



## Original Article

# Movements and geographic distribution of juvenile bluefin tuna in the Northeast Atlantic, described through internal and satellite archival tags

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Arregui, I., Galuardi, B., Goñi, N., Lam, C. H., Fraile, I., Santiago, J., Lutcavage, M., and Arrizabalaga, H. Movements and geographic distribution of juvenile bluefin tuna in the Northeast Atlantic, described through internal and satellite archival tags. – ICES Journal of Marine Science, 75: 1560–1572.

Received 20 October 2017; revised 28 March 2018; accepted 9 April 2018; advance access publication 25 May 2018.

From 2005 to 2010, 136 internal archival tags and 29 pop-up satellite archival tags were used to track juvenile Atlantic bluefin tuna in the Bay of Biscay. Information from 15 pop-up and 5 internal archival tags was recovered. The analysis was adapted for a common treatment of both types of tag data, allowing classification of overwintering distribution patterns, fidelity to the Bay of Biscay feeding area, as well as of horizontal and vertical habitat utilization. Results show substantial geographic dispersion from autumn to spring, with high habitat concentration in the Bay of Biscay during summer, when bluefin tuna inhabit in the mixed layer. Of the individuals that left the Bay of Biscay towards the end of the year, a high percentage returned the next year, suggesting a strong fidelity to the area. Thirty-three percent of records during the overwintering periods revealed residency in the Bay of Biscay and surrounding areas. Half of the fish overwintered in the mid-Atlantic, near the Azores or Madeira Islands, while three (17%) made trans-Atlantic round trips, and one individual travelled to and remained off the eastern coast of the United States. These findings challenge previous assumptions regarding the seasonality and annual movements of bluefin tuna from the Bay of Biscay, while demonstrating extensive spatio-temporal dispersion.

**Keywords:** Atlantic bluefin tuna, Bay of Biscay, depth distribution, dispersal, electronic tagging, habitat utilization, migration.

## Introduction

Atlantic bluefin tuna (ABFT), *Thunnus thynnus*, have been exploited for centuries. The International Commission for the Conservation of Atlantic Tunas (ICCAT) manages the species as two stocks, separated at 45°W. These stocks were considered to be overfished in recent decades (ICCAT, 2017). Recent studies using electronic tags (Walli *et al.*, 2009; Galuardi *et al.*, 2010; Galuardi and Lutcavage, 2012), otolith microchemistry (Rooker *et al.*, 2008, 2014; Schloesser *et al.*, 2010) and organochlorine tracers (Dickhut *et al.*, 2009) have improved knowledge of ABFT

geographic distribution, while revealing that the population structure and movements are far more complex (Galuardi *et al.*, 2010) and uncertain than those assumed in the stock assessments (Fromentin *et al.*, 2014; Arrizabalaga *et al.*, in press).

The Bay of Biscay (43–48°N, 0–10°W) supports a historically important ABFT bait boat fishery primarily comprised of juveniles (ages 1–3; 55–110-cm straight fork length [FL], Cort, 1990). The inter-annual consistency of this fishery and the targeting of early life stages, makes the Bay of Biscay assemblage a key component of the Eastern stock assessment (Rodriguez-Marin *et al.*, 2003;

Dufour *et al.*, 2010). However, little is known about juvenile ABFT (Galuardi and Lutcavage, 2012), the importance of the Bay of Biscay in ABFT life history, and the connectivity between the Bay of Biscay and other regions. The baitboat fishery in the Bay of Biscay targets albacore tuna and ABFT in summer and autumn. In late October or November, when catches of both species decrease and distance to fishing grounds increases, the vessels change their fishing gear to purse seine to target small pelagics. The juvenile ABFT distribution during the overwintering period (late autumn to early spring), until they show up in the Bay of Biscay the following summer, is basically unknown.

In the past, conventional tag data have provided important information on ABFT stock structure and general migratory patterns. Historic tagging programmes showed movement of juvenile ABFT between the Bay of Biscay and Mid-Atlantic coast of the United States (Mather *et al.*, 1967). Although conventional tagging data can be used to estimate movement rates, the data are dependent on fishing activity and do not provide information during the individuals' time at liberty. On the other hand, electronic tags provide detailed movement and habitat usage information which can be used to inform life history and stock assessments (Sippel *et al.*, 2015; Taylor *et al.*, 2011). Most electronic tagging of ABFT has occurred in the western Atlantic (e.g. Walli *et al.*, 2009; Galuardi *et al.*, 2010) or the Mediterranean Sea (e.g. Aranda *et al.*, 2013; Fromentin and Lopuszanski, 2014; Quilez-Badia *et al.*, 2013), but less information is available for the eastern Atlantic (Quilez-Badia *et al.*, 2013) where juveniles are most abundant (Cort, 1990). Moreover, given the relatively large size of external electronic tags, electronic tagging of juvenile tunas remains a challenge. Recently, subadult ABFT were successfully tagged with pop-up satellite archival tags (PSATs) and internal archival tags (IATs) in the northwest Atlantic (Galuardi and Lutcavage, 2012). Here we present the first results on geographic and vertical distribution of juvenile ABFT in the northeast Atlantic and findings in relation to their behaviour and ecology are discussed.

## Material and methods

Fish were placed in a tagging cradle, while live bait fishing, or on a padded plastic mat during rod and reel fishing. Internal tags (IATs and dummy tags) were implanted in the peritoneal cavity via a ventral incision. Amoxicillin solution was injected into the incision which was closed with one or two silk thread sutures as described in Galuardi and Lutcavage (2012). Fish were also tagged with orange conventional tags prior to release that identified fish with implanted internal tags. The entire process took less than three minutes. PSATs were secured by inserting an umbrella dart (Domeier *et al.*, 2005) through the base of the second dorsal fin across the pterygiophores. Tags were tethered with 10 cm of monofilament line covered with a silicone sleeve to increase stiffness and reduce tissue damage (Lutcavage *et al.*, 1999). A 200€ reward was established to motivate tag returns.

## Experimental design

Most juvenile ABFT caught in the Bay of Biscay are considered too small to attach external PSATs, e.g. 83% of the individuals caught during 2005 were < 90-cm FL. Although IATs have been used extensively in several tuna species, significant time and monetary investment is needed, especially if recovery rates are low, as in the case of juvenile ABFT in the northwest Atlantic

(Galuardi and Lutcavage, 2012). In order to test survivorship and recovery rates from implanted archival tagging, an experimental tagging survey using dummy IATs was conducted along the 2004 summer. Dummy tags were designed based on the characteristics of the Lotek LTD2410 IATs. The dummies were constructed in plastic moulds using leaded epoxy resin and a nylon monofilament emulating the light sensor stalk. They had the same dimensions as the genuine IAT, 37-mm length × 11-mm diameter and 6.2-g weight. A label with a contact number for recaptures was also embedded in the tags. We implanted 125 dummy tags in fish with 55- to 67-cm FL. The study and the reward for recovered tags were advertised through the distribution of posters to relevant research institutions, fishermen organizations as well as fishing and farming companies operating in the Atlantic and the Mediterranean. The internal dummy tag recovery rate over 2 years was 3.2% (and increased to 4.8% over 13 years). It is similar to that of conventional tags, demonstrating the feasibility of IATs for an affordable number of releases.

In addition, the availability of a small PSAT tag (X-Tag, Microwave Telemetry Inc., Columbia, MD, USA) allowed us to tag a wider size distribution of ABFT and recover data from more individuals. The size and orientation of the PSAT tag was appropriate for the size of the fish and did not impede locomotion nor behaviour (Lynch *et al.*, 2017).

## Electronic tagging

From 2005 to 2009, 136 IATs were implanted in juvenile ABFT (60- to 107-cm FL, Table 1) within the Bay of Biscay (42.91–45.41°N and 2.00–5.29°W). Deployed tag models were as follows: 2 Wildlife Computers MK9 tags in 2005; 79 Wildlife Computers MK9 and 8 Lotek LTD2410 tags in 2007; 1 Lotek LTD 2310 tag in 2008; 15 Lotek LTD 2310 and 31 Lotek LAT2510 tags in 2009. MK9 tags were programmed with a one minute sampling interval, except 15 tags that were programmed with a 30 second sampling interval. In the case of LAT2510 tags, the telescopic Log option was activated.

In 2009 and 2010, 29 PSATs (Standard Rate X-Tag) were deployed on juvenile ABFT onboard live bait fishing vessels between late August and September (Table 1). The sampling intervals for deployment durations of <4 months, 4–8 months, and >8 months were 15, 30, and 60 min, respectively. PSATs internally archive data at a two minute sampling interval, which is available when the PSATs are physically recovered. Mean FL was 95.9 cm (86–110 cm range), which corresponded to a mean age of 2.9 years (Cort, 1990).

## Horizontal movements

Light-based positions from PSATs were initially supplied by the manufacturer and post-processed with a state-space Kalman filtering workflow, using the R language (R Core Team, 2000), to obtain a better estimate of geolocation. Given the range of light-based geolocations, extreme outliers were first removed (e.g. positions in the Arctic and/or southern hemisphere). A sea surface temperature (SST) inclusive unscented Kalman filter (*ukfst* package, Lam *et al.*, 2008), was then fitted to all PSAT tracks containing adequate temperature information using Reynolds optimal interpolated SST (Reynolds *et al.*, 2002). Two short tracks (PSATs 49 885 and 49 826, with 4 and 43 days at liberty, respectively) lacked adequate SST measures and were processed with a light-only Kalman filter model (*kftrack* package, Sibert *et al.*, 2003).

