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## Association dynamics of tuna and purse seine bycatch species with drifting fish aggregating devices (FADs) in the tropical eastern Atlantic Ocean

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### Abstract :

Several pelagic fish species are known to regularly associate with floating objects in the open ocean, including commercially valuable species. The tuna purse seine industry takes advantage of this associative behavior and has been increasingly deploying free-drifting man-made floating objects, also known as fish aggregating devices (FADs). Using passive acoustic telemetry, this study describes the associative dynamics of the main targeted tropical tuna species (*Thunnus albacares*, *T. obesus* and *Katsuwonus pelamis*), as well as three major bycatch species, silky shark (*Carcharhinus falciformis*), rainbow runner (*Elagatis bipinnulata*) and oceanic triggerfish (*Canthidermis maculata*). Short-term excursions away from the FADs were frequently performed by all tuna species as well by silky sharks. These excursions were characterized by a marked diel pattern, mainly occurring during nighttime. Rainbow runners and oceanic triggerfish were much more present at the FADs and rarely performed excursions. Average continuous residence times (CRTs) ranged from 6 days, for silky shark, up to 25 days for bigeye tuna. Similar to silky shark, average CRTs for skipjack tuna and oceanic triggerfish were less than 10 days. For yellowfin tuna and rainbow runner, CRTs averaged 19 and 16 days, respectively. Bigeye and yellowfin tuna remained associated to a single drifting FAD for a record of 55 days and 607 km traveled.

**Keywords :** Behavior, Acoustic telemetry, Residence time, Floating objects, Pelagic fish, Tropical tuna

## 38 **1. Introduction**

39 Several pelagic fish species are known to regularly associate with floating objects in  
40 the open ocean (Lezama-Ochoa et al., 2018; Taquet et al., 2007). Commercially  
41 valuable species, such as tropical tunas, are among the most abundant species found  
42 around floating objects. The tuna purse seine industry takes advantage of this  
43 associative behavior, and has been increasingly deploying free-drifting man-made  
44 floating objects, also called drifting fish aggregating devices (dFADs), as a fishing  
45 strategy. This practice started in the early 1980's and, since the mid 2000's, its  
46 increase has been substantial (Fonteneau et al., 2013, 2000; Hall and Roman, 2013).

47 It is difficult to quantify how many drifting FADs have been deployed over the  
48 years (Dagorn et al., 2013a; Maufroy et al., 2015). A rough estimate suggests that the  
49 numbers could range from 50,000 up to 100,000 deployed worldwide every year  
50 (Baske et al., 2012). Furthermore, FAD fishing has undergone major technological  
51 improvements that have significantly increased their fishing power and efficiency.  
52 FADs are now equipped with echo sounder buoys that remotely provide biomass  
53 estimates, as well as their geographical position (Lopez et al., 2014). FADs are  
54 currently a key issue in tuna fisheries management (Davies et al., 2014; ICCAT Rec.  
55 16-02<sup>1</sup>; IOTC Res. 19-02<sup>2</sup>) and, to assure its sustainable use, it is imperative to  
56 understand the associative dynamics of tunas and other species vulnerable to this  
57 fishery.

58 Besides increasing fishing pressure, the effects of the substantial growth on FAD  
59 density could lead to an ecologically negative impact on the populations of associated  
60 species. The ecological trap hypothesis, for example, suggests that a strong  
61 associative behavior could potentially 'trap' individuals in unproductive zones that  
62 have a high density of FADs (Hallier and Gaertner, 2008; Marsac et al., 2000). It is  
63 still unknown whether FADs could act as ecological traps or disrupt the biology of the  
64 associated species in another way (Dagorn et al., 2013b). However, measuring the  
65 amount of time fish species spend in FAD-associated and unassociated states is a key  
66 factor to begin to understand these potential impacts.

67 The amount of time a fish tends to remain in FAD-associated and non-associated  
68 states can also be used to model the dynamics of fish abundance and thus provide  
69 fishery-independent abundance indices (Capello et al., 2016). Electronic tagging  
70 studies have successfully measured the residence and absence times of tropical tunas  
71 and other species associated with drifting and anchored FADs, although most of the  
72 studies have been conducted on anchored FADs (Dagorn et al., 2007b, 2007a;  
73 Filmalter et al., 2015; Govinden et al., 2013; Matsumoto et al., 2016, 2014; Mitsunaga  
74 et al., 2012; Ohta and Kakuma, 2005; Robert et al., 2013; Rodriguez-Tress et al.,  
75 2017; Schaefer and Fuller, 2013, 2010). Nonetheless, all of these studies were  
76 conducted in the Pacific and Indian Oceans, and the dynamics of FAD-associated  
77 species in Atlantic are yet to be described.

78 Using passive acoustic telemetry, this study aims to describe the associative  
79 dynamics of the main tropical tuna species (*Thunnus albacares*, *T. obesus* and  
80 *Katsuwonus pelamis*), as well as three key bycatch species, silky shark (*Carcharhinus*  
81 *falciformis*), rainbow runner (*Elagatis bipinnulata*) and oceanic triggerfish  
82 (*Canthidermis maculata*). These bycatch species were chosen because they are among  
83 the most frequently and abundantly caught by the purse seine fishery, and in the case

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<sup>1</sup> Recommendation by The International Commission for the Conservation of Atlantic Tunas (ICCAT) to establish an ad hoc Working group on FADs.

<sup>2</sup> Resolution by the Indian Ocean Tuna Commission (IOTC) to establish procedures on a FAD management plan.

84 of silky sharks, because of the concerns surrounding the impact of the fishery on their  
85 population (Amandè et al., 2010; Lezama-Ochoa et al., 2018; Rigby et al., 2017;  
86 Torres-Irineo et al., 2014). The primary objective of the study was to quantify  
87 residence and absence times around drifting FADs in the eastern Atlantic Ocean at a  
88 small and a large temporal scale. These metrics will serve as essential scientific  
89 knowledge for future modeling studies aiming to investigate the effects of FADs on  
90 the ecology of tuna and non-tuna species as well as potentially deriving local indices  
91 of abundance (Capello et al., 2016).

## 92 **2. Material and methods**

### 93 *2.1. Data collection*

94 During a research cruise carried out in October 2015, four drifting FADs, located off  
95 the coast of Guinea (Fig.1), were equipped with Vemco VR4-Global satellite-linked  
96 acoustic receivers (VEMCO, a division of Amarix Ltd., Canada). These receivers  
97 remotely relay the acoustic detection logs on a daily basis using the Iridium satellite  
98 system. The FADs were selected based on the presence and abundance of tuna and  
99 bycatch species. After the FADs were equipped with the acoustic receivers, fishing  
100 operations were conducted to catch and tag the fish, using rod and reel or hand line.  
101 Tagging activities were conducted within a short period of time, between 7-16  
102 October 2015, and limited to two tagging days at each FAD.

103 Once captured, each fish was carefully brought onboard in a scoop net and placed  
104 in a V-shaped tagging cradle where a hose supplying seawater was inserted into the  
105 buccal cavity to oxygenate the gills. Through a small surgical incision, a Vemco  
106 coded acoustic tag (120seconds nominal delay, 69kHz, 1H) was inserted in the  
107 peritoneal cavity of the fish. Pressure sensitive tags V9P and V13P were used  
108 depending on the size and species of fish. All tagged fish were released within close  
109 proximity (300 m) of the FAD and VR4 of capture.

