

1 Tracking Atlantic bluefin tuna from foraging grounds off the west coast of Ireland

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11

12 Abstract

13 Pop-up archival tags (n=16) were deployed on Atlantic bluefin tuna off the west coast of Ireland in
14 October and November 2016 (199 to 246cm Curved Fork Length, CFL), yielding 2799 days of location
15 data and 990 and 989 days of depth and temperature time-series data respectively, including
16 downloaded archives from three recovered tags. Most daily locations (96%, n=2,651) occurred east of
17 45°W, the current stock management boundary for Atlantic bluefin tuna. Key open ocean habitats
18 occupied were the Bay of Biscay and the Central North Atlantic, with two migratory patterns evident:
19 an east-west group and an eastern resident group. Five out of six tags that remained attached until
20 July 2017 returned to the northeast Atlantic after having migrated as far as the Canary Islands, the
21 Mediterranean Sea and the Central North Atlantic. Tracked bluefin tuna exhibited a diel depth-use
22 pattern occupying shallower depths at night and deeper depths during the day. Four bluefin tuna
23 visited known spawning grounds in the central and western Mediterranean Sea, and one may have
24 spawned, based on recovered data showing oscillatory dives transecting the thermocline on 15 nights.
25 These findings demonstrate the complexity of the aggregation of Atlantic bluefin tuna off Ireland and,
26 more broadly in the northeast Atlantic, highlighting the need for dedicated future research to
27 conserve this important aggregation.
28

29 Introduction

30 Atlantic bluefin tuna (*Thunnus thynnus*, hereafter ABT) are highly migratory, endothermic predators
31 that range widely throughout the North Atlantic Ocean (Block *et al.*, 2005). They were once frequently
32 encountered along the western coasts of Ireland until 2005 (Cosgrove *et al.*, 2008), before becoming
33 regionally scarce. In recent years, ABT have reappeared in coastal and offshore waters off Ireland (Ó
34 Maoiléidigh *et al.*, 2018), the United Kingdom, Sweden, Denmark (MacKenzie *et al.*, 2018) and Norway
35 (Ferber *et al.*, 2018) with catch indices from Japanese longline fleets working in the northeast Atlantic
36 also indicating a positive change in catchability (Kimoto and Itoh, 2017). However, the underlying
37 mechanisms behind these fluctuations in spatial distribution are complex and remain unclear (Ravier

38 and Fromentin, 2004; Fromentin, 2009).

39

40 The ABT population is comprised of two or more genetically distinct spawning stocks (Rooker *et al.*,
41 2008; Rodríguez-Ezpeleta *et al.*, 2019): the ‘eastern stock’ spawns in the Mediterranean Sea (Abascal
42 *et al.*, 2016) and the ‘western stock’ spawns in the Gulf of Mexico (Wilson *et al.*, 2015). ABT larvae and
43 mature adult fish (with fully developed gonads) have also been found in the Slope Seas between the
44 Gulf Stream and the northeast United States continental shelf seas, indicating that ABT may use other,
45 lesser-known spawning grounds in the North Atlantic Ocean (Richardson *et al.*, 2016). Throughout
46 their range, ABT stocks have been subjected to over-exploitation (Taylor *et al.*, 2011). In 2007, after
47 considerable stock depletion, a multi-annual stock rebuilding programme was implemented by the
48 International Commission for the Conservation of Atlantic Tunas (ICCAT). The most recent ICCAT stock
49 assessment suggested that the eastern stock had grown “substantially” (ICCAT, 2017), leading to a
50 revision of the recovery plan in 2018 and staged increases in total allowable catches up to 36,000
51 tonnes in 2020 (ICCAT, 2018). The status of the western Atlantic stock is more uncertain and recent
52 research has indicated that recovery of the eastern stock may have resulted in an increase in mixing
53 rates between sub-populations (Hanke *et al.*, 2017).

54

55 In order to avoid their repeated over-exploitation, understanding the complex spatio-temporal life-
56 history of ABT is key. ABT movements appear to vary ontogenetically, with larger ABT ranging further
57 and occupying more northerly regions (Block *et al.*, 2005; Walli *et al.*, 2009). There may also be
58 differences in the movement of ABT from different stocks (Aranda *et al.*, 2013; Fromentin *et al.*, 2014a;
59 Wilson *et al.*, 2015). Otolith microchemistry and tracking studies have linked ABT present in northeast
60 Atlantic aggregations to both eastern (east of the 45°W meridian) and western (west of the 45°W
61 meridian) stock management areas, and to spawning grounds in the Mediterranean Sea (Block *et al.*,
62 2005; Stokesbury *et al.*, 2007; Rooker *et al.*, 2019). While research into the underlying drivers behind
63 the changing abundance of ABT in the northeast Atlantic continues (e.g. Fromentin, Reygondeau, *et*
64 *al.*, 2014; Faillettaz *et al.*, 2019), aspects of the genetic provenance, migration patterns and putative
65 spawning behaviour of ABT that seasonally reside in the northeast Atlantic remain unclear. In the
66 present study, we build on the work detailed in Stokesbury *et al.* (2007) to further investigate the
67 movements, habitat preferences and area-specific behaviours of potentially sexually mature ABT
68 captured on their seasonal foraging grounds off the west coast of Ireland.

69

70 **Methods**

71 ***Electronic tagging***

72 Between October and November 2016, ABT (n=16, mean size 220 ± 13 cm, 1 Standard Deviation,
73 Curved Fork Length, CFL) were captured off the west coast of Ireland by recreational 'rod and line'
74 fishermen trolling lures. Tagging was conducted on-deck, during which a saltwater hose was used to
75 irrigate the gills and a cloth soaked in fish-slime replacement (PolyAqua) was placed over the eyes to
76 reduce stress. Electronic tags (Wildlife Computers MiniPAT 247A and 348F, tagware v2.4n, hereafter
77 'tags') were attached via percutaneous darts as detailed in Wilson *et al.* (2015) and programmed to
78 detach from ABT after 316 to 365 days. Tags recorded light, pressure (depth) and temperature every
79 15 seconds for model 247A tags (n=8) and every 5 seconds for model 348F tags (n=8). The entire
80 procedure (removal from the water to release) took 3 to 5 minutes. After detachment, tags were
81 programmed to transmit 8-hour long segments of depth or temperature time-series data at a 10-
82 minute resolution (hereafter 'transmitted time-series', n=9 tags). All tags were programmed to release
83 from the study animal if they remained at a constant depth (± 2.5 m) for a period of four days, which
84 may indicate death or premature detachment.

85

86 Animal locations were reconstructed using the Global Position Estimator 3 (GPE3, Wildlife
87 Computers), which uses the tag records of light, temperature, depth, and reference data on sea
88 surface temperature (NOAA OI SST, www.esrl.noaa.gov/psd) and bathymetry (ETOPO1-Bedrock,
89 Amante and Eakins, 2009) with a user-defined movement speed (set at 2 m per second) to determine
90 the most likely location. For each tag, up to seven estimates of location were available per day, which
91 were averaged (geodesic mean) to create 'daily locations'. All reported locations are most likely
92 locations and are subject to positional error (grand mean for all tags of $1.5 \pm 0.1^\circ$ longitude and $1.2 \pm$
93 0.1° latitude).

94

95 ***Behaviour classification***

96 Atlantic bluefin tuna that were tracked for longer than 60 days (n=14) were classified into two types
97 based on whether they crossed the Mid Atlantic Ridge (median longitude 28° W, 'east-west') or not
98 ('eastern resident'). Periods where distances between successive relocations indicated faster
99 movements were classified as 'fast migration' using the *adehabitatLT* package in R (Calenge, 2006;
100 further details of classification methods are supplied in the Supplemental Materials) and vertical
101 movements analysed separately. ABT with tags that remained attached after the 1st of July 2017 (the
102 year following tag attachment and the time of year schools of ABT begin to be observed off west
103 Ireland, *Pers. Comm.* A. Molloy) were classified as return migrants if either tag pop-up or daily
104 locations were present in the area east of 30° W and north of 50° N.

105

106 **Horizontal Movements**

107 Areas of relative importance for ABT were determined by dividing the number of summed daily
108 locations by counts of unique tags in 100 km diameter hexagonal bins (11,555 km² per hexagon;
109 maximum count 16). The study area was partitioned into ecoregions following Longhurst (2007, Fig.
110 S1).

