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Original Article

Migration, residency, and homing of bluefin tuna in the western Mediterranean Sea

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This study presents the results of an electronic tagging programme on mature Atlantic bluefin tuna (ABFT) that has been conducted since 2007 offshore of the French Mediterranean Coast. The spatial distributions of ABFT showed little year-to-year variation and the fish concentrated in a small area of the central northwestern Mediterranean, where they may stay for several months. The individual tracks display sinuous trajectories in this area, indicating the possibility of feeding behaviour. No fish went out to the North Atlantic, but several fish displayed some migration to the southern western Mediterranean Sea during winter and the central Mediterranean during the spawning season. The homing behaviour of one fish after a full year as well as the back and forth of several fish further indicates that this restricted feeding area is probably persistent from year to year. We hypothesize that this area could result from local enrichment due to permanent mesoscale oceanographic features related to the North Mediterranean Current and the North Balearic front. The option of a spatial management, through marine protected areas, for a highly migratory species, such as ABFT, thus deserves more careful consideration because those species displayed complex spatial dynamics (e.g. homing), and population structure (e.g. several subpopulations of different sizes).

Keywords: feeding area, front, marine protected area, pop-up archival tag, spatial distribution, *Thunnus thynnus*.

Introduction

Atlantic bluefin tuna (ABFT) is a commercial fish of a high market value that crystallises many of the problems found in fisheries in areas beyond national jurisdiction, i.e. severe overcapacity, open access in international waters, geographical expansion of the fisheries, and deficient governance at both the international and national levels. Although the scientific community has raised serious concern about the East Atlantic and Mediterranean stock status since the mid-1990s (ICCAT, 1997), management has not followed, until recently, the scientific advice (Fromentin and Powers, 2005). Furthermore, management regulations have largely been ineffective in limiting catches because of a lack of compliance and control (ICCAT, 2007). This has meant that catches were underreported until 2007 (and probably thereafter, but to a lesser extent) and overexploitation occurred for years (ICCAT, 2009). Such failure in management was unfortunately not specific to ABFT and can be found in many fisheries around the world (e.g. Garcia and Grainger, 2005; Hilborn *et al.*, 2005; Beddington *et al.*, 2007). This situation probably has resulted in the scientific community starting to consider alternative management options for the pelagic and highly migratory species, such as marine protected area (MPA, e.g. Halpern and Warner, 2002; Sumaila *et al.*, 2007).

However, highly migratory species, such as tuna and billfish, are likely to move out of the reserves, so that MPAs may be inefficient as conservation tools (Claudet *et al.*, 2010). Mobile marine species often display more population structure than usually assumed and have complex spatial dynamics, such as homing behaviour (e.g. Kritzer and Sale, 2004; Ruzzante *et al.*, 2006; Hauser and Carvalho, 2008; Rooker *et al.*, 2008; Secor, 2010). Such features could make MPAs more effective than expected if well designed to protect particular life-history phases, key habitats, or given subpopulations. Knowledge of spatial dynamics will also be important for developing simulation models that include plausible hypotheses about stock structure and fisheries dynamics for use in management strategy evaluation (e.g. Kell *et al.*, 2009).

Studies of highly migratory fish, such as ABFT, based on electronic tagging have been shown to be successful for investigating the spatial dynamics and to identify preferential feeding and spawning areas (e.g. Block *et al.*, 2005; Wilson *et al.*, 2005; Sibert *et al.*, 2006; Teo *et al.*, 2007). However, the great majority of studies on ABFT has been conducted in the western Atlantic and, therefore, has focused on the spatial dynamics of ABFT in the North Atlantic.

In this study, we present the results of an electronic tagging programme for ABFT in the northwestern Mediterranean that has been conducted since 2007. The objectives of the study are to: (i) better understand ABFT spatial dynamics in the Mediterranean Sea, especially the migration patterns within the Mediterranean and between the Mediterranean and the North Atlantic, (ii) identify the potential key feeding and spawning areas in the Mediterranean, and (iii) explore the appropriateness of MPAs as a management and conservation tool for ABFT in the Mediterranean Sea.

Methods

Pop-up archival tags

Pop-up archival tags record several times a day, water temperature, depth, and light intensity that are used to calculate the average daily location of the fish. The tag is fixed, through a tether, close by the second dorsal fin of the fish. After a period set by the scientists (here 10 or 12 months), the tag detaches itself and emits a summary of the recorded data to the closest satellites (e.g. Gunn and Block, 2001, for more details). However, premature detachment is a general problem with pop-up archival tags that usually truncate the time at liberty to a few months (Sibert *et al.*, 2006).

ABFT were caught using rod and reel on board of a recreational fishing boat. Tuna were brought on-board, through the back door, onto a wet vinyl mat. During the tagging operation, the eyes of the fish were covered by a wet tissue and the fish was irrigated with a deck hose with flowing seawater. Since 2008, the pop-up archival tag was also maintained along the body of the fish using a second tether. This avoids harm to the fish caused by the tag hitting and dragging the fish. The whole tagging operation lasts 1–2 min. All the tagging operations were performed on the same boat with the same crew (i.e. captain, recreational fishers, and scientist).