110 To be considered present at a FAD, the tagged fish must be within the detection  
111 range of the receiver. According to the manufacturer, the theoretical detection range  
112 of VR4 receivers vary from 550 to 682 meters for V13P tags and from 500 to 627 for  
113 V9P. Comparable detection ranges have been estimated in open ocean experiments  
114 conducted at drifting FADs (Schaefer and Fuller, 2013). The receiver cannot decode  
115 the simultaneous emissions of two or more tags due to acoustic collisions and this  
116 issue can impact the detection rate. The emission delay of the tags (nominal delay:  
117 120 seconds) was thus optimized to minimize acoustic collisions and their impact on  
118 the detection rates (Forget et al., 2015).

### 119 *2.2. Data analysis*

120 The association of pelagic species with drifting FADs was studied based on the  
121 concept of continuous residence times (CRTs) and continuous absence times (CATs).  
122 The CRT is defined as the amount of time during which a tagged fish is continuously  
123 detected by the receiver without absences of a pre-determined duration (Capello et al.,  
124 2015). Conversely, the CAT is defined as the period of time between two consecutive  
125 CRTs. The total residence time (TRT) is the period of time between the first and last  
126 detections, including absence periods, i.e. the sum of all CRTs and CATs. Fine-scale  
127 residence and absence times (FCRTs and FCATs) were calculated by considering  
128 absence periods of at least 1 hour to evaluate the fine-scale associative behavior  
129 (Capello et al., 2015; Govinden et al., 2013). For the long-term associative behavior,  
130 the CRTs and CATs were calculated using absence periods of at least 24 hours (Ohta  
131 and Kakuma, 2005). In this latter case, solely acoustic telemetry experiments lasting a

132 minimum of 30 days were considered. For these long-lasting experiments, the total  
133 drifting distance of each FAD was calculated by the cumulative sum of the distance  
134 between every consecutive point of the FAD's transmitted track. FAD's position is  
135 transmitted daily.

136 Following the methodology described in Capello et al. (2015), survival curves  
137 based on residence and absence times were computed for each species. These survival  
138 curves provide the probability of a CRT or CAT to be interrupted at a certain time,  
139 and they can be used to identify similarities between the associative dynamics of the  
140 various species. The survival curves were compared using the logrank statistical  
141 test (Harrington and Fleming, 1982), using the "survdiff" function of the "survival"  
142 package in R (Therneau, 2015).

143 For the long-term association dynamics, the survival curves of CRT and CAT  
144 were fitted with three models (single exponential, double exponential and power law)  
145 to define which biological process best described the data (Robert et al., 2013). The  
146 exponential models describe the association dynamics considering that the probability  
147 of a fish joining or leaving a FAD is independent of the time it remained associated or  
148 unassociated. Alternatively, the power law model implies a dependence on the time  
149 spent associated/unassociated. The double exponential model also indicates that two  
150 time-scales of associative behavior are occurring. The best-fitting models were chosen  
151 based on the Akaike Information Criterion (AIC) and quantile-quantile plots (Q-Q  
152 plots).

153 The FCRT and FCAT data were used to assess whether the short excursions  
154 performed by the tagged fish began or ended at regular times. Thus, the relative  
155 frequencies of departures and arrivals were calculated for each hour of the 24-hour  
156 cycle. The time data are expressed in GMT, which also corresponds to local times. As  
157 a reference point, sunset times were estimated based on the NOAA Solar Calculator  
158 (<https://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html>). To test if departures and  
159 arrivals were uniformly distributed throughout the day, Rao's spacing tests were  
160 performed using the "circular" package in R (Agostinelli and Lund, 2013). All  
161 statistical analyses were performed with a 0.05 significance level using the statistical  
162 computing software R (R Core Team, 2013).

### 163 **3. Results**

164 A total of 107 fish were tagged, consisting of 23 bigeye, 20 yellowfin and 7 skipjack  
165 tunas and 18 silky sharks, 19 rainbow runner and 20 oceanic triggerfish (Table 1).  
166 Only 1 bigeye tuna, 7 silky sharks and 2 oceanic triggerfish were never detected by  
167 the receivers. All fish were exclusively detected at the FAD of release. All four  
168 experiments were interrupted due to equipment malfunctions before all fish had left  
169 the FAD. The duration of each experiment ranged from 3 to 55 days (Fig.1).

#### 170 *3.1. Fine-scale association dynamics*

171 The FCRTs for bigeye, yellowfin and skipjack tuna averaged 18.82, 24.11 and 24.74  
172 hours respectively (Table 2). Rainbow runner and triggerfish had considerably higher  
173 average values of 98.81 and 80.40 hours respectively, whereas silky sharks produced  
174 the lowest average of 8.91 hours (Table 2). An overview of the FCRTs recorded for  
175 all species at each drifting FAD is shown on Fig.2. The survival curves constructed  
176 from the FCRTs evidenced the behavioral similarities between rainbow runners and  
177 triggerfish (logrank test,  $p=0.624$ ), as well as between all tuna species (logrank test,  
178  $p=0.66$ ) (Fig.3b). For the silky shark, the survival curve of FCRTs differed  
179 significantly from the other species (logrank test,  $p<0.05$ ) and decreased more rapidly,

180 indicating shorter fine-scale residence times in line with the trends observed for the  
181 mean FCRT (Table 2).

182 Considering small-scale absence times (FCAT), all species made excursions away  
183 from the FADs, but the frequency and duration of these excursions varied among  
184 species (Fig.2). The three tuna species exhibited a similar pattern, with frequent  
185 excursions lasting less than 3 hours on average (Table 2). Silky sharks frequently  
186 performed excursions as well, but they tended to last twice as long, averaging  
187 approximately 6 hours (Table 2). Conversely, rainbow runners and oceanic triggerfish  
188 were much more present at the FADs, in line with the high FCRT averages, and rarely  
189 performed excursions (Fig.2). The duration of the few excursions performed by these  
190 two bycatch species was relatively short, between 1 and 3 hours, with the exception of  
191 one rainbow runner that was away from the FAD for approximately 315 hours (Fig.2).  
192 The survival curves constructed using the calculated FCATs followed the same  
193 pattern described for the survival curves of FCRTs (Fig.3b), evidencing the  
194 similarities between rainbow runners and triggerfish (logrank test,  $p=0.76$ ) and  
195 between tuna species (logrank test,  $p=0.76$ ), as well as the differences between silky  
196 sharks and all the other species (logrank test,  $p<0.05$ ).

197 The time at which excursions were performed showed a clear difference between  
198 tunas and bycatch species. For the tuna species, the majority of the excursions began  
199 during the late afternoon, between 16:00h and 17:00h (Fig.4a). By 22:00h most of  
200 tunas were back at the FAD (Fig.5a). Similar to the tuna species, the majority of silky  
201 shark excursions began between 17:00h and 18:00h, although departures during the  
202 day were not uncommon (Fig.4b). For the other two bycatch species the departure  
203 times were not concentrated in any specific hour of the day, but occurred more  
204 frequently during daytime. For silky sharks the end of the excursions occurred mostly  
205 during the nighttime with a peak at 01:00h, while for rainbow runners and triggerfish,  
206 arrivals mainly occurred during the day (Fig.5b). The Rao's spacing tests confirmed  
207 that the frequency of departures and arrivals was not uniformly distributed throughout  
208 the day for all species ( $p<0.05$ ). For the duration of the experiments, local sunset  
209 times varied from 17:10h to 17:35h.