111

112 **Diving Behaviour from Time Series Data**

113 After detachment, tags transmitted each 8-hour time-series segment across three data messages,
114 which were often only partially recovered via satellite. Mean depth values derived from incomplete
115 transmitted time series (one or two messages received) were found to differ from values derived from
116 downloaded tag archives, where tags were physically retrieved, (see Supplemental Table 1 and Fig. S3
117 for details) and hence were removed from future time-series analysis. In addition to using transmitted
118 time series (three data messages received), downloaded datasets from three recovered tags were
119 down sampled to match transmitted time-series frequency and included in diving analyses. Time
120 series data for each tag were subset into day-time and night-time summary periods using tag-derived
121 sunrise and sunset times. Diving metrics (mean depth, vertical movement rate, mean temperature
122 and rate of ambient temperature change) were then calculated for each day-time or night-time period
123 for each tag. Vertical movement rate and rate of ambient temperature change were calculated by
124 summing the absolute depth and temperature change, respectively, and dividing by the time elapsed
125 in hours for a given summary period (either day-time or night-time). Generalised Linear Mixed Models
126 (GLMM, gamma family) were fit to log-normalised depth and temperature dive metrics, with fixed
127 terms for ecoregion and day or night and tag as a random effect using the package “lme4” (Bates *et*
128 *al.*, 2013). The most appropriate model was selected by removing individual fixed effects and
129 comparing with the null model using a likelihood ratio test. T-tests using Satterwaite’s method were
130 used to test the differences between fixed level effects. The final model was validated by visually
131 inspecting standardized residuals. All errors are reported as one standard deviation. In addition to
132 investigating general behaviours over longer periods (hours), putative spawning behaviour was
133 investigated using the downloaded archive of a recovered tag. For this analysis, rates are reported at
134 the base sampling rate of 5-seconds.

Results

135 **Fieldwork and tag performance**

136 Mean tag retention time was 224 ± 99 days (n=15, Fig. S4), with 3 tags remaining attached for the
137 entire programmed attachment period (307 to 365 days). One tag detached following a putative

138 mortality event, with the tag remaining at a constant depth for four days (14P0251, Fig. S6) and one
139 tag only transmitted for seven hours post-detachment. Three tags were physically recovered, and raw
140 time series data were downloaded. The resulting dataset comprised 2,779 days (n=14 tags) of
141 geolocation data.

142

143 **Horizontal movements**

144 Tracked ABT dispersed up to 4,628 km from the tagging site (cumulative along-track straight-line
145 distance, mean $2,780 \pm 721$ km, Fig. 1a), but most remained in the eastern Atlantic, with 96% of daily
146 locations occurring east of the 45°W meridian. No ABT moved north immediately after tagging and
147 98% of all daily locations were south of the tagging site. ABT moved west into sovereign waters of the
148 USA and Canada, as far south as the Canary Islands, as far east as the coast of Libya, and as far north
149 as the Faroe Islands, as well as visiting known spawning grounds in the eastern and central
150 Mediterranean Sea (Fig. 1a). Eight ABT travelled to the Bay of Biscay, where they either remained for
151 26 to 107 days (range, mean 48 ± 30 days) or migrated west to the Central North Atlantic (Fig. 1b).
152 ABT occupied eight different ecoregions in the North Atlantic and Mediterranean Sea (Fig. 2). Areas
153 of high relative mean residency for ABT (Fig. 1c) were in the Celtic Sea and Goban Spur area (maximum
154 19 days per tag per grid cell, NECS ecoregion), the Bay of Biscay (maximum 18 days per tag per grid
155 cell, NADR, NECS and CNRY ecoregions) and central North Atlantic/Flemish Cap region (maximum 12
156 days per tag per grid cell, NADR and NASE ecoregions). Ten ABT (77%) exhibited an east-west
157 migratory pattern, crossing the Mid Atlantic Ridge into the Newfoundland Basin, and three ABT (23%)
158 exhibited an eastern resident migratory pattern, remaining in waters east of 20°W and making
159 latitudinal migrations (Fig. 3). Six tags remained attached after the 1st of July 2017, of which five (83%)
160 showed a return migration to the northeast Atlantic (Table 1), with the sixth migrating to the Scotian
161 Shelf where the tag detached on the 5th of July 2017.

162

163 The grand mean speed of travel for all tracked ABT was 46 ± 9 km per day. Ninety-three percent of
164 pooled daily movements for ABT were less than 125 km per day (n=2,570 days) with 67% less than 50
165 km per day (n=1,850 days, Fig S2). The maximum distance (along-track straight-line, range <1 to 276
166 km) travelled by an ABT (234 cm CFL) in a single day was 276 km (1.4 body lengths per second). ABT
167 exhibited a fast migration behaviour for between 2 and 50 days per tag (mean 15 ± 12 days per tag),
168 which was observed in five out of eight ecoregions (CNRY, MEDI, NADR, NASE and NECS), with the
169 highest proportion occurring in the MEDI and CNRY ecoregions (30 and 13% of daily movements in
170 each region respectively, Table 2).

171

172 **Vertical movements**

173 The dataset of complete time-series dive data comprised 990 and 989 days of depth and temperature
174 time-series data, respectively (36% of days with geolocation data). Dive data were collected in all
175 ecoregions except the NASW, and only one ABT occupied the SARC for a period of 11 days. Due to the
176 paucity of data in these two regions they were excluded from modelling.

177

178 **Depth preferences from time-series data**

179 Tracked ABT occupied the shallowest depths in the MEDI ecoregion (19 ± 19 m, $t = 0.1$, $P = 0.32$), which
180 were similar to depths occupied in the CNRY (21 ± 3 m, Table 2) and GFST ecoregions (27 ± 19 m, $t =$
181 0.42 , $P = 0.68$). ABT occupied significantly greater depths in the NADR (49 ± 22 m, $t = 7.33$, $P = <0.001$),
182 NASE (45 ± 11 m, $t = 5.24$, $P = <0.001$) and NECS ecoregions (33 ± 7 m, $t = 5.6$, $P = <0.001$). ABT occupied
183 significantly shallower depths during the night whilst in the MEDI (day 24 ± 24 m, night 13 ± 3 m, $t = -$
184 2.3 , $P = 0.02$), NADR (day 64 ± 41 m, night 32 ± 11 m, $t = -2.5$, $P = 0.01$) and NECS (day 39 ± 11 m, night
185 $= 24 \pm 10$ m, $t = -4.7$, $P = <0.001$) ecoregions. ABT vertical movement rate was positively correlated
186 with mean occupied depth (Spearman's rank, $S = 25821^4$, $\rho = 0.78$, $P = <0.001$). Low ABT vertical
187 movement rates (less than 15 m per hour) were observed in all ecoregions and 90% of vertical
188 movement rates were less than 186 m per hour (Fig. S8).

189

190 **Temperature preferences from time-series data**

191 Mean ambient temperature experienced by ABT differed significantly between all ecoregions except
192 the CNRY and GFST ($17.3 \pm 1.7^\circ\text{C}$ and $17.7 \pm 0.7^\circ\text{C}$ respectively, $t = -1.6$, $P = 0.64$, Table 2) and the GFST
193 and NASE ecoregions ($17.7 \pm 0.7^\circ\text{C}$ and $17.3 \pm 1.1^\circ\text{C}$, respectively, $t = -0.42$, $P = 0.99$). Coolest ambient
194 temperatures were experienced by ABT in the SARC (day 12.0°C , night 12.5°C) and NECS ecoregions
195 (day $12.9 \pm 1.1^\circ\text{C}$, night $13.2 \pm 1.2^\circ\text{C}$) and the warmest in the MEDI ecoregion (day $21.0 \pm 3^\circ\text{C}$, night
196 $21.8 \pm 1.7^\circ\text{C}$). Additionally, mean temperatures occupied by ABT were significantly cooler between
197 day and night periods for all ecoregions (GLMM, cooler by 0.2°C , $df = 1$, $F = 11.6$, $P = <0.001$) and were
198 positively correlated with the rate of ambient temperature change (Spearman's rank, $S = 53521^4$, $\rho =$
199 0.35 , $P = <0.001$). Low rates of ambient temperature change (less than 0.5°C per hour) were observed
200 in ABT occupying every ecoregion and 90% of ambient temperature change rates were less than 3.1
201 $^\circ\text{C}$ per hour (Fig. S8).

202

203 **Spawning ground visitation and behaviour**

204 During the present study, four ABT entered the Mediterranean Sea between May and July - the known
205 period for spawning (Aranda *et al.*, 2013). ABT entered through the Straits of Gibraltar between the

206 16th and 23rd May 2017 (mean 19th May 2017), but only one (16P1265) was tracked returning to the
207 North Atlantic after 47 days residency (exit on 6th of July 2017, see below). A third ABT (16P1170)
208 experienced a similar temperature profile to 16P1265 indicating entry to the Mediterranean Sea but
209 lacked light data to reconstruct the track beyond the 3rd June 2017 (Fig. S7). Two eastern resident ABT
210 migrated to the central Mediterranean Sea and two east-west ABT migrated to the western
211 Mediterranean Sea (Fig. 3). Two of these four tags were physically recovered. Depth data from the
212 first tag (14P0031) suggests that the fish was caught near the Strait of Messina on the 4th of June 2017
213 and potentially towed to a fish farm off Malta, where the tag was recovered 76 days later. A second
214 tag (16P1265) detached from the fish after collecting a dataset over a full migratory cycle. The fish
215 (234 cm CFL) moved an estimated minimum straight-line distance of 17,173 km over 307 days (Fig. 4).
216 The ABT departed the NECS on the 7th of November 2016 and returned on the 21st of July 2017 after
217 having spent 47 days in the Mediterranean Sea over the spawning season. Archival data (5-second
218 resolution) reveal the fish undertook high frequency shallow (10 ± 10 m) diving around the
219 thermocline on 15 occasions over two periods (the 3rd to the 5th and 14th to the 24th of June 2017),
220 between 00:00 and 04:00 (UTC), whilst off the Balearic Islands (Fig. 5). Rates of vertical ascent /
221 descent peaked at 9 m per 5 seconds (mean 1.1 ± 1.1 m per 5 seconds) and the fish experienced
222 temperature fluctuations of up to 2.9°C per 5 seconds (mean 0.2 ± 0.3 °C per 5 seconds). Outside of
223 these periods, whilst still in the Mediterranean Sea, the fish occupied depths of 13 ± 30 m and
224 experienced mean ambient temperatures of 21.5 ± 2.8 °C with mean rates of vertical ascent / descent
225 of 0.8 ± 0.9 m per 5 seconds and rates of temperature change of 0.1 ± 0.2 °C per 5 seconds. Tags
226 attached to the other two ABT that entered the Mediterranean Sea detached 130 km off the Libyan
227 coast on the 25th of June 2017 (14P0330), and 300 km southeast of Iceland on the 1st of September
228 2017 (16P1264). The coarseness of transmitted depth and temperature time-series data received
229 from the tags prevents an investigation of putative spawning behaviour for these fish.

