recorded using a Vemco VR-60 receiver attached to a laptop computer running custom-designed software. Because we could determine an accurate bearing but not range to the transmitter, we assumed the position of the tracking vessel and the fish position were the same. Location data were recorded every minute using a global positioning system (GPS) receiver (Garmin Model 55 Olathe, Kansas, USA) attached to a second laptop computer running data acquisition software (Tunalog, Cascadia Research, Inc., Olympia, Washington). During the 1995 track, bluefin depth data and boat position were recorded manually every 5 min and when the fish exhibited sudden vertical or horizontal movements.

Changes in water temperature with depth were measured using an expendable bathythermograph (XBT) system (Sippican Inc., Marion, Massachusetts) with probes launched from the boat every 3 to 4 h. Complete vertical temperature profiles were not collected during the 1995 track. Sea surface temperatures were recorded every 10 min from the boat's sea surface temperature recorder (probe depth 1.5 m). Tracking vessels had dual frequency fish finders (Koden 8808 50/200 kHz) which were used to detect schools of bluefin tuna prey and the tuna themselves. Sonar targets were identified by the tracking vessel captain (J. Tutein), who has over 25 years of commercial fishing experience.

To examine fishes' movements and behaviors in relation to surface temperature and ocean fronts, synoptic sea surface temperature data from Advanced High Resolution Radiometry (AVHRR) images were used (NOAA Coastal Ocean Program Coast Watch Active Access System, NCASS). Selected images (from tracking days or adjacent days if cloud cover was extensive) were retrieved and displayed with the image processing program CCoast (Computer Based Coastal Observation and Analysis of Sea Temperature, R. Miller, NASA, Stennis Space Center, 1994) using an image resolution of 1.5 km × 1.5 km $pixel^{-1}$.

Speed over ground (henceforth referred to as "speed") was calculated from the GPS geolocation data. Water temperatures occupied by the fish were calculated by combining fish depth and XBT data using custom-designed software. Aggregate time at depth, time at specific temperatures, and speed distributions were calculated based on 3 m, 1 °C, and 0.4 km h^{-1} bins, respectively (Holland et al. 1990). These data were then expressed as a percentage of the total tracking time for each fish, and the means (±SEM) calculated for all fish. Fish 9501 served to evaluate the harpoon tagging technique and was planned as an 8 h track. Two tracks, Fish 9703 and 9704, ended prematurely (7 and 3.5 h, respectively) as a result of receiver failure and tag shedding, respectively. Data from these tracks were excluded from analyses of swimming depth and speed.

Results

A summary of all tracks is given in Table 1, and depth patterns in Table 2. Fish tracks are grouped below according to the geographic region where the fish were tagged.

Stellwagen Bank and Cape Cod Bay

Fish 9601 and its school traveled steadily east until evening, slowed and remained in the same area until dawn (Fig. 2). The next day, it resumed an easterly path to Franklin Swell, but then doubled back to the west. During the day it moved repeatedly through the thermocline and increased its vertical excursion range when it encountered changes in subsurface thermal structure on the edge of Stellwagen Bank. At sunset the fish made a single deep dive (Fig. 3). It remained within the relatively uniform temperature (>17 °C) surface layer until sunrise, when it made two deep dives before returning to shallower depth. Mean (±SD) swimming speed was 6.8 ± 3.1 km h^{-1} during daylight and 4.4 ± 2.9 km h^{-1} at night. During the day, its school preyed on surface schools of sand lance (*Ammodytes* sp.) and submerged prey concentrations were also detected at the same depth, in close proximity to the school with the tagged fish. The track was ended after 30 h because of weather.

Fish 9602 and its school moved repeatedly across a convergence zone (visible as a color change and debris line) on the northwest corner of the Bank, where sand lance, sunfish *(Mola mola)*, fin (*Balaenoptera physalus*) and humpback whales (*Megaptera noveangliae*), and other bluefin schools were feeding in the afternoon. It moved west off the Bank at night (Fig. 2). At dawn, Fish 9602 moved back onto the northeast corner, during daylight hours moved off the Bank, then returned to the southeast corner during the early evening hours. It

Table 1 *Thunnus thynnus*. Summary of hydroacoustic tracking for North Atlantic bluefin tuna in the Gulf of Maine, 1995 to 1997. Individual size estimated by tagger, school size estimated by spotter pilot, mean and maximum speed refer to the speed over ground (*EST* Eastern Standard Time; *SST* sea surface temperature; *Stw Bnk* Stellwagen Bank; *Grt S Chanl* Great South Channel; *NA* no observations)

