Population Structure, Migratory Behavior and Spawning Habitat of
East Atlantic and Mediterranean Bluefin Tuna Revealed by a
Multianual Electronic Tagging Programme
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Abstract

31	During 2008-2014, 101 pop-up satellite and 31 internal archival electronic tags were deployed in bluefin
32	tuna (12 to 250 kg in weight) in the Western and Central Mediterranean and in the Atlantic coast of
33	Morocco. Time at liberty spanned from 18 to 391 days. In the Western and Central Mediterranean, two
34	behavioral patterns / contingents (highly migratory and resident) were observed to co-occur. Imprinting
35	of early Atlantic migrants is hypothesized to explain the existence of the two contingents. None of the
36	"resident" individuals left the Mediterranean during the whole tracking period. None of the tuna present
37	in the Mediterranean at some point crossed over to the Eastern Mediterranean. The occurrence of
38	potential Mediterranean spawners in North Atlantic waters beyond the 45°W was also observed.
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43 INTRODUCTION

Atlantic bluefin tuna (*Thunnus thynnus*) has been a focus of marine fisheries research and a target of fishers since ancient times (1, 2), but its populations have suffered a sharp decline in the past four decades (3) and its breeding populations, both within the Gulf of Mexico and the Mediterranean Sea, have been at risk of fishery collapse (4, 5). Improving fisheries models of Atlantic bluefin tuna population structure, migration patterns and habitat use is necessary, particularly on their spawning grounds where they are heavily exploited. Understanding habitat utilization is, thus, critical for the design of more effective management measures.

51 Mature bluefin tuna of eastern origin have been hypothesized to undertake two types of 52 migrations: movements into the Mediterranean Sea during April and May to spawn (6), and a post-53 spawning foraging migration to the north Atlantic Ocean around the end of July and August (7, 8). While 54 a recent study using PSAT tags has confirmed the rapid migration of some post-spawning adults from 55 the Western Mediterranean to the Atlantic (9), other studies have recently highlighted the importance of 56 the Mediterranean habitats not only for spawning but also as an ecological foraging area significant 57 during overwintering periods (9-13). However, these past studies have focused only on one of the two 58 contingents, i.e. the "migrant" contingent (those individuals that perform the trophic migration from the 59 Mediterranean towards the Atlantic Ocean) or the "resident" contingent (those individuals that remain 60 in the Mediterranean Sea during the whole duration of their tracked trajectories and even overwinter in 61 the basin). And only Quílez-Badia, Cermeño (14) gives a glimpse of both contingents with data gathered 62 in 2011.

In order to increase our knowledge on the two different contingents, their habitat use, migration patterns and the possible population structure of bluefin tuna within the Mediterranean Sea, a thorough analysis was conducted with the data collected from 2008 to 2014 and the results are presented here. It is worth noting that the present study represents the most sustained effort that currently exists regarding electronic tagging of bluefin tuna in the Eastern Atlantic and Mediterranean Sea.

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69 MATERIAL AND METHODS

70 Atlantic bluefin tuna were tagged with electronic tags in expeditions that occurred between 2008 and 71 2013 in the Western Mediterranean, the Adriatic Sea and the Atlantic coast of Morocco (Table 1). The 72 tagging expeditions were conducted in locations along the eastern Spanish coast - Roses and Llançà 73 (NE Spain), Garraf (NE Spain), Moraira (E Spain) and Algeciras (SE Spain) -, in the Balearic Islands -74 Port of Pollença (N Majorca, Spain) -, in the Adriatic Sea - in San Benedetto del Tronto and Porto 75 Barricata (E and NE Italy, respectively) -, and in the Atlantic coast of Morocco - in Larache (NW 76 Morocco) - (Fig. 1). Tagging seasons started in May (at the earliest) and ended by November. Tagging 77 times depended on the accessibility of fishers to bluefin tuna.

78 Everywhere apart from Morocco, bluefin tuna were caught using recreational rod and reel 79 fishing: i.e., by means of chumming the water with sardines (for most bluefin tuna over 30 kg), or by 80 trolling lures (for most tuna under 30 kg). In 2008 and 2009 bluefin tuna were tagged in the water using 81 an aluminum tagging pole with only one insertion point and tag anchor. From 2010 to 2013, bluefin tuna 82 were brought on-board using a lip hook placed in the most rostral position of the lower jaw and pulled 83 from the water to a vinyl mat. For this (on-board) type of tagging, a second attachment loop was used to 84 prevent excessive motion of the pop-up satellite tag. Pop-up satellite tags were programmed to release 85 from the tuna between 150 and 300 days.

From 2011 to 2013, giant tunas (fork length (FL) > 2.10 m) trapped by the Moroccan tuna trap "Es Sahel" - operated by Maromadraba, s.a.r.l. - in Larache were also tagged. Approximately half of the individuals were tagged (with double attachment) on board one of the tuna trap vessels after being pulled out of the trap by means of a small crane and placed on to a mat. The other half were tagged in the water using an aluminum tagging pole. These tunas had entered the trap 24-48 h prior to the tagging operation and were all safely released at sea afterwards.