230

231 Discussion

232 The distribution of bluefin tuna in the Atlantic has fluctuated markedly over time (Fromentin *et al.*,
233 2014b) and positive abundance trends indicate a recent resurgence in northeast Atlantic (Kimoto and
234 Itoh, 2017; Faillettaz *et al.*, 2020). Consequently, understanding the movements and habitat selections
235 (e.g. Walli *et al.*, 2009; Galuardi *et al.*, 2010) that constitute the overall distribution of ABT is a key step
236 in conserving them throughout their range. Here we show that ABT tagged off Ireland appear to spend
237 most time in eastern management regions, were comprised of at least two migratory groups and
238 visited known spawning grounds in the Mediterranean Sea, where in at least one case, diving
239 behaviour consistent with spawning was observed.

240

241 **Irish ABT Migrations**

242 To meet the requirements of a metabolically demanding lifestyle while storing sufficient energy
243 reserves to reproduce, ABT must prioritise prey capture by exploiting a patchwork of seasonally
244 productive feeding areas (Walli *et al.*, 2009; Wilson and Block, 2009). Records indicate that ABT have
245 been present off Ireland since at least the 1970s and they have been caught by commercial pelagic
246 trawlers and recreational fishers since 1999 (Cosgrove *et al.*, 2008), although no commercial fishery
247 exists. A pilot recreational catch, tag and release programme was recently sanctioned to aid data
248 collection for management (ICCAT, 2018). ABT arrive in Irish waters from foraging grounds in the
249 Atlantic and spawning grounds in the Mediterranean from July onwards to feed on a diverse array of
250 forage fish including sprat (*Sprattus sprattus*), Atlantic saury (*Scomberesox saurus*) and Atlantic
251 mackerel (*Scomber scomber*, Cosgrove *et al.* 2008). The continental shelf edge is closest to Ireland and
252 the UK in this area (ca. 100 km) and is a region of seasonally high productivity (Van De Poll *et al.*, 2013)
253 and an established migratory pathway for pelagic forage fish (Jansen *et al.*, 2012). ABT leave these
254 foraging grounds for the Bay of Biscay and/or the Central North Atlantic in the late autumn when
255 stratification of the water column breaks down and the water cools (Van Aken, 2001). The Bay of
256 Biscay hosts small (55 to 110 cm straight fork length) ABT throughout the summer and autumn
257 (Rodríguez-Marín *et al.*, 2003; Arregui *et al.*, 2018). Here, we show large ABT tagged off Ireland (199
258 to 224 cm CFL) do not occupy the area until winter and spring (October – April), highlighting
259 differential, age-structured use of the area between conspecifics. The Central North Atlantic is a region
260 of high productivity (Daniault *et al.*, 2016) that has been shown to attract sharks (Queiroz *et al.*, 2016),
261 birds (Dias *et al.*, 2012), whales (Silva *et al.*, 2013) and multiple size cohorts of ABT (Block *et al.*, 2005;
262 Stokesbury *et al.*, 2007; Arregui *et al.*, 2018) from both eastern and western stocks (Rodríguez-
263 Ezpeleta *et al.*, 2019), including ABT from foraging aggregations off Ireland.

264

265 Understanding and characterising the movements of large ABT is a key step in conserving the
266 spawning stock. Wilson *et al.* (2015) tracked ABT that had visited the Gulf of Mexico spawning ground
267 and showed they exhibited high fidelity to the foraging ground they were first captured on whilst also
268 remaining west of the 45°W meridian. Stokesbury *et al.* (2007), albeit with a small sample size (n=3
269 ABT), demonstrated that ABT tagged off Ireland visited the Mediterranean Sea and western Atlantic
270 regions. Here, we build on this work, demonstrating that ABT tagged off Ireland constitute two
271 movement types (east-west and eastern resident) and visit known spawning grounds in the central
272 and western Mediterranean Sea. Furthermore, we show a high degree of spatiotemporal variability
273 in individual fish movements, with multiple ecoregions inhabited simultaneously (although we note

274 not all ecoregions are similar in area) by fish of a size considered to be sexually mature. Reasons
275 underlying this are likely varied and reflect the challenge of locating sufficient forage fish in a
276 heterogenous environment. Some ABT tracked in the present study did not visit known spawning
277 grounds, which is consistent with other ABT electronic tagging studies (Block *et al.*, 2005; Walli *et al.*,
278 2009; Galuardi *et al.*, 2010; Wilson *et al.*, 2015) and may be because they, i) use alternate spawning
279 locations, for instance the Slope Sea (Richardson *et al.*, 2016; e.g. Fig. S5h) or waters off the Canary
280 Islands (Druon *et al.*, 2016; e.g. Fig. S5f), ii) could be immature fish from the proportion of the western
281 stock that spawn in the Gulf of Mexico (these fish show first spawning ground visitation at larger sizes
282 than the eastern stock, Block *et al.* 2005), or, iii) as with other iteroparous fishes, may choose to defer
283 breeding due to a deficient diet or poor nutritional condition (Rideout and Tomkiewicz, 2011).

284

285 In recent years, ABT have been observed more frequently in waters off Denmark, Sweden and Norway
286 after having been rare since the 1960's (Ferber *et al.*, 2018; MacKenzie *et al.*, 2018). Here, we provide
287 no evidence of connectivity between foraging grounds off Ireland and these Nordic regions. However,
288 it is likely that the migration of ABT into waters north of the study site, such as these, is under-
289 represented in this dataset due to premature tag shedding. Given the similar sizes of ABT in the Nordic
290 (Denmark and Sweden, mean 232 ± 16 cm CFL, MacKenzie *et al.*, 2018) and Irish aggregations, it could
291 be that ABT tracked from Irish foraging grounds, i) visited Nordic regions but the temporal range of
292 geolocation data in this study did not capture this part of the annual migration, or, ii) show foraging
293 ground fidelity (as for spawning grounds, i.e. Rooker *et al.*, 2008) and Ireland and Denmark represent
294 unique cohorts of the ABT population with differing spatial habits.

295

296 **Patterns in diving behaviour**

297 Many marine fishes dive extensively for reasons including foraging (Wilson and Block, 2009; Thorrold
298 *et al.*, 2014; Whitlock *et al.*, 2015), thermoregulation (Teo *et al.*, 2007), reproduction (Aranda *et al.*,
299 2013; Cermeño *et al.*, 2015) and navigation (Brunnschweiler *et al.*, 2009) and employ different diving
300 strategies depending on their movement mode (i.e. transiting - Walli *et al.*, 2009) and the time of day
301 (Gilly *et al.*, 2006; Queiroz *et al.*, 2016; Jansen *et al.*, 2019). Here we demonstrate that ABT dive
302 extensively and follow a diel diving pattern, which likely reflects foraging effort as ABT follow the
303 vertical migrations of their prey (Darbyson *et al.*, 2003; Gilly *et al.*, 2006; Olson *et al.*, 2016; Jansen *et al.*
304 *et al.*, 2019). Additionally, low rates of ambient temperature change across all except the MEDI
305 ecoregion, indicate that the ABT in this study spent most time in the mixed layer. This behaviour has
306 been observed previously for ABT (Walli *et al.*, 2009; Lawson *et al.*, 2010; Galuardi and Lutcavage,
307 2012). An explanation for the relationship could be physiological, as ABT seek warmer (near-surface)

308 temperatures after visiting deeper (cooler) depths. ABT likely trade-off between maintaining internal
309 temperatures at 12 to 20°C above ambient (Lawson *et al.* 2010), and visiting colder but more
310 productive waters to replenish depleted energy reserves after migration or spawning by foraging on
311 an energy rich food source (e.g. spawning Atlantic herring, Pleizier *et al.*, 2012; Wilson *et al.*, 2015).
312 To further this, we present the first data showing ABT residing in inshore waters of the Inner Hebrides,
313 Scotland and the Celtic Deeps off Wales, the coolest regions inhabited by ABT in this study (mean
314 temperature 12.6°C).

