Complex migration routes of Atlantic bluefin tuna (Thunnus thynnus) question current population structure paradigm

Article *in* Canadian Journal of Fisheries and Aquatic Sciences · June 2010

DOI: 10.1139/F10-033

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Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm

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Abstract: Movements of Atlantic bluefin tuna (*Thunnus thynnus*, ABFT) from specific western Atlantic forage grounds are not well described, and the extent of their spawning areas is mainly surmised. In 2005 and 2006, we deployed 41 pop-up satellite archival tags (PSATs) on adult Atlantic bluefin tuna off the coast of Nova Scotia, Canada, and on Georges Bank. During the assumed spawning period, 56% of the tagged ABFT occupied a known spawning area, while 44% were located in distant oceanic regions. Assuming obligate annual spawning, these results are inconsistent with the notion of spawning site fidelity to the Gulf of Mexico. The ocean-wide migrations of adult ABFT tagged on a common forage ground suggest evidence of a metapopulation requiring more spatially explicit management than the current simple two-stock structure.

Résumé : On n'a pas décrit adéquatement les déplacements des thons rouges de l'Atlantique (*Thunnus thynnus*, ABFT) à partir de zones d'alimentation spécifiques de l'ouest de l'Atlantique et on a en grande partie présumé de l'étendue de leurs aires de reproduction. En 2005 et 2006, nous avons fixé 41 étiquettes satellites enregistreuses détachables (PSAT) à des thons adultes au large de la côte de la Nouvelle-Écosse, Canada, et sur le banc Georges. Durant la période de reproduction présumée, 56 % des ABFT porteurs d'étiquettes se retrouvaient sur une aire connue de reproduction, alors que 44 % étaient dans des régions océaniques éloignées. Si nous supposons que la fraie annuelle est obligatoire, ces données sont incompatibles avec la notion de fidélité au golfe du Mexique comme site de fraie. Les migrations à l'échelle de l'océan des ABFT adultes marqués dans une aire commune d'alimentation laissent croire à l'existence d'une métapopulation qui requiert une gestion plus explicite à l'échelle spatiale que la structure simple de deux stocks utilisée couramment.

[Traduit par la Rédaction]

Introduction

Though ICCAT (International Commission for the Conservation of Atlantic Tunas) manages Atlantic bluefin tuna (*Thunnus thynnus*, ABFT) as eastern and western stocks, divided at 45°W, all size classes have been documented crossing this management line (Block et al. 2005; Lutcavage et al. 1999; Mather et al. 1995). Over the past 50 years, ABFT have been the target of intense commercial fishing pressure across their entire Atlantic range. Management efforts to rebuild the western stock and reduce overfishing of the eastern stock have had little impact, and ABFT were recently proposed for listing under the Convention on International Trade in Endangered Species (CITES, appendix 1, http://www.cites.org/eng/app/index.shtml). Despite the 1998 implementation of a rebuilding plan for the western stock, catches from 2005–2008 have declined. The US commercial fishery, which operates primarily in New England, caught only 10%–27% of the allocated western quota (National Marine Fisheries Service Fisheries Statistics Division). ABFT fisheries on the adjacent shelf of the Canadian Maritimes have thrived over the same time period but have not made up for the stock-wide loss in catches. The precipitous decline in the US commercial ABFT fishery, combined with continued high exploitation rates in the Mediterranean Sea and eastern Atlantic fisheries, has caused concern worldwide for the stability and future commercial viability of this species (Fromentin and Powers 2005). The current biological and management paradigms are that mature western ABFT reside within the western management boundary where they annually migrate between spawning grounds in and around the Gulf of Mexico (GOMEX) and feeding grounds on the Northwest Atlantic shelf. Understanding the complexities in movement patterns expressed by ABFT between spawning

Received 1 September 2009. Accepted 8 March 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 26 May 2010. J21379

Paper handled by Associate Editor Ray Hilborn.

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Table 1. Summary of Nova Scotia bluefin (*Thunnus thynnus*), 2005–2006.

Tag ID	Tagging date	Weight (kg)	CFL (cm)	Tag latitude, °N	Tag longitude, °W	Report date	Report latitude, °N	Report longitude, °W	Days at liberty	Distance (km)
2005-03497	19 Oct. 2005	341	315	44.205	64.208	26 Dec. 2005	39.745	60.132	80/330	2 320
2005-03815	18 Oct. 2005	193	265	44.216	64.242	21 Nov. 2005	33.941	76.907	35/330	2 025
2005-03817	19 Oct. 2005	205	270	44.201	64.235	17 Nov. 2005	35.224	75.038	30/330	1 781
2005-04233	19 Oct. 2005	273	294	44.223	64.210	19 Sept. 2006	44.567	62.896	336/330	23 056
2005-04234	18 Oct. 2005	261	291	44.214	64.234	4 Dec. 2005	31.831	76.837	58/330	2 876
2005-04366	19 Oct. 2005	352	318	44.220	64.216	3 Apr. 2006	27.132	91.904	167/330	6 900
2005-04368	18 Oct. 2005	303	304	44.214	64.238	18 Sept. 2006	44.363	63.912	336/330	14 634
2005-04745	21 Oct. 2005	227	279	44.213	64.228	14 Apr. 2006	26.614	94.747	176/330	7 346
2005-08775	17 Oct. 2005	273	294	44.215	64.235	2 Mar. 2006	33.885	76.057	102/330	4 187
2005-08777	19 Oct. 2005	205	270	44.223	64.233	2 Mar. 2006	33.885	76.057	135/330	4 352
2005-12922	19 Oct. 2005	318	308	44.231	64.216	12 Mar. 2006	23.037	94.753	145/330	6 230
2006-03495	9 Oct. 2006	227	279	44.221	64.241	1 May 2007	37.894	63.135	205/330	8 499
2006-03496	9 Oct. 2006	273	294	44.221	64.241	16 Apr. 2007	27.757	92.711	190/330	6 617
2006-03816	10 Oct. 2006	148	245	44.212	64.253	10 Sept. 2007	43.829	64.306	336/330	9 685
2006-04364	10 Oct. 2006	250	287	44.210	64.248	7 Mar. 2007	22.889	74.675	149/330	5 730
2006-04367	11 Oct. 2006	273	294	44.211	64.248	4 Mar. 2007	26.879	90.240	145/330	6 120
2006-04744	11 Oct. 2006	136	239	44.213	64.279	4 July 2007	37.509	65.155	268/330	9 379
2006-04933	16 Oct. 2006	318	308	44.203	64.257	12 Feb. 2007	25.184	85.383	121/330	5 326
2006-12924	19 Aug. 2006	221	296	42.082	65.586	5 Dec. 2006	40.913	63.260	109/330	3 159
2006-12925	19 Aug. 2006	221	296	42.082	65.589	19 Feb. 2007	29.017	51.794	184/330	6 685
2006-13975	17 Oct. 2006	250	287	44.213	64.247	17 Nov. 2006	34.214	76.382	32/365	2 089
2006-14077	19 Oct. 2006	227	279	44.215	64.249	18 Dec. 2006	34.225	76.674	61/365	2 417
2006-14078	19 Oct. 2006	227	279	44.215	64.249	26 Nov. 2006	33.664	77.616	39/365	2 216
2006-14079	18 Oct. 2006	159	250	44.215	64.237	22 Nov. 2006	34.417	76.572	36/364	2 038
2006-14148	19 Oct. 2006	216	274	44.215	64.249	14 Feb. 2007	35.074	75.573	119/365	3 977
2006-14215	8 June 2006	91	173	40.380	66.430	26 Aug. 2006	43.337	66.483	80/150	3 625
2006-14536	19 Oct. 2006	273	294	44.215	64.249	11 Jan. 2007	34.300	76.870	85/365	3 597
2006-14539	16 Oct. 2006	318	308	44.214	64.247	16 May 2007	28.822	86.995	213/365	6 402
2006-14655	18 Oct. 2006	250	287	44.214	64.245	5 June 2007	24.125	79.833	231/365	9 630
2006-14656	19 Oct. 2006	273	294	44.214	64.244	14 Aug. 2007	43.416	61.005	300/364	21 564
2006-14657	17 Oct. 2006	273	294	44.213	64.244	18 Feb. 2007	38.995	68.812	125/365	4 455
2006-14658	19 Oct. 2006	227	279	44.215	64.249	14 Feb. 2007	39.084	39.916	122/365	6 293