Bluefin tuna that were brought on board had a soft cloth soaked in fish slime replacement (PolyAqua, Novalek) placed over their eyes while a seawater hose oxygenated their gills. A clip of a fin was kept for future genetic analyses, and curved fork length (CFL) was measured to the nearest 0.5 cm. CFL was transformed to fork length (15) and then to weight using the formulas adopted by the International Commission for the Conservation of Atlantic Tunas (ICCAT) for Mediterranean and Atlantic tuna (Arena (*unpublished*) and Rey and Cort (*unpublished*) for Mediterranean and Atlantic

98 individuals, respectively, and cited in: 99 http://iccat.int/Documents/SCRS/Manual/Appendices/Appendix%204%20III%20Length-weight.pdf). 100 For those tuna tagged in the water a conservative estimation of the weight was made by the tagging team 101 and the tagging expert diver. 102 Electronic tagging was conducted with Pop-up Satellite Archival Transmitting tags (PAT 103 MK10 and MiniPAT built by Wildlife Computers, Redmond Washington, using PAT Hardware version 104 2.0). Both types of tags were placed on juveniles and adults in the base of the second dorsal fin. In 105 addition, archival tags (MK9, Wildlife Computers), were surgically deployed in juvenile bluefin tunas 106 considered too small for an external satellite tag. 107 Pop-up satellite tags recorded pressure, light and water temperature every 60 seconds interval 108 and were grouped in 6-, 12- or 24-hour binned histograms (for 2012 and 2013, 2008 to 2010, and 2011 109 tags, respectively). Pop-up satellite tag number # 10P0648 was returned by a fisherman, getting access 110 to the 5-second interval archival record. 111 The MK9 archival tags were surgically implanted in the peritoneal cavity of juvenile tuna and 112 programmed to record pressure, light, external temperature and internal temperature every 60 seconds. 113 To implant the archival tags, a 3-4 cm incision with a sterile surgical blade was carefully placed in the 114 ventral musculature of the tuna following the surgery methodology described in Cermeño, Quílez-Badia 115 (11). A conventional green external tag (Floy Tags) was also inserted close to the second dorsal fin to 116 inform about the existence of an archival tag inside the tuna 117 Bluefin tuna geolocations were estimated from light level and sea surface temperature (SST) 118 data recorded by the tags. All tracks were processed by CLS (Collecte Localisation Satellites) using a 119 tool based in state-space models (SSM). SSM's constitute a robust statistical approach to refine satellite 120 tracking data by accounting for observation errors and stochasticity in animal movement. The algorithm 121 uses SST and bottom topography data to better constrain the tracks. An ensemble Kalman filter is applied 122 to solve for the trajectory, thus estimating the state vector and its covariance from a set of samples rather 123 than the usual deterministic equations (16, 17).

A utilization distribution (UD) was subsequently created from the satellite tracking following the methodology explained in Cermeño, Quílez-Badia (11). Statistical analyses for the utilization areas 126 were performed with the Statistics Toolbox in Matlab 8.0.0 (18).

In order to infer potential spawning behavior we took into account the timing of spawning in
the Mediterranean Sea, oceanographic features that have been associated to the spawning strategy in the
Mediterranean and in the Gulf of Mexico, the residential and more sinuous movement during the
breeding phase, the prolonged surface intervals during nighttime, and the well-defined thermocline
(Cermeño, Quílez-Badia (11) and references therein).

132 FAO's Major Fishing areas in the Mediterranean were adopted to separate the different basins133 (19) (Fig. 1).

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135 RESULTS

A total of 132 electronic tags were deployed during the duration of this study: 101 pop-up satellite and 31 archival tags. From the 101 pop-up satellite tags deployed, 65 (i.e. 18 from 29 MK10 and 47 from 72 MiniPAT) transmitted data and were at liberty for at least 18 days, which was the minimum time that we chose to include in this study (Table 1). From the 31 surgically implanted archival tags, 2 were recovered (Table 1), although only one (ID # 890138) provided a complete archival time series record. The second one (ID # 890152) had the external temperature sensor damaged and its thermal data could not be taken into account in the analyses.

143 Out of the 66 analyzed tunas, 56 were in the Mediterranean Sea at some point, i.e. 39 fish were 144 tagged within the Mediterranean and 17 entered the basin after being tagged in the Atlantic coast of 145 Morocco. These 56 tags provided a wide time-span: from 18 up to 304 days at liberty for pop-ups and 146 up to 391 for the archival tag. The remaining 10 fish did not enter the Mediterranean Sea after having 147 been tagged in the Atlantic coast of Morocco. None of the tagged fish ever went to the southern Atlantic 148 Ocean. The research presented in this manuscript involved no endangered or protected species and no 149 harm to the animals. No special permission was required for the study in any of the locations as it was 150 not required, however a special permit was granted by the Spanish Ministry "Agricultura, Alimentación 151 v Medio Ambiente" for the 2011 tagging operations in Roses and Llancà.