315

316 **Spawning behaviour of Irish ABT**

317 Archival tags have been previously used to identify ABT putative spawning behaviours (e.g. Teo *et al.*,
318 2007; Aranda *et al.*, 2013; Cermeño *et al.*, 2015; Hazen *et al.*, 2016). During spawning, Teo *et al.* (2007)
319 proposed that heat production through metabolic processes likely increases (internally placed tags
320 demonstrated visceral warming) and Reglero *et al.* (2018) demonstrate that oocytes need to be
321 released into warmest surface waters to maximise growth and development. Consequently, high
322 frequency shallow dives intersecting the thermocline detailed in the present study in the MEDI
323 ecoregion, may reflect a thermoregulatory behaviour to balance the physiological effects of potential
324 heat stress (Teo *et al.*, 2007) whilst also releasing oocytes and sperm above the thermocline at
325 temperatures best for growth and development (Reglero *et al.*, 2018). This specific behaviour, coupled
326 with warm surface waters and the shallow, intense stratification in the MEDI ecoregion likely resulted
327 in observed high rates of ambient temperature change over comparatively small changes in depth,
328 reflecting behavioural thermoregulation.

329

Overview

330 Recent years have seen ABT return to waters of the northeast Atlantic, including the waters off Ireland.
331 Here we show that the ABT in this aggregation spend most of their time in eastern stock management
332 units and exhibit high fidelity to foraging grounds of the northeast Atlantic. We link ABT present in
333 aggregations off northwest Ireland to established high-use areas of the Central North Atlantic, Bay of
334 Biscay and known spawning areas in the western and central Mediterranean Sea, but only tentatively
335 to western stock management units and not at all to Nordic regions. The re-appearance of large ABT
336 into the northeast Atlantic represents an opportunity to study the full cycle of foraging and
337 reproductive behaviours of this important cohort of the eastern Atlantic spawning stock in a period of
338 increasing fishing pressure in the eastern Atlantic.

339

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345 not have been possible.

References

- Abascal, F. J., Medina, A., De La Serna, J. M., Godoy, D., and Aranda, G. 2016. Tracking bluefin tuna reproductive migration into the Mediterranean Sea with electronic pop-up satellite archival tags using two tagging procedures. *Fisheries Oceanography*, 25(1): 54–66.
- Amante, C., and Eakins, B. W. 2009. ETOPO1 Global Relief Model converted to PanMap layer format. NOAA-National Geophysical Data Center.
- 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(10): e76445.
- Arregui, I., Galuardi, B., Goñi, N., Lam, C. H., Fraile, I., Santiago, J., Lutcavage, M., *et al.* 2018. 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(5): 1560–1572.
<https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsy056/5004410>.
- Bates, D., Maechler, M., and Bolker, B. 2013. lme4: Linear mixed-effects models using Eigen and S4 classes. R package version 1.1-7.
- Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J., Weng, K. C., *et al.* 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature*, 434(7037): 1121–1127.
<http://dx.doi.org/10.1038/nature03463>.
- Brunnschweiler, J. M., Baensch, H., Pierce, S. J., and Sims, D. W. 2009. Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of Fish Biology*, 74(3): 706–714. Wiley/Blackwell (10.1111). <http://doi.wiley.com/10.1111/j.1095-8649.2008.02155.x> (Accessed 6 July 2018).
- Calenge, C. 2006. The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197(3–4): 516–519.
- Cermeño, P., Quílez-Badia, G., Ospina-Alvarez, A., Sainz-Trápaga, 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(2): e0116638.
- Cosgrove, R., Stokesbury, M. J. W., Browne, D., Boustany, A., Block, B. A., and Farrell, M. 2008. Bluefin tuna tagging in Irish waters. *Fisheries Resource Series*, 6(6): 1–16.
- Daniault, N., Mercier, H., Lherminier, P., Sarafanov, A., Falina, A., Zunino, P., Pérez, F. F., *et al.* 2016. The northern North Atlantic Ocean mean circulation in the early 21st century. *Progress in Oceanography*, 146(August): 142–158. Elsevier Ltd. <http://dx.doi.org/10.1016/j.pocean.2016.06.007>.
- Darbyson, E., Swain, D. P., Chabot, D., and Castonguay, M. 2003. Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. *Journal of Fish Biology*, 63(5): 1235–1257.
- Dias, M. P., Granadeiro, J. P., and Catry, P. 2012. Do Seabirds Differ from Other Migrants in Their Travel Arrangements? On Route Strategies of Cory’s Shearwater during Its Trans-Equatorial Journey. *PLoS ONE*, 7(11): e49376.

- Druon, J.-N., Fromentin, J.-M., Hanke, A. R., Arrizabalaga, H., Damalas, D., Tičina, V., Quílez-Badia, G., *et al.* 2016. Habitat suitability of the Atlantic bluefin tuna by size class: An ecological niche approach. *Progress in Oceanography*, 142: 30–46. <http://www.sciencedirect.com/science/article/pii/S0079661116000070>.
- Faillettaz, R., Beaugrand, G., Goberville, E., and Kirby, R. R. 2019. Atlantic Multidecadal Oscillations drive the basin-scale distribution of Atlantic bluefin tuna. *Science Advances*, 5(1): eaar6993.
- Faillettaz, R., Beaugrand, G., Goberville, E., and Kirby, R. R. 2020. Atlantic Multidecadal Oscillations drive the basin-scale distribution of Atlantic bluefin tuna (January 2019): 2–10.
- Ferter, K., Tracey, S., Hinriksson, J., Bjelland, O., Onandia, I., and Nøttestad, L. 2018. Tagging of Atlantic bluefin tuna (*Thunnus thynnus*) with pop-up satellite archival tags (PSAT) in western Norway during 2018 Final project report prepared for the International Commission for the Conservation of Atlantic Tunas (ICCAT) / Grand Bluefin.
- Fromentin, J.-M. 2009. Lessons from the past: investigating historical data from bluefin tuna fisheries. *Fish and Fisheries*, 10(2): 197–216. <http://doi.wiley.com/10.1111/j.1467-2979.2008.00311.x>.
- Fromentin, J.-M., Bonhommeau, S., Arrizabalaga, H., and Kell, L. T. 2014a. 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., Reygondeau, G., Bonhommeau, S., and Beaugrand, G. 2014b. Oceanographic changes and exploitation drive the spatio-temporal dynamics of Atlantic bluefin tuna (*Thunnus thynnus*). *Fisheries Oceanography*, 23(2): 147–156.
- Galuardi, B., Golet, W., Lutcavage, M., Logan, J., Royer, F., and Neilson, J. 2010. Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(6): 966–976.
- 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(5): e37829.
- Gilly, W., Markaida, U., Baxter, C., Block, B., Boustany, A., Zeidberg, L., Reisenbichler, K., *et al.* 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series*, 324: 1–17.
- Hanke, A., Macdonnell, A., Dalton, A., Busawon, D., Rooker, J. R., and Secor, D. H. 2017. Stock Mixing Rates of Bluefin Tuna From Canadian Landings : 1975-2015. *Collect. Vol. Sci. Pap. ICCAT*, 74(6): 2622–2634.
- Hazen, E. L., Carlisle, A. B., Wilson, S. G., Ganong, J. E., Castleton, M. R., Schallert, R. J., Stokesbury, M. J., *et al.* 2016. Quantifying overlap between the Deepwater Horizon oil spill and predicted bluefin tuna spawning habitat in the Gulf of Mexico. *Scientific Reports*, 6: 33824. <https://www.ncbi.nlm.nih.gov/pubmed/27654709>.
- ICCAT. 2017. Report of the 2017 ICCAT bluefin stock assessment meeting. *Collect. Vol. Sci. Pap.*, 74(6): 2372–2535. http://iccat.int/Documents/Meetings/Docs/2017_BFT_ASS_REP_ENG.pdf.
- ICCAT. 2018. BFT 18-02: Recommendation by ICCAT establishing a multi-annual management plan for bluefin tuna in the eastern Atlantic and the Mediterranean Sea. 18–02. Madrid, Spain. 1–46 pp.
- Jansen, T., Campbell, A., Kelly, C., Hátún, H., and Payne, M. R. 2012. Migration and Fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter. *PLoS ONE*, 7(12).
- Jansen, T., Post, S., Olafsdottir, A. H., Reynisson, P., Óskarsson, G. J., and Arendt, K. E. 2019. Diel vertical feeding behaviour of Atlantic mackerel (*Scomber scombrus*) in the Irminger current. *Fisheries Research*, 214: 25–34. Elsevier. <https://linkinghub.elsevier.com/retrieve/pii/S0165783619300207>.
- Kimoto, A., and Itoh, T. 2017. The standardized bluefin CPUE of Japanese longline fishery in the Atlantic up to 2017 fishing year. *ICCAT SCRS*, 25(2): 1–23.
- Lawson, G. L., Castleton, M. R., and Block, B. A. 2010. Movements and diving behavior of Atlantic bluefin tuna *Thunnus thynnus* in relation to water column structure in the northwestern Atlantic. *Marine Ecology Progress Series*, 400: 245–265.
- Longhurst, A. R. 2007. *Ecological Geography of the Sea 2nd Edition*. Academic Press. 560 pp.