Pop-up archival tags were primarily deployed on fish of 125–255 cm (fork length) offshore of the French Mediterranean Coast, slightly west of Marseille (at 43°14′N 04°58′E, Table 1). We released 11, 6, 9, 5, and 8 pop-up archival tags from 2007 to 2011, respectively. All the tags, except tag 92109, have successfully transmitted (Table 1). Past pop-up archival surveys on different biological platforms (fish and birds) suggested problems with the transmission in the Argos band over the Mediterranean Sea (de Metrio et al., 2001; Fromentin, 2010). After an inquiry from Argos-France, it appeared that the Argos band is subject to interference due to various sources of noise over the Mediterranean Sea, so that a minimum transmission power of 0.3 W is needed (Argos, unpublished). Therefore, we only deployed Mk-10 pop-up archival tags from Wildlife Computers, which have a transmission power of ~0.5 W.

Geolocation estimates

Observed geolocations estimated from light intensity alone are known to be incomplete and/or impaired by large observation errors (Sibert and Fournier, 2001). To circumvent this difficulty, we used a state-space model developed by Royer *et al.* (2005) and improved later on to integrate constraints from coastlines, bathymetric limits, and sea surface temperature information from oceanic models in the optimisation function (Royer and Lutcavage, 2009). This constrained non-linear and non-Gaussian estimation method partly corrects for erroneous sunrise and sunset times, which are known to explain most of common error patterns in latitude deduced from light-based geolocations (Nielsen *et al.*, 2006). However, in our case study, the main limitations in estimating unbiased tracks from pop-up archival tags mostly result from the transmission. In average, we obtained 24% of the daily geolocations (from 12% in 2007 to 30% in 2009) and ~37% of temperature and depth profiles (from 25% in 2007 to 50% in 2011). The quality of the Argos transmission also varied considerably among tags: from 3.3% of daily geolocations for tag 68409 (over 139 days-at-sea) to 84% of information for tag 87643 (over 55 days-at-sea). The paucity of data for some tags was thus a key limitation because this leads to a monotonic and poorly informative trajectory. This was the case for six tracks (tags 68406, 68408, 68409, 87642, 34261, and 61958). Note that the tags 68407, 92109, and 73422 did not send any archived data because of transmission failure, so that the locations of release and pop-off are the only available information for those three tags (Table 1).

Mapping

To identify the potential key areas of ABFT, we calculated the probability distribution from the geolocations, using a two-dimensional kernel density estimation with an axis-aligned bivariate normal kernel (Venables and Ripley, 2002). The kernel density was evaluated on a square grid of $n = 500$ in both directions. Kernel density plots have been computed for each year (from 2007 to 2011) as well as for the whole period by pooling all the tracks together. All the calculations have been performed using the libraries "MASS", "fields", "mapdata", and "Hmisc" of R software 2.15.0 (http://www.r-project.org/).

Results

Tagging release and recapture

Twenty pop-up archival tags were deployed on medium-size fish of 124–172 cm (i.e. young spawners of 4–7 years old when referring to the von Bertalanffy equation used by the scientific committee of ICCAT), whereas 19 were deployed on larger-size fish of 180–255 cm (i.e. spawners from 8 to 16 years old, Table 1). Large fish (>190 cm) were tagged in all years, but smaller fish (124 cm < ABFT < 144 cm) were tagged during the first 2 years and fish of 160–190 cm were mostly tagged during the 3 subsequent years. Although small size fish were available during all the period, medium-size fish (i.e. 160–190 cm) were mostly abundant in the last years. The overall average of time at liberty is 110 d, ranging from 68 d in 2007 to 160 d in 2011 (Table 1). This substantial increase in the duration of the tag attachment is probably due to an anchorage through the pterygiophores and the use of a double dart since 2008. Nonetheless, all the tags, except tag 61964, popped-off prematurely. As mentioned in the "Methods" section, premature detachment is a well-known problem for pop-up archival tags. In our study, we identified three main causes: (i) premature rupture of the tag pin (confirmed on the single premature detached tag that has been recovered), (ii) fishing, as for tag 68407 and possibly for 1–3 other fish, and (iii) death of the fish just after release (i.e. tags 37333, 80083, and 62008).

Geolocations and tracks

Deployment mostly occurred in August and September, so most of the tracks start in late summer and end in early spring of the following year and summer for a few tags (Table 1). The rather low

Table 1. Detailed information about the 39 pop-up archival tags deployed between 2007 and 2011, i.e. the time and place of release, size of the fish at release, place of pop-off (or recapture), and time at liberty (in days).