Note: Days at liberty is out of total possible, determined by tag programming. CFL, curved fork length.

and feeding grounds and their relationships to current management boundaries in the Atlantic is an important step towards revealing why the western ABFT stock has dramatically declined despite rebuilding efforts.

Electronic tagging has provided a substantial contribution to our understanding of ABFT biology by revealing movement patterns of fish tagged in the southern Gulf of Maine (GOM) (e.g., Lutcavage et al. 1999; Royer and Lutcavage 2009; Wilson et al. 2005), off North Carolina, and in the GOMEX (Block et al. 1998, 2001, 2005). Interannual variability in dispersal patterns is high and varies by size (Block et al. 2001; Royer and Lutcavage 2009; Sibert et al. 2006), with smaller ABFT (<200 cm) generally more constrained to coastal regions and larger individuals (>200 cm) occupying offshore waters. Although the mechanisms triggering trans-Atlantic crossings remain unclear, it has been suggested this may occur due to a change in environmental conditions (Mather et al.1995; Rodewald 1967) or, in the case of mature ABFT, a return to natal spawning grounds (Block et al. 2005; Rooker et al.2008).

In 2005, we focused tagging efforts in waters near southwestern Nova Scotia (NS) to better understand the spatial distribution of large, mature ABFT that, based on recent catch history, appeared to be bypassing the Gulf of Maine forage grounds and fisheries (National Marine Fisheries Service Fisheries Statistics Division). In 2005 and 2006, 41 pop-up satellite archival tags (PSATs) were deployed on ABFT with estimated weights of 91–352 kg (median = 250 kg). We used PTT-100 PSATs (Microwave Telemetry, Inc., Columbia, Maryland) on fish released from commercial fishing vessels from inshore locations off Riverport, Nova Scotia, in October 2005 and 2006 (n = 36), on Georges Bank in August 2005 (n = 2), and from a US-based longline vessel just west of the International Maritime Boundary in June 2006 (n = 3) (Table 1). Using currently accepted length-to-weight relationships (Parrack and Phares 1979) and length and age curves (Fromentin and Powers 2005; Neilson and Campana 2008; Turner and Restrepo 1994), median age was between 18 and 20 years. All fish tagged were therefore considered mature fish given that the age of first maturity is generally taken to be 8–10 years for western ABFT (Mather et al.1995).

Tracks returned from these fish were used to identify duration of occupancy in differing oceanic regions, restricting our analysis here to horizontal movements. Based on their estimated ages, it is reasonable to expect, under the current biological paradigm, that most if not all fish tagged would enter the GOMEX or Straits of Florida to spawn during the known spawning period (April–June) (Block et al. 2005; Richards 1977; Rooker et al. 2008). Here, we show complex seasonal dispersals over the course of a year, which illustrate the susceptibility of the western stock to eastern fishing mortality and identify migration patterns that are inconsistent with the current spawning area paradigms.