**Table 1.** Summary of tags released in the Bay of Biscay.

Tagging type	Year(s)	Number released	FL mean $\pm$ SD (range)	Fishing gear	Tagging cruises	Number recovered
Dummy	2004	125	60.6 $\pm$ 2.7 (55–67)	Bait-boat	Opportunistic	6
Internal	2007	87	64.9 $\pm$ 1.7 (62–70)	Bait-boat	Directed	3
Internal	2005–2009	49	73.3 $\pm$ 19.4 (60–107)	Bait-boat Rod and reel	Opportunistic	2
Pop-up	2009	4	104.2 $\pm$ 5.6 (97–110)	Bait-boat	Directed	3
Pop-up	2010	25	94.6 $\pm$ 2.9 (86–100)	Bait-boat	Directed	12

FL is straight fork length of the fish in cm. “Number recovered” refers to the number of tags with archived information retrieved or physically recovered (in the case of dummy tagging).

Bathymetric correction was then applied using 1-min bathymetry (Amante and Eakins, 2009) through the *analyzepsat* package (Galuardi *et al.*, 2010; Galuardi, 2011).

For the Lotek IAT 90813, the procedure was equal to that of the PSATs, and a similar procedure was also followed for the remainder IAT track estimation. Initial positions were calculated through manufacturer-provided software (DAP Global Position Estimator V2 in MK9host v1.09.1029 software for Wildlife Computers, Inc. IAT data, and Viewer 2000 ver. 2.5.8 (2004) for Lotek IAT data) using light intensity and attenuation coefficients for each day (Hill and Braun, 2001; Ekstrom, 2004). Daily light curves derived from Wildlife Computers, Inc. tags were manually supervised and, where necessary, discarded when surface light intensity estimates were not congruent to the theoretical light curve found by the manufacturer algorithm. Geolocation outliers were removed based on the Wildlife Computers, Inc. software default procedure.

Resulting geolocations were processed using *ukfsst* with a daily SST product (GHRSSST Level 4 AVHRR\_OI Global Blended Sea Surface Temperature Analysis Ver. 1.0, <http://dx.doi.org/10.5067/GHAAO-4BC01>). Data for IATs 790068 and 790071 showed substantial clock drift, and several years with no data after the memory were filled. Consequently, estimated geolocations using default time drift correction, as well as *ukfsst* fits fell consistently on land. Thus, new time drifts were iteratively estimated until no gain on log likelihood was attained in *ukfsst* fitting. Where no geolocation was available, daily locations were interpolated considering the uncertainty bounds, through Waveform Distortion Data for Bivariate Interpolation (Akima, 1978).

Fidelity to the Bay of Biscay was characterized based on return rates to the Bay of Biscay using sufficiently long times at liberty (at least until mid-May of the year after tagging). Overwintering behaviour types were classified for the tagged individuals that remained at liberty for >4 months. Considering that most juveniles were tagged in late summer and that they are known to leave the Bay of Biscay in autumn (Cort, 1990), a 4-month threshold was chosen to characterize behaviour during the whole autumn and at least half of the winter (i.e. early February). A trans-Atlantic dispersal movement pattern (TRN) was defined when the 45°W stock boundary was crossed during the overwintering period, and a mid-Atlantic movement pattern (MID) when overwintering occurred outside the Bay of Biscay, but east of the 45°W management boundary. A local movement pattern (LOC) was assigned when overwintering was centred in, or associated to, the Bay of Biscay (defined as waters east of 10°W and north of 43°N), allowing occasional outside excursions. In multiyear tracks, each overwintering period was classified separately, so that the same individual can show alternative overwintering

behaviours in subsequent years. For all behaviour types, and each journey out of the Bay of Biscay, the dates of leaving and re-entering the Bay of Biscay were obtained, when available, from reconstructed tracks.

### Habitat utilization

Habitat utilization (Calenge, 2006; Galuardi and Lutcavage, 2012) was determined directly from the position estimate error covariates of all fish across the whole tracks. A bivariate normal probability distribution was estimated from the uncertainty bounds of the reconstructed track (or interpolated values for missing days) via Monte Carlo sampling (2500 samples per day and individual, *i*). Habitat use by tagged fish was estimated by adding density of presence in each solid angle on the earth projection cells from each tagged individual. Each solid angle was divided by its area according to a 0.2° latitude  $\times$  longitude grid (Equations 1 and 2) to generate overall seasonal utilization probability distributions.

$$H_a^s = \frac{\sum_{d \in s} \sum_i p_{i,d,a}}{A_a} \quad (1)$$

$$\%H_a = H_a / \max(H_a) \cdot 100 \quad (2)$$

$H_a^s$  habitat use index during the season *s*, in the solid angle on a globe projection *a*;

$p_{i,d,a}$  probability of individual *i* during day *d* to be in the solid angle *a*;

*a*, solid angle of a latitude–longitude rectangle on a globe ( $\Delta a = 0.2^\circ$  in latitude and longitude);

$A_a$ , area (Km<sup>2</sup>) of the solid angle *a*;

*s*, season, approximated by calendar trimester (e.g. winter = January, February, March).

Core-use habitat was defined as the 50% cumulative probability of %*H*, and wide-use habitat as the 95% cumulative probability of %*H*.

### Vertical movement analysis

The lower sampling frequency and sampling coverage in PSATs conditioned the vertical resolution for seasonal and diel analysis. The bin width increased with depth, while keeping higher resolution in frequently visited depths near the surface: 2.5-m bins between 0- and 20-m depth, 5-m bins between 20- and 50-m depth, 25-m bins between 50- and 200-m depth, and 100-m bins between 200- and 1000-m depth. Depth density histograms were calculated as the proportion of time by depth for each individual,

**Table 2.** IAT and PSAT release and recovery dates and positions.

Tag type	ID	FL (cm)	Release			Recovery			Recorded days
			Date	Lati. (°N)	Long. (°W)	Date	Lati. (°N)	Long. (°W)	
Xtag	93714	103	22 September 2009	45.8	3.8	18 May 2010	44.3	7.9	238
Xtag	93712	107	22 September 2009	45.8	3.8	1 February 2010	44.7	3.9	132
Xtag*	93709	110	22 September 2009	45.8	3.8	16 March 2010	40.6	10.6	175
Xtag*	80001	95	23 August 2010	43.9	2.7	25 September 2010	43.6	2.4	33
Xtag	93710	91	23 August 2010	43.9	2.7	2 February 2011	38.8	28.2	163
Xtag	79999	92	23 August 2010	43.9	2.7	19 October 2010	33.5	17.3	57
Xtag	93713	92	23 August 2010	43.9	2.7	14 September 2010	43.6	4.9	22
Xtag	93715	97	23 August 2010	44.4	4.2	23 May 2011	44.8	2.5	273
Xtag*	80003	90	23 August 2010	44.3	4.2	NA	NA	NA	176
Xtag	49826	95	23 September 2010	43.9	2.9	4 January 2010	43.5	1.8	42
Xtag	49856	98	29 September 2010	45.0	3.3	19 June 2011	44.0	2.7	263
Xtag	49880	93	29 September 2010	45.0	3.3	2 June 2011	42.7	13.1	246
Xtag	49889	95	29 September 2010	45.0	3.3	11 October 2010	45.2	6.1	12
Xtag	49885	95	29 September 2010	45.0	3.3	2 October 2010	44.5	2.7	3
Xtag	49827	97	29 September 2010	45.0	3.3	29 January 2011	37.1	17.1	122
Mk9	390579	67	1 September 2005	43.6	2.0	14 June 2006	43.7	2.8	378
Mk9	390540	64	18 August 2007	43.6	2.5	2 August 2009	44.5	2.1	715
Mk9#	790068	70	18 August 2007	43.6	2.5	7 November 2012	55.3	29.1	768
Mk9#	790076	65	18 August 2007	43.6	2.5	1 December 2014	36.0	-14.4	1594
LTD	90813	89	26 August 2008	43.5	2.0	10 August 2009	44.7	2.8	349
X-Tag	all	96.6					42.2	8.6	<b>1957</b>
X-Tag*	all								<b>384</b>
IAT	all	71					44.8	4.4	<b>3804</b>

In the case of PSATs, the recovery information refers to dates and positions where they transmitted from. Physically recovered PSATs are identified with an asterisk (\*) and IATs that filled memory prior to recapture are identified with an ash key (#). "Recorded days" refers to the number of days at liberty with recorded data. FL, straight fork length; NA, not available.

month, year, and day or night as well as for each individual, area, and day or night. Then, an average of the proportion of time weighted by the number of days was calculated. This portion of the study was delineated into three areas: the Bay of Biscay, the Mid-Atlantic Bight (US continental shelf, defined as positions to the west of 67°W), and oceanic waters (when positions were out of the other two areas). A criteria of 450 depth measurements per strata was established. This represents a minimum of 12 days by month covered in PSATs to ensure representative profiles. Diel and crepuscular periods were determined with solar elevation angle ( $\alpha$ ), as follows: day when  $\alpha < -9$ , night when  $\alpha > 0$  and dusk or dawn when  $0 > \alpha > -9$ . The solar declination was calculated daily for all estimated and interpolated positions. These solar definitions are the same as those used to derive light-based geolocations within manufacturers' software. This definition of dusk and dawn is similar to civil twilight (Hill and Braun, 2001).