	Year/ID					
	9501	9601	9602	9603	9604a	9604b
Date	10 Oct	11–12 Sep	20–22 Sep	26–27 Sep	6–8 Oct	12–14 Oct
Origin of track	Grt S Chanl	SW Stw Bnk	NW Stw Bnk	SW Stw Bnk	Grt S Chanl	Grt S Chanl
Individual size (kg)	136	136	159	227	340	340
School size	> 200	500+	150–200	1000+	40–50/ > 200 d2	NA
Length of track (h)	8	30	48	30	46	45.6
Start track EST	10:22	11:26	12:41	12:50	12:10	10:25
Horizontal displacement (km)	31	93	116	0.2	18.3	12.8
Distance (km)	54	133	131	76	115	72
Mean speed (km h^{-1})	3.6	3.2	3.7	2.3	2.7	3.1
Maximum speed (km h^{-1})	NA	25	18	18.5	15	15
SST range (°C)	14.8–16.4	16.8/18.2	13.3/17.0	13.2/15.6	12.4/13.6	11.5/12.7
Minimum temperature (°C)	NA	7.2	< 9.0	< 9.0	< 9.0	< 9.0
	9605	9701	9702	9703	9704	9705
Dates	12–13 Oct	15–17 Aug	19–21 Aug	25 Aug	16 Sep	17–19 Sep
Origin of track	Grt S Chanl	W Stw Bnk	Cape Cod Bay	Cape Cod Bay	NW Stw Bnk	NW Stw Bnk
Individual size (kg)	318	317	317	318	136	113
School size	300+	12	6	12	200–300	200
Length of track (h)	18.4	48	30.2	7	3.5	48
Start track EST	11:35	11:31	17:47	12:20	14:35	14:51
Horizontal displacement	17.2	86	66	16	3	51
Distance (km)	44.5	153	126	18		126
Mean speed (km h^{-1})	4.7	2.9	2.9			3.7
Maximum speed (km h^{-1})	31	15	13	NA	NA	17
SST range (°C)	12.3/12.7	18.5–20.5	18.0–22.0	18.8–21.6	17.3–18.6	14.1–19.3
Minimum temperature (°C)	< 9.0	6	6	8.5	6	6

Table 2 *Thunnus thynnus*. Depth records for North Atlantic bluefin tuna tracked with hydroacoustic tags, 1995 to 1997, in the Gulf of Maine

Track	Mean (m) ± SD	Median (m)	Maximum (m)	Percent time at 0–1 m	Percent time at 0–4 m
9501	24 ± 19.1	9	128	3.6	22.8
9601	12 ± 16.3	9	128	3.6	22.8
9602	20 ± 10.9	18	68	0.1	1.5
9603	14 ± 6.6	13	40	0.3	5.9
9604a	16 ± 14.8	16	80	22.3	31.7
9604b	16 ± 14.7	12	67	4.1	15.9
9605	15 ± 8.5	14	57	0	4.7
9701	5 ± 11.6	2	215	39.6	70.3
9702	8 ± 8.0	5	60	16.8	45.4
9703	8 ± 3.3	8	22	0.6	7.1
9704	17 ± 10.0	13	38	0	0.8
9705	20 ± 17.3	17	203	0	0

continued on a steady southeasterly heading away from the Bank until the track ended after 48 h. Fish 9602 moved primarily between 8 and 20 m, but made only four or five trips to the surface (Fig. 3).

Fish 9603 was tagged on the southwest corner where it spent over 75% of its time, except for a 7 h foray up the western side of the Bank and then back again (Fig. 2). A large, mixed assemblage of seabirds, minke whales (*Balaenoptera acutorostrata*), and humpback whales was repeatedly sighted during this track. We briefly lost this fish at dawn and dusk, when it made rapid changes in direction and speed, probably to feed (Fig. 3). Fish 9603 remained above 25 m for all but the brief period when it traveled off Stellwagen in midmorning; it approached the surface on numerous occasions, but spent little time there (Table 2). It regularly traveled to the bottom at Stellwagen Bank (Fig. 3), where the sonar showed concentrations of unidentified bait, but its school also fed at the surface on sand lance. Fish 9603 made its deepest excursions during light transitions (Fig. 3). This fish was < 0.2 km from where it was tagged when contact was finally lost.

Fish 9701 was tagged on the western edge of the Bank, not far from a group of basking sharks (*Cetorhinus maximus*). It traveled steadily east until nightfall, when it made a slight diversion to the north before