Tag Ids	Release date	Release latitude (°E)	Release longitude (°N)	Fish size (cm)	Recapture latitude (°E)	Recapture longitude (°N)	Time at liberty (days)	Total distance (nm)	Mean distance/ day (nm)
68402	24 September 2007	4.73	43.23	124	9.87	38.17	15	688	45.9
68403	03 October 2007	4.97	43.28	235	4.86	38.44	40	756	18.9
68404	24 September 2007	4.73	43.25	128	2.68	40.96	59	872	14.8
68405	21 September 2007	4.73	43.23	127	4.06	41.14	88	946	10.8
68406	24 September 2007	4.73	43.23	128	7.17	43.58	122	847	6.9
68407	02 November 2007	4.92	43.27	130	0.25	36.2	69	*Transmission Failure*	
68408	22 September 2007	4.73	43.23	132	11.68	41.95	91	829	9.1
68409	22 September 2007	4.73	43.23	127	12.27	35.74	139	1 280	9.2
37332	03 November 2007	4.93	43.23	128	5.68	39.3	7	282	40.2
37333	03 November 2007	4.93	43.23	133	6.16	41.07	4	161	40.4
37334	03 November 2007	4.93	43.23	130	4.92	41.12	112	916	8.2
37331	31 July 2008	5.4	43.05	225	6.27	41.23	18	209	11.6
80082	08 November 2008	4.92	43.23	144	14.49	40.08	168	1 717	10.2
87641	21 August 2008	5.4	43.05	228	6.9	38.6	71	835	11.8
87642	26 October 2008	4.91	43.26	210	18.33	31.88	239	2 537	10.6
87643	26 October 2008	4.91	43.26	143	3.95	42.03	55	509	9.2
87644	21 August 2008	5.4	43.05	188	3.52	41.07	14	357	25.5
80083	20 August 2009	4.8	43.27	197	4.79	43.28	1	*Death after Release*	
80084	16 August 2009	4.82	43.27	198	4.95	41.32	149	1 540	10.3
80085	07August2009	4.82	43.27	190	8.92	44.36	1	*Death after Release*	
92107	21 August 2009	4.8	43.27	192	5.98	37.99	112	854	7.6
92108	20 August 2009	4.8	43.27	180	7.08	38.77	309	2 098	6.8
92109	26 August 2009	4.85	43.27	172	*Transmission failure*				
92110	28 August 2009	4.98	43.27	180	11.03	37.42	129	1 290	10
92111	26 September 2009	4.82	43.28	156	2.32	37.72	33	659	20
92115	11 September 2009	4.82	43.27	160	8	38	151	1 466	9.7
92112	10 August 2010	4.92	43.27	255	3.97	41.85	19	526	27.7
92113	28 August 2010	4.82	43.27	160	5.22	43.06	166	1 493	9
92114	01 September 2010	4.89	43.27	160	3.97	41.85	176	1 588	9
92116	24 September 2010	4.87	43.27	160	4.38	42.85	234	1 692	7.2
34261	24 September 2010	4.87	43.27	156	13.13	40.89	125	1 345	10.8
34273	06 August 2011	4.78	43.27	165	7.29	43.6	101	3 039	30
34274	18 August 2011	4.91	43.27	160	4.13	43.04	228	3 931	17.2
61954	24 August 2011	4.9	43.27	165	13.04	41.15	170	3 316	19.5
61958	19 August 2011	4.91	43.27	169	11.28	42.23	105	1 883	17.9
61964	16 September 2011	4.93	43.28	185	16.25	41.31	362	8 460	23.4
61966	17 September 2011	4.93	43.3	207	4.79	41.91	75	2 085	27.8
62008	16 September 2011	4.93	43.28	237	4.96	43.3	1	*Death after Release*	
73422	21 August 2011	4.91	43.28	159	8.45	40.26	238	*Transmission Failure*	

Total distance is the sum of the distances between each daily geolocations while the mean distance per day is the total distance divided by the time at liberty.

temporal resolution of pop-up archival tags and the limitations of the transmission in the Mediterranean Sea probably mean that the actual tracks underestimate the distance travelled. However, both the total distance (as the sum of the distances between each daily geolocations) and the mean distance per day (as the total distance divided by the time at liberty) were calculated to get an order of magnitude and for comparison purposes (Table 1).

The mean distances per day (i.e. a minimum estimate) mostly ranged from 7 to 30 nm d^{-1}. The mean distance did not depend on the type of the trajectory (i.e. migration vs. residency), nor the quality of the transmission. The great majority of fish remained in a rather small area, i.e. the central part of the northwestern Mediterranean (Figure 1), where they may stay for several months (tag 92108, Figure 2). In this area, all individual tracks display sinuous trajectories, indicating the possibility of feeding behaviour (Figures 2 and 3). Even if those fish remained in a restricted area, the total covered distance can be rather long. For instance, fish 92108 covered at least 2100 nm in this area over 300 d (Figure 2).

Without including tag 73422 (for which no track is available, see Table 1), six tag durations are long enough to include data up to and including April and could thus be informative on the reproductive migration patterns. Of these six tracks, two ABFT (tags 80082 and