Plotting the daily positions of the 56 tuna that were in the Mediterranean Sea at some point, weobserved that there is a coexistence of two behavioral/demographic contingents in the Western and

154 Central Mediterranean Sea. On one hand, we found individuals (N = 39) of a wide size range (from 17 155 up to 250 kg) clearly "resident" in the Mediterranean basin for a substantial period of time - but 156 eventually carrying out long intra-Mediterranean migrations, e.g. from the Gulf of Lions to Libya (11) -157 which even overwintered there (Fig. 2a and 3). And on the other, we observed highly migratory 158 individuals (N = 11) that performed the rapid trophic migration into the Atlantic Ocean (time-span ranged from 42 up to 300 days at liberty) (Fig. 2b). The remaining 6 individuals entered the 159 160 Mediterranean from the Atlantic coast of Morocco but their tags released relatively shortly after (from 161 19 up to 36 days at liberty), while still in the basin.

162 When analyzing the 39 "resident" individuals tagged within the Mediterranean, we observed 163 that none of them ever left this sea (the Alboran Sea being the furthest west, i.e. ID # 14P0186), nor 164 ventured into the Eastern Mediterranean (the Ionian Sea being the furthest east, i.e. ID # 08A0390) (Fig. 165 2a, 2c and 3). In fact, even though we could not have the complete geolocation track from the archival 166 tag that had the external temperature sensor damaged (Table 1, ID # 890152), we were able to use the 167 light level longitude record to establish its position and concluded that this bluefin tuna neither left the 168 Mediterranean, nor visited the Eastern Mediterranean during the nearly 3 years of monitoring. This bluefin inhabited waters comprised between the 0 and the 18th meridian east. 169

170 Therefore, if we include this latter tuna to the other 56 aforementioned, we realized that none171 of the 57 ever crossed over to the Eastern Mediterranean basin (Fig. 2c).

After analyzing those individuals who showed potential reproduction, we observed that spawning shows considerable geographical plasticity within the Western and Central Mediterranean, it being contingent upon the occurrence of the adequate oceanographic features and environmental conditions. Potential spawning was observed to occur only south of 40° N, where adequate environmental and oceanographic conditions occurred (Fig. 4). In addition, it is worth noting that breeding individuals from the two contingents ("resident" – orange - and migratory – yellow -, Fig. 4) met in the same spawning areas.

An individual tagged in the Atlantic coast of Morocco (ID # 11P0474), after entering the
Mediterranean during the breeding season, engaged in the trophic migration towards the Atlantic Ocean
and its tag released off Newfoundland (Canada) (Fig. 5).

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183 DISCUSSION AND CONCLUSIONS

184 A hypothesis about the Eastern Atlantic bluefin tuna constituted by at least three sub-populations (i.e. 185 (1) a highly migratory one over all the North Atlantic which would spawn in the Western and Central 186 Mediterranean, (2) a more resident one in the Mediterranean spawning in the Central and Eastern 187 Mediterranean) and (3) a more resident one in the West Atlantic spawning in the Gulf of Mexico) was 188 formulated by Fromentin (20) based on fisheries data of the 20th century, including total catch and size 189 composition. In the present study we have observed that two behavioral patterns or contingents appear 190 to occur in the Western and Central Mediterranean: on one hand that corresponding to the highly 191 migratory fish – already studied since Aristotle's time and more recently confirmed by electronic tagging 192 studies (21, 22), which quickly return to the Atlantic feeding areas, and on the other, that defined by the 193 "resident" fish that do not leave the Mediterranean during the whole tracked period and even overwinter 194 there, which has also been hypothesized by scientists for centuries (Di Natale (13), Fonteneau (23) and 195 references therein) and has recently been documented with tagging studies (Cermeño, Quílez-Badia (11) 196 and references therein). It is still unknown if those fish remaining in the Mediterranean for more than 197 one year will stay in the Mediterranean for several years or for their entire life, therefore, the definition 198 of "resident" includes this clear incertitude (13).

199 Consequently, the question arisen here is what might be the demographic relationship between 200 these two contingents. Several hypotheses are discussed: (1) two different population units, (2) a single 201 population with distinct size/age dependent migratory behaviors, and (3) a single population with early 202 imprinted determination of migratory behaviors.

In the present study we observed that potential spawning – inferred from the tuna behavior and the environmental and oceanographic features stated in Materials and Methods – took place where adequate environmental and oceanographic conditions occurred, showing considerable geographical plasticity within the Western and Central Mediterranean. It is important to highlight that individuals from both contingents (highly migratory and "resident") shared the same spawning areas in the Mediterranean basin (Fig. 4), thus making very unlikely the possibility of two genetically different populations; on the contrary, it would appear quite likely the existence of a single panmictic population.

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As there is still no consensus on the genetic population structure of bluefin tuna in the Atlantic Ocean
and the Mediterranean Sea (Carlsson, McDowell (24); Cannas, Ferrara (25); Riccioni, Stagioni (26);
Puncher, Massari (27) and references therein), more genetic studies are needed in order to confirm this
statement.