- MacKenzie, B. R., Aarestrup, K., Birnie-Gauvin, K., Cardinale, M., Casini, M., Harkes, I., Onandia, I., *et al.* 2018. Electronic tagging of adult bluefin tunas by sport fishery in the Skagerrak, 2017. ICCAT SCRS(164): 18 pp.
- O'Farrell, M., and Molloy, A. 2004. Bluefin Tuna (*Thunnus thynnus*) Big Game Fishing in Irish Coastal Waters: Results of Year 2003 Angling Trials and Compilation of Supporting Documentation. Killiney, Ireland. 24 pp.
- Ó Maoiléidigh, N., Connolly, P., Drumm, A., Neill, O., Maxwell, H., Co, J., Bunn, R., *et al.* 2018. Final report on tagging activities in the Celtic Seas Area 2018. (ICCAT GBYP 07/2018-PHASE 8), 2018.
- Olson, R. J., Young, J. W., Ménard, F., Potier, M., Allain, V., Goñi, N., Logan, J. M., *et al.* 2016. Bioenergetics, Trophic Ecology, and Niche Separation of Tunas. *Advances in marine biology*. Volume 35, 74: 199–344.
- Pleizier, N. K., Campana, S. E., Schallert, R. J., Wilson, S. G., and Block, B. A. 2012. Atlantic bluefin tuna (*Thunnus thynnus*) diet in the Gulf of St. Lawrence and on the eastern Scotian Shelf. *Journal of Northwest Atlantic Fishery Science*, 44: 67–76.
- Queiroz, N., Humphries, N. E., Mucientes, G., Hammerschlag, N., Lima, F. P., Scales, K. L., Miller, P. I., *et al.* 2016. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceedings of the National Academy of Sciences*, 113(6): 1582–1587. <http://www.pnas.org/lookup/doi/10.1073/pnas.1510090113>.
- Ravier, C., and Fromentin, J. M. 2004. Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? *Fisheries Oceanography*, 13(3): 145–160.
- Reglero, P., Ortega, A., Balbín, R., Abascal, F. J., Medina, A., Blanco, E., de la Gándara, F., *et al.* 2018. Atlantic bluefin tuna spawn at suboptimal temperatures for their offspring. *Proceedings of the Royal Society B: Biological Sciences*, 285: 20171405.
- Richardson, D. E., Marancik, K. E., Guyon, J. R., Lutcavage, M. E., Galuardi, B., Lam, C. H., Walsh, H. J., *et al.* 2016. Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*). *Proceedings of the National Academy of Sciences*, 113(12): 201525636. <http://www.pnas.org/lookup/doi/10.1073/pnas.1525636113>.
- Rideout, R. M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: More common than you might think. *Marine and Coastal Fisheries*, 3(1): 176–189.
- Rodríguez-Marín, E., Arrizabalaga, H., Ortiz, M., Rodríguez-Cabello, C., Moreno, G., and Kell, L. T. 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(6): 1216–1231.
- Rodríguez-Ezpeleta, N., Díaz-Arce, N., Walter, J. F., Richardson, D. E., Rooker, J. R., Nøttestad, L., Hanke, A. R., *et al.* 2019. Determining natal origin for improved management of Atlantic bluefin tuna. *Frontiers in Ecology and the Environment*: 1–6.
- Rooker, J. R., Secor, D. H., De Metrio, G., Schloesser, R., Block, B. A., and Neilson, J. D. 2008. Natal Homing and Connectivity in Atlantic Bluefin Tuna Populations. *Science*, 322(5902): 742–744.
- Rooker, J. R., Fraile, I., Liu, H., Abid, N., Dance, M. A., Itoh, T., Kimoto, A., *et al.* 2019. Wide-Ranging Temporal Variation in Transoceanic Movement and Population Mixing of Bluefin Tuna in the North Atlantic Ocean, 6(July): 1–13.
- Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., and Santos, R. S. 2013. North Atlantic Blue and Fin Whales Suspend Their Spring Migration to Forage in Middle Latitudes: Building up Energy Reserves for the Journey? *PLoS ONE*, 8(10): e76507.
- 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(12): 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): 1–18.
<http://link.springer.com/10.1007/s00227-006-0447-5>.

- Thorrold, S. R., Afonso, P., Fontes, J., Braun, C. D., Santos, R. S., Skomal, G. B., and Berumen, M. L. 2014. Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nature Communications*, 5: 1–7. Nature Publishing Group. <http://dx.doi.org/10.1038/ncomms5274>.
- Van Aken, H. M. 2001. The hydrography of the mid-latitude Northeast Atlantic Ocean - Part III: The subducted thermocline water mass. *Deep-Sea Research Part I: Oceanographic Research Papers*, 48(1): 237–267.
- Van De Poll, W. H., Kulk, G., Timmermans, K. R., Brussaard, C. P. D., Van Der Woerd, H. J., Kehoe, M. J., Mojica, K. D. A., *et al.* 2013. Phytoplankton chlorophyll *a* biomass, composition, and productivity along a temperature and stratification gradient in the northeast Atlantic Ocean. *Biogeosciences*, 10(6): 4227–4240.
- Walli, A., Teo, S. L., 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(7): e6151. <https://www.ncbi.nlm.nih.gov/pubmed/19582150>.
- Whitlock, R. E., Hazen, E. L., Walli, A., Farwell, C., Bograd, S. J., Foley, D. G., Castleton, M., *et al.* 2015. Direct quantification of energy intake in an apex marine predator suggests physiology is a key driver of migrations. *Science Advances*, 1(8): 1–10.
- Wilson, S. G., and Block, B. A. 2009. Habitat use in Atlantic bluefin tuna *Thunnus thynnus* inferred from diving behavior. *Endangered Species Research*, 10: 355–367. <http://www.int-res.com/abstracts/esr/v10/p355-367/%5Cnhttp://www.int-res.com/articles/esr2010/10/n010p355.pdf>.
- Wilson, S. G., Jonsen, I. D., Schallert, R. J., Ganong, J. E., Castleton, M. R., Spares, A. D., Boustany, A. M., *et al.* 2015. Tracking the fidelity of Atlantic bluefin tuna released in Canadian waters to the Gulf of Mexico spawning grounds. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(11): 1700–1717. NRC Research Press. <http://dx.doi.org/10.1139/cjfas-2015-0110>.