### 210 *3.2. Large-scale association dynamics*

211 Two experiments, FAD 92 and FAD 96, lasted more than 30 days (Fig.2) and were  
212 thus included in the large-scale analyses. On average, longer residence times were  
213 observed for bigeye and yellowfin tunas and rainbow runners, while shorter CRTs  
214 were observed for silky shark, skipjack tuna and oceanic triggerfish (Table 3). These  
215 mean values, however, are associated with high standard deviations, especially for  
216 bigeye and yellowfin tuna (Table 3). Only three individuals performed excursions  
217 away from the FADs that lasted 24 hours or more, and only 6 continuous absence  
218 times (CATs) were calculated: 1 for bigeye tuna 1 for rainbow runner and 4 for silky  
219 shark (Table 3). This means that, for most cases, long-scale CRTs were equivalent to  
220 total residence times (TRTs). The longest CAT was recorded for one rainbow runner  
221 that stayed away from the FAD for 13 days. The CAT recorded for bigeye tuna lasted  
222 1 day, whereas silky shark's absence times varied from 1 to 3 days (Table 3). The  
223 recorded CATs from silky shark were all from the same individual and the first one  
224 occurred shortly after tagging, lasting almost 2 days.

225 The longest total association periods (maximum TRTs) were recorded for bigeye  
226 and yellowfin tuna at 55 days, which corresponded to the duration of the experiment  
227 on FAD 92. Considering this association period, these tunas followed the FAD for at  
228 least 607 km (Fig.6). Unlike the other tuna species, skipjack exhibited the shortest

229 maximum TRT at 15 days and 104 km traveled. For the bycatch species, maximum  
230 TRT and corresponding traveled distance were 28 days and 229 km for silky shark, 41  
231 days and 363 km for rainbow runner and 33 days and 273 km for triggerfish (Fig.6).

232 With the exception of skipjack tuna and rainbow runner, for which the only  
233 converging model was the single exponential, the double exponential was consistently  
234 the best fit based on both Q-Q plots and AICs (Table 4; Figs 7 and 8). The double  
235 exponential describes two modes of residence times, characterized by short  
236 association periods and long association periods (L1 and L2 in Table 4). However, for  
237 the species in which this model converged, the p-value corresponding to the L1  
238 parameter was not significant. The obtained parameters indicate long associations of  
239 50 days (1/L2) for bigeye tuna and long associations of 33.33 days for yellowfin tuna.  
240 In contrast, the parameter obtained for skipjack tuna from the single exponential fit  
241 characterized residence times of only 9.09 days (1/L).

242 Regarding bycatch species, the model parameters indicated that they remained  
243 associated with FADs for shorter periods of time compared to bigeye and yellowfin  
244 tunas. The periods of long associations characterized by the longer timescale of  
245 double exponential fits (1/L2) for silky shark and oceanic triggerfish were similar to  
246 the residence times observed for skipjack tuna, varying respectively from 6.67 to 9.09  
247 days (Table 4). As mentioned above, the periods of short associations (1/L1) were not  
248 significantly different from zero. For rainbow runner, the single exponential fit  
249 characterized residence times (1/L) of 16.67 days, however, this fit did not perform  
250 well based on the Q-Q plot (Fig.8).

## 251 **4. Discussion**

### 252 *4.1. Fine-scale association dynamics*

253 The analyses on the fine-scale associative dynamics showed distinct behavioral  
254 patterns among the three groups of species; 1) tunas, 2) silky shark, and 3) rainbow  
255 runner and oceanic triggerfish. The behavior of the tuna species resulted in very  
256 similar survival curves, with average FCRTs ranging from 18 to 24 hours. Excursions  
257 away from the FAD were frequently observed. These excursions usually lasted less  
258 than 3 hours and consistently started at late afternoon. This marked pattern of pre-  
259 sunset excursions has been previously reported for yellowfin and bigeye tuna  
260 associated with anchored FADs off Okinawa Islands (Ohta and Kakuma, 2005). As  
261 observed here, the authors of the Okinawa study found that both species performed  
262 excursions away from the FADs with high temporal regularity, mainly leaving at  
263 17:00h and returning before 22:00h. In turn, yellowfin and skipjack tuna associated  
264 with anchored FADs in the Maldives did not exhibit temporal patterns in their  
265 excursions (Govinden et al., 2013). The authors of the Maldivian study hypothesized  
266 that the lack of patterns in the excursions may imply that tuna do not rely on regular  
267 environmental cues when deciding to move away from a FAD (Govinden et al., 2013).  
268 However, the results obtained in the Maldivian study appear to be atypical. In the  
269 Indian and Pacific oceans, skipjack, yellowfin, and bigeye tuna displayed a diel  
270 pattern, and were generally found to be more closely associated with drifting FADs  
271 during the day than during the night (Forget et al., 2015; Matsumoto et al., 2014;  
272 Schaefer and Fuller, 2013). These findings suggest that tunas tend to perform  
273 excursions away from the FADs during nighttime, as observed in the Okinawa (Ohta  
274 and Kakuma, 2005) and present studies. This is an interesting result given that the  
275 Okinawa study was conducted on anchored FADs and the current study on drifting  
276 FADs.

277 The survival curves of FCRTs for silky sharks differed significantly different from  
278 the other species, and its average FCRT of 8.91 hours was the lowest. However,  
279 similar to tuna species, silky sharks frequently performed excursions away from the  
280 FADs, although they tended to last twice as long. Interestingly, the majority of silky  
281 shark excursions also occurred during the night, starting just after the tunas (between  
282 17:00h and 18:00h) and finishing at around 1:00h. In the Indian Ocean, silky sharks  
283 associated with drifting FADs displayed the same behavior, with nearly all excursions  
284 starting after dark and ending before sunrise (Filmlalter et al., 2015). Furthermore, the  
285 similarity between tunas and silky sharks observed in the present study are also  
286 present in the Indian Ocean (Filmlalter et al., 2015; Forget et al., 2015). The authors of  
287 these studies also observed a time lag between the departures of tunas and sharks,  
288 with the sharks typically leaving a few hours after the tunas. The similarity in the  
289 findings of the Atlantic (present study) and Indian Ocean studies further endorses the  
290 occurrence of a marked diel pattern on the behavioral modes of silky sharks and tuna  
291 species.