## Results

Archived information from 20 juvenile ABFT ( $90.2 \pm 13$ -cm FL at tagging) was recovered. Of the 29 PSATs deployed, information was obtained for 15 PSATs (52%, Table 2), with a mean time at liberty of 131.4 days (range = 4–274 days). Fourteen PSATs transmitted via the ARGOS satellite system (48% reporting rate). Satellite communications returned, on average, 56% of archived data (range: 11–97%). Two PSATs were physically recovered after transmissions ended, and another that failed to transmit was physically recovered 7 months after its scheduled release date.

Five IATs were recovered with 760 days of data on average (range: 349–1594 days, Table 2), corresponding to a 3.7% recovery rate, just below the recovery rate of the dummy tag study.

The five recovered IATs provided a disproportionately high number of records ( $8.39 \times 10^6$ , compared with 539 932 from all PSATs) due to the higher sampling frequency. From the 5761 archived days at liberty in the entire dataset, 66% were from internal tags. IAT records were also distributed throughout the year and encompassed four overwintering periods. IATs provided 3804 days with geolocation estimates, whereas PSATs yielded 632 days (11.6% obtained from physically recovered PSATs). Because most tagging activity occurred in late summer, the number of days with data decreased progressively after autumn, but all seasons were reasonably well covered (range: 1138–1904 days of information by season).

After filtering, the average standard deviation in IAT geolocations during autumn months (geolocation is most uncertain near the autumn equinox) was  $0.29^\circ$  for the longitudinal component and  $0.36^\circ$  for the latitudinal component. These are lower than for PSAT geolocations, which had a standard deviation of  $1.32^\circ$  for longitude and  $0.75^\circ$  for latitude during the same period.

## Horizontal movements and distribution

Of the 20 tags for which data were recovered, 14 electronic tags allowed characterization of 18 overwintering periods (Table 3).

Six tunas displayed local residency patterns (LOC, 33%). Five of these made excursions to surrounding areas outside the Bay of Biscay with a mean duration of 39 days, and a maximum of 72 days (i.e. Figure 1a). They did not visit any shallow or putative feeding areas during these rapid excursions. The sixth LOC tuna remained in the Bay of Biscay during the whole overwintering period.



**Table 3.** Summary of electronic tags with enough archived data to characterize the overwintering period (OVW) and transit dates from/to the Bay of Biscay.

ID	RY	OVW	Start date	Leaving date	Entering date	Finish date
93714	2009	LOC	22 September 2009	26 December 2009 27 March 2010	20 January 2010 18 May 2010	18 May 2010
93712	2009	LOC	22 September 2009			1 February 2010
93709	2009	LOC	22 September 2009	28 February 2010		16 March 2010
93710	2010	MID	23 August 2010	28 December 2010		2 February 2011
93715	2010	LOC	23 August 2010	5 December 2010	27 December 2010	23 May 2011
80003	2010	LOC	23 August 2010	28 January 2011		15 February 2011
49856	2010	MID	29 September 2010	12 November 2010	7 May 2011	19 June 2011
49880	2010	MID	29 September 2010	19 January 2011	2 June 2011	2 June 2011
49827	2010	MID	29 September 2010	29 November 2010		29 January 2011
390579	2005	MID	1 September 2005	9 December 2005	8 May 2006	14 June 2006
390540	2007	MID	18 August 2007	31 December 2007	27 May 2008	
	2008	TRN		1 December 2008	5 June 2009	2 August 2009
790068	2007	MID		3 December 2007		24 September 2009
790076	2007	MID	18 August 2007	16 December 2007	27 May 2008	
	2008	MID		25 November 2008	20 May 2009	
	2009	TRN		26 November 2009	20 May 2010	
	2010	TRN		14 November 2010	22 June 2011	
	2011			7 December 2011		28 December 2011
90813	2008	LOC	26 August 2008	29 November 2008 15 January 2009 4 March 2009	20 December 2009 26 February 2009 15 May 2009	10 August 2009

Each OVW is characterized as local pattern (LOC), mid-Atlantic pattern (MID), or transatlantic migration pattern (TRS). The Reference Year (RY) is determined by the beginning of each OVW. Start date and finish date refer to the period of data recorded by each tag. Leaving and entering dates indicate all the dates when fish were observed to traverse the Bay of Biscay boundary (10°W). Each individual can have successive overwintering periods, and each overwintering period can have successive excursions in and out the Bay of Biscay.

Nine tag tracks showed a MID pattern, spending, on average, 158 days outside the Bay of Biscay (i.e. Figure 1b). These tuna mainly overwintered in areas north of the Azores Islands, and to a lesser extent, west of Madeira (i.e. Figures 1c and 2, upper panel). Fish 790068, tracked for 768 days, was the only juvenile ABFT that did not display fidelity to the Bay of Biscay (Figure 1d). After leaving the Bay of Biscay in December 2007, this fish overwintered near the Azores prior to travelling to the Grand Banks and the Mid-Atlantic Bight (northeastern US coast) the following spring. It remained off the east coast of the US for the entire second year at liberty (Figure 1d).

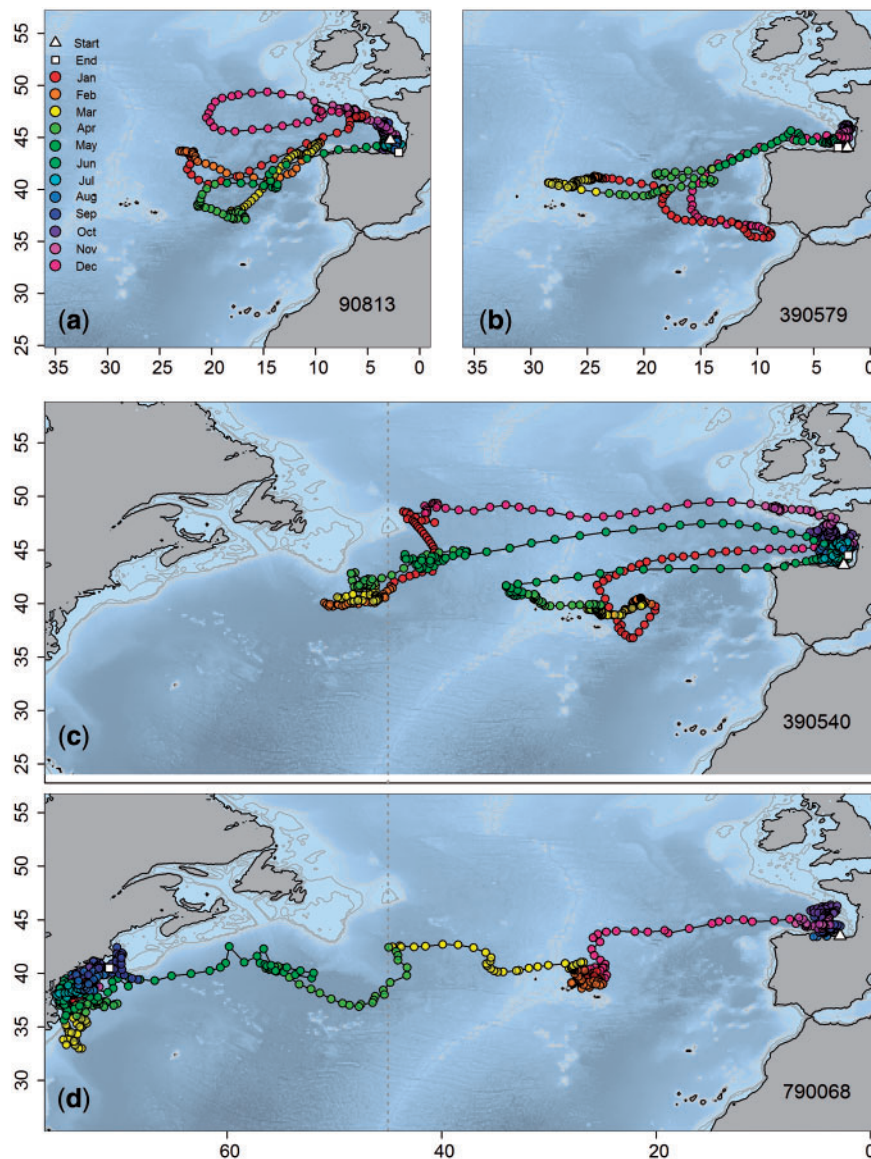
Two ABFT showed three TRN movement patterns after departing from the Bay of Biscay. In both cases, these individuals showed a MID pattern in previous overwintering periods. Fish 390540 showed a MID pattern the first winter (2007–2008), and a TRN pattern in the second winter (2008–2009). Likewise, fish 790076 showed a MID pattern during the first two winters (2007–2009) followed by a TRN pattern the following two winters (2009–2011). During these TRN overwintering trips, the two juvenile ABFT travelled from the Bay of Biscay to the south of the Grand Banks, and were absent from the Bay of Biscay for 194 days on average.