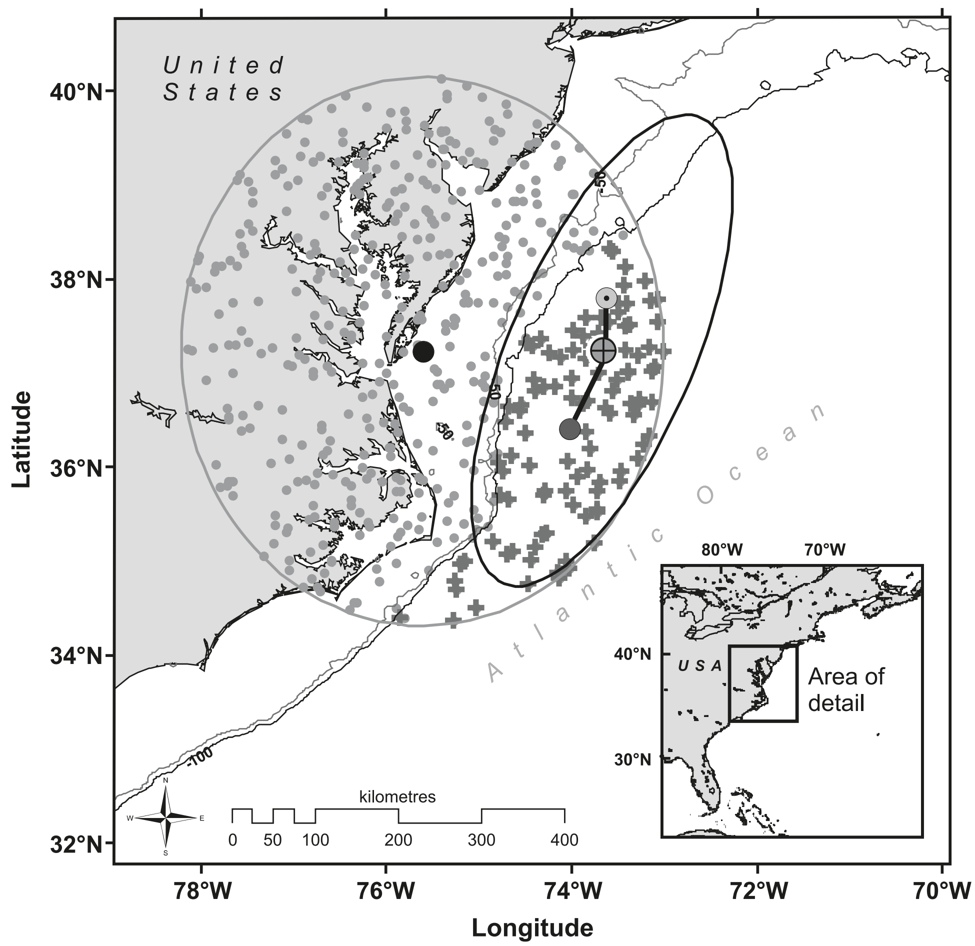
Materials and methods

In this study, we used PTT-100 PSATs (Microwave Telemetry, Inc.) tethered via monofilament to a nylon dart (Lutcavage et al. 1999). Fishing aboard the F/V *High Rider* and F/V *Fin Seeker* was with rod and reel using circle hooks. Fish condition was assessed, and fish that were undamaged and hooked in the gape were tagged from the gunwale of the boat while the fish remained in the water. Tags were implanted in the dorsal musculature at the base of the second dorsal fin. Fish were then swum alongside the boat and hooks were removed to ensure proper revival after the catch and tagging process. Fish weight was estimated by the captain and senior crew members in 25 lb (~12 kg) increments. The estimated mean (± standard deviation (SD)) weight of tagged fish was 268 kg (±56 kg) and 227 kg (±58 kg) for 2005 and 2006, respectively. According to accepted conversions, the age of tagged fish was ≥8 years and likely 15–20 years (Neilson and Campana 2008; Parrack and Phares 1979; Turner and Restrepo 1994).

The generation of PTT-100 tags used recorded temperature (±0.17 °C) and depth (5 m bins) at 15-min intervals. These tags also determined sunrise and sunset times, based on light thresholding, from which a geolocation was calculated by the manufacturer. Because ABFT swim rapidly and tend to be at depth during sunrise and sunset (Block et al. 1998; Brill et al. 2001; Lutcavage et al. 2000), our light-based locations were generally poor. To improve this, we used a state–space Kalman filter to estimate position based on sunrise and sunset times and sea surface temperature (SST) (Royer and Lutcavage 2009). Following the methods of Royer and Lutcavage (2009), we used an unscented Kalman filter model (Lam et al. 2008; Nielsen and Sibert 2007; Wan and van de Merwe 2001) utilizing filtered sunrise and sunset times and tag-measured sea surface temperatures (SST), <10m depth, in the observation equations and satellite-measured SST built into a correlated random walk model in the state equations. Daily, 3-day interpolated SST data from the AMSR-E sensor (National Aeronautics and Space Administration) were used. AMSR-E SST is a microwave-based (7–89 GHz) product, making it fairly insensitive to clouds. Minimal interpolation was required, and where needed, a bicubic spline was applied to estimate pixels with no values. Movement parameter estimation proved difficult for this data set, as adding SST to the observation record made estimation unstable. Many local minima prevented proper convergence of likelihood maximization methods. All movement parameters were therefore held constant and set to default values. Diffusion coefficients of D = 2000 $km^2 \cdot day^{-1}$, σ_{sun} = 20 min, $b_{sunset} = b_{sunrise}$ = 0 min, b_{SST} = 0 °C, and $u = v$ = 0 $km \cdot day^{-1}$ were used.

Following state–space estimation, we applied a secondary bathymetric correction that constrained estimated locations based on daily maximum depth (Hoolihan 2005; Teo et al. 2007). This ensemble-rejection method is especially helpful in nearshore areas and along shelf breaks. By using a two-step process, we removed depth from the state estimation but maintained the nature of the covariance-based error position estimate as follows. We sampled depth measurements from within the 95% or 99% error bounds around each estimated location, rejecting depths less than the daily maximum, and found our final location estimate by minimizing the distance between the previous day's final estimated location and the geographic mean of the resampled depths. Our final error estimate is calculated by taking the spatial covariance of the remaining depth estimates about the final estimated location (Fig. 1).

Fig. 1. Bathymetric correction to unscented Kalman filtered locations. The solid black circle and lighter-shaded ellipse are the initial filtered location (using sunrise, sunset, and sea surface temperature (SST)) and confidence region, respectively. The dotted circle is the previous day's final estimated location. The smaller, lighter-shaded circles are rejected sampled points (shallower than maximum daily depth) and the darker-shaded crosses are the accepted depths. The large, darker-shaded circle is the spatial mean of the accepted samples, and the circle with cross and darker-shaded ellipse are the final estimated location (minimum distance) and spatial covariance, respectively.