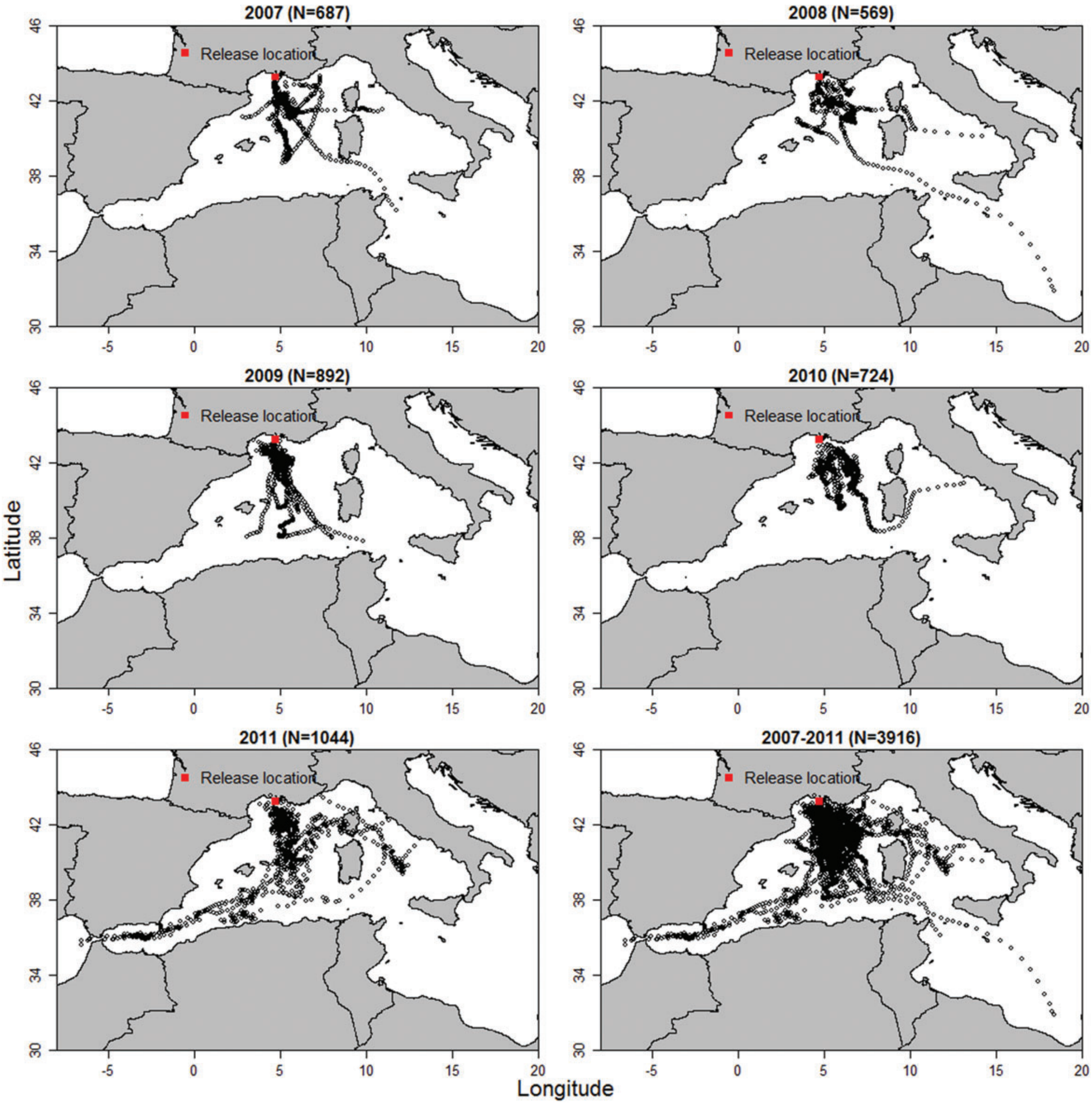

Figure 1. Daily geolocations of ABFT by year and over the whole period (2007–2011). Note that the individual tracks may extend over 2 consecutive years (the year of release and the following year, see Table 1). The total numbers of geolocations for each map is given in parentheses. The release location (red square) is ~43.2°N 4.7°E.

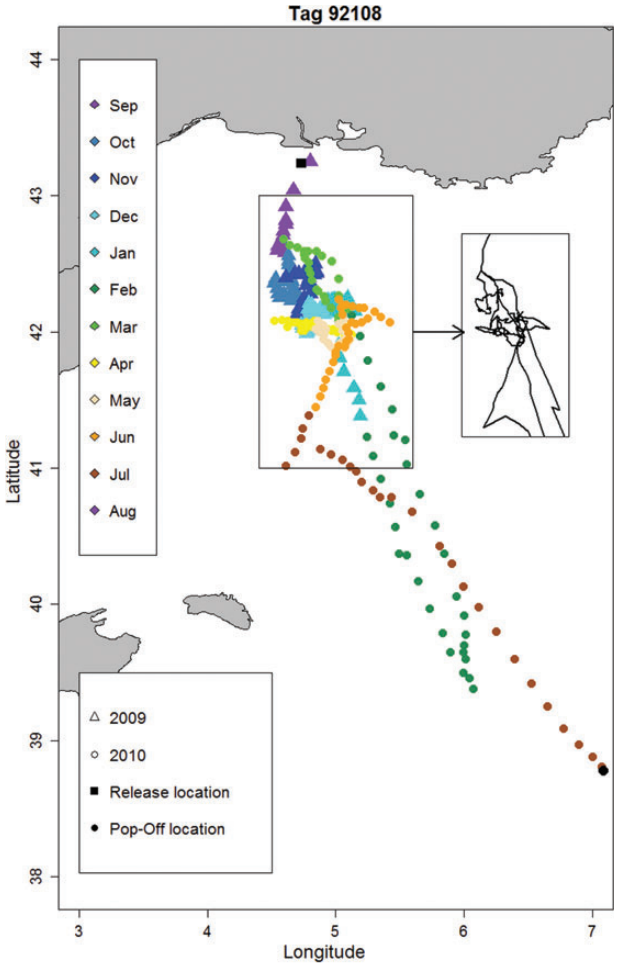

Figure 2. Track of tag 92108 with the release (black square) and pop-off (black circle) locations. Information about the month and year is provided by colour and symbol, respectively. The rectangle indicates the potential key area where details of the track are given in a subplot.