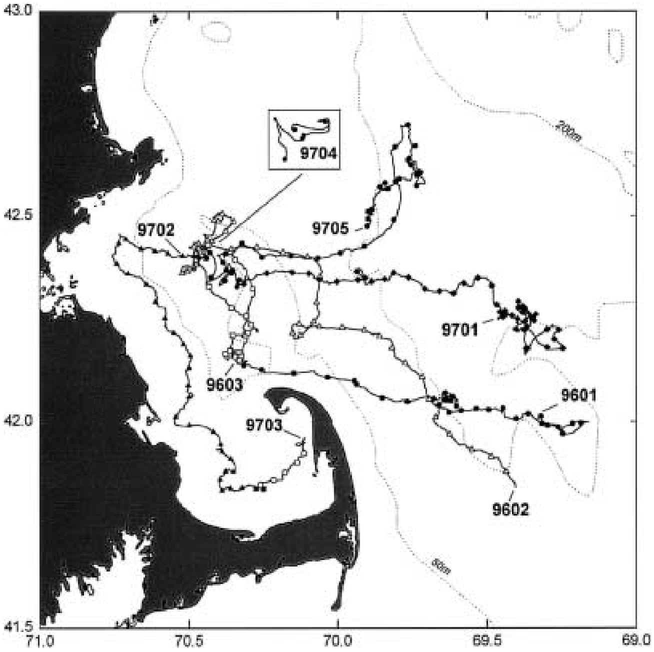
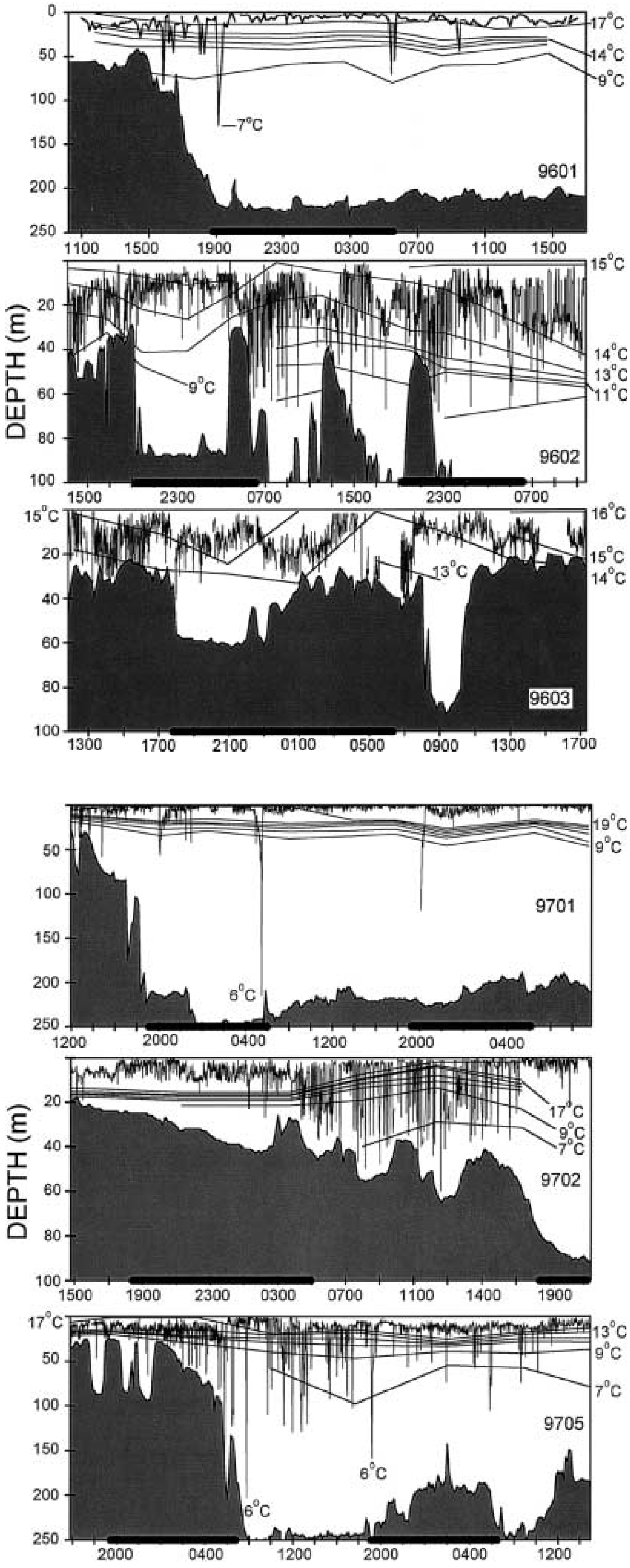


Fig. 2 *Thunnus thynnus*. Horizontal movement of bluefin tuna tagged on Stellwagen Bank [Fish 9601, 9602, 9701, 9704 (shown as inset), and 9705 originated on northwest corner; 9603 originated on southwest corner] or in Cape Cod Bay (Fish 9702, 9703) (*symbols* hourly ticks; end of track indicated with fish identifier)



resuming an easterly heading (Fig. 2). It traveled primarily in the top 5 m of warm surface water (18 to 19 °C), with the exception of single, deep excursions at each of four dusk or dawn transitions (Fig. 3). At sunrise and sunset on the second day, it descended to 215 m (nearly to the bottom, water temperature 6 °C).

Fish 9702 was tagged in Cape Cod Bay (Fig. 2), where it remained in warm (19 °C) shallow water through the night (Fig. 3). In the morning, the fish moved out of Cape Cod Bay, traveling north parallel to bathymetric contours as it headed into deeper water. At 05:00 to 07:00 hrs, we encountered a strong temperature front; sea surface temperatures decreased 6 °C and the fish made repeated deep descents through the thermocline (Fig. 3), sometimes reaching the bottom (7 °C). On the second afternoon a low pressure system brought rain squalls and tornados just west of our track. As we traveled over deep water west of Stellwagen Bank, Fish 9702 abruptly shifted back to a shallow diving pattern, remaining primarily in the warm surface layer. At sunset it took an easterly heading, and was close to the northwest corner of Stellwagen when we abandoned the track due to rapidly deteriorating weather.

Fish 9703 was tagged on a very calm, clear day in Cape Cod Bay, where small squid (unidentified species) were unusually abundant in surface waters (Fig. 2). We had repeated visual contact with all six members of this school during the track. The school was milling slowly eastward, ~18 km from the tagging location into very shoal water, when the ultrasonic receiver failed after 7 h.

Fig. 3 *Thunnus thynnus*. Vertical movements of adult bluefin tuna (Fish 9601, 9602, 9603, 9701, 9702, and 9705). Fish 9702 started in Cape Cod Bay. Data are incomplete for Fish 9601. Water column temperature isotherms from expendable bathythermograph data and bottom depths also shown. Solid bars along the time axis indicate night

Fish 9704 was tagged on the northwest corner of Stellwagen Bank near foraging humpback and minke whales, sand lance, and other tuna schools (Fig. 2). Feeding activity was centered on a thermal front (17.3 to 18.6 °C) at a visible surface convergence. Schools of bluefin tuna were airborne in pursuit of prey, and the movements of Fish 9704 suggested it was foraging at the surface with its school. From 15:00 to 16:30 hrs we saw the school several times amid the feeding aggregation. At approximately 3.5 h into the track the transmitter plummeted to the bottom, having been shed. We surmised that the transmitter was dislodged in the feeding frenzy.