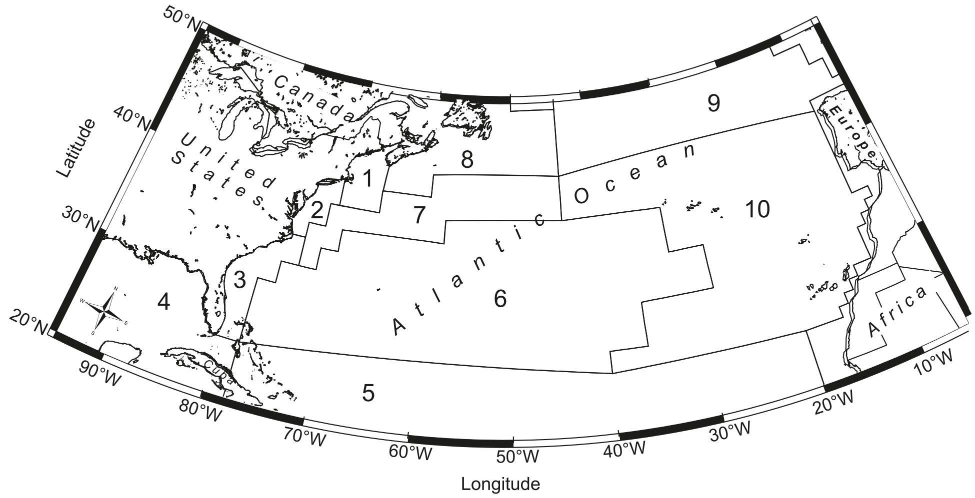


With these locations, we assessed areas of occupation and residency. Because Kalman filter methods inherently provide estimates of uncertainty for final estimates, there is a natural link to home range theory, which postulates the probable area inhabited by individuals or populations (Worton 1987, 1989). Kernel densities assuming Gaussian distributions have the same probability density construct as the confidence intervals returned from Kalman filter estimation (Royer and Lutcavage 2009). This creates a convenient framework for determining home range from state–space models using Kalman filters and removes the trial and error and inherent ambiguity associated with choosing an appropriate smoothing parameter in classic kernel density estimation. The final confidence intervals from our estimated tracks were used to create estimates of ABFT utilization distribution. We used the bivariate kernel functionality in the GenKern (version 1.1-2) library for the R statistical language (http://www.r-project.org). This allowed us to construct continuous probability densities in two dimensions, weighted by the covariance of the estimated uncertainty at the individual position estimates. Distributions were summarized seasonally for all fish for each tagging year. We termed each season based on the schedule of feeding and migration as follows: October–December (fall), January–March (winter), April–June (spring), and July–September (summer). The spring designation represents the putative spawning period for western ABFT. ABFT are typically found in northerly waters including the Gulf of Maine and Gulf of St. Lawrence from summer to early fall (Clay 1986; Mather et al. 1995; Paul et al. 2008).

ABFT make rapid ascents and descents and can encounter a wide range of temperatures in a relatively short period of time (e.g., Brill et al. 2001; Lutcavage et al. 2000; Teo et al. 2007). Given the temporal resolution of the PTT-100 tags (15 min), a fish could easily spend short periods in warm water near the surface and descend to cooler water before temperature was recorded. We therefore used the maximum daily temperature encountered to identify when ABFT may have experienced temperatures conducive to larval development (≥24 °C).

To classify ABFT habitat use, we used a modified Longhurst region definition (Longhurst 1995). To introduce some regional precision, we split the western Atlantic continental shelf region (roughly, the 200 m bathymetric contour) into three subregions: the Gulf of Maine, Mid-Atlantic shelf, and North Carolina – South Atlantic Bight (NC/SAB) (Fig. 2).

Fig. 2. Bioregions modified from Longhurst (1995): 1, Gulf of Maine; 2, Mid-Atlantic shelf; 3, North Carolina – South Atlantic Bight; 4, Gulf of Mexico; 5, Caribbean; 6, Central Atlantic; 7, Gulf Stream; 8, Canadian shelf; 9, North Atlantic; 10, North Atlantic Subtropical Gyral.



This more accurately reflects areas of interest for ABFT distribution. We also reduced the original size of the grid from 1° to 1/10° to coincide with the greater spatial precision possible from today's satellite ocean observing systems. We extracted numeric values representing our modified Longhurst regions at each final location for each tagged fish and summarized the regions visited over the time at liberty for each fish. Maps of completed fish tracks were produced using R (R Development Core Team 2008), ArcGIS 9.3 (ESRI, Redlands, California), and generic mapping tools (Wessel and Smith 1991).

Results

We received data from 36 tagged fish; five tags failed to report. Three of the 36 reporting tags came off within a week and a fourth tag remained attached for 259 days but failed to transmit archived data. For the remaining 32 tags, four reported on the programmed pop-up date (11 months after release), and 28 detached prematurely. Tags remained on fish at liberty between 30 and 336 days (2005, 145 ± 28 days (mean ± SD); 2006, 150 ± 76 days; Table 1). We used state–space Kalman filtering and bathymetric corrections to the raw light-based locations to produce locations for all 32 tracks, with an estimated combined total dispersal of 205 210 km for all individuals (Fig. 3). Longhurst regions (Longhurst 1995) were used to summarize occupancy in distinct oceanic habitat (Fig. 4).

Tagging off Riverport, Nova Scotia, occurred near the end of the ABFT's foraging season in the Gulf of Maine and Canadian Maritimes (Figs. 3*a*, 3*b*). Once tagged fish left the area, they either traveled directly south through the Gulf Stream or remained on the shelf. In the first 4–8 weeks after tagging (November – December), fish were distributed off North Carolina, in the South Atlantic Bight (SAB), and in the Gulf Stream. Several tags (n = 11) jettisoned early while fish were in the shallow Outer Banks area off North Carolina. Seasonal 95% utilization distributions (UD) indicate an extremely varied and extensive range for ABFT tagged off Nova Scotia. Autumn distributions extended to 60°W, across the eastern seaboard of the United States to the GOMEX (Figs. 5*a*, 5*b*). Winter UD shows a strong affinity for the SAB, the Caribbean Sea, the GOMEX, and to a lesser extent, the central and Northeast Atlantic (Figs. 5*c*, 5*d*). The range approaches a bimodal distribution in springtime, with most tagged fish mainly in the Gulf of Mexico and Gulf Stream regions, and two in the Northeast Atlantic regions (Figs. 5*e*, 5*f*).

By the following summer, all remaining tagged fish (n = 4) returned to the Mid-Atlantic shelf (MATL) and continued on to the Canadian shelf. When the tags reported, these four fish were within 20–360 km of their tagging location (Figs. 3*c*–3*f*). One fish (2005-04233) demonstrated striking fidelity to a prior feeding area and was recaptured by a vessel moored to the same anchor from which it was tagged the previous year.

Two of these fish (2005-04233 and 2006-14656) crossed the Atlantic and spent several months northeast of the Azores. One (2005-04233) followed the continental shelf south to the Caribbean Sea before heading to the Northeast Atlantic. The other (2006-14656) spent several months in the Gulf Stream region before heading due east in March. The two fish making trans-Atlantic crossings each ceased their transit east in May near 45°N and 15°W. Return trips to Nova Scotia were made within six weeks, with both fish occupying the Gulf Stream margin for several weeks before they returned to the Nova Scotia area. These individuals spent 68 and 153 days, respectively (20% and 51% of total days at liberty), in the eastern management area. Two additional fish tagged in 2006 appeared to be heading across the management boundary when the tags jettisoned (Fig. 3*b*).