The mean departure date from the Bay of Biscay for overwintering (including the first short outward journey of the LOC movements) was the 31 December, ranging from mid-November to end of February of the following year (Table 3). For the TRN and MID migrants, the mean departure date was earlier (7 December). These fish returned to the Bay of Biscay after an average of 5.5 months outside of the area (Table 3).

Thirteen tracks were long enough to inform fidelity rates. Twelve (92.3%) of these tracks showed tunas returning to the Bay of Biscay feeding area in consecutive feeding seasons. These results suggest a high fidelity of juvenile ABFT to the Bay of Biscay, with fish 790068 being the only exception that foraged in the western Mid-Atlantic Bight.

### Habitat utilization

Habitat utilization distributions showed high usage of the southeastern Bay of Biscay for nearly all individuals during spring and summer (Figure 2 mid panels). During summer, ABFT were highly concentrated in the southeastern corner, south of 45°N and east of 5°W, except for a small area along the eastern US coast, 37–42°N, due to an individual which remained there for 16 months. In autumn, the core-use (50th percentile) and wide-use (95th percentile) areas expanded by a factor of 3.4 and 3.7, respectively (Table 4). The core habitat spread towards the northwest along the French shelf break and the Celtic Sea shelf, and the wide-use area dispersed all along the North Atlantic, including areas between the Portuguese coast towards the Strait of Gibraltar and Madeira (Figure 2 lower panel). In the Bay of Biscay, the autumn core-use area was along the Cantabrian and the French shelf breaks. Individuals displaying a TRN movement pattern travelled along the warm northern edge of the Gulf Stream to the Canadian shelf break area. In winter, habitat use was concentrated in several widely separated areas: the Bay of Biscay, where the core-use area is displaced toward the south-west; north of the Azores and west of Madeira, where the MID tunas overwintered; and south of the Grand Banks, where the TRN individuals inhabited the warm margin of the Gulf Stream (Figure 2, upper panel).



**Figure 1.** Examples of dispersal patterns from recovered archival tags. These individuals occupied the Bay of Biscay during summer months and initiated migrations in November (a and c) or December (b and d). (a) shows an individual that stayed east of the Azores and made three 1- to 2-month loops from the coast to offshore and back. The individual in (b) travelled to southwest Spain in January before moving to areas north of the Azores. The individuals in (c and d) displayed a similar dispersal to north of the Azores. The fish in (c) made a second trip to the western Atlantic, south of the Grand Banks. All individuals returned to the Bay of Biscay in May or June; except for the individual in (d) which continued heading westward in March. This individual arrived off the east coast of the United States in April, and remained there for more than 1 year.

Core-use area in winter and spring was 10.3 and 6.5 times larger than in summer (Table 4). During the spring, the wide-use area was similar to that in winter, extending throughout the mid-Atlantic to the Canadian shelf.

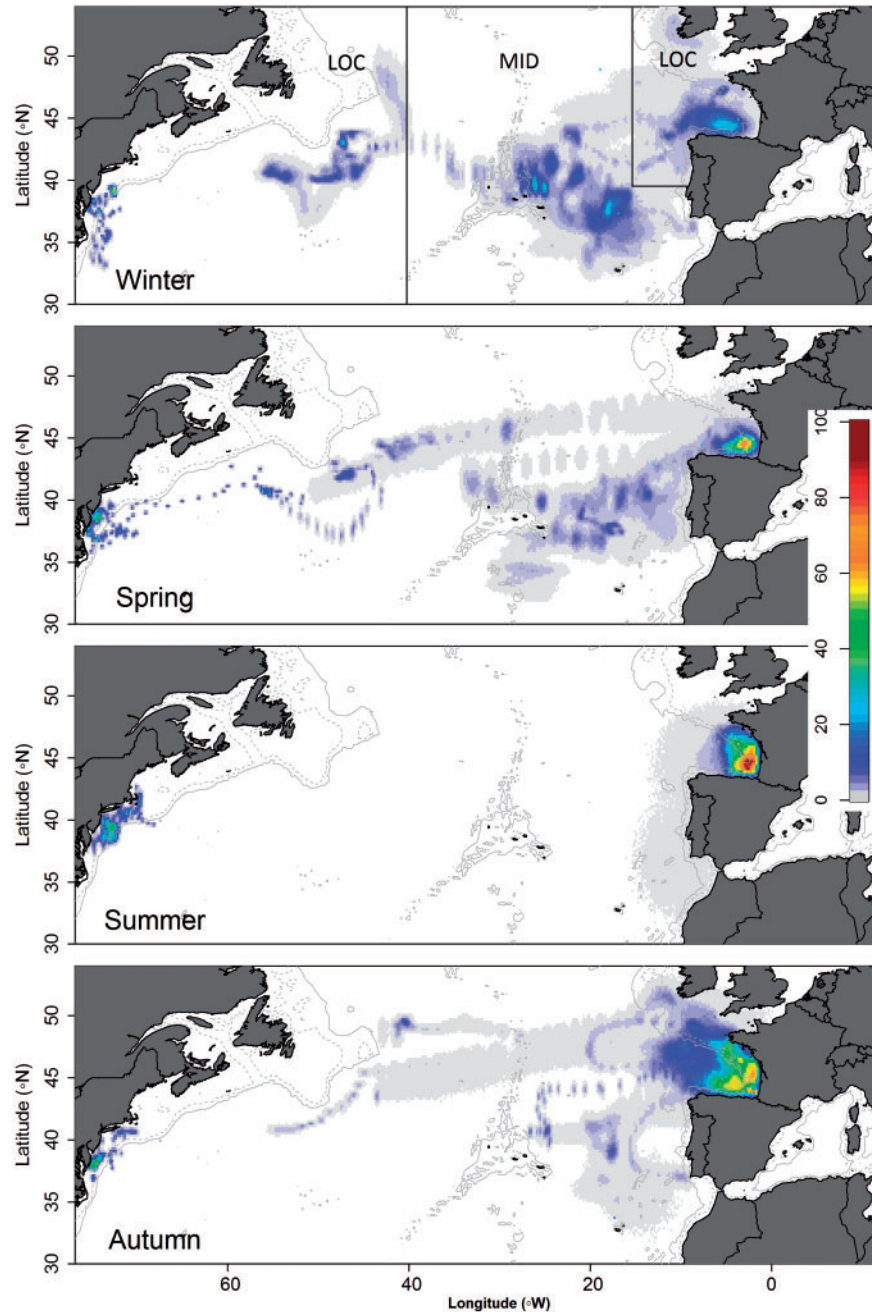
### Vertical distribution

Tagged fish had shallow distribution concentrated above 40 m in spring and summer. In autumn and winter depths below 50 m were visited, mostly between December and May (Figure 3).

From December to August, fish concentrated near the surface (above 7.5-m depth) during 47% of the time (Figure 3), decreasing to 29% from September to November. During this early

autumn period, proportion of time spent between 20 and 40 m was 2.7 times higher than during the rest of the year. Changes in depth distribution from summer to autumn are in accordance with the thermocline depth. In fact, ABFT largely remained within the mixed layer (e.g. Figure 4a), except for short excursions to deeper depths (e.g. Figure 4b). The change in depth preference occurred towards the end of the season, following the deepening of the thermocline.

Occasional dives during dusk and dawn periods were observed (Figure 5a) but not as often as Kitagawa *et al.*, (2004) found for juveniles in the East China Sea and Kuroshio-Oyashio region. Therefore, the twilight period was included in the day period for



**Figure 2.** Habitat utilization of tagged fish, aggregated to a  $0.2^\circ$  grid. Colours represent habitat use estimates (% $H$ ) and dark grey lines represent 250 m (dashed line) and 2000 m (solid line) isobaths. In autumn, tagged fish expanded throughout the Bay of Biscay and westward. Fish were most dispersed in winter, but still showed heavy use of the southwestern Bay of Biscay. In spring, an eastward contraction of habitat was observed. Use of the Bay of Biscay increases during spring and is most intense during the summer, when fish are concentrated in the southeastern Bay of Biscay near the continental slope.

our analysis. Diel differences in proportion of time at depth were consistent across months, with slightly higher proportions near the surface during the night (Figure 3).

In the Bay of Biscay depths between 7 and 50 m show a higher use than in oceanic waters (Figure 6) but differences are less remarkable than those obtained seasonally. Nevertheless, the individual on the Mid-Atlantic Bight show a higher proportion of time in shallow water during night time and a secondary maximum below during day time.

## Discussion

Electronic tagging of juvenile tuna remains a challenge. Although development of miniaturized PSATs has provided a fisheries-independent tool suitable for smaller individuals, these tags were considered still too large for external attachment for the majority of ABFT entering the Bay of Biscay (<85-cm FL). Moreover, they provide significantly shorter data records than IATs, and in this study, close to 50% of the PSATs failed to report. On the other hand, given the low recovery rates of conventional and dummy



**Table 4.** Area (in thousands of km<sup>2</sup>) covered at given cumulative probability of habitat (H) use by season for electronically tagged juvenile Atlantic bluefin tuna.

Seasons	km <sup>2</sup> 10 <sup>-3</sup> by H probability percentile	
	95%	50%
Spring	2762	320
Summer	534	49
Autumn	1961	165
Winter	2875	507

The 50% H shows the seasonal fluctuation in core-use areas, while the 95% column shows the wide-use area.