Fish 9705 was tagged on the northwest corner of Stellwagen (Fig. 2) in the vicinity of feeding whales, seabirds, basking sharks, and several commercial fishing vessels. In the afternoon, this fish remained primarily in the surface layer near Stellwagen, but made a single deep descent through the thermocline at sunset when it had moved west off the bank (Fig. 3). From about midnight until first light the fish traveled east across Stellwagen, repeatedly moving through the thermocline. The school then traveled east over deep water and as it neared Wildcat Knoll, it increased its speed and depth excursions (Fig. 3). While conditions were sunny (08:00 to 10:00 hrs), Fish 9705 traveled in the surface layer, but under cloudy conditions near noon, it resumed travel through the thermocline, experiencing a vertical temperature gradient from 17 to 6 °C. Fish 9705 made a single deep excursion at sunset and then traveled primarily in the surface layer (under a bright full moon) until first light, when it again made several deep descents. The next day, as fog cleared at 07:50 hrs we noted seabirds and schools of bait fish in the vicinity of the school within range of the fish carrying the transmitter. At 11:00 hrs, two separate schools coalesced into the school containing Fish 9705, and schools were present on all sides of the tracking vessel. As we completed the last 5 h of the track in Wilkinson Basin, the school containing Fish 9705 slowly milled in a zone of clear water teeming with salps and cnidarians, indicating an area of high productivity.

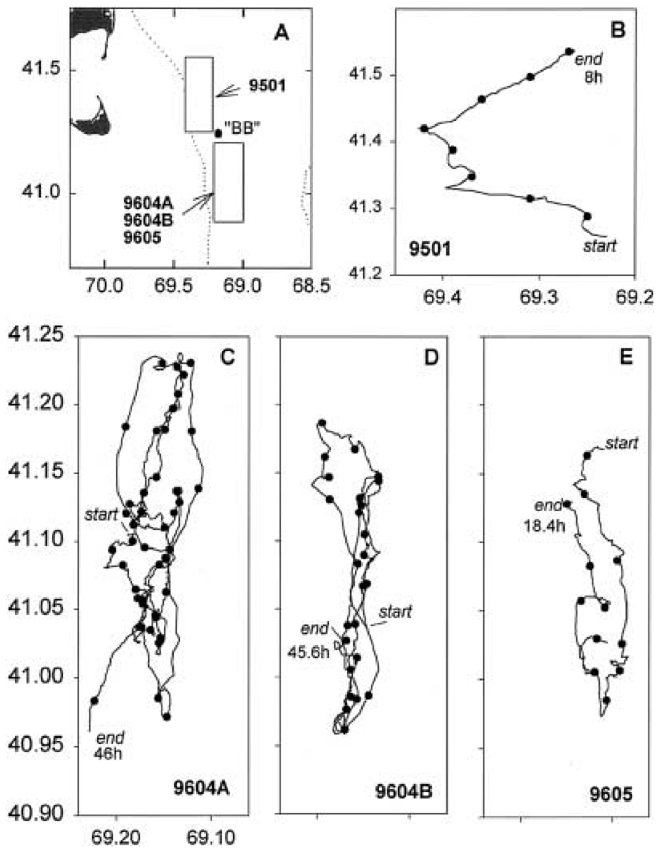


Fig. 4A–E *Thunnus thynnus*. Horizontal movements of Fish 9501, 9604, and 9605 tagged in the area in the Great South Channel near the BB buoy (**A**). Fish 9501 was planned as an 8 h track to test feasibility of the tagging method (**B**). Fish 9604 was followed for 48 h (**C**), then relocated 6 d later (**D**) just before a second transmitter was attached to Fish 9605 (**E**). Fish 9604 and 9605 moved in north–south directions within a relatively narrow corridor ~11 km wide (*circles* hourly positions)

Great South Channel tracks

Fish 9501 moved from east of the BB buoy (Fig. 4A, B) northwesterly into shallow areas east of Nantucket Shoals, diving frequently to the bottom (40 to 60 m) in the afternoon, when the school was also observed feeding at the surface. The area was active with feeding pilot whales (*Globicephala melaena*) and masses of bait on sonar, and was marked by debris lines. The fish maintained a north/northeasterly heading into deeper water and remained in the top 40 m before making its deepest dive (93 m) just after sunset.

Fish 9604, the largest fish that we tracked, was tagged just south of the BB buoy (Fig. 4A, C). Bluefin tuna schools of different sizes were abundant on the surface and at depth, within a mixed assemblage of pilot whales and humpback whales. At sunset, this fish dove to the bottom (about 75 m) and remained there with its school (marked on the fish finder as the tracking vessel passed over it) for approximately 45 min (Fig. 5). Water temperature at the bottom was 9 °C. Shortly thereafter we detected herring (*Clupea harengus*) schools rising off the bottom, and Fish 9604 returned to shallower depths. At first light the next day, this fish made another series of deep excursions to the bottom, and then returned to a shallow diving pattern (Fig. 5). On the second day, a spotter pilot confirmed that the fish being tracked was in a school nearly four times as large as the school of the previous day. During the 46 h track, Fish 9604 traveled along a 6 to 9 km wide by 28 km long corridor, nearly parallel to the axis of the Great South Channel (Fig. 4C). It consistently made its deepest excursions at sunrise and sunset, and returned to shallow depths immediately afterwards. Most of the time it remained above the thermocline and repeatedly visited the relatively cool (12 to 13.6 °C) surface water (Fig. 5). Fish 9605 was tagged with a 50 kHz transmitter near the BB buoy