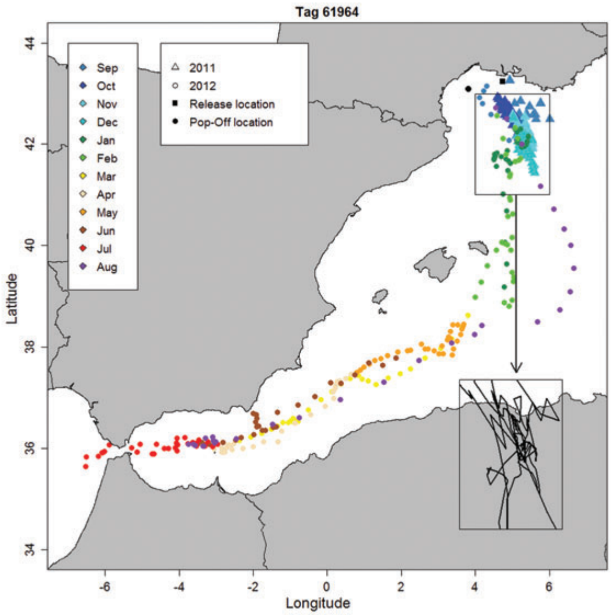

Figure 3. Track of tag 61964 with the release (black square) and pop-off (black circle) locations. Information about the month and year is provided by colour and symbol, respectively. The rectangle indicates the potential key area where details of the track are given in a subplot.

87642) showed clear migration towards North Sicily and the Gulf of Sidra in 2008, i.e. two known spawning locations in the Mediterranean (Figure 1). Three other tags (i.e. 92108, 92116, and 34274) remained in the northwestern Mediterranean and did not display any migration towards a known spawning ground during the spawning season. The last ABFT (tag 61964) clearly migrated from the northwestern Mediterranean to Gibraltar from February to April then went back to the southern part of the Balearic Islands in May to move back to Gibraltar in June–July (Figure 3). This individual fish did not show any clear residency in the Balearic Islands spawning ground during the spawning season (usually occurring from early June to early July in that area). Finally, none of the other tagged fish (which were all mature) showed any clear migration to this spawning location, though it is the closest and most important one in the Western basin.

No fish migrated to the North Atlantic, except tag 61964. This fish only stayed 7 d in mid-July 2012 at the entrance of the Gibraltar Sea then went back to the northwestern Mediterranean (Figure 3). More interestingly, this fish displayed a clear homing behaviour (i.e. the ability of the fish to return to a given place when displaced from it over great distances) to the Northwestern Mediterranean. It remained in this area from September 2011 to February 2012 and went back to it in August/September 2012. The release and pop-off locations are only separated by 40 nm, while the fish had travelled 1250 nm away from the release location a few weeks before pop-off and covered a distance of at least 8460 nm during the year (Table 1, Figure 3).

Several other fish also displayed clear migration patterns towards the southern western Mediterranean Sea during winter (ABFT offshore Tunisia and Algeria in 2007, 2009, and 2011 on Figure 2). Our sample size is too small to deduce any robust relationship between fish size and migration patterns. The two longest migrations (i.e. towards Gulf of Sidra or the Gibraltar Sea) have been performed by large fish (i.e. 180 and 210 cm long), but some small fish (i.e. 127–144 cm long) also displayed long migrations to wintering/feeding grounds in the southern Mediterranean Sea.

Spatial distributions

ABFT spatial distributions (using a two-dimensional kernel density estimation) showed little year-to-year variation. In all the years, the core of the distribution is concentrated in this rather small area of the northwestern Mediterranean that was already noted from the individual tracks, i.e. between the Gulf of Lions, the Balearic Islands, and Corsica (Figure 4). The spatial distribution does not seem to be affected by the number of geolocations, which differs substantially from year to year (Figure 1). ABFT spatial distributions appear more widely spread in 2008, 2010, and 2011 than in 2007 and 2009 (Figure 4). This is due to a few fish displaying longer migration patterns in those years. Nonetheless, the core of the ABFT spatial distribution observed over the 5 years (2007–2011) is very similar to those observed during an individual year and is always highly concentrated within the northwestern Mediterranean (Figure 4).