IATs, the use of IATs implies larger investments when compared with other areas, such as the eastern Pacific, where recovery rates were 51.6% for Pacific bluefin tuna (*Thunnus orientalis*) of similar size (Whitlock *et al.*, 2012). Both tag types are complementary, with PSATs providing tracks for a larger number of individuals, and IATs providing larger times at liberty for the smallest juveniles prevalent in the area. Surprisingly, the PSATs (Xtags) deployed in this study had relatively high non-reporting rates in comparison with other studies (e.g. Galuardi *et al.*, 2010; Lutcavage *et al.*, 2015). Although smaller tags produce less drag and should be retained longer than larger tag models (Musyl *et al.*, 2011), there appeared to be unidentified issues, as suggested by non-reporting PSATs found on land, as in this study, or recovered still attached to tunas (Lutcavage *et al.*, 2015).

### Horizontal movements and distribution

This study is the first to analyse seasonal movements and habitat-use of juvenile bluefin tuna tagged in the northeast Atlantic, as well as quantify the importance of the Bay of Biscay as a juvenile habitat. The Bay of Biscay is clearly an important feeding ground from late spring to early autumn (Goñi and Arrizabalaga, 2010; Logan *et al.*, 2011), with intense use of the western Bay of Biscay during summer. Tracked individuals showed a high degree of fidelity to this feeding area based on their returning proportion in subsequent years. Moreover, this study shows that the Bay of Biscay is an important winter habitat as well, based on a proportion of tagged individuals. The historical view that ABFT spent the winter outside the Bay of Biscay was inferred from fishery data (Dufour *et al.*, 2010) and conventional tagging information that showed ABFT visiting warmer waters during winter (Cort, 1990). However, warm-bodied bluefin tuna tolerate a wide range of environmental conditions (Arrizabalaga *et al.*, 2015), which may explain this LOC pattern, despite lower ambient temperatures. The traditional bait boat fishery takes place from June to October, which is consistent with the observed average timing of movements to and from the Bay of Biscay for the MID and TRN migrants (late May and early November, respectively).

The observed TRN dispersal movement rate (18% from East to West,  $n = 17$ ) is higher than previous estimates of 0.4–10% based on conventional tags across the whole age range of the population (Porch *et al.*, 2001; Fromentin, 2002; Arregui *et al.*, 2006). However, it is closer to the estimates for the younger individuals where, based on organochlorine tracers, recent migration rates from the Bay of Biscay into the northwest Atlantic were 24–33% for ages 2–4, (Graves *et al.*, 2015). The magnitude of the movement rate observed in our study is also comparable to that observed for larger conspecifics tagged in the northwestern Atlantic

off North Carolina, USA (Walli *et al.*, 2009). All those studies are based in a reduced number of data. Movement rate estimates using conventional tags are typically sensitive to fishing effort data and reporting rate assumptions (Arrizabalaga *et al.*, 2004), while organochlorine tracers detect mostly recent migrants. Consequently, it is advisable to use a multidisciplinary approach, including tracking tools (e.g. conventional tags, electronic tags, and organochlorine tracers), as well as genetics or otolith chemistry to assign origin to individuals of different age groups over a wide range of years to better understand migrations and the life cycle of ABFT populations (Arrizabalaga *et al.*, in press; Briscoe *et al.*, 2016).

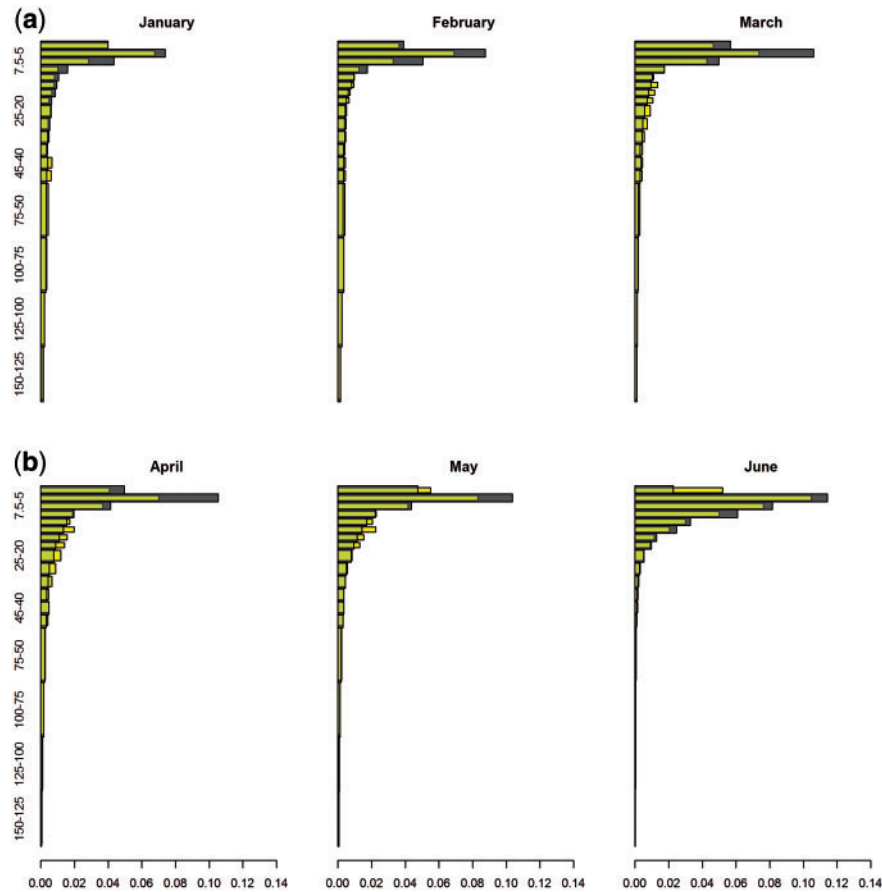
Bluefin tuna tagged in the Bay of Biscay showed a similar seasonal habitat utilization compared with juvenile ABFT tagged in the northwest Atlantic (Galuardi and Lutcavage, 2012). There, seasonal foraging habitat concentrated in spring and summer from the mid-Atlantic coastal area to New England, and expanded in autumn towards warmer pelagic regions further south. However, individuals tagged in the present study showed a much higher dispersion in winter, with high use areas identified in the eastern, mid, and western Atlantic. Another difference is that during summer, the results show maximum habitat use around the shelf break, but not on the continental shelf.

Juvenile ABFT tagged in the western Atlantic and tracked during 1–2.3 years at liberty were not observed to cross the Atlantic (Galuardi and Lutcavage, 2012), while conventional tag recoveries (ICCAT database) and results from more recent PSAT tagging (Lutcavage, unpublished data) confirmed trans-Atlantic movements. PSAT missions of sufficient duration (~1 year) also confirm that shorter observation periods may strongly affect evaluation of habitat utilization of highly migratory species (e.g. Lam *et al.*, 2016).

The Bay of Biscay juveniles (tagged at ages 1–3) share overwintering areas with adult ABFT (Walli *et al.*, 2009) and their habitat dispersal from autumn to spring is comparable to that of adults. In addition, return migration to summer feeding locations in the Bay of Biscay can be rapid. For example, a 3-year-old tuna crossed the Atlantic (~3000 km) moving into the Bay of Biscay in 22 days during early June. The importance of this feeding area could be linked to the presence of European anchovy, one of juvenile ABFT's preferred prey in the Bay of Biscay (Logan *et al.*, 2011). ABFT may follow the pattern of anchovy during its early life cycle, where large anchovy larvae first disperse off the shelf, and then young of the year anchovy recruit to shelf areas (Irigoién *et al.*, 2008; Boyra *et al.*, 2016). This spatial pattern is in accordance with ABFT core use habitat changes from summer to autumn within the Bay of Biscay: transitioning from the southeastern part, mainly off the shelf, to the shelf break and continental shelf (Figure 2, lower panels).

Among adult ABFT tagged electronically, a few were documented to enter the Bay of Biscay (e.g. Aranda *et al.*, 2013) during their post-spawning migration out of the Mediterranean. In contrast, those tagged in the northwest Atlantic that performed transatlantic movements (Walli *et al.*, 2009; Galuardi and Lutcavage, 2012), or those tagged in the northeast Atlantic and western Mediterranean (Stokesbury *et al.*, 2007; Fromentin and Lopuszanski, 2014; Aranda *et al.*, 2013; Cermeño *et al.*, 2015) visited surrounding areas but did not move into the Bay of Biscay. This apparent avoidance by adults and the high fidelity by juveniles observed in this study suggests that the Bay of Biscay is mostly a summer-autumn residence area for juvenile ABFT, as depicted from fishery data (Rodríguez-Marin *et al.*, 2003).





**Figure 3.** Mean proportion of time by depth of tagged tuna. The depth bin width is 2.5 m from 0- to 20-m depth, 5 m from 20- to 50-m depth, and 25 m from 50- to 150-m depth. Proportion of time in deeper bins is not appreciable. Day is indicated with clear bars while night is indicated with dark grey bars.