The two remaining fish with year-long tracks had markedly different migrations. Fish 2005-04368 traveled through the Gulf of Maine and south along the shelf break, arriving off North Carolina in November. After spending several months there, it entered the GOMEX in April, left in early June, and returned directly to the Nova Scotian shelf. The last ABFT (2006-03816) traveled south along the shelf break to North Carolina in November, passing through the Gulf of Maine. It spent most of its time at liberty in the

Fig. 3. Final estimated tracks for ABFT tagged in (*a*) 2005 and (*b*) 2006. Shaded areas indicate confidence intervals returned from a sea surface temperature (SST) inclusive unscented Kalman filter and bathymetric correction. (*c*) ABFT 2005-04233 and (*e*) ABFT 2006-14656 displayed similar dispersal patterns transiting the Atlantic and spending April–June in the eastern Atlantic. (*d*) ABFT 2005-04368 made a round trip to the Gulf of Mexico, whereas (*f*) ABFT 2006-03816 spent the entire time at liberty along the eastern seaboard of the United States and Canada. All four fish exhibited site fidelity to a common foraging ground.

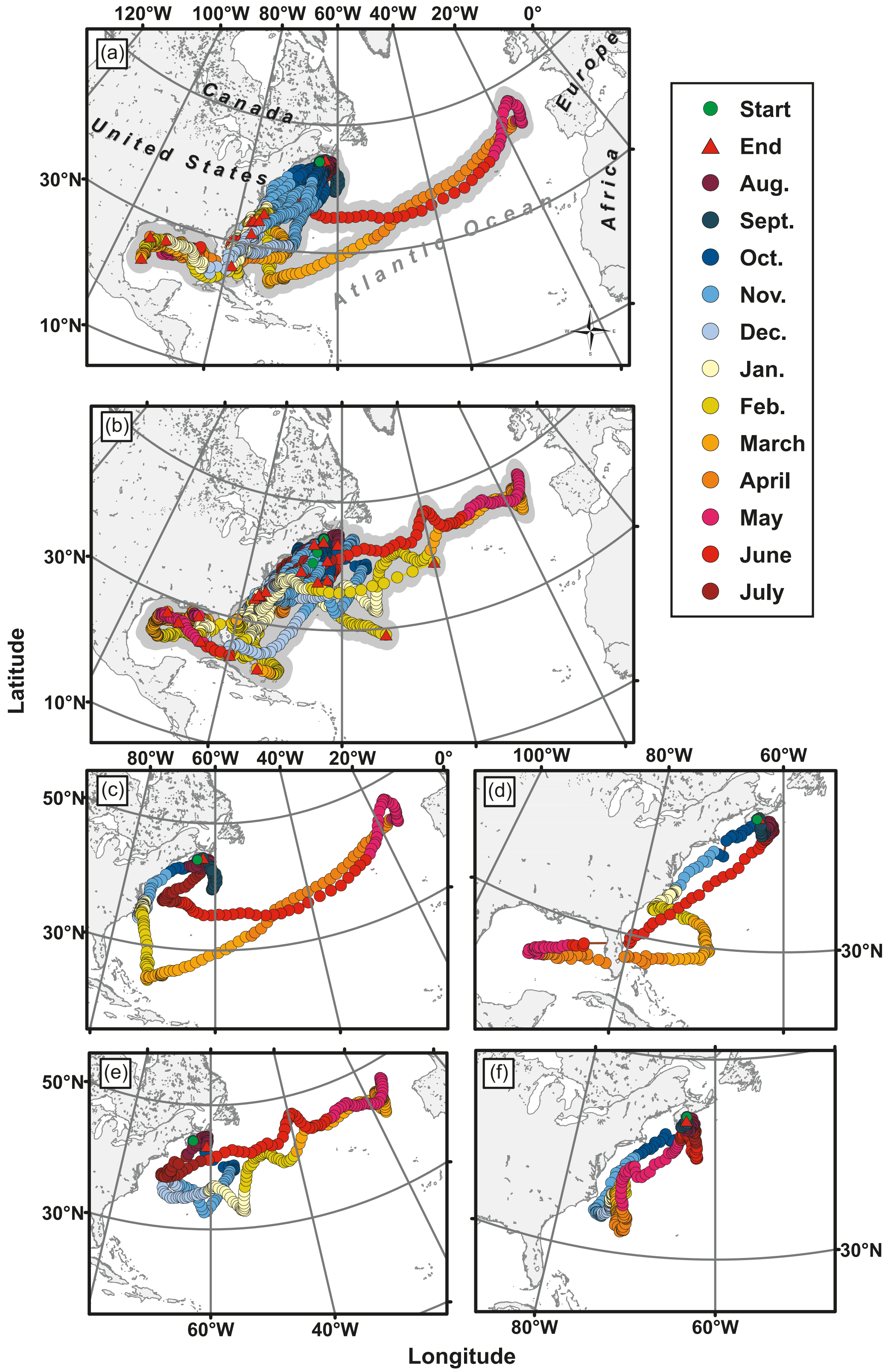
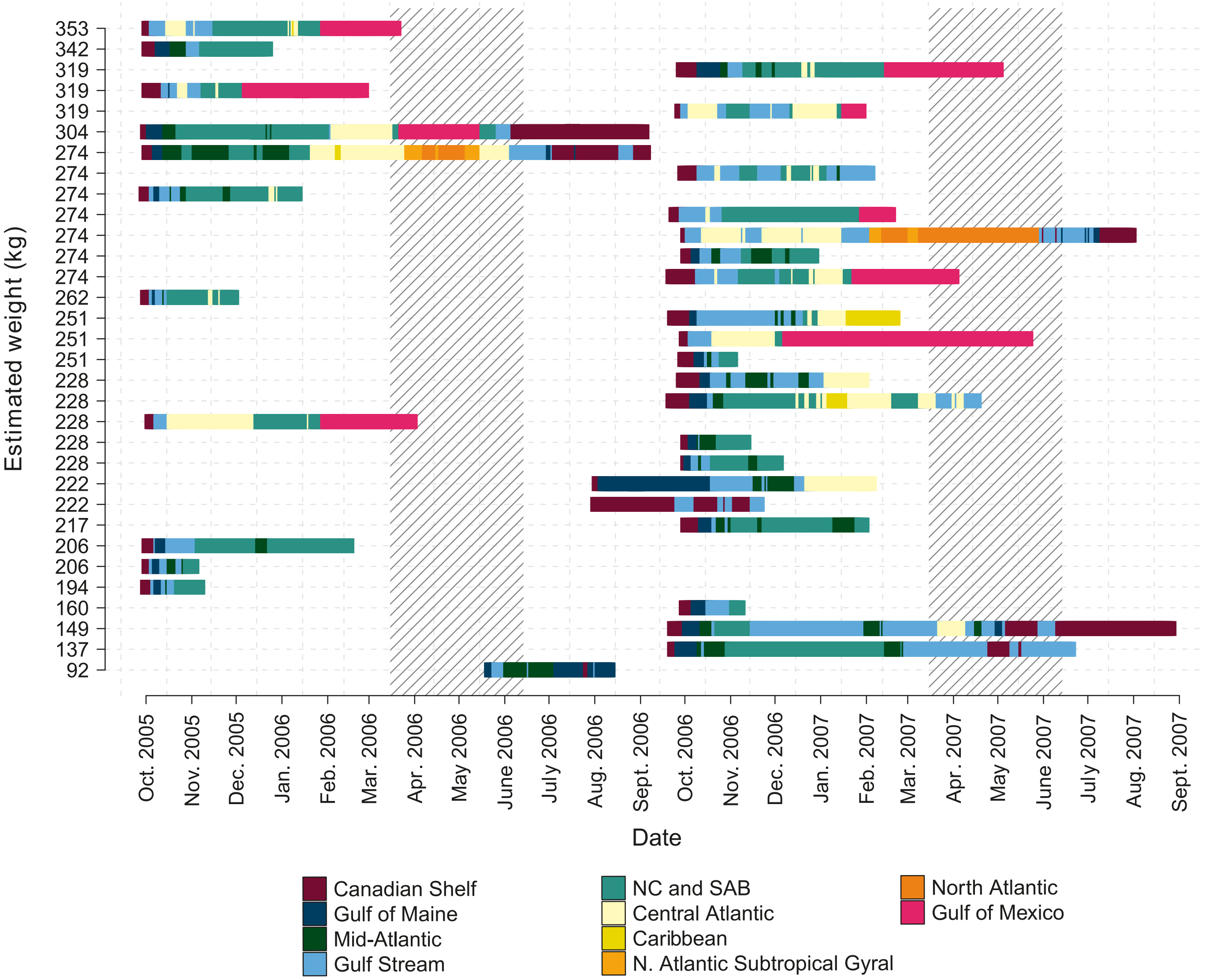