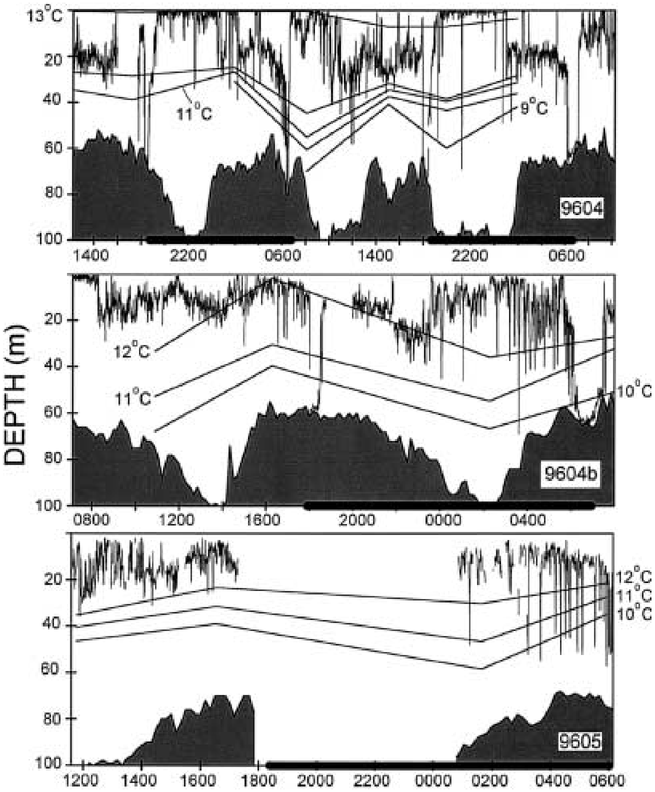


Fig. 5 *Thunnus thynnus*. Vertical movements of Fish 9604 and 9605 tracked in the Great South Channel

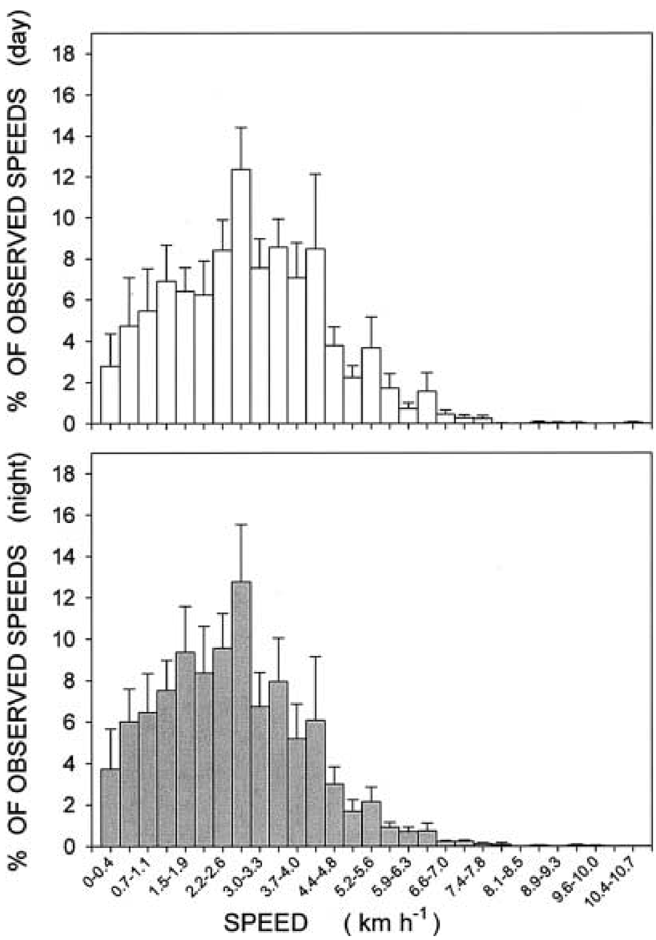


Fig. 6 *Thunnus thynnus*. Frequency histogram (mean ± SEM) of observed speeds over ground for adult bluefin tuna. Frequency of each speed interval was calculated as a fraction of the total number of observations for each fish, and intervals were averaged across fish ($n = 8$)

(Fig. 4A, E) amidst a large surface feeding school. Unexpectedly, before starting this track we detected the signal from the 38 kHz transmitter carried by Fish 9604. We intermittently received signals from both tags over the next 18.4 h as the fish seemed to be going in the same direction (Fig. 4D, E). Contact with Fish 9605 was lost at sunset when it abruptly picked up speed to over 13 km h^{-1}. By retracing the previous trackline, we relocated Fish 9604 at midnight, and Fish 9605 shortly thereafter, suggesting that these fish had similar travel paths but were not in the same school.

During the first 6 h that we followed Fish 9605, it remained primarily above 20 m (Fig. 5). When relocated after midnight, it was traveling through the thermocline. At dawn we lost contact for the final time as it made a series of rapid course changes and picked up speed. For the 18.5 h it was followed, Fish 9605 avoided the bottom and the surface. In contrast, during the second track Fish 9604 behaved as it had in its first 46 h track 6 d earlier. It visited the surface and descended to the bottom at dusk and dawn (Fig. 5). At first light it spent nearly an hour on the bottom close to dense schools of benthic prey (probably herring), as it had previously. During the second track, Fish 9604 traveled ~72 km, but after 46 h was only < 14 km from where we first detected its signal. Tracks of Fish 9604 and 9605 in the Great South Channel showed that they consistently traveled with the tidal currents and reversed direction following slack tides.

Swimming speed, time at depth, and time at temperature

Mean swimming speed ($n = 8$ fish) was 5.9 ± 1.24 km h^{-1}, but modal travel speeds were 2.6 to 3.0 km h^{-1}, both day and night (Fig. 6). Maximum swim speeds were 13 to 31 km h^{-1} (Table 1). On average, adult bluefin spent about 8% of their time in the surface layer (0 to 1 m), 19% of their time from 0 to 4 m, and > 90% of their time above 30 m (Fig. 7A). Although mean depth was not significantly different between years (15.3 m, 1996; 11.5 m, 1997), taking individual differences into account, bluefin tuna tracked in 1996 spent more time in deeper water than in 1997. With all tracks combined, fish spent about the same amount of time in the top 3 m in daytime as at night (mean ± SD: 12.8 ± 7.7% and 12.0 ± 7.0%, respectively) (Fig. 7A), but in 1996, spent < 4% of their time in the top 3 m in daylight, increasing to 12% at night.