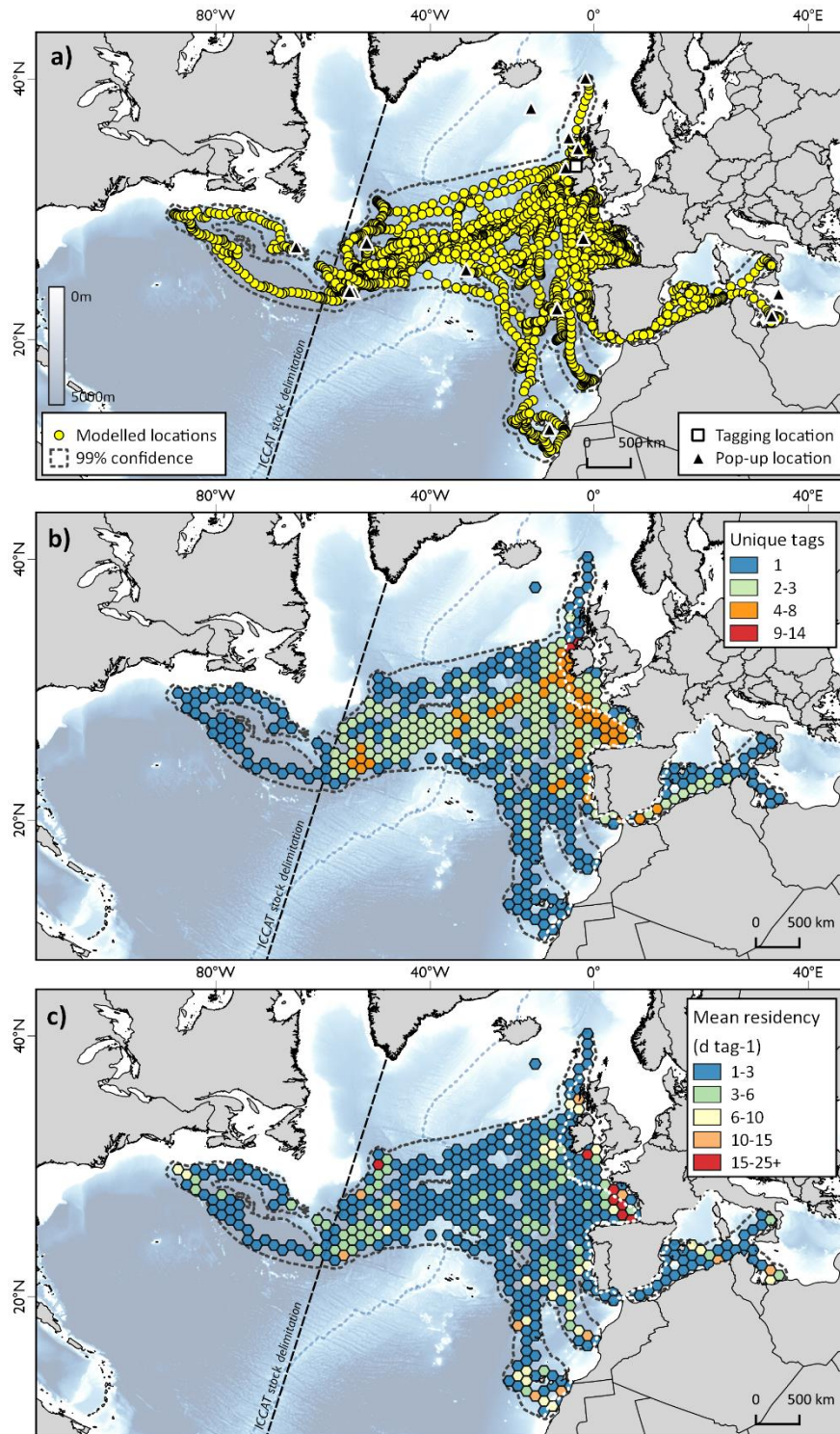


Figure 1. Bluefin tuna horizontal movements in the North Atlantic. a) Estimated daily locations obtained from 14 electronic tags attached to ABT in 2016 (n=2,779 tracking days). b) 100 km hexagon grid showing the number of unique tags in each grid cell for the 14 tags that yielded data, and, c) 100 km hexagon grid showing mean residency of tagged ABT (days per tag). Black broken line at the 45°W meridian denotes the ICCAT stock delimitation line and blue broken line denotes the Mid-Atlantic Ridge. White broken line (b and c) denotes 200 m depth contour.

Tag Serial	CFL (cm)	Tag type	Programming	Deployment			Pop-Up				Days at large	Trajectory	Return migrant?	Xmit days (light days)
				Date	Latitude	Longitude	Date	Latitude	Longitude	Release Reason				
14P0337	216	MiniPAT 247A	HS (24h)	09/10/2016	54.53	-8.80	23/01/2017	39.82	-41.48	Premature	106	E-W	-	18 (96)
14P0307	216	MiniPAT 247A	HS (24h)	09/10/2016	54.53	-8.79	26/06/2017	42.38	-50.91	Pin Broke	260	E-W	-	16 (235)
14P0359	224	MiniPAT 247A	HS (24h)	11/10/2016	54.54	-8.74	31/07/2017	63.69	-4.17	Pin Broke	293	East	Y	18 (237)
14P0251*	230	MiniPAT 247A	TS (5min)	11/10/2016	54.54	-8.78	14/10/2016	54.54	-8.79	Mortality	0	-	-	6 (2)
14P0031*Φ	220	MiniPAT 247A	TS (5min)	11/10/2016	54.53	-8.82	05/08/2017	35.85	14.64	Pin Broke	298	East	-	16 (283)
14P0330	206	MiniPAT 247A	HS (24h)	12/10/2016	54.54	-8.78	25/06/2017	34.01	12.74	Pin Broke	256	East	-	18 (184)
14P0062	215	MiniPAT 247A	TS (5min)	12/10/2016	54.55	-8.82	01/07/2017	47.04	-9.17	Pin Broke	262	E-W	N	16 (200)
14P0441	212	MiniPAT 247A	HS (24h)	12/10/2016	54.54	-8.84	19/08/2017	57.60	-9.39	Pin Broke	311	-	Y	0 (7)
16P1170	199	MiniPAT 348F	TS (5min)	12/10/2016	54.53	-8.81	12/10/2017	54.50	-10.62	Complete	365	E-W	Y	12 (79)
16P1268*	206	MiniPAT 348F	HS (24h)	22/10/2016	54.53	-8.63	06/03/2017	44.09	-26.63	Pin Broke	135	E-W	-	19 (128)
16P1253	207	MiniPAT 348F	TS (5min)	25/10/2016	54.71	-8.87	08/01/2017	45.07	-41.52	Premature	75	E-W	-	3 (34)
16P1264	224	MiniPAT 348F	TS (5min)	28/10/2016	54.70	-8.86	01/09/2017	61.10	-16.18	Complete	308	E-W	Y	15 (156)
16P1267	220	MiniPAT 348F	TS (5min)	28/10/2016	54.78	-8.81	10/03/2017	39.78	-42.04	Pin Broke	133	E-W	-	20 (121)
16P1249	240	MiniPAT 348F	TS (5min)	29/10/2016	54.74	-8.82	19/05/2017	27.56	-15.79	Premature	202	E-W	-	18 (147)
16P1265*	234	MiniPAT 348F	TS (5min)	29/10/2016	54.76	-8.81	01/09/2017	53.92	-9.57	Complete	307	E-W	Y	16 (111)
16P1263	246	MiniPAT 348F	HS (24h)	01/11/2016	54.59	-8.59	28/12/2016	40.11	-13.94	Premature	56	-	-	17 (27)

Table 1. Deployment and pop-up satellite tag metadata. Summary statistics for 16 electronic tags attached to ABT off the northwest coast of Ireland during 2016. * denotes tags that were physically recovered. Φ denotes an ABT that is thought to have been caught by a fishing vessel on approximately the 4th of June 2017. For programming: “HS” = Histogram and “TS” = Time-Series with respective sampling frequencies shown in parentheses. “Xmit day” denotes the length of time the tag transmitted for post-release with the number of days with light data given in parentheses.

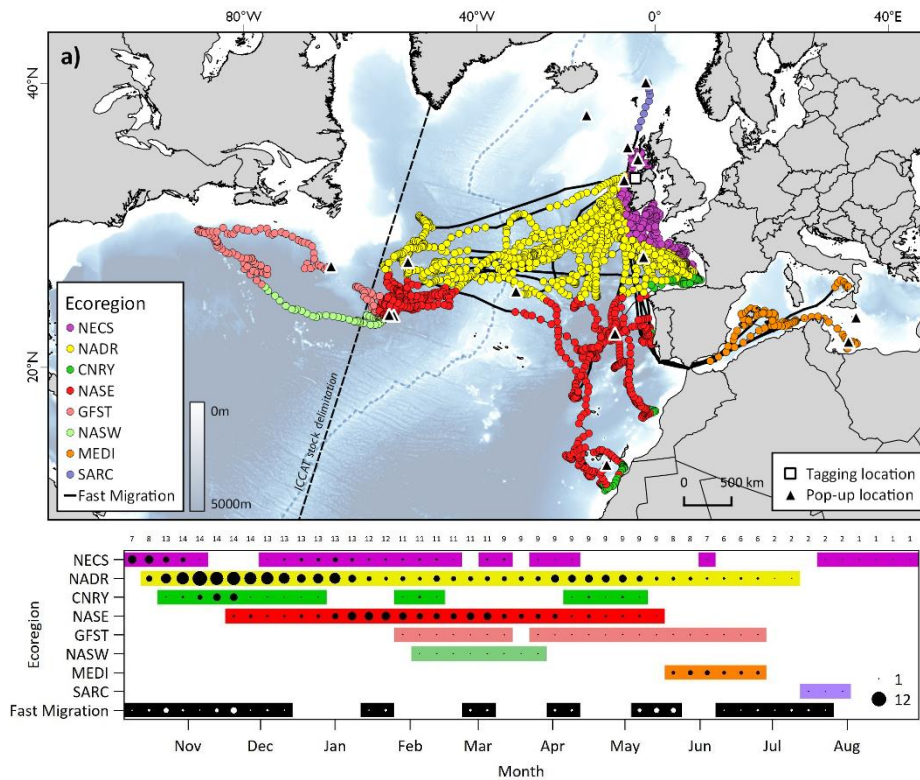


Figure 2. Seasonal occupancy of North Atlantic ecoregions by Atlantic bluefin tuna. a) Map of the North Atlantic displaying estimated daily locations obtained from 14 electronic tags attached to ABT in 2016. Black broken line at the 45°W meridian denotes the ICCAT stock delimitation line and blue broken line denotes the Mid-Atlantic Ridge. b) A gantt chart displaying the temporal pattern of ecoregion usage for all electronically tagged ABT. Numbers above the plot denote the total number of active tags and filled circles indicate the number of active tags in each ecoregion, both at a weekly resolution. NECS - NE Atlantic Shelves; NADR - N. Atlantic Drift; CNRY - Canary Coastal; NASE - N. Atlantic Subtropical Gyre (East); GFST - Gulf Stream; N. Atlantic Subtropical Gyre (West); MEDI - Mediterranean Sea; SARC- Atlantic Subarctic; Fast Migration – periods where distances between successive relocations indicate faster movements (thick black lines).