### Vertical distribution

Adult bluefin tuna display a wide variety of depth patterns, presumably related to foraging, travelling and spawning (Lutcavage *et al.*, 1999; Teo *et al.*, 2007; Walli *et al.*, 2009), supported by their unique physiological thermoregulation capabilities (Carey, 1973). Diel variations in vertical distribution and use of particular depths, such as the thermocline or deep scattering layer, are hypothesized as a strategy to optimize the probability of encountering/detecting prey, or may even serve an orientation function (Lutcavage *et al.*, 2000; Willis *et al.*, 2009; Marcek *et al.*, 2016). For northwest Atlantic juveniles, Galuardi and Lutcavage (2012) and Brill *et al.* (2002) showed sharp compression in vertical habitat during summer months and a broader and bimodal distribution in winter months with no difference in diel activity, while Marcek (2016) detected deeper distribution during the day in late summer. In the present study, diel differences per month and area were small. Regarding day and night, bluefin tuna concentrated between 0 - 30 m and restricted to 50 m overall, from June to October, while from December to March, the depth range expanded to 100-125 m. Tagged juveniles did not show a clear bimodal depth distribution, except in the US coast, as also observed by Galuardi and Lutcavage (2012) and Marcek *et al.* (2016). The modal depth deepened from 16 m to 22.5 m and 27.5 m in August, September and October, respectively. The variability of juvenile bluefin vertical distribution in the northwestern Pacific

was related to anchovy depth (Kitagawa *et al.*, 2004). Similarly, the broader depth distribution of juvenile ABFT from late summer to early autumn is concordant with the mixed layer depth and probably associated with preying on juvenile anchovy in the Bay of Biscay. These anchovies are widely available and distributed across the continental shelf between the surface and 25 m, and then deepen through the season with their ontogenetic growth (Boyra *et al.*, 2013).

The highly aggregated summer distribution of juvenile bluefin tuna in the Bay of Biscay described in this study likely determined the specialization of the fishing fleets in the Bay of Biscay. The ports of Hondarribia and Saint Jean de Luz (Cort, 1990) have historically specialized in catching bluefin tuna, while the other fishing ports along the Spanish and French coasts around the Bay of Biscay mostly targeted albacore tuna (*Thunnus alalunga*). These two ports, located at both sides of the Spanish-French border, are closest to the summer core habitat of ABFT (Figure 2). This proximity likely lead to relatively higher catch rates of this species and subsequent specialization. Our results further demonstrate that limitations of fishery-dependent data have resulted in an underestimation of bluefin tuna presence in the Bay of Biscay during late autumn and winter. After the emigration of most individuals in autumn, remaining resident individuals might have been undetected for several reasons. We hypothesize that, besides the unfavourable environmental

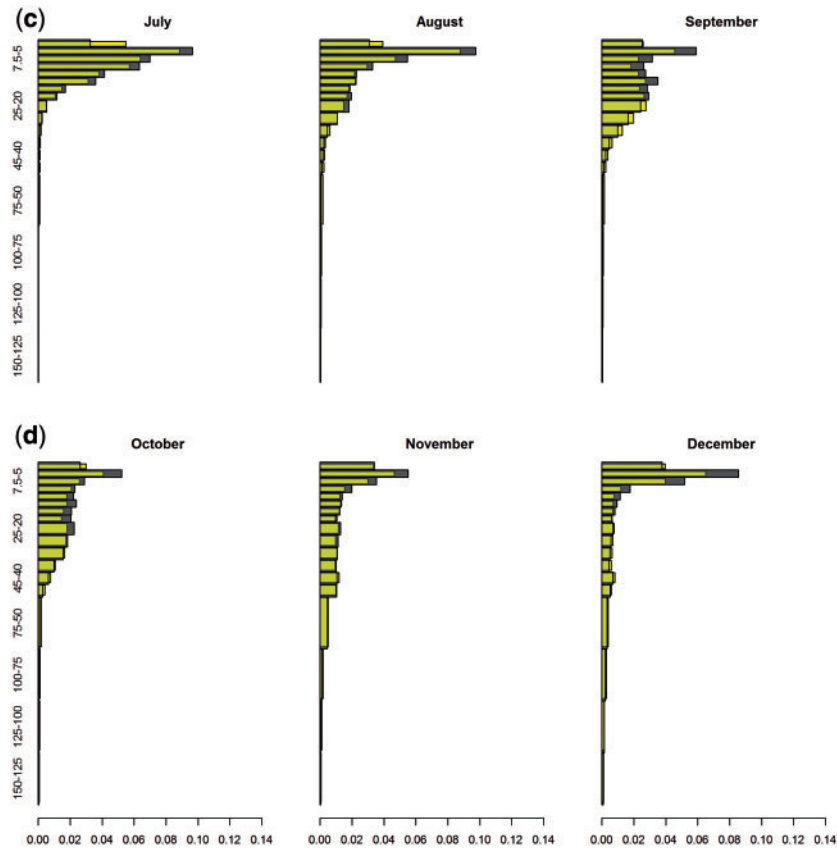


Figure 3. Continued

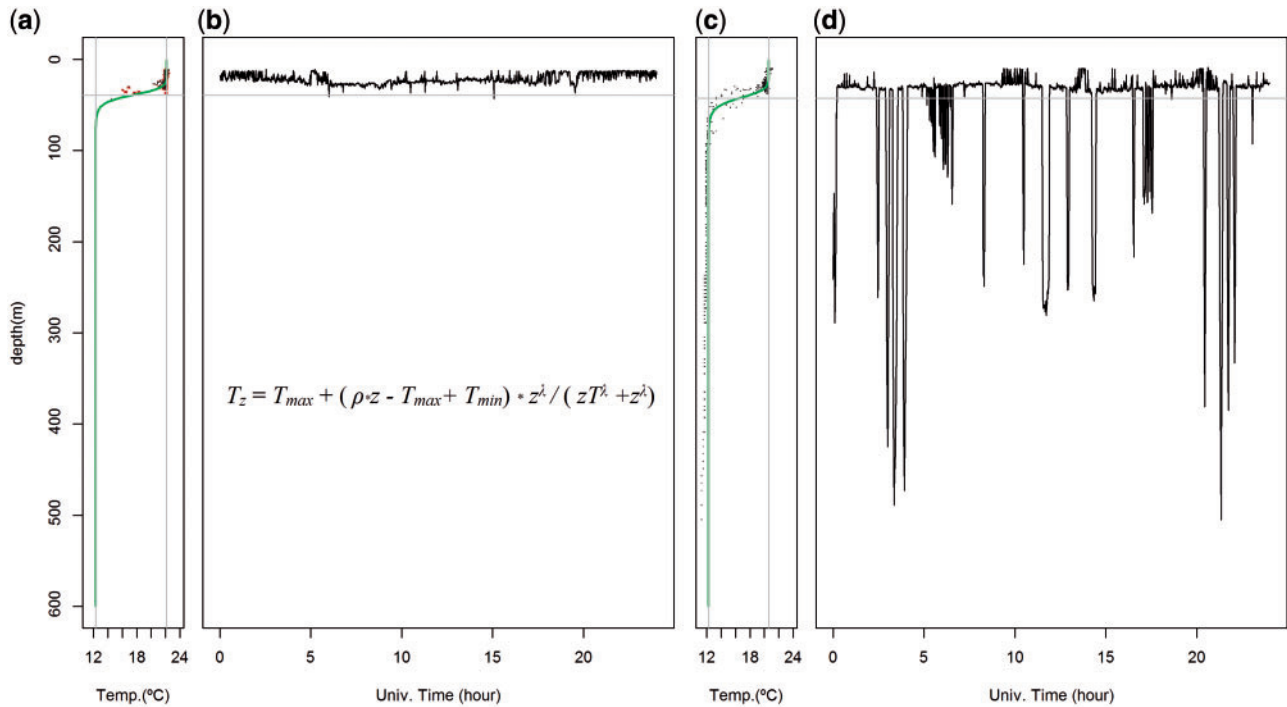
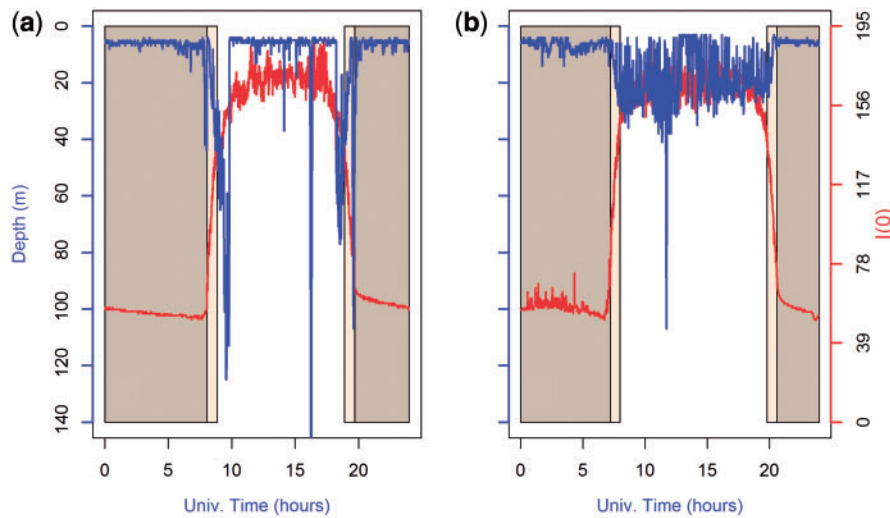
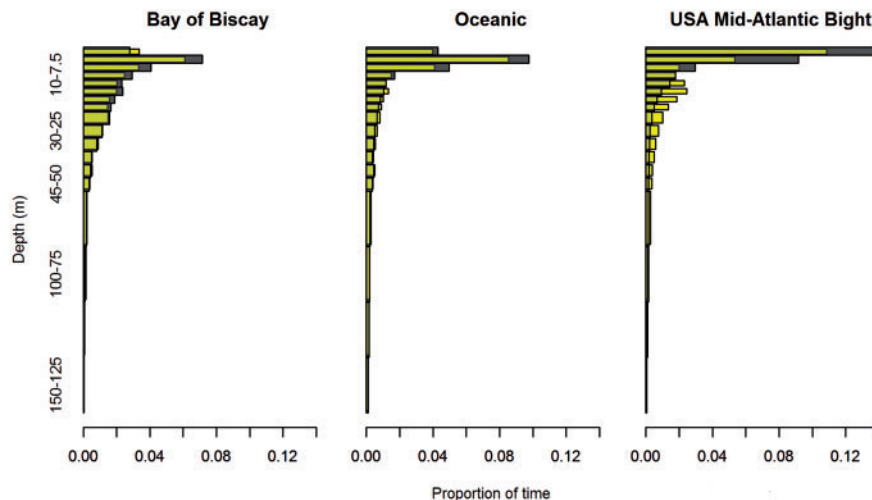