Modal temperatures were 12 to 13 °C, but bluefin spent > 51% of the daytime and 62% of the night in

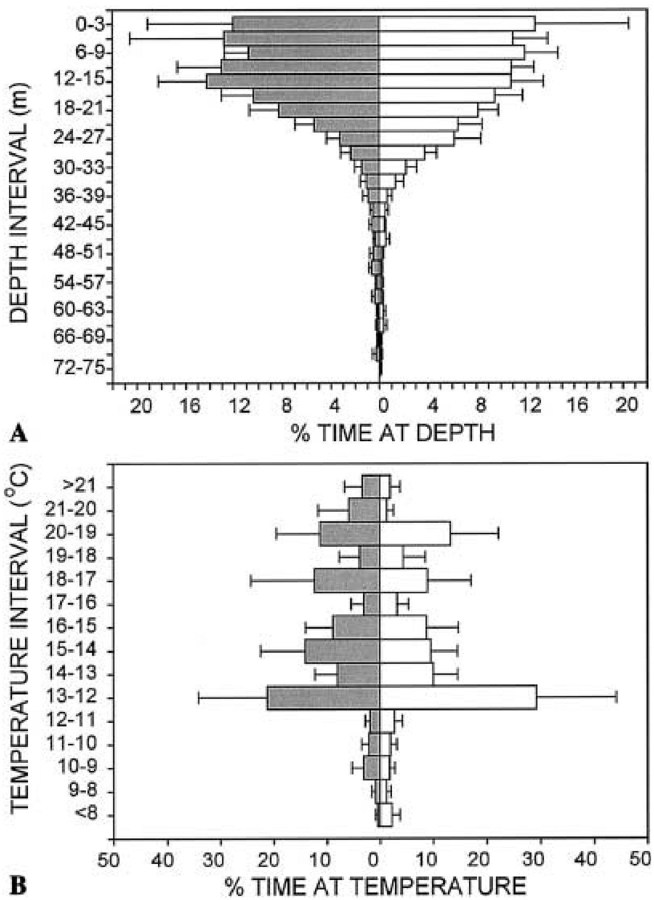


Fig. 7A, B *Thunnus thynnus*. **A** Vertical distribution for adult bluefin tuna expressed as percentage (mean ± SEM) of time spent at specific depths. **B** Vertical distribution for adult bluefin tuna expressed as percentage (mean ± SEM) of time spent at specific temperatures (*open bars* day; *filled bars* night)

water > 15 °C, and < 10% of the day and < 9% of the night in water colder than 12 °C (Fig. 7B). Minimum temperatures were 6 to 9 °C.

Discussion and conclusions

This is the first study to report on the movements of North Atlantic bluefin tuna in which the transmitters were placed on free-swimming fish in schools using the harpoon method (Chaprales et al. 1998), and our results differ from previous studies where fish were tracked following confinement or handling and were not tracked with schools (Carey and Lawson 1973; Carey and Olson 1981). Adult bluefin tuna released after capture from traps in St. Margarets Bay, Nova Scotia usually sounded and then headed directly offshore, and traveled in the surface layer above the thermocline, with no sign of having joined a school (Carey and Olson 1981). The only exception was a fish released from longline fishing gear (off Block Island, Rhode Island, USA), which joined a feeding school and repeatedly traveled through the thermocline to the bottom. Carey and Olson (1981) speculated that bluefin tuna in schools might behave differently than fish traveling alone (and, presumably, that have been disturbed); our results confirm this. Harpoon tag attachment is an effective means of obtaining spatial information (on both individuals and schools) necessary for the development of direct assessments. Tracking data combined with spotter pilot observations also confirmed the dynamic nature of schools, since in at least two cases (9604, 9705) the size and composition of schools changed dramatically over 24 h.

Horizontal movements, travel speeds, and residency

Our data showed no consistent differences in bluefin day–night travel patterns. For example, during the first night they were followed, some fish (e.g. Fish 9601 and Fish 9602) had smaller displacements than during the day, but this pattern seemed to be specific to geographic area and activity (i.e. feeding versus traveling). In both cases the fish covered much larger distances on the second night.

Four of the five bluefin tuna tagged on Stellwagen Bank took an easterly course, but three of these had doubled back to the west when the track was terminated (Fig. 2). Although we have no way of knowing whether these individuals eventually returned to Stellwagen Bank, aerial surveys have documented the presence of bluefin schools there until mid-October (M. Lutcavage and J. Goldstein, unpublished). Fish 9703 traveled to Stellwagen Bank from Cape Cod Bay, but deteriorating weather conditions prevented us from establishing if this fish completed a circuit between the two locations, as some bluefin fishermen believe.

Although one fish tagged on Stellwagen Bank (Fish 9603) showed site fidelity during the time it was followed, all of the fish tagged there visited the "corners" and traveled primarily along the bank's boundaries rather than directly over the shallow portions of the bank itself, a pattern that was also observed in northern Pacific bluefin tuna near the Oma bank in the Tsugaru Strait (Nishimura 1963).