Residency and homing

Figures 2–5 indicate a potential ABFT hotspot in the northwestern Mediterranean Sea. As this area is just south of the release location (∼50 nm), we investigated if the time at liberty could be the main

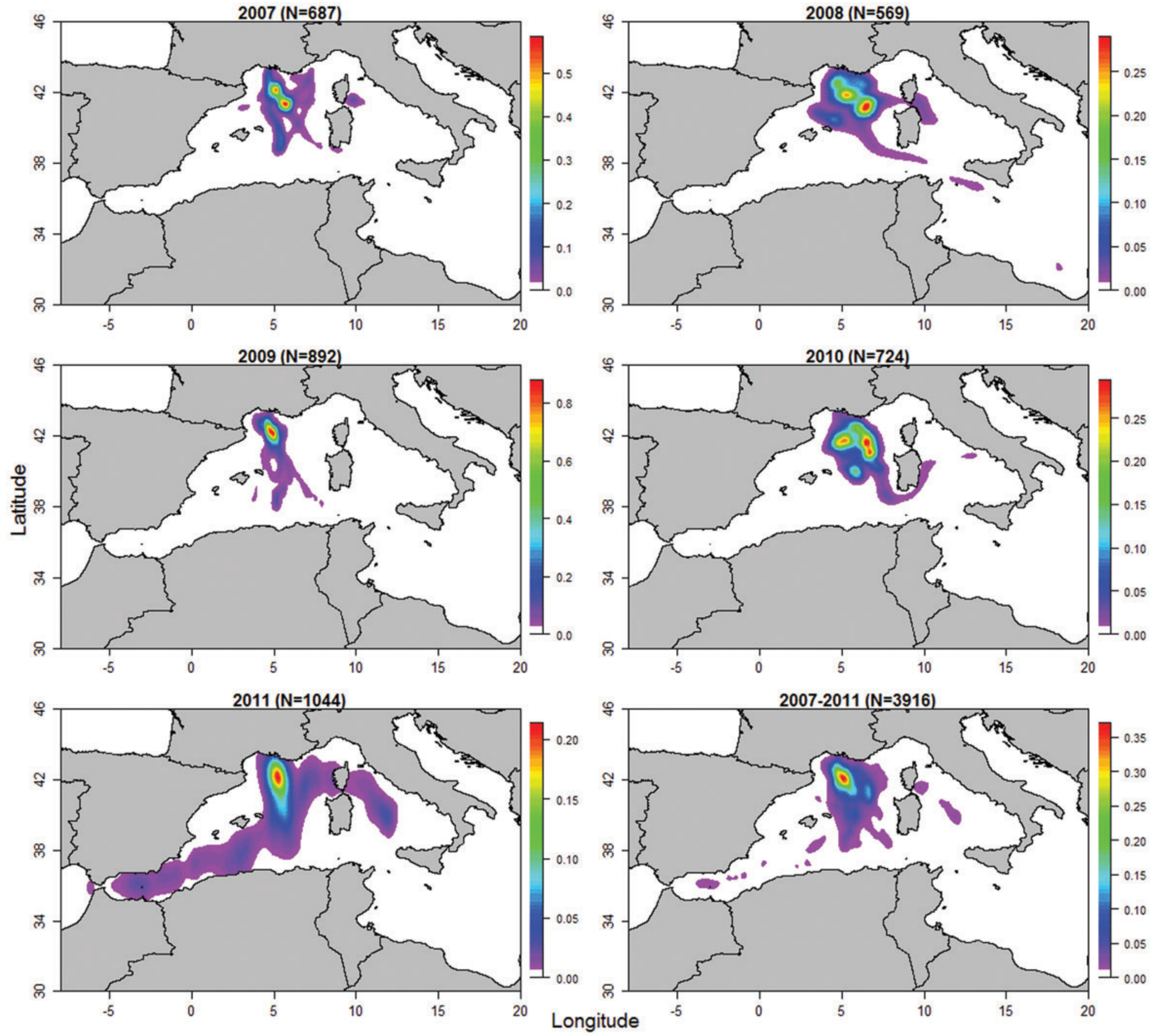

Figure 4. Annual and overall (2007 – 2011) spatial distributions of ABFT, using a two-dimensional kernel density function on the daily geolocations (number given in parentheses).

factor explaining dispersion and thus the concentration in that area. There is no apparent relationship between the time at liberty and the distance from the release location (Figure 5). The latter does not increase (either linearly or non-linearly) with the former, as would be expected if the proximity of release location affected ABFT dispersion and spatial distribution.

As noted above, a majority of fish spent several months in the Northwestern Mediterranean, at a distance of 30–150 nm from the release location (such as tags 34274, 61964, and 92108 in Figure 5). Fewer fish, however, seem to disperse more (such as tag 61954 or 87642 after 180 d, Figure 5), but they nonetheless spent several months near the same area. The northwestern Mediterranean could be a key area for ABFT; a hypothesis that is further supported by the homing behaviour of tag 61964 and the back and forth to this area of tags 92108 and 34274 (Figure 5).