Figure 4. Vertical thermal structure (a and c), and depth time series (b and d) for two representative days (7 and 23 September 2005, respectively) for individual 390579 in the Bay of Biscay. Thermal structure (green line) was determined from observed data and interpolation from the closest time period when necessary. The model equation describing the thermal structure is shown in (b).  $T_{max}$ ,  $T_{min}$ , and  $T_z$  are maximum temperature, minimum temperature and temperature at depth ( $z$ ), respectively. Depth at the middle of the thermocline ( $zT$ ) is 37.7 m for (a and b) and 42.8 m for (c and d). Constant and thermocline thermal decrease are parameterized by  $\rho$  and  $\lambda$ , respectively.



**Figure 5.** Example of two different behavioral patterns of bluefin tuna from the central Atlantic. Depth (m) is indicated in blue and estimated surface irradiance ( $I_0$ ) in red. Crepuscular periods, calculated from solar declination, are represented with light grey rectangles, night with dark grey, and day with white. (a) (1 February 2006) shows vertical excursions during crepuscular periods while (b) (18 March 2006) shows shallower vertical excursions during daylight. Data are from Wildlife Computers Mk9 IATs 390579.



**Figure 6.** Area specific day (clear bars) and night (dark grey bars) mean proportion of time at depth. The depth bin width is 2.5 m from 0- to 20-m depth, 5 m from 20- to 50-m depth, and 25 m from 50- to 150-m depth. Proportion of time in deeper bins is not appreciable.

conditions for fishing, their progressively deeper distribution after autumn (Figure 3) could result in a lower detectability by traditional surface gears such as bait boat or trolling.

## Conclusion

This is the first fisheries-independent characterization of the movements, seasonal habitat use, and depth preferences of juvenile bluefin tuna in the northeast Atlantic. The Bay of Biscay was revealed as important summer feeding area for juveniles, as well as an overwintering area for an unexpected portion of this population. Transient individuals spent the winter in areas around the Azores, Madeira, the Gulf Stream margins and the Canadian–USA coasts. The estimated return rate to the Bay of Biscay in the following summer was 93% suggesting high fidelity for the group of ages 1–3. The capability of juvenile eastern ABFT to conduct

extensive, even transoceanic, dispersal movements and expand their habitats approaches that of adults. Given the amplitude and complexity of the movements during the overwintering period, a larger dataset (particularly of IAT data) would allow to make stronger conclusions about juvenile movements at the population level. This, together with other approaches (e.g. genetics and otolith chemistry) as part of a multidisciplinary effort, is necessary to characterize ABFT mixing rates and their variability, so as to improve the stock assessment and management of this valuable resource.

## Acknowledgements

European Data Collection Programme (ROJOCAN 2007), Basque Government. Institutions cooperating with AZTI: Instituto Español de Oceanografía (IEO, Dr Enrique Rodriguez



Marin) and recreational fishing organizations (Basque Nautical and the Recreational Fishery Federation “FASNAPER” and “Club Nautico Hondarribia”). Archival tags were released from FV “Nuevo Horizonte Abierto”, live bait FV “Berriz Gure Naia”, and recreational FV “Tia Rosario”. FV “Tuku-tuku” and “Attalaya Berria” contributed in pop-up tagging during 2010. All vessels were based at the Hondarribia fishing port, Basque Country, Spain. The continued support of their captains and crew has been indispensable for the success of the releases in this study. Three anonymous reviewers made useful suggestions that improved the article.

## References

- Akima, H. 1978. A method of bivariate interpolation and smooth surface fitting for irregularly distributed data points. *ACM Trans. Math. Software*, 4: 148–159.
- Amante, C., and Eakins, B. W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. p. 19. NOAA Technical Memorandum NESDIS NGDC.
- Aranda, G., Abascal, F. J., Varela, J. L., and Medina, A. 2013. Spawning behaviour and post-spawning migration patterns of atlantic bluefin tuna (*Thunnus thynnus*) ascertained from satellite archival tags. *PLoS One*, 8: e76445.
- Arregui, I., Arrizabalaga, H., and de la Serna, J. M. 2006. Preliminary approach to the experimental design of tagging campaigns for movement rates estimation of East Atlantic bluefin tuna. *ICCAT Collective Volume Science Paper*, 59: 769–788.
- Arrizabalaga, H., Arregui, I., Medina, A., Rodríguez-Ezpeleta, N., Fromentin, J. M., and Fraile, I. In press. Life history and migrations of Mediterranean bluefin populations. *In* *Bluefin Futures*. Ed. by B. Block. Johns Hopkins University Press, Baltimore, Maryland, US.
- Arrizabalaga, H., Costas, E., Juste, J., González-Garcés, A., Nieto, B., and López-Rodas, V. 2004. Population structure of albacore *Thunnus alalunga* inferred from blood groups and tag-recapture analyses. *Marine Ecology Progress Series*, 282: 245–252.
- Arrizabalaga, H., Dufour, F., Kell, L., Merino, G., Ibaibarriaga, L., Chust, G., and Irigoien, X. 2015. Global habitat preferences of commercially valuable tuna. *Deep-Sea Research Part II*, 113: 102–112.
- Boyra, G., Martínez, U., Cotano, U., Santos, M., Irigoien, X., and Uriarte, A. 2013. Acoustic abundance estimates of juvenile anchovy (*Engraulis encrasicolus*) in the Bay of Biscay as an indicator of the next year's recruitment. *ICES Journal of Marine Science*, 70: 1354–1368.
- Boyra, G., Peña, M., Cotano, U., Irigoien, X., Rubio, A., and Nogueira, E. 2016. Spatial dynamics of juvenile anchovy in the Bay of Biscay. *Fisheries Oceanography*, 25: 529–543.
- Brill, R., Lutcavage, M., Metzger, G., Bushnell, P., Arendt, M., Lucy, J., Watson, C. *et al.* 2002. Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of western North Atlantic, determined with ultrasonic telemetry. *Fisheries Bulletin of National Oceanic and Atmospheric Administration*, 100: 155–167.
- Briscoe, D. K., Hobday, A. J., Carlisle, A., Scales, K., Eveson, J. P., Arrizabalaga, H., Druon, J. N. *et al.* 2016. Ecological bridges and barriers in pelagic ecosystems. *Deep Sea Research*.
- Calenge, C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Model*, 197: 1035.
- Carey, F. G. 1973. Fish with warm bodies. *Scientific American*, 228: 36–44.
- Cermeño, P., Quílez-Badía, G., Ospina-Alvarez, A., SainzTrápaga, S., Boustany, A. M., Seitz, A. C., Tudela, S. *et al.* 2015. Electronic tagging of Atlantic Bluefin Tuna (*Thunnus thynnus*, L.) reveals habitat use and behaviors in the Mediterranean Sea. *PLoS One*, 10: e0116638.
- Cort, J. L. 1990. Biología y pesca del atún rojo *Thunnus thynnus* (L.) del Mar Cantabrico. *In* *Publicaciones Especiales Instituto Español de Oceanografía*, Madrid, Spain, p. 272.
- Dickhut, R. M., Deshpande, A. D., Cincinelli, A., Cochran, M. A., Corsolini, S., Brill, R. W., Secor, D. H. *et al.* 2009. Atlantic Bluefin Tuna (*Thunnus thynnus*) population dynamics delineated by organochlorine tracers. *Environmental Science & Technology*, 43: 8522–8527.
- Domeier, M. L., Kiefer, D., Nasby-Lucas, N., Wagschal, A., and O'Brien, F. 2005. Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. *Fisheries Bulletin of National Oceanic and Atmospheric Administration*, 103: 292–306.
- Dufour, F., Arrizabalaga, H., Irigoien, X., and Santiago, J. 2010. Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. *Progress in Oceanography*, 86: 283–290.
- Ekstrom, P. A. 2004. Advance in geolocation by light. *Memoirs of National Institute of Polar Research*, 58: 210–226.
- Fromentin, J.-M., Bonhommeau, S., Arrizabalaga, H., and Kell, L. T. 2014. The spectre of uncertainty in management of exploited fish stocks: the illustrative case of Atlantic bluefin tuna. *Marine Policy*, 47: 8–14.
- Fromentin, J.-M., and Lopuszanski, D. 2014. Migration, residency, and homing of bluefin tuna in the western Mediterranean Sea. *ICES Journal of Marine Science*, 71: 510–518.
- Fromentin, J. M. 2002. Descriptive analysis of the ICCAT bluefin tuna tagging database. *ICCAT Collective Volume Science Paper*, 54: 343–362.
- Galuardi, B. 2011. analyzepsat, R library for reading MTI fish reports, estimating tracks and plotting results nicely. <http://code.google.com/p/analyzepsat/>.
- Galuardi, B., and Lutcavage, M. 2012. Dispersal routes and habitat utilization of juvenile Atlantic Bluefin Tuna, *Thunnus thynnus*, tracked with Mini PSAT and archival tags. *PLoS One*, 7: e37829.
- Galuardi, B., Royer, F., Golet, W., Logan, J., Neilson, J., and Lutcavage, M. 2010. Complex Migration routes of Atlantic Bluefin tuna question current population structure paradigm. *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 966–976.
- Goñi, N., and Arrizabalaga, H. 2010. Seasonal and interannual variability of fat content of juvenile albacore (*Thunnus alalunga*) and bluefin (*Thunnus thynnus*) tunas during their feeding migration to the Bay of Biscay. *Progress in Oceanography*, 86: 115–123.
- Graves, J. E., Wozniak, A. S., Dickhut, R. M., Cochran, M. A., MacDonald, E. H., Bush, E., Arrizabalaga, H. *et al.* 2015. Transatlantic movements of juvenile Atlantic bluefin tuna inferred from analyses of organochlorine tracers. *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 625–633.
- Hill, R. D., and Braun, M. J. 2001. Geolocation by light level - the next step: latitude. *In* *Methods and Technologies in Fish Biology*, pp. 315–330. Ed. by J. R. Sibert, and J. Nielsen. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- ICCAT. 2017. Report of the 2017 ICCAT bluefin stock assessment meeting. *ICCAT Collective Volume Science Paper*, In press.
- Irigoien, X., Cotano, U., Boyra, G., Santos, M., Alvarez, P., Otheguy, P., Etxebeste, E. *et al.* 2008. From egg to juvenile in the Bay of Biscay: spatial patterns of anchovy (*Engraulis encrasicolus*) recruitment in a non-upwelling region. *Fisheries Oceanography*, 17: 446–462.
- Kitagawa, T., Kimura, S., Nakata, H., and Yamada, H. 2004. Diving behavior of immature, feeding Pacific bluefin tuna (*Thunnus thynnus orientalis*) in relation to season and area: the East China