214 The second hypothesis is that there could be a single population which would stay in the 215 Mediterranean Sea until its individuals reached a certain age or size, well beyond the size at maturity in 216 the Mediterranean. Even though the sampling we conducted in the Western and Central Mediterranean 217 was biased towards juveniles and young adults, tuna of large size were also found in the resident 218 contingent (i.e. up to 248 kg). In addition, catches of age class 0 were found to be common in a tuna trap 219 near Ceuta (North Africa) towards the end of autumn when fishing the tuna on their way out to the 220 Atlantic (28). Moreover, the documented live-bait boat fishery in the Bay of Biscay is partly made of 221 juveniles most likely of Mediterranean origin (Cort and Rey, (29) and review in Rooker et al. (2)). 222 Furthermore, the exit flow of Mediterranean natal origin juveniles has been confirmed using otolith 223 chemistry composition, which had led to the conclusion that approximately 60 % of adolescent (20-70 224 kg) bluefin tuna from foraging areas in eastern United States are originally from the Mediterranean Sea 225 (30). Hence, this second hypothesis has to be refuted.

226 Lastly, we could be facing a single population whose individuals would "decide" to stay or 227 leave the Mediterranean at some point early in their development. This "decision", which could be 228 triggered by environmental conditions or have an individually-based genetic origin, would then be 229 imprinted in the tuna resulting in it being "resident" or highly migratory (meaning either staying all its 230 life within the Mediterranean or periodically returning to the Mediterranean briefly to spawn from the 231 moment they reach a certain age in the Atlantic, respectively). This would be the "Early imprinted 232 migration determination" hypothesis. Rivas (31) stated that the active migratory behavior of bluefin tuna 233 spawned in the Gulf of Mexico starts at an age of 14 days, and surveys conducted in the '60s found 234 bluefin tuna of age 0 in the Ibero-Moroccan area (Di Natale (32) and references therein); both in 235 accordance with our hypothesis. Resident tuna, on the other hand, would still perform important intra-236 Mediterranean migrations between feeding and spawning areas, as the ones recorded in this study 237 between the NW Mediterranean and the waters off Libya and the Adriatic. Rooker et al (33) found that

the percentage of adolescent tunas from Mediterranean origin in foraging areas in eastern USA declined drastically when sampling tuna over 140 kg, suggesting a migration towards eastern Atlantic and Mediterranean waters for the adult stage. In addition, two individuals over 120 kg tagged in the eastern coast of USA showed a homing behavior with annual visits to the Western Mediterranean during the spawning season (21). Both studies, hence, would be consistent with this third hypothesis.

243 In addition to these two contingents in the western and central area of the Mediterranean Sea, none of 244 the 56 tuna that were in the Mediterranean Sea at some point (including the archival - ID # 890152 -245 with the external temperature sensor damaged) ever crossed over to the Eastern Mediterranean basin 246 (Fig. 2c), which would be consistent with a more sedentary, isolated population in the Eastern 247 Mediterranean. This hypothesis is supported by Karakulak and Oray (34) who stated that a sub-248 population of bluefin tuna exists in the northern Levantine Sea; and by histological and larval studies 249 where they found a bluefin tuna spawning ground in the eastern Mediterranean basin (35, 36). In 250 addition, the preliminary results obtained from recent genetic studies carried out within the ICCAT 251 GBYP framework (27) are pointing out to a potential separate subpopulation in the eastern 252 Mediterranean basin, possibly originating from the ancient Black Sea-Eastern Mediterranean area (37). 253 Previous tagging work conducted in the Eastern Mediterranean by De Metrio et al. (8, 38) found that 254 most of the tagged tuna remained in the Eastern Mediterranean, while two moved toward the Central 255 and Western Mediterranean. Unfortunately, as some of these fish were tagged in cages, there is no 256 reliability regarding the exact origin of their capture prior caging, therefore, we cannot know if the 257 mixing between Eastern and Central/Western Mediterranean really happened. On the other hand, the 258 preliminary results obtained from the 2015 ICCAT GBYP electronic tagging program (39) have shown 259 that some mixing does exist both between the NE Atlantic and the Eastern Mediterranean basin and 260 within the Mediterranean Sea. In particular, from the 18 electronic tags that had popped-off at the time 261 (out of the 20 deployed in Larache, west coast of Morocco), one fish went to the Eastern Mediterranean, 262 reaching the southern part of Crete. Moreover, from the 30 electronic tags deployed in Turkey, two 263 popped-off in the NE Atlantic - one off the Faroe Islands and the other one off the NW Galician coast – 264 , one popped-off in Libyan waters and 2 popped-off in the Ionian Sea. Other tuna-like species, such as 265 Sarda sarda or Xiphias gladius, have been found to have significant genetic differentiation between

sampling areas within the Mediterranean Sea (40). In the case of Bluefin tuna, and because the
aforementioned results of Di Natale et al (39) are still preliminary, an in-depth analysis of these tagging
data are needed before being able to state any conclusions on the differentiation of the Eastern
Mediterranean basin.

270 Regarding the Tyrrhenian Sea, only three out of the 56 tuna that were in the Mediterranean Sea 271 at some point visited this basin, while both historical and fishery data strongly indicate that the southern 272 Tyrrhenian Sea is a typical and intense spawning area (Di Natale, Mangano (41); Piccinetti, Di Natale 273 (42) and references therein). This result could be partly due to the recently reported hydrological changes 274 in the Mediterranean Sea (i.e. the Mediterranean transient) (43, 44). As a matter of fact, even though 275 catches in the area resumed in 2014 and 2015, bluefin tuna catch records in the Tyrrhenian had been 276 decreasing in the past years, and no purse seine catches were reported in 2012 (based on information 277 reported to ICCAT); this, however, could have partly been due to changes in the fishery strategies, also 278 constrained by the lower quota per vessel.