The bluefin tuna tagged in 1996 in the Great South Channel had horizontal displacements that were roughly 10 to 25% of Stellwagen fish, suggesting that their foraging needs were met on smaller spatial scales. The Channel area is characterized by persistent thermal fronts, strong tidal currents, and high productivity associated with the shallow, warm water over Nantucket Shoals and Georges Bank on the east. The productivity, in turn, attracts large aggregations of demersal and pelagic fishes, seabirds, and cetaceans, and in recent years this area has consistently yielded high catch rates of giant bluefin tuna. Two of the three fish tagged here had similar median depth and diving patterns and their nearly identical travel paths, synchronized with the tide, suggested that their schools targeted similar prey. Their travel paths probably reflected the tidal current's influence on the distribution of herring and mackerel (*Scomber* spp.).

Fish 9501, which was tracked in the Great South Channel the previous year, exhibited slightly different behavior and greater horizontal displacement and median depth. For most of the track this fish moved west against the tide into shallower water to feed on the bottom, similar to the behavior of the Stellwagen fish.

Fish 9604 was probably in the Great South Channel region for at least 8 d, but there is only indirect evidence on bluefin residency patterns there, and whether fish arrive directly from other regions within the Gulf of Maine. In 1995 and 1996, aerial surveys first detected bluefin tuna in the Great South Channel beginning in August (Lutcavage et al. 1997a; M. Lutcavage and J. Goldstein, unpublished), and schools were abundant through mid-October in a much broader area than that indicated by the travel paths of the three fish that we followed. Based on temperature data, 14 out of 15 giant bluefin tuna captured and released in the Great South Channel with pop-up satellite tags in September 1997 migrated to warmer water (presumably the Gulf Stream) within 10 d, whereas only one individual remained in the Great South Channel for > 30 d (Lutcavage et al. 1999). Bluefin tuna schools near Stellwagen Bank do not seem to be spatially linked by either aerial survey data or hydroacoustic tracks with schools in the Great South Channel. This supports the hypothesis that the Gulf of Maine bluefin are comprised of diverse assemblages having distinct behaviors and origins (Crane 1936; Bigelow and Schroeder 1953), but this awaits confirmation.

Giant bluefin tuna had modal speeds of 2.2 to 3.3 km h^{-1} (Fig. 6), near the estimated migration speeds of giants swimming from the Bahamas to Norway (3.5 km h^{-1}, Mather et al. 1995), and mean speeds (8.7 to 9.8 km h^{-1}, Table 1) only slightly lower than those given for adult yellowfin tuna (Brill et al. 1999). Their peak speeds ranged from 14.8 to 28.7 km h^{-1}, but lasted only for brief periods, and none exceeded 13 km h^{-1} for more than 45 min. Maximum sustained swimming speeds of a penned, captive school of bluefin tuna (54 to 433 kg) were 15 km h^{-1} (Wardle et al. 1989). In yellowfin tuna and skipjack tuna, individuals tended to travel at approximately 1 body length s^{-1}, regardless of size (Holland et al. 1990; Brill et al. 1999). Within the 2.5-fold range in estimated body mass (136 to 340 kg) of the fish we tracked, travel speeds fell within this range (roughly 0.6 to 1 body length s^{-1}).

Vertical movements and depth distribution patterns

Three consistent patterns of movement emerged from tracking: repetitive travel through the thermocline with small to moderate daily displacements (< 5 to 40 km d^{-1}, e.g. Fish 9604, 9605, 9702), travel primarily in the surface layer with large displacements (40 to 76 km d^{-1}, e.g. Fish 9601, 9701), and deep bounce dives at dusk and dawn (majority of fish tracked). Benthic feeding seemed to occur most commonly in shallower regions (i.e. < 60 m depth), and schools that traveled extensively through the water column rarely (with the exception of the light transition periods) went to the bottom when traveling over deep water (defined as > 60 m). Their most consistent vertical pattern was a single deep bounce dive (or on rare occasions two or three), which usually occurred between first light and sunrise, and again at sunset or shortly thereafter, a behavior also documented in juvenile southern bluefin tuna with implanted archival tags (Gunn et al. 1994).

Predation rates by bluefin on herring and sandlance increase at light transition periods (Hobson 1986), and the fish appear to exploit these enhanced feeding opportunities, as we observed increases in speed and course changes at dawn and dusk, suggesting heightened foraging activity. Simultaneous observations of sonically tracked yellowfin and bigeye tuna against sonar records also showed vertical movements linked with that of their prey (Josse et al. 1998), but there were no significant day/night differences in depth patterns. In contrast, Pacific yellowfin, skipjack, and bigeye tunas show striking and repetitive diurnal rhythms, tight associations with the mixed layer, and distinct day–night differences in swimming depth that suggest close association with coastal topography and fish aggregating devices (Yuen 1970; Carey and Olson 1981; Holland et al. 1990; Brill et al. 1993, 1999; Block et al. 1997). These species occur over much deeper oceanic waters than the New England shelf and have different schooling and foraging patterns than bluefin tuna.

The two bluefin tuna that had the highest displacements (9701, 9601) remained primarily in the surface layer. If traveling schools have different vertical patterns than foraging schools, as noted for yellowfin tuna (Carey and Lawson 1973), giant bluefin tuna might conceivably change their depth preferences when they leave the continental shelf for deep ocean basins, where their prey becomes mesopelagic squid and epipelagic fishes (Dragovitch 1969; Mather et al. 1995). From 17 pop-up satellite tag records of mean ambient daily temperatures, giant bluefin tuna moving from the Gulf of Maine to the deep mid-Atlantic favored significantly warmer (23 to 26 °C) waters than those recorded during their presumed stay in the region (15 °C, Lutcavage et al. 1999). Two smaller fish tagged with archival tags off Cape Hatteras also showed similar temperature patterns (Block et al. 1998). Though limited, these data suggest that giant bluefin tuna remain primarily at shallow depths (i.e. < 60 m) throughout their migrations. Ultrasonic tracking studies of juvenile bluefin tuna off the eastern shore of Virginia (Northwest Atlantic) show that when fish moved into deeper water east of the continental shelf they remained primarily at shallow depth but also made brief descents, to ~140 m (Brill et al., unpublished).