Discussion

Pop-up archival tagging has several limitations, especially premature detachment (Sibert *et al.*, 2006), which make large-scale studies (in both time and space) difficult. Nonetheless, it is one of the rare approaches that can provide fisheries-independent information, which is crucial to understand the spatial dynamics of highly migratory species, such as tuna, swordfish, marlin, and pelagic shark (Block *et al.*, 2011). The tagging programme described in this study, which is still ongoing, has produced new information about ABFT migratory patterns in the Mediterranean; this includes ~4000 geographical locations and 1500 observed depth and temperature profiles. Such a programme would have been of limited scientific interest if it had been restricted to a few tagged fish in a given year, but the replication of the same tagging protocol over 5 consecutive years has allowed to the study to

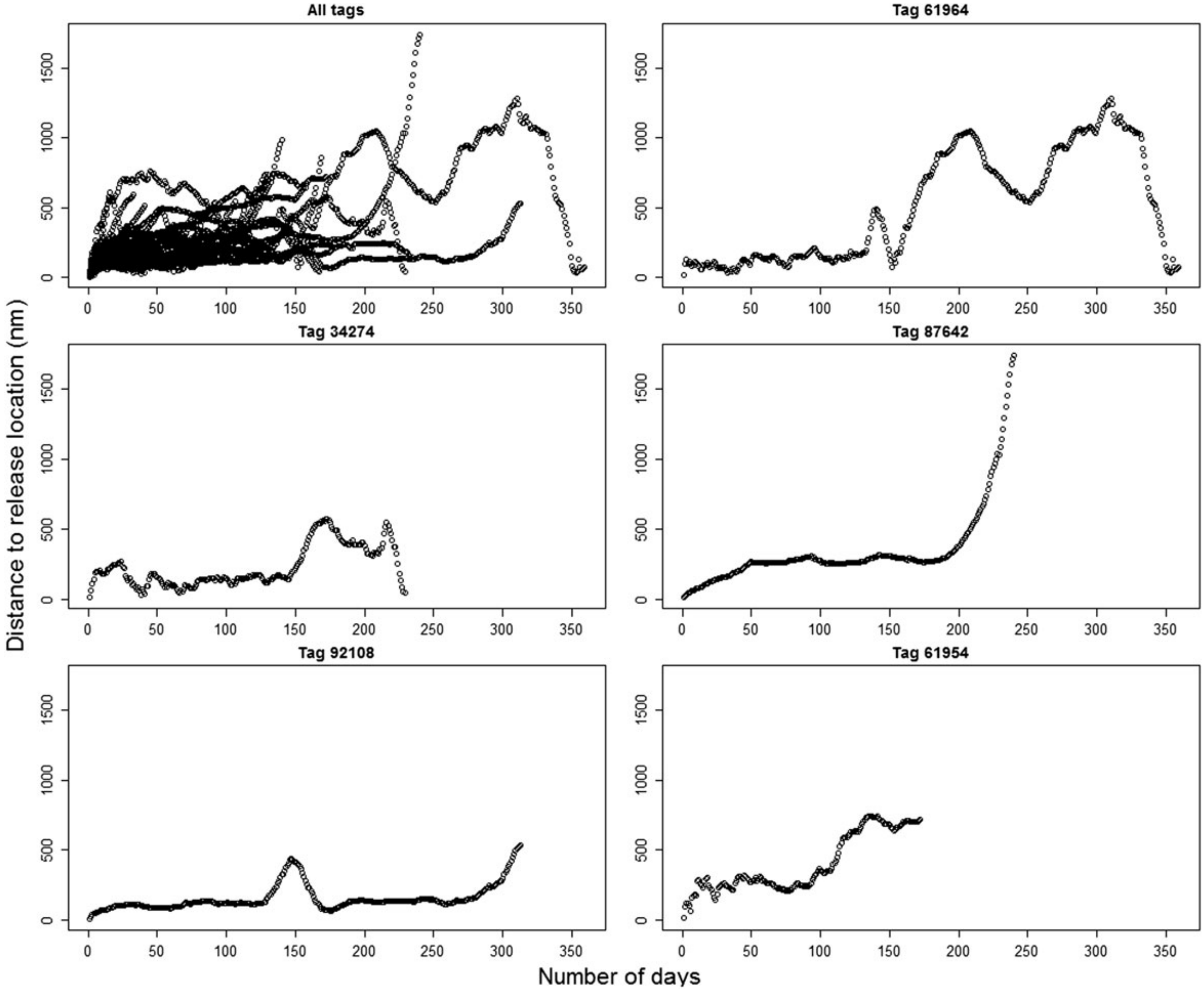

Figure 5. Distance between each daily geolocation and the release location (in nautical miles) against the number of days after release for all the tags (top left) and for a few illustrative individual tags.

identify some recurrent patterns and a possible key area in the western Mediterranean.

Our results clearly showed that ABFT can remain in the Mediterranean Sea all year long. During the spawning season, only one tagged fish was near the closest spawning ground, i.e. the Balearic Islands, but it did not display any clear spawning behaviour in that area. Two other tagged fish clearly migrated to rather distant spawning grounds, whereas the remaining three tagged fish were far from any known spawning locations during the spawning season. It is not possible to draw any conclusion on such a low sample size, but it is of interest to note that a more intensive electronic tagging programme on ABFT in the northwestern Atlantic also showed that a substantial proportion of the tagged ABFT were far from any known spawning grounds during the spawning season, which lead the scientists to postulate to the occurrence of some unknown spawning locations/seasons and/or the possibility of ABFT to skip spawning in some years (Lutcavage *et al*., 1999; Galuardi *et al*., 2010).