292 The nightly excursions away from the FADs performed by bigeye, yellowfin,  
293 skipjack tuna and silky sharks are most probably driven by foraging behavior. This  
294 hypothesis has been proposed by numerous studies (Filmlalter et al., 2015; Forget et  
295 al., 2015; Matsumoto et al., 2014; Ohta and Kakuma, 2005; Schaefer and Fuller, 2013,  
296 2005). Filmlalter et al. (2015) also added that the temporal precision in departures  
297 (during or just after sunset) might indicate that a change in luminosity is a major  
298 stimulus for the species to shift their behavioral mode, which seems plausible. During  
299 the night, forage fauna within the deep scattering layer (DSL) migrate vertically to  
300 shallow depths, where pelagic predators such as sharks, tunas and billfishes, are  
301 known to feed (Bernal et al., 2009; Dagorn et al., 2000). It is not likely a coincidence  
302 that these pelagic predators move away from the FADs at the same time the DSL  
303 migration is occurring. Additionally, Filmlalter et al. (2017) found that a large portion  
304 (30-40%) of the silky shark diet in the Indian Ocean consisted of the vertically  
305 migrating swimming crab *Charybdis smithii*, lending further weight to the nocturnal  
306 feeding argument.

307 Rainbow runners and oceanic triggerfish remained more closely associated to the  
308 FADs than the other species, with FCRTs averaging approximately 98 hours for  
309 rainbow runner and 80 hours for triggerfish. Indeed, these two species rarely  
310 performed excursions. The few observed excursions mainly occurred during daytime  
311 and were relatively short, lasting from 1 to 3 hours. In the Indian Ocean, rainbow  
312 runners and triggerfish were found to be more closely associated with drifting FADs  
313 during the night (Forget et al., 2015). The results of the cited research suggest that  
314 both species perform excursions mostly during the day, corroborating the findings of  
315 the present study. Although opposite to the behavioral pattern observed for silky shark  
316 and tuna species, these diurnal excursions could still be motivated by foraging.  
317 Studies on stomach contents of tunas have suggested that FADs are not rich in food  
318 due to the high proportion of empty stomachs observed (Jaquemet et al., 2011;  
319 Marsac et al., 2000). For other species that are usually less numerous at FADs,  
320 different feeding patterns have been observed. Taquet (2004) and Filmlalter et al.  
321 (2017), for instance, found that dolphin fish (*Coryphaena hippurus*) and silky sharks  
322 find more than half of their prey while associated to FADs. Despite their different  
323 results, all of these studies indicate that prey present at FADs are usually insufficient  
324 to fulfill predators needs. If this is the case, associated species would need to regularly  
325 move away from the FAD to feed. The time at which feeding excursions would occur  
326 could be a matter of strategy. In the case of rainbow runners and triggerfish daytime



327 seems to be the preferred period. During the night, when large predators are feeding,  
328 the FAD might serve as a shelter enabling these two species to reduce predation.

329 With the exception of silky shark, most of the tagged fish were detected by the  
330 receivers, although some exhibited immediate excursions. This suggests that the stress  
331 associated with tagging operations was minor and did not significantly impact the  
332 fish's associative behavior as measured by temporal statistical units (FCRT and CRT).  
333 Previous studies, using surgical incision, also concluded that handling and tagging did  
334 not appear to impact associative behavior (Dagorn et al., 2007b; Holland, 1990;  
335 Matsumoto et al., 2014, 2013; Musyl et al., 2003). However, for juvenile silky shark,  
336 the effects of capture, handling and tagging seams to be significant (Filmlalter et al.,  
337 2015, 2011). The authors described that the behavioral response to tagging occurred  
338 within the first 24 hours after release and resulted in immediate excursions, with a few  
339 sharks never being detected by the receivers. The silky sharks tagged in the present  
340 study displayed the same behavioral response. Nevertheless, it is important to note  
341 that the results presented here are not significantly impacted by the tagging effect.  
342 The measurements of residence times only start after the first consecutive detections,  
343 and not after tagging.

#### 344 *4.2. Large-scale association dynamics*

345 The majority of monitored individuals remained continuously at the FADs without  
346 performing day-scale excursions (CATs). Consequently, long-scale CRTs were often  
347 equivalent to total residence times (TRTs). Bigeye and yellowfin tuna exhibited the  
348 longest TRTs, totaling 55 days. It is important to note that these TRTs were truncated  
349 because experiments ended prematurely due to equipment failure. Therefore, the  
350 maximum TRT of 55 days is likely underestimated. In any case, the values observed  
351 here for yellowfin and bigeye tuna are comparable to what was observed in other  
352 studies on anchored FADs (Dagorn et al., 2007a; Ohta and Kakuma, 2005;  
353 Rodriguez-Tress et al., 2017), but were never observed for drifting FADs (Dagorn et  
354 al., 2007b; Matsumoto et al., 2016; Schaefer and Fuller, 2010). It is also worth noting  
355 that these previously reported TRTs were calculated at the scale of an array of  
356 anchored FADs and not on a single drifting FAD, as in our study. Skipjack tuna did  
357 not remain associated with the FADs for such long periods and the maximum  
358 observed TRT for this species was 15 days. Most studies have observed that skipjack  
359 tuna generally associate with FADs for shorter periods of time, with reported  
360 maximum TRTs varying from 6.4 to 12.8 days (Govinden et al., 2013; Matsumoto et  
361 al., 2016, 2014). As an exception to this general finding, a skipjack tuna remained  
362 associated for a record of 40.9 days at an array of anchored FADs in Mauritius  
363 (Rodriguez-Tress et al., 2017). For the bycatch species, the maximum observed TRTs  
364 were 28 days for silky sharks, 41 days for rainbow runner and 32 days for triggerfish.  
365 Filmlalter et al. (2015) reported a comparable TRT of 30 days for silky shark in the  
366 Indian Ocean, while Forget (2016) reported much longer TRTs for both rainbow  
367 runner (85 days) and oceanic triggerfish (66 days).

368 Furthermore, our study shows that during the 55 days associated to the same FAD,  
369 these yellowfin and bigeye tuna travelled about 600 km when the experiment was  
370 prematurely ended due to equipment failure. The other species did not remain  
371 associated for so long and over such distances with a same FAD. These long  
372 association periods and travelled distances exhibited by yellowfin and bigeye tuna can  
373 lead to interrogations concerning the possibility of an ecological trap, as suggested by  
374 some authors (Dagorn et al., 2013b; Hallier and Gaertner, 2008; Marsac et al., 2000).  
375 This hypothesis states that tunas could be “trapped” by drifting FADs and

376 consequently be entrained to areas that could be less favorable to their biology. Until  
377 this study, the TRTs measured at single drifting FADs for tunas were relatively short  
378 (a few days), suggesting that if an ecological trap were to happen, it would have to be  
379 at the scale of large clusters of floating objects, and not at single floating objects. The  
380 long TRT and traveled distance measured for yellowfin and bigeye tuna clearly show  
381 a strong residence of these individuals to the FAD. However, without information on  
382 their physiological condition and a proxy for habitat quality, in particular in terms of  
383 prey availability, it is difficult to ascertain if such prolonged associations could have  
384 negatively impacted their biology. Dedicated studies with simultaneous observations  
385 of local habitat conditions and physiology are required to determine whether the  
386 seeding of thousands of drifting FADs can impact the biology of tuna. Nonetheless,  
387 observation tools required for such challenging investigations have not yet been  
388 developed, but technological innovation should allow scientists to address this issue  
389 in the near future.