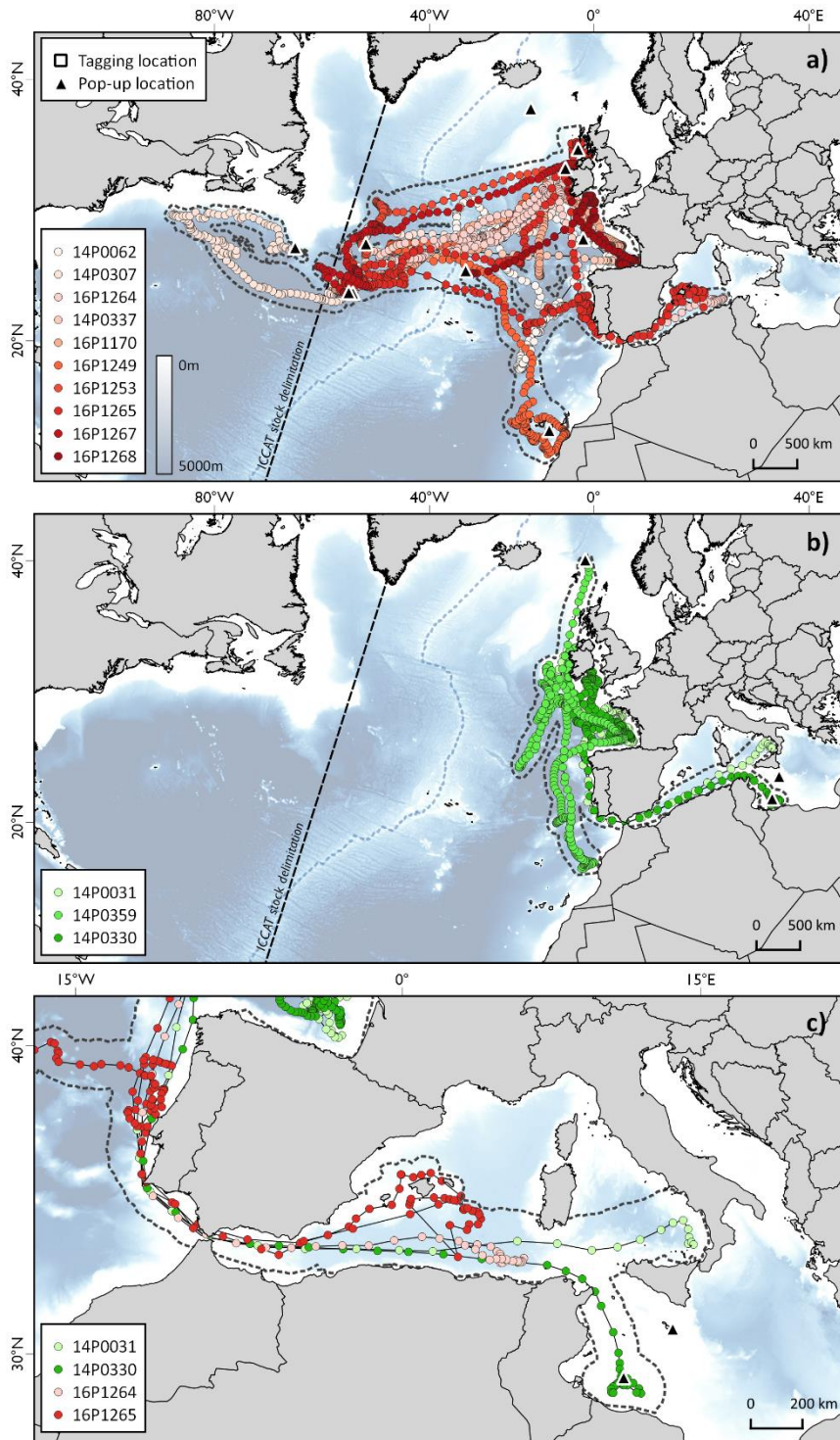


Figure 3. Migration patterns and spawning ground visitation of Atlantic bluefin tuna. a) East-west ABT that exhibited movements crossing the Mid-Atlantic Ridge, b) eastern resident ABT that remained east of the Mid-Atlantic Ridge, and c) ABT from both categories that visited previously described spawning areas in the Mediterranean Sea (unique colours for tags are the same for all plots). Black broken line at the 45°W meridian denotes the ICCAT stock delimitation line and blue broken line denotes the Mid-Atlantic Ridge.

Region	Tags (days)	Fast Migration (%)	T-S Tags (nD nT)	SST (°C)	Mean Depth (m)	VMR (m h ⁻¹)	Mean Temp. (°C)	ATC (°C h ⁻¹)
CNRV	8 (145)	13	5 (81 83)	16.6 ± 2 (14.1)	22 ± 5 (775)	77 ± 19 (212)	17.2 ± 1.5 (10.7) ^a	2.5 ± 2.6 (11.8)
					19 ± 2 (698)	56 ± 8 (167)	17.4 ± 1.9 (10.7) ^a	1.2 ± 0.9 (4.4)
GFST	2 (117)	0	2 (19 17)	17.2 ± 1.6 (10.8)	25 ± 16 (609)	87 ± 47 (233)	17.7 ± 0.7 (0) ^{a, b}	1 ± 0.5 (3.6)
					29 ± 21 (531)	108 ± 62 (324)	17.8 ± 0.6 (11.1) ^{a, b}	1.5 ± 0.9 (2.3)
MEDI	4 (107)	30	4 (76 72)	22.4 ± 2 (16.8)	24 ± 24 (482) Φ	92 ± 59 (391)	21 ± 3 (13.3)	6.3 ± 3.1 (17.3)
					13 ± 3 (454) Φ	53 ± 13 (426)	21.8 ± 1.7 (13.3)	4.4 ± 2.3 (14.7)
NADR	14 (1217)	8	10 (353 358)	14.5 ± 1.9 (9.5)	64 ± 41 (756) Φ *	113 ± 33 (359)	14.7 ± 1.4 (3.7)	1 ± 0.6 (5.9)
					32 ± 11 (871) Φ *	103 ± 28 (332)	14.7 ± 1 (7.1)	0.7 ± 0.3 (5.4)
NASE	9 (623)	5	7 (277 265)	17.2 ± 1.5 (12.9)	43 ± 14 (958) *	105 ± 45 (515)	17.2 ± 0.9 (7.2) ^b	1.4 ± 1.5 (7.2)
					45 ± 17 (931) *	136 ± 63 (568)	17.3 ± 1.2 (7.9) ^b	1.2 ± 1.5 (9.6)
NASW	1 (51)	0	0	-	-	-	-	-
					-	-	-	-
NECS	14 (299)	8	7 (165 166)	12.6 ± 1.7 (9.7)	39 ± 11 (195) Φ *	114 ± 52 (228)	12.9 ± 1.1 (9.7)	0.9 ± 1.1 (8.4)
					24 ± 10 (196) Φ *	92 ± 42 (207)	13.2 ± 1.2 (9.9)	0.5 ± 0.4 (4)
SARC	1 (11)	0	1 (3 5)	12.5 ± 0.3 (11.6)	16 (199)	56 (68)	12 (4.6)	2.5 (3.2)
					13 (190)	46 (88)	12.5 (5.1)	1.2 (2.6)
Fast Migration	14 (209)	N/A	7 (16 23)	15 ± 1.9 (12.1)	30 ± 30 (365)	77 ± 59 (214)	14.6 ± 1.3 (10.2)	0.7 ± 0.5 (2.8)
					41 ± 31 (710)	146 ± 119 (698)	15.1 ± 1.8 (9.9)	1 ± 0.5 (3.3)
Totals	14 (2,779)	8	14 (990 989)	Day	40 ± 29 (958)	98 ± 45 (515)	15.7 ± 2.6 (0)	1.6 ± 2 (17.3)
				Night	30 ± 19 (931)	101 ± 66 (698)	16.1 ± 2.8 (5.1)	1.4 ± 1.4 (14.7)
				All	35 ± 25 (958)	100 ± 56 (698)	15.9 ± 2.7 (0)	1.5 ± 1.7 (17.3)

Table 2. Vertical habitat use of tagged Atlantic bluefin tuna. NECS - NE Atlantic Shelves; NADR - N. Atlantic Drift; CNRY - Canary Coastal; NASE - N. Atlantic Subtropical Gyre (East); GFST - Gulf Stream; N. Atlantic Subtropical Gyre (West); MEDI - Mediterranean Sea; SARC- Atlantic Subarctic; Fast Migration – periods where distances between successive relocations indicate faster movements. Maximum depth, maximum vertical movement rate (VMR) and maximum rate of ambient temperature change (ATC) are shown in parentheses for “Mean Depth (m)”, “VMR (m h⁻¹)” and “ATC (°C h⁻¹)”, respectively. Minimum temperature is shown in parentheses for “Mean Temp. (°C)”. “T-S Tags” denotes the number of tags that transmitted useable time-series data, with the number of days given in parentheses for each of depth (nD) and temperature (nT), respectively. White boxes denote day-time and grey shaded boxes denote night-time periods. For “Mean Depth”, Φ denotes ecoregions where mean occupied depths were significantly deeper than the GFST ecoregion and * denotes ecoregions where mean occupied depths were significantly different between day and night summary periods (at the 5% level). For “Mean Temp” letters denote similarity between mean occupied temperatures, ecoregions without letters are statistically unique (at the 5% level).