279 It is also worth noting that the Alboran Sea was the furthest west any of these 56 resident tuna 280 went to (Fig. 2a and 2c). In particular it was tuna ID # 14P0186 which, after being in the waters between 281 the south of the Balearic Islands and North Africa during the spawning season, went west towards the 282 Alboran Sea. This individual stayed in the waters of the Alboran Sea from the beginning of August until 283 the 30th of November (when its tag popped-off), never crossing the Strait of Gibraltar. This result is 284 consistent with the study from De la Serna, Alot (7) where they state that bluefin tuna with lengths 285 ranging from 60 to 250 cm are captured with live bait in the middle of the Strait of Gibraltar from August 286 until March.

In the present study we also observed that out of the 27 analyzed tuna from Morocco (i.e. with tags that lasted ≥ 18 days at liberty), 10 did not follow their expected behavior and did not enter the Mediterranean Sea during the spawning season. This result could either be due to the potential presence of other alternative spawning areas, to a small percentage of tuna naturally skipping spawning, or to an artifact caused by one of the two tagging methodologies used in the Moroccan trap (i.e. on-board tagging, although some of the fish tagged in the water also did not enter the Mediterranean for spawning).

293 The electronic tagging activities carried out from 2011 to 2013 in the Moroccan Atlantic trap 294 showed that some adult individuals moved towards the Ibero-Moroccan Bay, the Canary Islands, 295 Madeira and the Azores Islands during the usual spawning season, without entering into the 296 Mediterranean Sea (Quílez-Badia, Cermeño (14) and unpublished results). From the preliminary 297 analyses conducted so far on these tags, the oceanographic conditions recorded in those areas for some 298 of them were potentially suitable for bluefin tuna spawning, but further detailed analyses – which are 299 currently being carried out – are needed before being able to be conclusive. In fact, Druon et al (45) has 300 recently predicted the Azores area and the area off Morocco to Senegal as secondary potential spawning 301 grounds for Atlantic bluefin tuna. In addition, historically it has been hypothesized that there could be 302 bluefin tuna spawning in in the Ibero-Moroccan Bay, in the area between the Canary Islands, Mauritania 303 and Morocco, in the area around the Azores Islands and in the Gulf of Guinea (Di Natale et al. (46) and 304 references therein). Even though larval surveys carried out in all these areas (apart from the Gulf of 305 Guinea), were never able to find any bluefin tuna larvae, individuals of age 0 have been reported in the 306 past in the Ibero-Moroccan area (Di Natale (32) and references therein). Bearing in mind that the 307 aforementioned larval studies were very limited, larval dispersion can be very high in the open ocean, 308 bluefin tuna are opportunistic spawners that follow environmental signals and adapt to variability (11, 47), and the preliminary results obtained from the 10 tags indicate potential suitable oceanographic 309 310 conditions, this hypothesis could still be valid.

Previous electronic tagging studies have indicated that some adult Atlantic bluefin tuna are not present in the known spawning areas during the known spawning times (21, 48, 49) and experiments in captivity (50) found that spawners did not spawn every year. These observations have prompted some authors to suggest that either bluefin tuna were using currently unknown spawning areas or times, or were skipping spawning in some years (49, 51, 52).

The third option we have suggested is the possibility of the tagging methodology affecting the natural behavior of the tuna. From these 27 tags, 16 were deployed on board one of the tuna trap vessels and 11 were deployed in the water. Bearing in mind we observed a notable difference in the percentage of tuna entering the Mediterranean Sea – i.e. 44 % for those deployed on board versus 91 % for those

deployed in the water -, it is reasonable to assume that the stress caused to the tuna during the on-boardtagging might have aborted their natural migration.

Recent data, presented by GBYP to SCRS in 2015, shows a different motivation: the high variability in presence of Bluefin tuna spawners having different natal origin in the Moroccan and Canary areas. As a matter of fact, spawners from the two stocks (western and eastern Atlantic) are present there during the main fishing seasons, as confirmed by the microchemical and isotope analyses. The presence of the western component may range inter-annually in a considerable way, providing a very reasonable motivation for the different behavior of these fish.

Nonetheless, before being able to state something definitive, it is clear further studies areneeded in order to elucidate this unexpected behavior.

330 Since 1982, and based on assumed separate and exclusive spawning grounds, low levels of 331 mixing between stocks, and widely different maturity schedules, ICCAT manages Atlantic bluefin tuna 332 fisheries as two separate stocks, i.e. eastern and western stock, divided by the 45°W meridian (53). But, 333 as the Standing Committee on Research and Statistics (SCRS) states in its 2014 report 334 (http://www.iccat.int/Documents/Meetings/Docs/2014-SCRS-REP ENG.pdf), "Although the Atlantic 335 bluefin tuna population is managed as two stocks, conventionally separated by the 45°W meridian, its 336 population structure remains poorly understood and needs to be further investigated. Recent genetic and 337 microchemistry studies as well as work based on historical fisheries tend to indicate that the bluefin tuna 338 population structure is complex". In fact, the occurrence after the spawning season of potential 339 Mediterranean spawners in North Atlantic waters beyond the 45°W was observed in the present study 340 (Fig. 5), which stresses the importance of mixing and points to a link between spawning grounds in the 341 Mediterranean Sea and feeding grounds off Newfoundland.