390 The exponential models (double and single) were the best to describe the long-  
391 term association dynamics of all six species. Exponential survival models reflect the  
392 properties of a memoryless process, in which the likelihood of something happening  
393 in the future has no relation to what has happened in the past (Aczél, 1966). This  
394 implies that the probability of these species to leave a FAD does not depend on the  
395 time they have spent associated with the FAD. The best fit for yellowfin and bigeye  
396 tuna was the double exponential model, indicating that there were two timescales in  
397 the association duration. However, the estimated L1 parameter was not significant for  
398 either species and the presence of this mode on the survival curves appear to be driven  
399 by individuals that left the FAD shortly after being tagged. The long association  
400 timescale estimated by the inverse L2 parameter of the double exponential model (50  
401 days for bigeye and 33 days for yellowfin tuna) is likely to represent a better estimate  
402 of the residence of the two species. These values are considerably higher than the  
403 mean CRTs reported in other studies on drifting FADs, which range from 1.0 to 6.1  
404 days for yellowfin tuna and from 1.4 to 5.1 days for bigeye (Dagorn et al., 2007b;  
405 Matsumoto et al., 2016). On anchored FADs, the reported mean CRTs were higher for  
406 both species, reaching 23.2 days for yellowfin tuna and 7.0 for bigeye (Dagorn et al.,  
407 2007a; Govinden et al., 2013; Mitsunaga et al., 2012; Ohta and Kakuma, 2005;  
408 Robert et al., 2013; Rodriguez-Tress et al., 2017). For skipjack tuna, the single  
409 exponential model described a mean association duration of 9.09 days. This value is  
410 also higher than previously reported CRT means for the species on drifting FADs,  
411 which ranged from 0.2 to 2.4 days (Dagorn et al., 2007b; Matsumoto et al., 2016,  
412 2014). On anchored FADs the highest reported mean for skipjack tuna is 3.5 days  
413 (Govinden et al., 2013; Rodriguez-Tress et al., 2017).

414 The three tuna species displayed considerably longer residence in the Atlantic  
415 Ocean compared to other studies conducted both on anchored and drifting FADs in  
416 the Indian and Pacific Ocean. The substantial difference observed between ocean  
417 basins is difficult to explain because the factors influencing residence times of tunas  
418 around FADs remain unknown. It is conceivable that factors such as physiological  
419 condition, presence of conspecifics, density of predators and prey availability could  
420 have an effect. Residence times could as well be influenced by oceanographic  
421 conditions, albeit Ohta and Kakuma (2005) did not observe any relationship between  
422 tuna CRTs at FADs and abiotic oceanographic conditions. In other words, Ohta and  
423 Kakuma (2005) concluded that the biological environment (prey availability,  
424 predators, and productivity) and the internal state of the individual might be more  
425 influential than the abiotic environmental cues for inducing changes in associative

426 behavior. No other studies have attempted to investigate the effects of biotic or abiotic  
427 factors on the residence of tuna at FADs. As suggested by Dagorn et al. (2007b), the  
428 association dynamics should be considered within the context of the larger  
429 environment in which they occur (abiotic, geographic, biotic).

430 As for the bycatch species, the exponential model estimates indicate that they all  
431 remain associated with FADs for shorter periods of time when compared to bigeye  
432 and yellowfin tuna. This result is quite surprising and does not correspond to what has  
433 been observed on drifting FADs the Indian Ocean (Dagorn et al., 2007b; Filmalter et  
434 al., 2015; Forget, 2016). This could be due to particular conditions for FADs 92 and  
435 96 during the current study, and to the few individuals of these species tagged at these  
436 two FADs. Clearly, more data are here needed to make any conclusions.

## 437 **5. Conclusion**

438 The associative behavioral dynamics of tuna and other FAD associated species, which  
439 are key bycatch species of the tropical tuna purse seine fishery, were characterized for  
440 the first time in the Atlantic Ocean. Indeed, few other studies investigated the  
441 behavior of tuna and bycatch species simultaneously at drifting FADs (e.g., Forget et  
442 al 2015).

443 The diel pattern in the excursions performed by silky sharks and the three tuna  
444 species in the Atlantic Ocean appears to be consistent with what has been described  
445 for the Indian and Pacific oceans. Surprisingly, in the Atlantic Ocean, yellowfin and  
446 bigeye tuna appear to remain associated with drifting FADs for longer periods of time  
447 when compared to the other oceans. Records of association times, up to 55 days and  
448 over 600 km for some individuals, can lead to interrogations concerning the  
449 ecological trap hypothesis. Explaining differences observed between study areas are  
450 difficult, as factors influencing the residence of tuna at FADs remain unknown.  
451 Nonetheless, the longer residence times displayed by these tuna species imply that  
452 they are more vulnerable to FAD fishing in the Atlantic Ocean.

453 FAD densities and species social behavior could play an important role in the  
454 associative dynamics and spatial distribution of tuna (Sempo et al., 2013). FAD  
455 densities and biomass estimations (from echo-sounder buoys) are two additional  
456 variables that will soon be accessible to scientists and will clearly improve the  
457 interpretation of the residence times and absence times of tuna (and other species) at  
458 FADs. More electronic tagging data will also allow independent abundance indices to  
459 be derived (Capello et al., 2016), another challenge for tuna regional fisheries  
460 management organizations, and will contribute to provide sound scientific advice for  
461 sustainable use of drifting FADs.

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633

**Table 1.** Summary of the tagging experiments conducted on drifting FADs off the coast of Guinea in October 2015. NT= number of fish tagged, ND= number of tagged fish that were detected, avg= average size, min= minimum size, max= maximum size. BET= bigeye tuna, YFT= yellowfin tuna, SKJ= skipjack tuna, FAL= silky shark, ELA= rainbow runner and TRI= oceanic triggerfish. Fish sizes are expressed as fork length, except for triggerfish, which is expressed as total length.

	FAD92					FAD94					FAD95					FAD96					TOTAL				
	NT	ND	size (cm)			NT	ND	size (cm)			NT	ND	size (cm)			NT	ND	size (cm)			NT	ND	size (cm)		
			avg	min	max			avg	min	max			avg	min	max			avg	min	max			avg	min	max
BET	7	7	51	49	53	5	5	51	49	58	4	3	60	59	61	7	7	51	45	58	23	22	52	45	61
YFT	5	5	55	35	73	5	5	43	34	72	5	5	72	59	82	5	5	54	44	66	20	20	56	34	82
SKJ	3	3	51	42	61	1	1	47	47	47	-	-	-	-	-	3	3	43	39	46	7	7	47	39	61
FAL	7	3	124	78	143	6	4	120	90	146	2	2	85	84	86	3	2	106	99	120	18	11	116	78	146
ELA	5	5	38	34	41	5	5	33	30	38	5	5	36	33	40	4	4	38	35	40	19	19	36	30	41
TRI	5	4	52	49	54	5	5	55	46	79	5	5	60	45	87	5	4	64	43	115	20	18	58	43	115