Environmental associations

The vertical temperature gradients bluefin tuna encountered (from ~22 °C at the surface to 6 to 9 °C at depth) in the Gulf of Maine are comparable to the horizontal range (e.g. SSTs of 10 °C in the Bay of Fundy to 22 °C in Cape Cod Bay, Lutcavage et al. 1997a) but are several orders of magnitude steeper. Some of the fish we tracked encountered 6 °C, which is considered to be the lower temperature limit for bluefin tuna (Carey and Gibson 1983). None remained at this temperature for more than a few minutes. On two occasions Fish 9604 (the largest individual tracked) and its school remained near the bottom in 9 °C water for 30 to 45 min, but this pattern was exceptional. Given their large size and thermal inertia, it is unlikely that giant bluefin cooled significantly during their short stays at depth (Carey et al. 1971; Neill and Stevens 1974; Brill et al. 1994).

Based on concurrent observations and SST readings every 10 m by the tracking vessel, the resolution of composite satellite imagery was insufficient to detect all surface fronts and thermal structures experienced by the sonically tracked bluefin tuna over tidal cycles. Nonetheless, their movements superimposed on satellite sea surface temperature imagery (see electronic supplementary material) show that they traveled on the warm side of surface fronts, and that eastward movement generally coincided with offshore warming over deep basins. A consistent finding from direct observations (7 out of 11 tracks) was that bluefin tuna foraged in mixed feeding assemblages at surface fronts near Stellwagen Bank and in the Great South Channel. Links between ocean frontal systems and tuna abundance are extensively documented (e.g. Nakamura 1969; Laurs and Lynn 1977; Maul et al. 1984; Fiedler and Bernard 1987; Olson et al. 1994; Bakun 1996; Polvina 1996). Tracked bluefin also traveled near or with basking sharks, which selectively forage along persistent thermal fronts linked with peaks in phytoplankton biomass (Sims and Quayle 1998).

In the Great South Channel, bluefin tuna fed on dense schools of benthic and midwater herring and mackerel, and on Stellwagen Bank we usually saw them feeding on surface schools of sand lance, which have a lower fat content than herring and mackerel (1.2%, 6 to 9%, vs. 16%, respectively, Iverson et al. 1997; Kirsch et al. 1998). Feeding studies on both North Atlantic and southern bluefin tuna found significant differences in prey type and weight among geographic subregions (Chase 1995; Young et al. 1997). With a ration of up to 20 kg prey d^{-1} (Crane 1936; Chase 1995), the daily displacements of bluefin tuna schools (up to 76 km) may reflect distances required to locate optimum-quality prey patches, assumed to be a rate-maximizing process (Mangel and Clark 1986; Boyd 1996).

Sonically tracked bluefin tuna held a steady heading most of the time and on occasion reversed their travel paths. An analysis of horizontal trajectories of schools shows that their migration paths are not random (Newlands and Lutcavage, unpublished). There is evidence that highly migratory fishes use a map sense with memory to orient on smaller spatial scales, e.g. 1 to 100 km^2 (Carey and Robison 1981; Milinski 1994) and geomagnetic cues to orient during long-range migration, e.g. 1,000 km^2 (Carey and Scharold 1990; Walker 1984). In the tunas, olfaction (Atema et al. 1980), vision (Cahn 1972), and a magneto-reception system (Walker 1984; Walker et al. 1997) have all been implicated in navigation.

Movements in relation to direct aerial population assessment

This is the first tracking study on a North Atlantic tuna species accompanied by coincident aerial observations and regional migration data. A significant advantage of this new approach is that the database on vertical and horizontal movements can be encompassed within a direct population assessment program, such as those under development for southern bluefin tuna (Cowling et al. 1996) and for Pacific yellowfin and bigeye tuna (Marsac and Cayré 1998; Dagorn and Fréon 1999). Our tracking results show that bluefin tuna schools in the Gulf of Maine spend $<19\%$ of their time in the visual detection zone (0 to 4 m), but $>90\%$ of their time within the expected detection zone of LIDAR (30 to 60 m; Oliver et al. 1994; Schoen and Silber 1996), which has the potential to determine total biomass of schools (Hunter and Churnside 1995; Schoen and Silber 1996). Migration patterns link the surface counts from aerial surveys to biomass below, and help determine the probability of detection or capture; horizontal displacements identify the spatial extent of the fishery and its variability in time and space. These components are usually missing from CPUE-based assessments (Clark and Mangel 1979), but can now be inputs to models supporting more accurate interpretation of sightings (Lutcavage et al. 1997a; Lutcavage and Newlands in press) and fishery-based CPUE data (Sharp 1978; Hillborn and Walters 1992; Giske et al. 1998; Josse et al. 1998; Pennington and Strømme 1998).

Although 48 h tracking periods were insufficient to establish residency patterns of Gulf of Maine bluefin tuna, they revealed fine-scale (e.g. 1 to 100 km^2) movements of schools in relation to their environment and prey. When integrated with mesoscale (>100 km^2) movements, temperature and depth data from new pop-up satellite and archival tags, multiscale direct observations can lead to improved bluefin tuna stock assessments and more effective, equitable resource conservation.

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