Fig. 4. Habitat occupancy for the 2005 and 2006 ABFT. ABFT entered the Gulf of Mexico as early as December and stayed as late as June. Shaded areas are the putative spawning times for ABFT in the western Atlantic. The North Atlantic and North Atlantic Subtropical Gyral regions are within the eastern management area, whereas the Caribbean and Central Atlantic regions extend across 45°W. The remaining regions are contained within the western management area. NC, North Carolina; SAB, South Atlantic Bight.



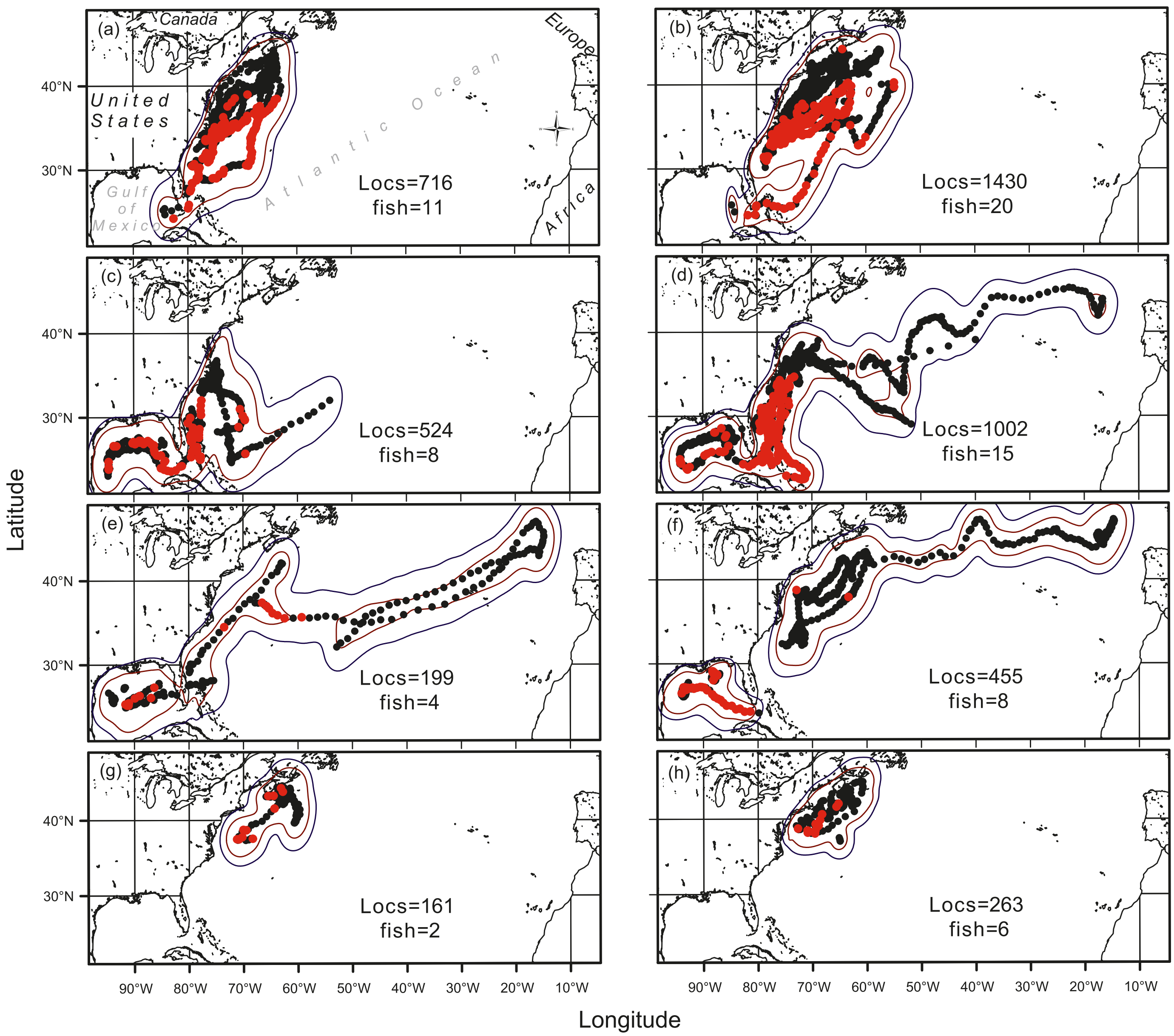
Gulf Stream area before returning in summer to the Canadian shelf.