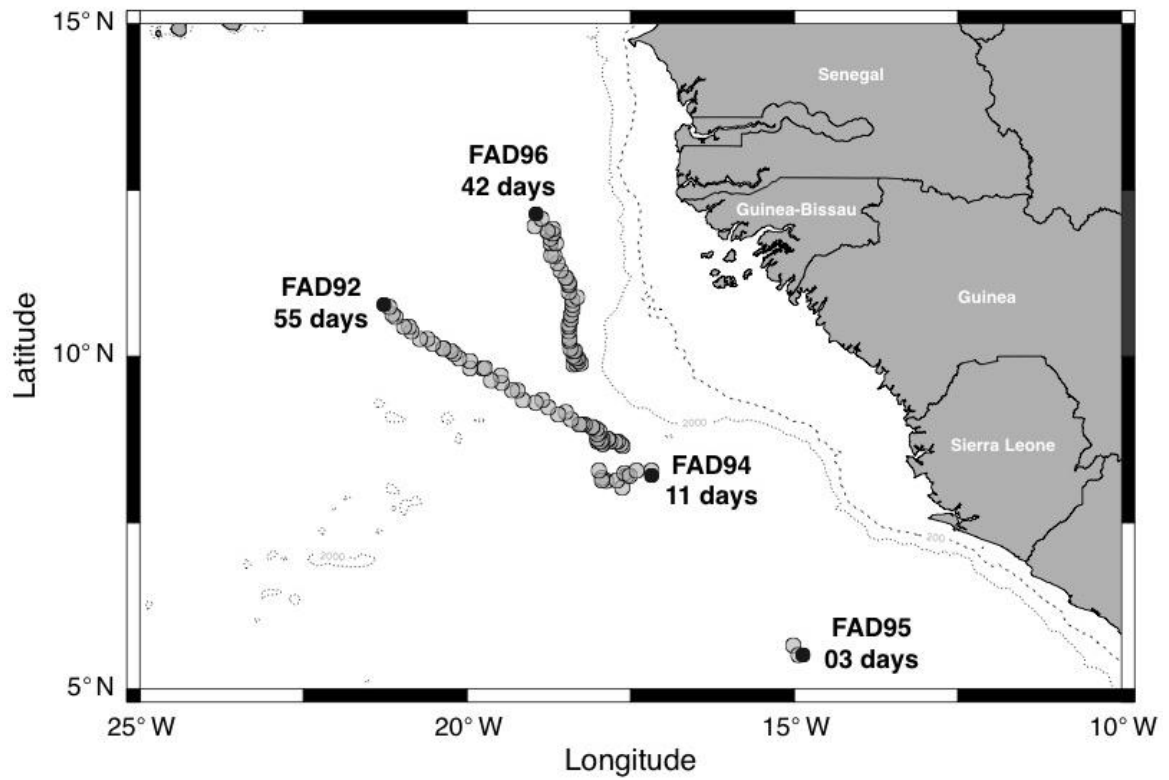
**Table 2.** Summary statistics of fine-scale continuous residence and absence times (FCRTs and FCATs) based on four acoustic telemetry experiments performed on drifting FADs off the coast of Guinea from October to December 2015. BET= bigeye tuna, YFT= yellowfin tuna, SKJ= skipjack tuna, FAL= silky shark, ELA= rainbow runner and TRI= oceanic triggerfish. N= total number of FCRTs/FCATs, Avg N= average number of FCRTs/FCATs per individual, Mean= average FCRT/FCAT duration, Med= median of FCRT/FCAT duration, Min= minimum FCRT/FCAT duration, Max= maximum FCRT/FCAT duration, SD= standard deviation of FCRT/FCAT duration.

	FCRT (time unit = hour)							FCAT (time unit = hour)						
	N	Avg N	Mean	Med	Min	Max	SD	N	Avg N	Mean	Med	Min	Max	SD
BET	447	20.31	18.82	18.4 5	0.04	303.60	24.70	425	22.37	2.79	2.09	1.00	24.16	2.37
YFT	201	10.05	24.74	15.7 5	0.05	370.88	48.29	181	11.38	2.98	1.70	1.00	23.78	3.39
SKJ	42	7.00	24.11	15.5 6	0.17	125.26	29.95	36	7.20	2.55	1.99	1.02	9.71	2.07
FAL	129	11.73	8.91	5.37	0.03	65.58	10.05	118	14.75	6.26	2.18	1.00	119.42	14.18
ELA	51	2.68	98.81	46.4 1	0.05	374.48	113.72	32	3.56	11.17	1.22	1.02	315.49	55.53
TRI	29	1.61	80.40	35.3 0	0.05	376.20	103.10	11	2.2	2.50	1.13	1.01	15.72	4.39

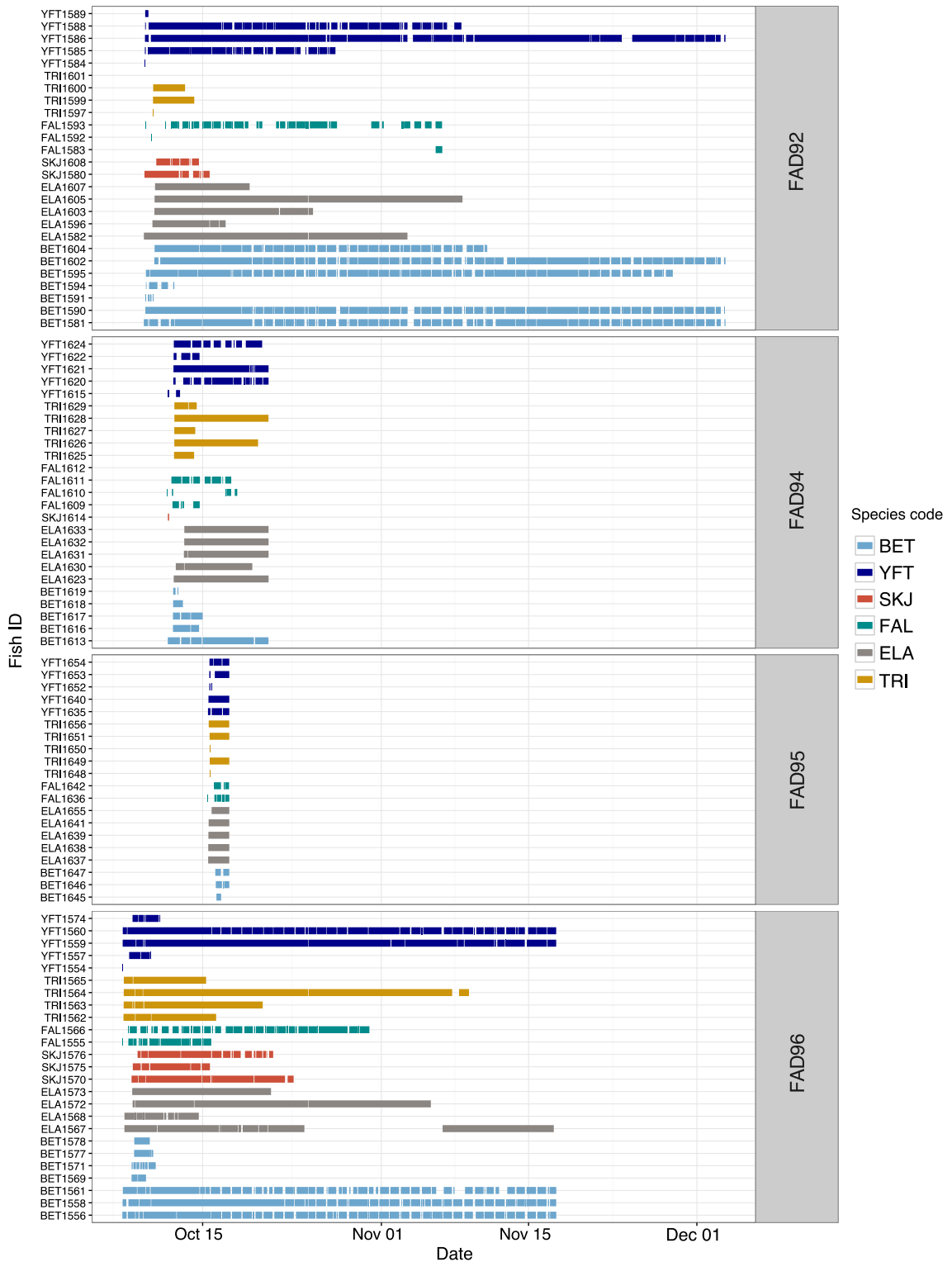
**Table 3.** Summary statistics of long-scale continuous residence and absence times (CRTs and CATs) based on the acoustic telemetry experiments performed on two drifting FADs (FAD92 and FAD96) off the coast of Guinea from October to December 2015. BET= bigeye tuna, YFT= yellowfin tuna, SKJ= skipjack tuna, FAL= silky shark, ELA= rainbow runner and TRI= oceanic triggerfish. N= total number of CRTs/CATs, Mean= average CRT/CAT duration, Med= median of CRT/CAT duration, Min= minimum CRT/CAT duration, Max= maximum CRT/CAT duration, SD= standard deviation of CRT/CAT duration.