Overall, the results obtained in the present study show the need for further studies on electronic tagging, otolith microchemistry and genetics, which in combination will allow to ascertain the precise demographic relationship between the two contingents (highly migratory and "resident"), as well as to be able to answer the questions about any possible discrimination of sub-populations, tribes or other entities in all ICCAT convention areas, including those fish living in South Atlantic. Furthermore, with

- 347 regards to management, it is evident that more detailed information is needed to ensure a proper, science-
- 348 based management of the Atlantic bluefin tuna fisheries.
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FIGURE LEGENDS

Figure 1. Different tagging locations: 1. Roses/Llançà (NE Spain), 2. Garraf (NE Spain), 3. Pollença (N Mallorca, Spain), 4. Moraira (E Spain), 5. Algeciras (S Spain), 6. San Benedetto del Tronto (E Italy), 7. Porto Barricata (NE Italy), and 8. Larache (NW Morocco). Red lines indicate the separation between the different Mediterranean basins based on FAO Fishing area criteria.

Figure 2. Daily positions of (a) the tuna tagged within the Mediterranean (N = 39), i.e. 38 deployed with pop-up tags (white dots) and one with an archival tag (orange dots). Tuna weight ranging from 12 up to 250 kg. Time-span ranging from 18 up to 304 days at liberty (pop-ups) and up to 391 (archival). (b) those giant tuna (all but one over 2 m CFL) tagged in the Atlantic coast of Morocco which entered the Mediterranean during the spawning season and then performed the trophic migration into the Atlantic Ocean (N = 11). Time-span ranged from 42 up to 300 days at liberty. And (c) the tuna tagged in the Mediterranean (N = 39, white dots) and the tuna tagged in the Atlantic coast of Morocco which visited the Mediterranean Sea at some point while having their tag attached (N = 17, red dots).

Figure 3. Seasonal Utilization Distributions (UDs) of all bluefin tuna analyzed in this study (N = 66). The locations of the tunas were examined for the (a) spawning period (i.e. May 15 to July 15) and the seasonal periods of (b) spring, (c) summer, (d) autumn and (e) winter. UDs were computed using the Kernel method through the ad hoc method (h = Sigma*n^(-1/6), Sigma = 0.5*(sd(x)+sd(y))). The graphs show the UDs cumulative frequencies up to 99.9% (the color attributed to a given percentage p applies to areas comprised between p and p–1.62% isopleths).

Figure 4. Places where tunas showed potential reproductive behavior. Orange areas represent those individuals tagged within the Mediterranean basin and yellow areas are for those tagged in the Atlantic coast of Morocco. Dashed white line is the 40° N parallel.

Figure 5. Trajectory of the tuna with ID # 11P0474 tagged in the Atlantic coast of Morocco on the 25th of May 2013.



FIGURE 1

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40°0'0"N 30°0'0"N--30°0'0"N 10°0'0"W 0°0'0" 10°0'0"E 20°0'0"E

FIGURE 2







FIGURE 3



FIGURE 4



FIGURE 5

TABLES

Table 1. Summary information on the deployments of pop-up electronic tags (\geq 18 days on fish) and implanted archival tags - from 2008 to 2014 in Western Mediterranean, Adriatic Sea and Moroccan bluefin tuna –, analyzed in this study. Different tagging locations: 1. Roses/Llançà (NE Spain), 2. Garraf (NE Spain), 3. Pollença (N Mallorca, Spain), 4. Moraira (E Spain), 5. Algeciras (S Spain), 6. San Benedetto del Tronto (SBT) (E Italy), 7. Porto Barricata (NE Italy) and 8. Larache (NW Morocco). Notes: * Tuna with implanted archival tags, † Two darts were used to anchor the tag.