In total, we observed three distinct dispersal routes to and from the Nova Scotian shelf by mature ABFT. Of the fish whose tags jettisoned prematurely (n = 17), the two individuals tagged on the northern edge of Georges Bank behaved differently than the others, moving northeast as far as the Grand Banks (2006-12924) and southeast to the Sargasso Sea (2006-12925). The majority of fish (n = 20) traversed the Gulf of Maine for short periods, mostly occupying its southern and eastern-most regions (Figs. 3*a*, 3*b*).

Over the two-year tagging campaign, nine tagged fish entered the GOMEX (2005, n = 4; 2006, n = 5) between early December and late March, with minimum residence times between 8 and 161 days. Six tags released in the GOMEX, so maximum residency could not be determined. Fish 2005-04368 returned to Nova Scotia, completing a round trip of about 14 634 km after spending 55 days in the GOMEX (Fig. 3*d*). All individuals observed there were present (or were presumably present based on their last known location) during the spawning season (April–June). In contrast, seven additional fish were observed between March and June but did not enter a known spawning area during their time at liberty (Fig. 4).

ABFT tracked from the Northwest Atlantic feeding grounds encountered temperatures optimal for ABFT larval development (≥24 °C) (Nishida et al.1998; Piccinetti and Piccinetti 1993; Rivas 1955) during all seasons across a broad range of Atlantic regions (Fig. 5). In autumn, these areas included the Gulf Stream, SAB, and Caribbean Sea. In winter, tagged fish in the SAB and GOMEX experienced the warmest conditions, although the number of days when temperatures were greater than 24 °C was highest in the SAB. In springtime, tagged fish encountered mainly warm conditions in the GOMEX and a few scattered locations in the Gulf Stream. The two fish that dispersed to the eastern

Fig. 5. Seasonal utilization distribution (red lines, 50%; blue lines, 95%) for bluefin tuna tagged in 2005 and 2006, determined from estimated tracks and confidence intervals. Red points indicate where water temperatures were 24 °C or above. (*a*, *c*, *e*, and *g*) ABFT tagged in 2005, and (*b*, *d*, *f*, and *h*) ABFT tagged in 2006. (*a* and *b*) Fall distributions (October–December) ranged from the Canadian shelf to the Gulf of Mexico; (*c* and *d*) winter (January–March) distributions covered the Gulf of Mexico to the eastern and central Atlantic; (*e* and *f*) spring (April–June) distributions were similar to winter distributions, but approached bimodality because the SAB was largely unoccupied; (*g* and *h*) summer (July–September) distributions showed ABFT return to the Northwest Atlantic. "Locs" and "fish" represent the number of individual locations and fish, respectively, in each panel.

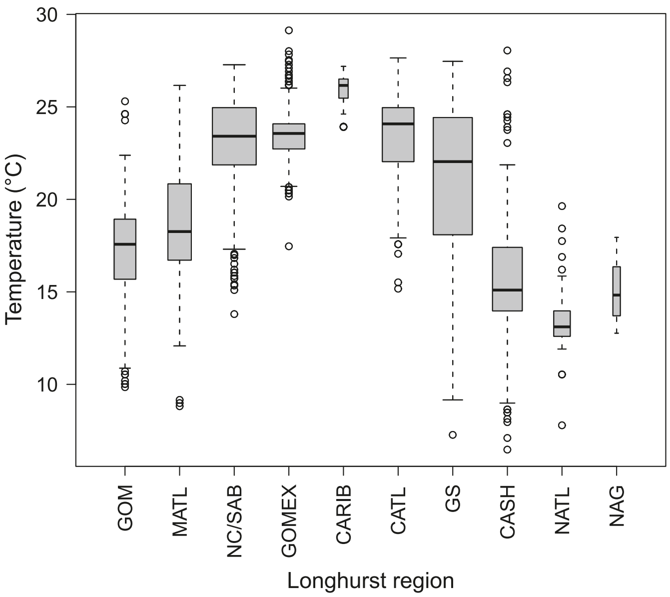


Atlantic did not experience temperatures above 24 °C until June and July, when they returned west to the Gulf Stream (Fig. 5). All fish tracked in this study spent from 1 to 146 days in the Gulf Stream region.

Discussion

Large, mature ABFT of similar size tracked from the same Northwest Atlantic shelf foraging areas exhibited diverse dispersal patterns and occupied distant ocean regions. In four cases where we observed individuals for an annual migratory cycle, individuals exhibited three distinct ocean-scale dispersal patterns and all returned to the tagging area, one homing to its exact release location after traveling to the eastern Atlantic. The dispersal routes identified from our year-long records are similar to those of smaller ABFT tagged with archival tags (mean curved fork length (CFL) = 204 cm) off North Carolina (Block et al. 2001) with the exception that we did not observe ABFT enter the Mediterranean Sea. In that study, it was assumed that individuals that did not enter either known spawning area were sexually immature. Our use of PSATs precluded multiyear records, but we were able to show site fidelity to specific forage areas, a view advanced by experienced commercial bluefin fishers.

Fig. 6. Maximum daily temperature by Longhurst region. Width is proportional to the number of days that fish were in each region. GOM, Gulf of Maine; MATL, Mid-Atlantic shelf; NC/SAB, North Carolina and South Atlantic Bight; GOMEX, Gulf of Mexico; CARB, Caribbean; CATL, Central Atlantic; GS, Gulf Stream; CASH, Canadian shelf; NATL, North Atlantic; NAG, North Atlantic Subtropical Gyral.



All tagged fish were >230 cm CFL (except one that was 179 cm CFL) and would presumably be mature fish capable of spawning, yet only nine of the 16 individuals (~56%) that retained tags during the known spawning period entered the GOMEX. This suggests that not all tagged fish spawned, or that they spawned elsewhere, or at a different time, which would be consistent with hypotheses presented in seminal pop-up tagging studies of ABFT in this region (Lutcavage et al. 1999; Sibert et al. 2006). We clearly delineate mature fish that did not occupy known spawning areas at presumed spawning times and leave assumptions of annual spawning and spawning site fidelity as open questions. Although our sample size was fairly small, these varied dispersals and feeding site fidelity indicate that the population structure of ABFT is spatially complex and may reflect reproductive patterns other than those assumed in the two-stock management scheme.