	CRT (time unit = day)						CAT (time unit = day)					
	N	Mean	Med	Min	Max	SD	N	Mean	Med	Min	Max	SD
BET	15	25.31	31.54	0.71	55.32	23	1	1.01	1.01	1.01	1.01	-
YFT	10	19.15	10.40	0.02	55.21	21	-	-	-	-	-	-
SKJ	5	9.19	7.34	4.06	15.41	4.8	-	-	-	-	-	-
FAL	9	5.90	3.89	0.01	23.33	7.4	4	2.02	1.76	1.31	3.26	0.85
ELA	10	16.18	14.14	6.97	29.29	8.6	1	13.15	13.15	13.15	13.15	-
TRI	8	8.71	5.87	0.002	32.83	11	-	-	-	-	-	-

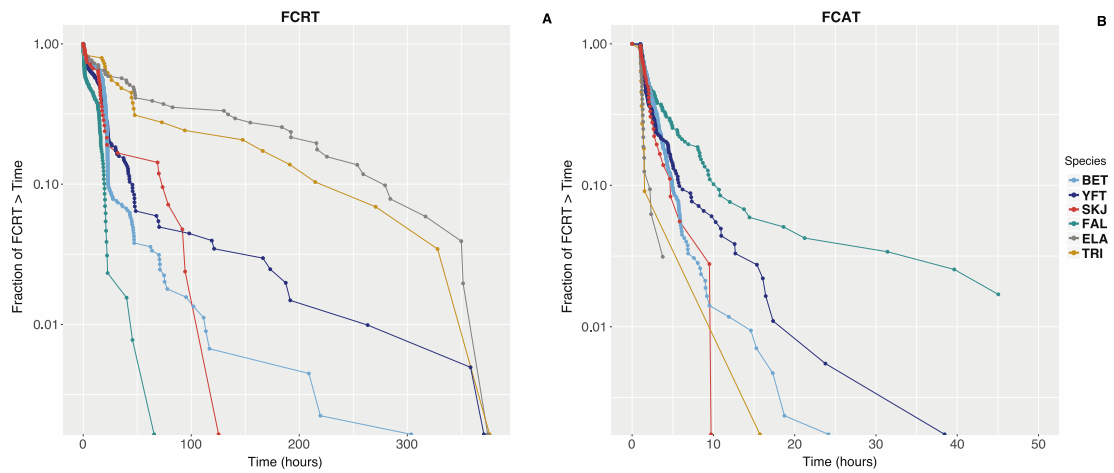




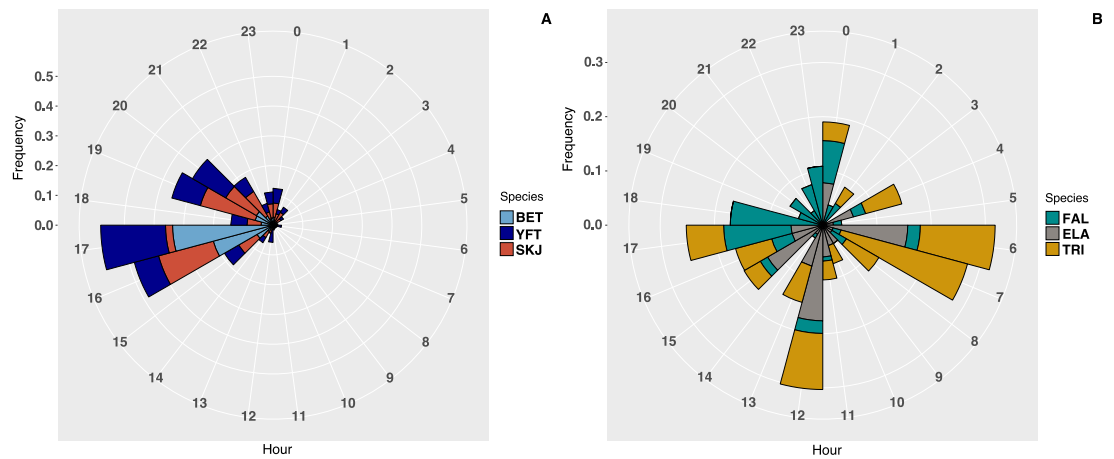
**Figure 1.** FAD drifts and corresponding duration of the acoustic telemetry experiments conducted from October to December 2015 in the eastern Atlantic Ocean. The black circles mark the time and location of equipment failures and the end of the experiments.



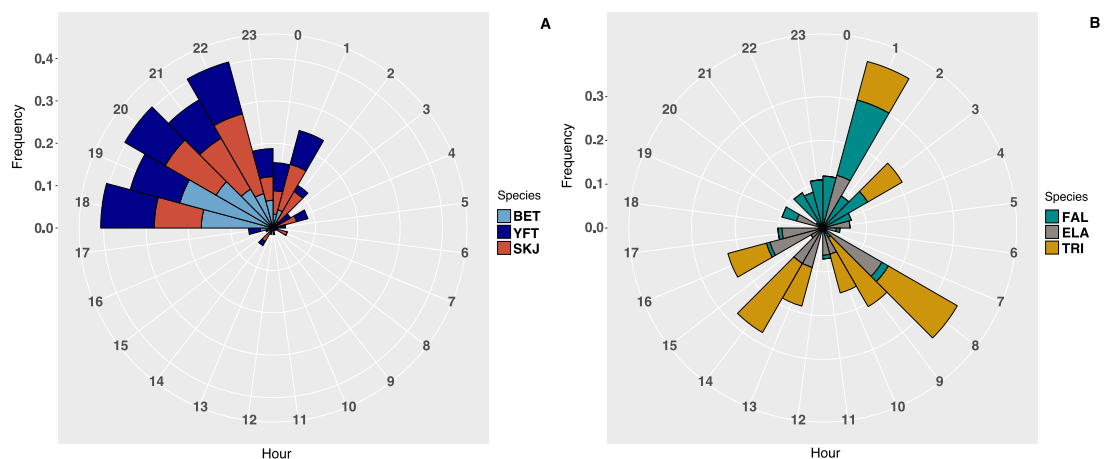
**Figure 2.** Residence times of tuna and bycatch species associated with drifting FADs off the coast of Guinea from October to December 2015. The solid colors represent fine-scale continuous residence times (FCRTs) and blank spaces represent absences of 1 hour or more (FCATs). BET= bigeye tuna, YFT= yellowfin tuna, SKJ= skipjack tuna, FAL= silky shark, ELA= rainbow runner and TRI= oceanic triggerfish.