Year	Pop-up ID	Area	Deployment position	Deployment Date	CFL (cm)	Weight (kg)	Pop-off / Recapture* position	Pop-off / Recapture* Date	Days at liberty	Dart
2008	08A0398	Mallorca, Spain	40°00'N 03°09'E	16/08/2008	-	100	37°88'N 01°74'E	15/10/2008	60	Umbrella
	08A0391	Mallorca, Spain	40°00'N 03°09'E	16/08/2008	-	150	35°88'N 00°49'E	19/12/2008	125	Umbrella
	08A0393	Mallorca, Spain	40°00'N 03 09'E	17/08/2008	-	150	38°96′N 00° 21′E	26/10/2008	70	Umbrella
	08A0405	Mallorca, Spain	40°00'N 03°09'E	17/08/2008	-	50	40°26′N 04°29′E	29/10/2008	73	Umbrella
	890138*	Roses, Spain	41° 56'N 03° 36'E	31/08/2008	-	12	41°01′N 02°45′E	26/09/2009	391	-
	890152*	Roses, Spain	41° 56′N 03° 36′E	31/08/2008	-	13	37°30′N 11°30′E	23/04/2011	965	-
2009	08A0407	Mallorca, Spain	40°01′N 03°01′E	14/08/2009	-	110	39°46′N 02°40′E	23/10/2009	70	Umbrella
	08A0390	Mallorca, Spain	40°01´N 03°01´E	15/08/2009	-	65	39°58′N 03°37′E	14/09/2009	30	Umbrella
	08A0399	Roses, Spain	42°20′N 03°20'E	27/08/2009	160	73.2	38°09′N 14°00′E	07/12/2009	102	Umbrella
	08A0385	SBT, Italy	42°48′N 14°35′E	13/09/2009	-	45	43°46′N 13°42′E	25/12/2009	103	Umbrella
	08A0394	SBT, Italy	42°49′N 14°37′E	14/09/2009	132	41.1	30°38′N 19°02′E	05/03/2010	172	Titanium†
	08A0409	Roses, Spain	42°23′N 03°20′E	04/09/2009	-	45	38°58′N 05°19′E	17/12/2009	104	Prince
2010	08A0403	Mallorca, Spain	40°02'N 03°10'E	08/08/2010	190	122.8	38°16'N 07°01'E	25/09/2010	48	Titanium†
	10P0049	Roses, Spain	42°15′N 03°40′E	01/09/2010	95	15.3	39°52' N 6°20'E	11/11/2010	71	Titanium†
	10P0052	Roses, Spain	41°51′N 03°50′E	05/09/2010	96	15.7	37°48' N 9°27'E	02/11/2010	58	Titanium†
	08A0390	SBT, Italy	42°55′N 14°14′E	13/09/2010	143	52.2	41°34'N 15°57'E	18/05/2011	247	Titanium†
	08A0396	Barricata, Italy	44°49 N 12°51'E	24/09/2010	153	64	42°34'N 15°49'E	20/03/2011	177	Titanium†
2011	10P0044	Larache, Morocco	35°18'N 06°11'W	26/05/2011	260	259	27°2'N 17°44'W	19/07/2011	54	Titanium†

	10P0035	Larache, Morocco	35°18'N 06°11'W	27/05/2011	210	139	38°18'N 27°14'W	22/03/2012	300	Titanium†
	08A0395	Larache, Morocco	35°18'N 06°11'W	27/05/2011	237	198	38°23'N 22°25'W	18/072011	52	Titanium†
	10P0406	SBT, Italy	43°01'N 14°09'E	26/07/2011	155	66.6	40°55'N 18°05'E	02/09/2011	38	Titanium†
	10P0400	SBT, Italy	43°01'N 14°09'E	26/07/2011	136	44.9	44°05'N 14°57'E	30/09/2011	66	Titanium†
	10P0038	SBT, Italy	42°57'N 14°16'E	06/08/2011	125	34.8	40°40'N 01°16'E	05/04/2012	243	Titanium†
	10P0401	SBT, Italy	42°56'N 14°17'E	06/08/2011	134	43	32°23'N 17°47'E	09/02/2012	187	Titanium†
	08A0389	Mallorca, Spain	40°03'N 3°08'E	12/08/2011	177	99.2	39°58'N 02°57'E	30/09/2011	49	Titanium†
	10P0398	Moraira, Spain	39°06'N 0° 29'E	29/05/2011	135	43.9	39°46'N 0°59'E	25/08/2011	88	Titanium†
	10P0402	Roses, Spain	42°21'N 3°19'E	31/08/2011	144	53.4	37°48'N 10°36'E	30/06/2012	304	Titanium†
	10P0546	Roses, Spain	42°20'N 3°09'E	01/09/2011	135	43.9	35°55'N 13°25'E	30/06/2012	303	Titanium†
	10P0547	Roses, Spain	42°20'N 3°20'E	01/09/2011	149	59.1	40°55'N 04°59'E	29/09/2011	28	Umbrella
	08A0388	Roses, Spain	42°20'N 3°20'E	01/09/2011	240	248.1	41°58'N 03°43'E	03/11/2011	63	Titanium†
	09P0412	Llançà, Spain	42°20'N 3°20'E	03/09/2011	199	141.2	37°09'N 04°29'E	26/09/2011	23	Titanium†
2012	11P0150	Larache, Morocco	35°18'N 06°11'W	14/05/2012	254	242	30°08'N 20°20'W	19/01/2013	250	Titanium†
	11P0134	Larache, Morocco	35°18'N 06°11'W	14/05/2012	247	223	49°18'N 26°45'W	17/09/2012	126	Titanium†
	09P0437	Larache, Morocco	35°18'N 06°11'W	14/05/2012	251	234	34°53'N 14°22'E	05/06/2012	22	Titanium†
	11P0531	Larache, Morocco	35°18'N 06°11'W	14/05/2012	243	213	46°35'N 27°30'W	19/01/2013	250	Titanium†
	11P0533	Larache, Morocco	35°18'N 06°11'W	14/05/2012	226	172	35°29'N 14°48'W	14/06/2012	31	Titanium†
	08A0390	Larache, Morocco	35°18'N 06°11'W	14/05/2012		200-300	62°25'N 3°08'W	16/08/2012	94	Titanium
	11P0138	Larache, Morocco	35°18'N 06°11'W	14/05/2012		200-300	39°32'N 35°41'W	31/07/2012	78	Titanium
	11P0133	Larache, Morocco	35°18'N 06°11'W	14/05/2012		200-300	47°12'N 12°11'W	26/09/2012	135	Titanium
	08A0386	Larache, Morocco	35°18'N 06°11'W	14/05/2012		200-300	34°04'N 12°31'E	02/06/2012	19	Titanium
	11P0530	Larache, Morocco	35°18'N 06°11'W	14/05/2012		200-300	51°05'N 20°01'W	24/10/2012	163	Titanium
	11P0378	Larache, Morocco	35°18'N 06°11'W	16/05/2012	265	273	35°36'N 24°51'W	20/06/2012	35	Titanium†
	11P0363	Larache, Morocco	35°18'N 06°11'W	16/05/2012	203	126	31°28'N 17°07'E	20/06/2012	35	Titanium†
	11P0372	Larache, Morocco	35°18'N 06°11'W	16/05/2012	238	200	35°29'N 17°30'W	24/06/2012	39	Titanium†
	11P0375	Larache, Morocco	35°18'N 06°11'W	16/05/2012	206	132	38°23'N 6°50'E	21/06/2012	36	Titanium†