No fish migrated in the North Atlantic if we ignore the 7 d when tag 61964 was at the entrance of Gibraltar Sea. Such a result was unexpected because ABFT is a highly migratory species that is known to enter and leave the Mediterranean for reproduction (e.g. Mather *et al*., 1995; Ravier and Fromentin, 2001). ABFT migration patterns within the Mediterranean remain, nonetheless, poorly known, as most of the electronic tagging programmes were conducted in the Northwestern Atlantic and thus mostly described ABFT dynamics in the North Atlantic (e.g. Walli *et al*., 2009). Interestingly, another current electronic ABFT tagging programme in the western and central Mediterranean, using both pop-archival and archival tags, also showed that none of the tagged ABFT left the Mediterranean Sea (Tudela *et al*., 2011). Results from recent genetic studies (Carlsson *et al*., 2004; Riccioni *et al*., 2010; Viñas *et al*., 2011) and retrospective analysis of fisheries data (Fromentin, 2009) clearly indicate that ABFT population structure is more complex than the current two-stocks hypothesis, with probably one or two subpopulations within the Mediterranean. This likely hypothesis is thus in agreement with the results of our study (and those from Tudela *et al*., 2011) and could explain the relative residence of ABFT within the Mediterranean Sea. In other words, there could be more diversity in ABFT migratory behaviour and spatial range than currently assumed and ABFT from the Mediterranean subpopulation(s) could be more resident (or displaying a different spatial range) than ABFT from the North Atlantic subpopulation(s).

Our results also showed similar spatial distributions from 2007 to 2011, with a high concentration in a rather small area of the northwestern Mediterranean that has never been documented before (Mediterranean ABFT fisheries indeed operated more North, in the Gulf of Lions, or more South, in the Balearics area, Fromentin and Powers, 2005). Most of the tagged fish spent a long time in this rather small area and displayed sinuous tracks. This area could thus be a key feeding ground for ABFT in the western Mediterranean. The homing behaviour of a fish to this area after a full year and the back and forth of several ABFT to this area indicate that this feeding area is probably persistent from year to year. We put forward that this feeding area could be related to the general circulation in the northwestern basin (Millot, 1999), especially the North Mediterranean Current and the North Balearic Front, which displayed permanent frontal zones that are known to concentrate abundant vertebrate and invertebrate prey for ABFT and marine mammals (e.g. Royer *et al.*, 2004; Gannier and Praca, 2007). Such a hypothesis, however, needs deeper investigations of the mesoscale oceanic circulation, which could be performed through a comprehensive analysis of the remote sensing information (e.g. Belkin and O'Reilly, 2009).

The results suggest that properly design MPAs used alongside with other management measures could be a useful tool for Mediterranean ABFT because the ABFT in this study were highly resident in the northwestern Mediterranean and highly concentrated in a small area. This area that could be roughly delimited by a box of 4–6°E longitude and 43–41°N latitude (i.e. ~49 400 km^2 and 5.8% of the surface of the whole western Mediterranean Basin) includes 50% of all the daily geolocations. This percentage increases up to 60–70% from August to November and is lower during ABFT spawning season (June–July, Figure 6). This area could thus be a key hotspot for ABFT feeding, especially during autumn and secondarily in winter and early spring. These findings are in agreement with a recent study on Mediterranean ABFT habitat derived from satellite information (Druon *et al.*, 2011), which also showed a main potential ABFT feeding habitat during late summer and autumn in the northwestern Mediterranean. Although our tagging study remains preliminary, it indicates that the option of a spatial management, through MPAs, for a highly migratory species, such ABFT, deserves more careful consideration. ABFT, like most of the migratory species, displayed complex spatial dynamics through homing to spawning and feeding locations, which may lead to restricted seasonal areas, such as the northwestern Mediterranean box of this study. Furthermore, ABFT is likely to display a complex population structure that could include several subpopulations of different size, migratory behaviour, and spatial range.

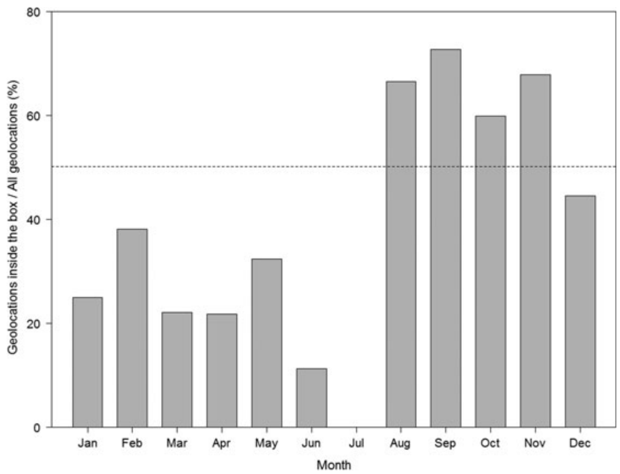

Figure 6. Monthly percentage of daily geolocations inside the key feeding area (delimited by a box of 4–6°E longitude and 43–41°N latitude). The calculation has been performed for each month using all the data.

These two key features make MPAs a potential useful tool, but those processes have to be better understood and quantified before any comprehensive study on MPAs efficiency. For Mediterranean ABFT, this should be soon possible, as genetic and tagging large-scale studies have been ongoing in the last few years and should substantially improve our understanding of ABFT population structure and spatial dynamics.

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