- Sea and the Kuroshio-Oyashio transition region. *Fisheries Oceanography*, 13: 161–180.
- Lam, C. H., Galuardi, B., Mendillo, A., Chandler, E., and Lutcavage, M. E. 2016. Sailfish connect productive coastal areas in the Northwest Atlantic Ocean. *Scientific Reports Nature*, 6: 3816.
- Lam, C. H., Nielsen, A., and Sibert, J. R. 2008. Improving light and temperature based geolocation by unscented Kalman filtering. *Fisheries Research*, 91: 15–25.
- Logan, J. M., Rodríguez-Marín, E., Goñi, N., Barreiro, S., Arrizabalaga, H., Golet, W., and Lutcavage, M. 2011. Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Marine Biology*, 158: 73–85.
- Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., Goldstein, J. L., and Tutein, J. 2000. Tracking adult North Atlantic bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. *Marine Biology*, 137: 347–358.
- Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., and Howey, P. W. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do north Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 173–177.
- Lutcavage, M. E., Lam, C. H., and Galuardi, B. 2015. Seventeen years and \$3 million dollars later: performance of psat tags deployed on Atlantic bluefin and bigeye tuna. *ICCAT Collective Volume Science Paper*, 71: 1757–1765.
- Lynch, S. D., Marcek, B. J., Marshall, H. M., Bushnell, P. G., Bernal, D., and Brill, R. W. 2017. The effects of pop-up satellite archival tags (PSATs) on the metabolic rate and swimming kinematics of juvenile sandbar shark *Carcharhinus plumbeus*. *Fisheries Research*, 186: 205–215.
- Marcek, B. J., Fabrizio, M. C., and Graves, J. E. 2016. Short-term habitat use of juvenile atlantic bluefin tuna. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 8: 395–403.
- Mather, III, F. J., Bartlett, M. R., and Beckett, J. S. 1967. Transatlantic migrations of young bluefin tuna. *Journal of the Fisheries Research Board of Canada*, 24: 1991–1997.
- Musyl, M. K., Domeier, M. L., Nasby-Lucas, N., Brill, R. W., McNaughton, L. M., Swimmer, J. Y., Lutcavage, M. S. *et al.* 2011. Performance of pop-up satellite archival tags. *Marine Ecology Progress Series*, 433: 1–28.
- Porch, C. E., Turner, S. C., and Powers, J. E. 2001. Virtual population analyses of atlantic bluefin tuna with alternative models of transatlantic migration: 1970-1997. *ICCAT Collective Volume Science Paper*, 52: 1022–1045.
- Quílez-Badia, G., Cermeño, P., Tudela, S., Trápaga, S. S., and Graupera, E. 2013. Spatial movements of bluefin tuna revealed by electronic tagging in the Mediterranean Sea and in Atlantic waters of Morocco in 2011. *ICCAT Collective Volume Science Paper*, 69: 435–453.
- R Core Team 2000. R Language Definition. Version 3.4.1 edn. R foundation for statistical computing, Vienna, Austria
- Reynolds, R. W., Rayner, N. A., Smith, T. M., Stokes, D. C., and Wang, W. 2002. An improved in situ and satellite SST analysis for climate. *Journal of Climate*, 15: 1609–1625.
- Rodríguez-Marin, E., Arrizabalaga, H., Ortiz, M., Rodríguez-Cabello, C., Moreno, G., and Kell, L. 2003. Standardization of bluefin tuna, *Thunnus thynnus*, catch per unit effort in the baitboat fishery of the Bay of Biscay (Eastern Atlantic). *ICES Journal of Marine Science*, 60: 1216–1231.
- Rooker, J. R., Arrizabalaga, H., Fraile, I., Secor, D. H., Dettman, D. L., Abid, N., Addis, P. *et al.* 2014. Crossing the line: migratory and homing behaviors of Atlantic bluefin tuna. *Marine Ecology Progress Series*, 504: 265–276.
- Rooker, J. R., Secor, D. H., Metrio, G. D., Schloesser, R., Block, B. A., and Neilson, J. D. 2008. Natal homing and connectivity in Atlantic bluefin tuna populations. *Science*, 322: 742–744.
- Schloesser, R. W., Neilson, J. D., Secor, D. H., and Rooker, J. R. 2010. Natal origin of Atlantic bluefin tuna (*Thunnus thynnus*) from Canadian waters based on otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ . *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 563–569.
- Sibert, J. R., Musyl, M. K., and Brill, R. W. 2003. Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. *Fisheries Oceanography*, 12: 141–151.
- Sippel, T. J., Eveson, P., Galuardi, B., Lam, C., Hoyle, S., Maunder, M., Kleiber, P. *et al.* 2015. Using movement data from electronic tags in fisheries stock assessment: a review of models, technology and experimental design. *Fisheries of Research*, 163: 152.
- Stokesbury, M. J. W., Cosgrove, R., Boustany, A., Browne, D., Teo, S. L. H., O’Dor, R. K., and Block, B. A. 2007. Results of satellite tagging of atlantic bluefin tuna, *Thunnus thynnus*, off the coast of Ireland. *Hydrobiologia*, 582: 91–97.
- Taylor, N. G., McAllister, M. K., Lawson, G. L., Carruthers, T., and Block, B. A. 2011. Atlantic Bluefin Tuna: a novel multistock spatial model for assessing population biomass. *PLoS One*, 6: e27693.
- Teo, S. L. H., Boustany, A., Dewar, H., Stokesbury, M. J. W., Weng, K. C., Beemer, S., Seitz, A. C. *et al.* 2007. Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Marine Biology*, 151: 1–18.
- Walli, A., Teo, S. L. H., Boustany, A., Farwell, C. J., Williams, T., Dewar, H., Prince, E. *et al.* 2009. Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS One*, 4: e6151.
- Whitlock, R. E., Mc Allister, M. K., and Block, B. A. 2012. Estimating fishing and natural mortality rates for Pacific bluefin tuna (*Thunnus orientalis*) using electronic tagging data. *Fisheries Research*, 119-120: 115–127.
- Willis, J., Phillips, J., Muheim, R., Diego-Rasilla, F. J., and Hobday, A. J. 2009. Spike dives of juvenile southern bluefin tuna (*Thunnus maccoyii*): a navigational role? *Behavioural Ecology and Sociobiology*.

Handling editor: Caroline Durif