Skipped spawning has been presented as a survival strategy in iteroparous fishes (Rideout et al. 2005), and although previous tagging studies have suggested the possibility in western Atlantic ABFT, definitive conclusions from tagging studies have been complicated by sampling a mixture of age classes and by technological limitations (Block et al. 2001; Lutcavage et al. 1999; Wilson et al. 2005). ABFT tagged with PSATs in the GOM in 2002 (n = 61) showed utilization distributions constrained to the continental shelf, Gulf Stream, and western central Atlantic (Wilson et al. 2005). None of the presumably mature fish in that study (n = 6 during spawning season) entered the Gulf of Mexico.

Here, our results show distinct spatial and temporal areas where mature ABFT, outside the known spawning area and season, occupy thermally suitable larval development conditions, although a thorough treatment of additional biophysical features, including flow fields (i.e., larval retention areas) and productivity (Garcia et al. 2002; McGowan and Richards 1989; Richards et al. 1989), is needed to define potential spawning habitat. ABFT experienced temperatures of 24 °C between November and August. The warmest individual temperatures encountered were in the GOMEX in May and June, but the longest duration above 24 °C occurred in the SAB, Gulf Stream, and Central Atlantic Longhurst regions, and the most consistently warm temperatures were in the Caribbean (Fig. 6). The two tagged ABFT making trans-Atlantic journeys did not enter a known spawning area, but both stopped in the warm Gulf Stream region for several weeks before returning to the Canadian shelf. (Figs. 3 and 4)

Our cumulative tagging results support scenarios proposed by Goldstein et al. (2007) and Mather et al. (1974) that ABFT have asynchronous reproductive schedules and may spawn in the warm waters (>24 °C) of the Gulf Stream or Caribbean Sea. Thus, an alternative hypothesis could be that ABFT in the western Atlantic have spatially or temporally stratified spawning according to size (Goldstein et al. 2007), as is the case in the Mediterranean Sea (Heinisch et al. 2008) and with Pacific bluefin tuna (*Thunnus orientalis*) (Itoh 2006). Another explanation for the observed dispersal patterns of mature fish is that the decadal-scale decrease in somatic condition and lipid stores documented for ABFT in this region (Golet et al. 2007) has impacted their reproductive patterns, resulting in skipped spawning and changes in migration patterns (Goldstein et al. 2007). These alternative life history scenarios would each have significant impact on current western ABFT stock assessments and rebuilding plans.

Our tagging results and historic fisheries records support the stock dynamic scenario that ABFT comprise a metapopulation (Fromentin 2009; Fromentin and Powers 2005; Hanski 1998). ABFT have distinct reproductive and foraging behaviors and electronic tagging data show unequivocally that local populations, managed as a single unit, do not have synchronous spatial and temporal dynamics. Population levels can be influenced by environmental changes, and historical fisheries records confirm that local assemblages may emigrate permanently (Fromentin 2009; Tiews 1978). Whether or not emigration has occurred in the US (New England) fishery is uncertain, but our results clearly show ABFT foraging on an adjacent shelf bypass presumably suitable habitat (Overholtz et al. 2004).

In 2008, a stock assessment conducted by ICCAT estimated that the total allowable catch of ABFT in the eastern Atlantic and Mediterranean Sea was three times the maximum sustainable yield (ICCAT 2007). In the western Atlantic, the biomass has not increased, despite a rebuilding program instituted in 1998. Current ABFT management sets catch limits for each side of the Atlantic assuming low mixing between eastern and western stocks. Recent work presenting evidence of spawning site fidelity to the GOMEX for the western stock and the Mediterranean for the eastern stock appears to support the general tenets of this management structure (Block et al. 2005; Carlsson et al. 2007), yet our tagging results do not support key assumptions underlying these studies. The three (or more) dispersal routes of adult ABFT tagged in our study indicate movements of contingent groups and imply additional substructure as suggested by historic fisheries catch records (Fromentin 2009).

Otolith chemistry and genetic evidence have shown that significant mixing occurs on some forage grounds of the western Atlantic (Boustany et al. 2008; Rooker et al. 2008) but do not indicate if mixing is permanent or temporary. Additional efforts to delineate otolith chemical differences between the Gulf of Mexico and areas noted in this study such as the Gulf Stream would help determine whether additional spawning areas have gone undetected. Without a rigorous effort to determine the extent of natal homing in ABFT, the existence of other spawning areas will remain inconclusive.

Although current generation PSAT tags cannot detect ABFT spawning events, the complex dispersal patterns that they identify do not support their current "simple" biological life history paradigm. Which of the reproduction scenarios apply must be determined through a complete analysis of biological and physiological dynamics of ABFT. The varied and distant dispersal patterns indicate that fish on common feeding grounds are susceptible to fishing pressure on an ocean-wide scale. Subsequently, current ICCAT management regulations would not protect ABFT contingents subject to regional depletion, even if catches were reduced in those regions. Consideration of alternative spawning strategies and recognition of a complex stock substructure may yield a more realistic view of ABFT population dynamics and could enhance fisheries management rebuilding efforts. It is well recognized that the current management approach of two stocks represents a simplification that was appropriate prior to the development of new tools such as satellite archival tags (Anonymous 2002). Our findings, along with mixing rates estimated through examination of otolith microchemistry (Rooker et al. 2008) and organochlorine tracers (Dickhut et al. 2009), contribute to a more realistic and complete synthesis of the movement of bluefin tuna in the Atlantic. Consideration of alternative spawning strategies and recognition of a complex stock substructure may yield a more realistic view of ABFT population dynamics and could enhance fisheries management rebuilding efforts.

Acknowledgements

We are grateful for the skill and dedication of our fishermen tagging partners, Captains Eric Jacquard, Joel Jacquard, Chris Malone, and crew members Timothy Nickerson, Camille Jacquard, Bernie Pothier, Taylour Lamrock, Devan Boudreau, and Captains John Caldwell and Scott Drabinowicz. Their long-term support made this work possible. We thank Sam Elsworth, SW Nova Tuna Assocociation, Robert Conrad and the St. Margaret's Bay Tuna / Trap Association, Gerard Chidley and the Newfoundland Tuna Association, Andrew McMaster (Fisheries and Oceans Canada), Charles Blaney, and Richard Ruais, Executive Director, East Coast Tuna Assocociation, for extensive logistical support of our research. We are indebted to Captain Frank Cyganowski, Fairhaven, Massachusetts, for valuable historical information and inspiration. This work was supported by NOAA Grant NA04NMF4550391 to M. Lutcavage.

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