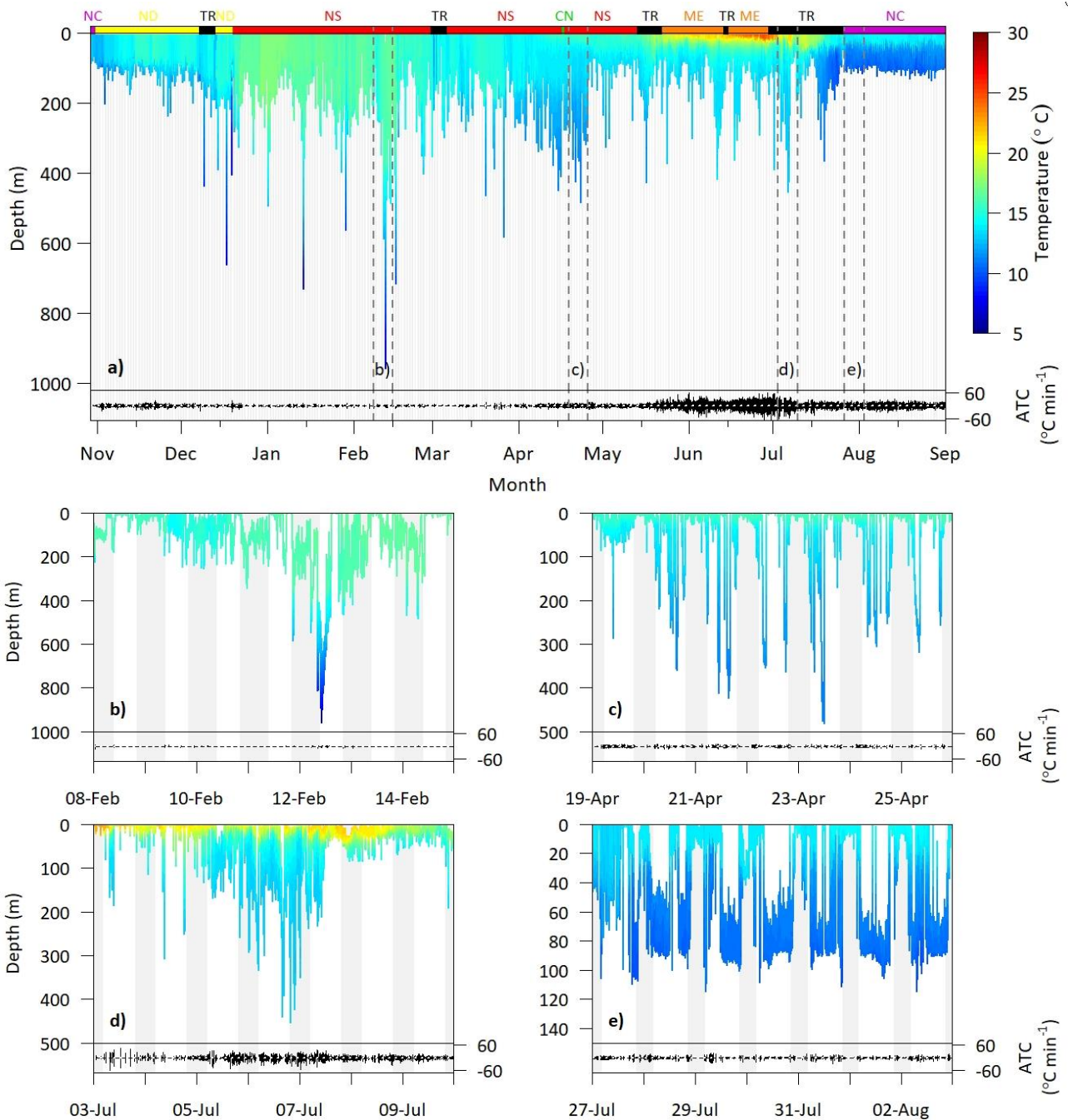


Figure 4a-e. High resolution diving behaviour of an Atlantic bluefin tuna. Physical archive time-series (5-second resolution) of depth, temperature and rate of ambient temperature change (ATC) for a tag recovered from the Outer Hebrides in September 2017 (16P1265). a) The full time-series with a labelled horizontal colour bar denoting which ecoregion the tag was in (colours *as per* Fig. 2), vertical dashed lines represent temporal range of subsequent plots, b) the deepest recorded dive of any bluefin tuna in this study, c) mesopelagic diving in the NADR region, d) deep-diving during exit from the Mediterranean Sea, and, e) diel vertical migration in the NECS ecoregion.

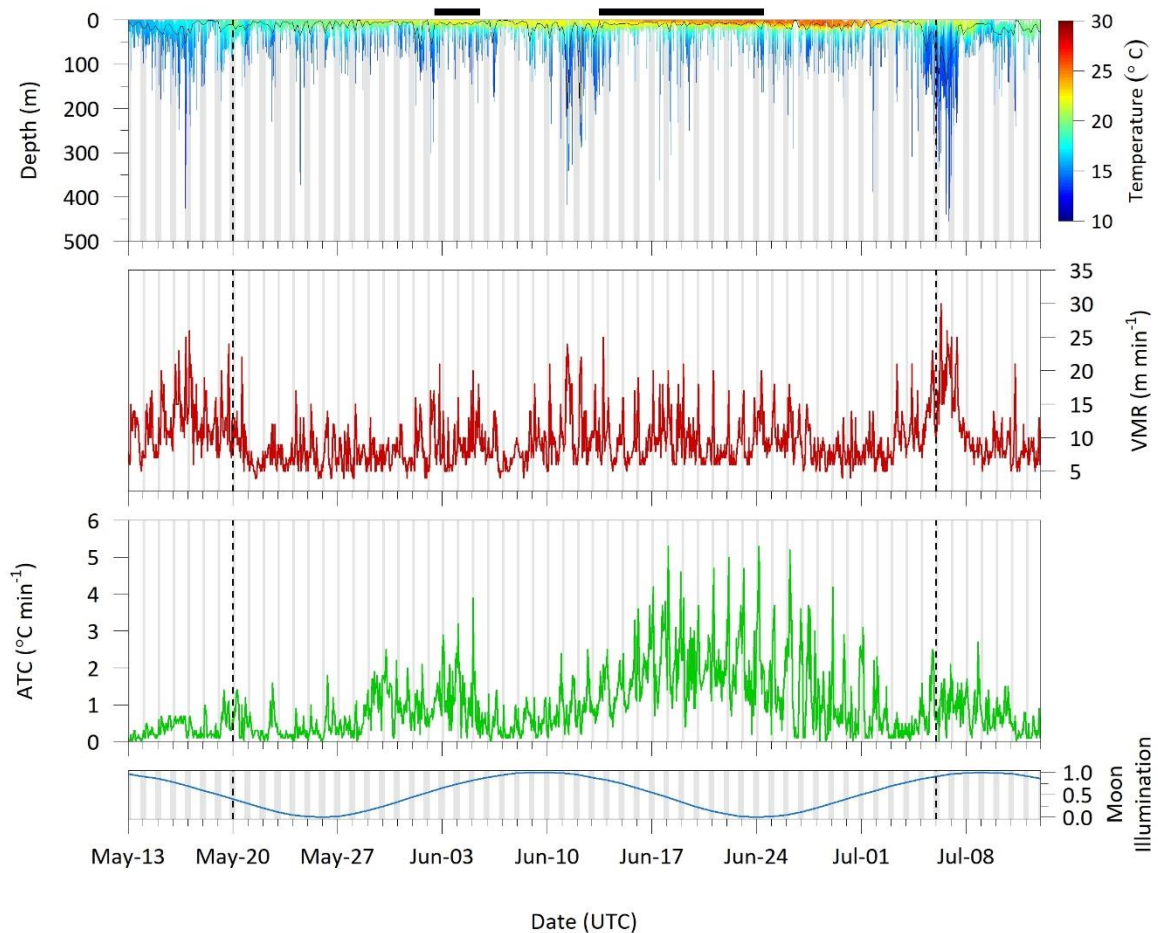


Figure 5a-d. Putative spawning behaviour of an Atlantic bluefin tuna in the Mediterranean Sea. a) Time-series of depth and ambient temperature at 5 second resolution. Black line denotes 4-hourly mean depth and black bar denotes periods when high-frequency shallow diving profiles were observed (see Fig. S8 for individual profiles and classification details), b) time-series of hourly vertical movement rate (VMR), c) time series of the hourly rate of ambient temperature change (ATC), and, d) daily time series of Moon illumination as a fraction. For all plots, vertical dashed lines represent date of entry and exit from the Mediterranean Sea. Grey shaded boxes in a) and d) represent full night-time periods and in b) and c) the period 00:00 – 04:00, the putative spawning time.