	10P0648	SBT, Italy	43°03N 14°08'E	12/05/2012	135	43.9	43°17′N 16°4′E	07/11/2012	179	Titanium†
	10P0632	SBT, Italy	45°16'N 13°07'E	09/23/2012	138	46.9	43°39'N 13°40'E	11/21/2012	84	Titanium†
	11P0483	Mallorca, Spain	40°01'N 3°09'E	11/08/2012	179	103	39°46'N 3°12'E	19/04/2013	251	Titanium†
	11P0468	Mallorca, Spain	40°02'N 3°09'E	11/08/2012	161	75	36°49'N 11°55'E	18/04/2013	250	Titanium†
	11P0482	Mallorca, Spain	40°02'N 03°10'E	24/11/2012	102	18.9	38°18'N 4°01'E	16/12/2012	22	Titanium†
	11P0480	Llançà, Spain	42°01'N 3°19'E	08/09/2012	179	102.7	37°27'N 8°18'E	11/01/2013	125	Titanium†
	11P0455	Llançà, Spain	42°21'N 3°19'E	09/09/2012	174	94.3	38°31'N 8°30'E	18/05/2013	251	Titanium†
	11P0481	Llançà, Spain	42°21'N 3°19'E	09/09/2012	199	141.2	30°38'N 19°52'E	06/02/2013	150	Titanium†
	11P0465	Llançà, Spain	42°20'N 3°20'E	09/09/2012	142	51.2	38°40'N 3°44'E	31/10/2012	52	Titanium†
	11P0452	Algeciras, Spain	35°57'N 5°29'W	16/09/2012	214	175.8	42°55'N 13°47'W	29/03/2013	194	Titanium†
2013	11P0028	Larache, Morocco	35°18'N 06°11'W	20/05/2013	245	218	35°55'N 5°44'W	18/07/2013	59	Umbrella+Titanium
	12P0133	Larache, Morocco	35°18'N 06°11'W	20/05/2013	240	205	54°34'N 10°18'W	07/10/2013	140	Umbrella+Titanium
	12P0134	Larache, Morocco	35°18'N 06°11'W	20/05/2013	235	193	51°56'N 17°29'W	24/07/2013	65	Umbrella+Titanium
	12P0136	Larache, Morocco	35°18'N 06°11'W	20/05/2013	227	175	38°54'N 10°15'W	01/07/2013	42	Umbrella+Titanium
	12P0139	Larache, Morocco	35°18'N 06°11'W	21/05/2013	240	205	35°56'N 5°50'W	19/07/2013	59	Umbrella
	12P0140	Larache, Morocco	35°18'N 06°11'W	21/05/2013	212	143	38°14'N 10°28'E	06/09/2013	108	Umbrella
	11P0474	Larache, Morocco	35°18'N 06°11'W	21/05/2013	230	181	44°40'N 49°54'W	14/10/2013	146	Titanium
	11P0467	Larache, Morocco	35°18'N 06°11'W	21/05/2013	242	210	34°04'N 14°1'E	11/06/2013	21	Titanium
	11P0445	Larache, Morocco	35°18'N 06°11'W	21/05/2013	246	220	35°40'N 14°51'W	29/06/2013	39	Titanium
	11P0446	Larache, Morocco	35°18'N 06°11'W	21/05/2013	260	259	48°50'N 11°12'W	06/09/2013	108	Titanium
2014	14P0186	Garraf, Spain	41°06'N 01°48'E	31/05/2014	160	73.3	36°16'N 5°12'W	30/11/2014	183	Titanium
	14P0182	Garraf, Spain	41°08'N 1°57'E	01/06/2014	165	80.4	39°42'N 2°19'E	19/06/2014	18	Titanium†