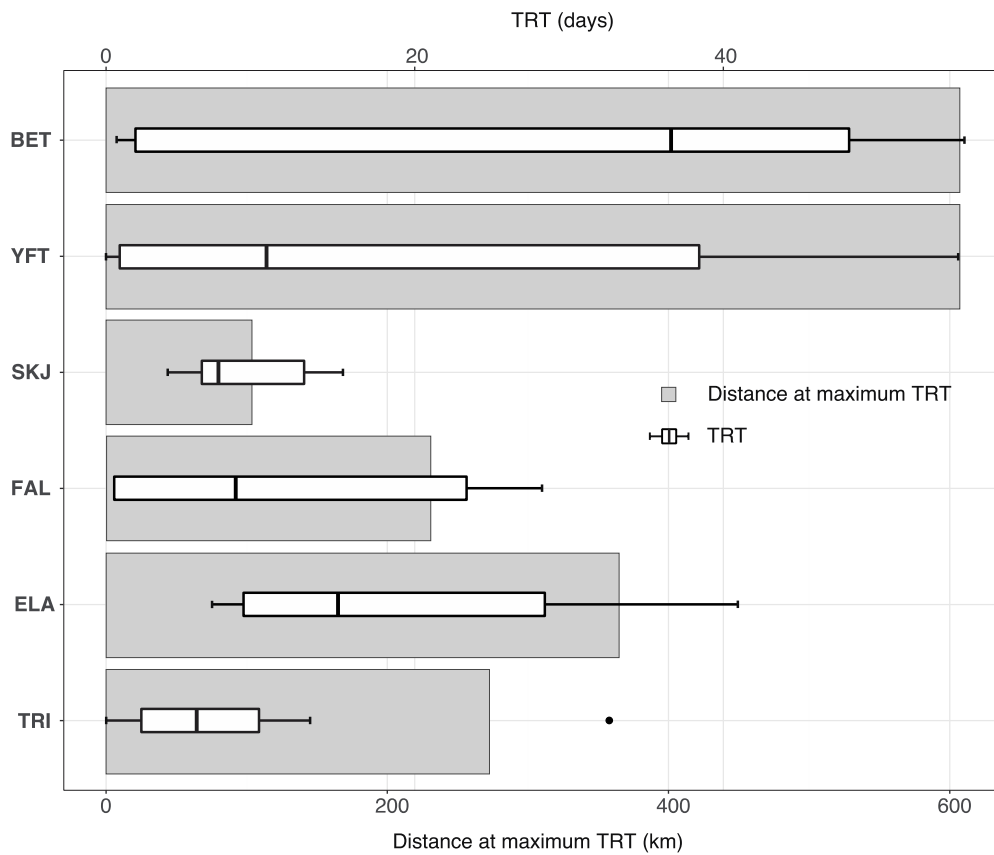
**Figure 3.** Survival curves of fine-scale continuous residence and absence times (FCRTs – panel A and FCATs – panel B) for tunas and bycatch species associated with drifting FADs off the coast of Guinea from October to December 2015. The y-axis is in logarithmic scale.



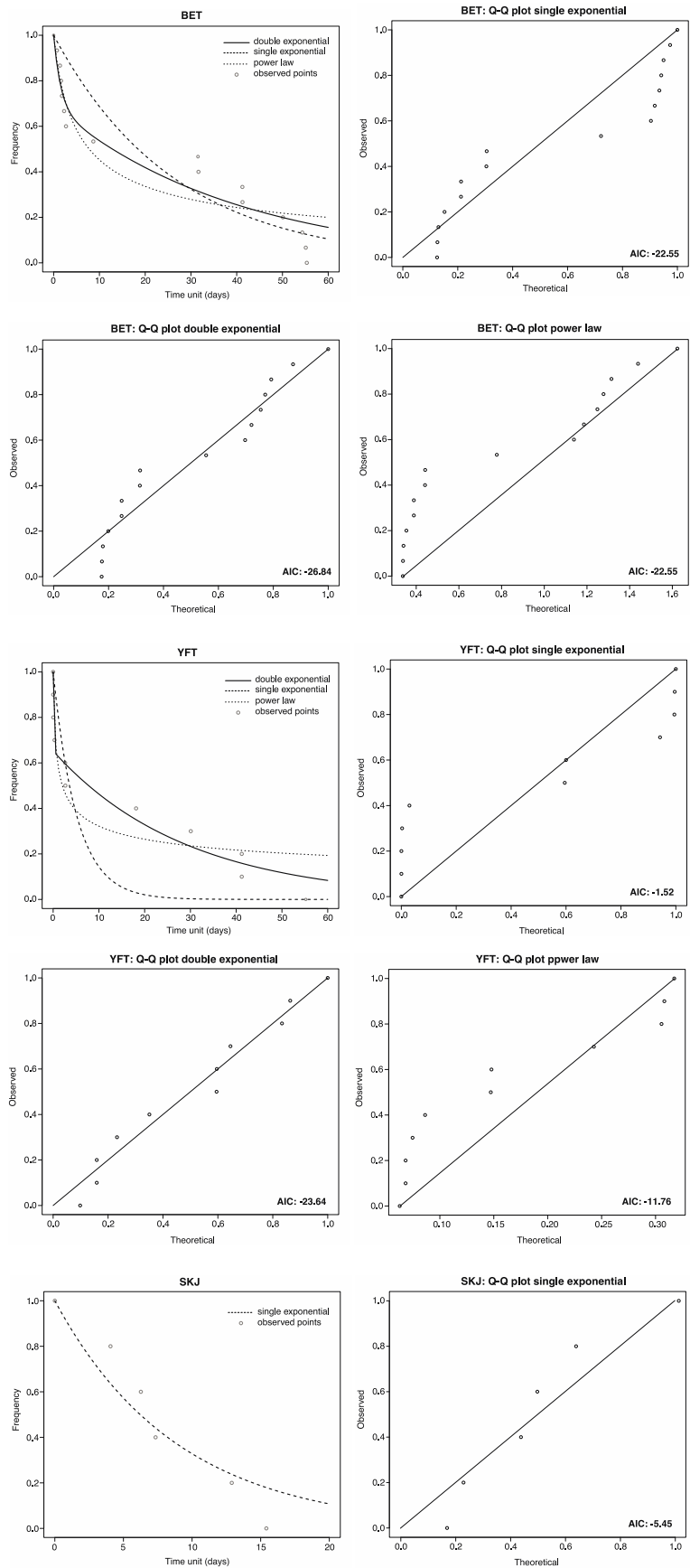
**Figure 4.** Frequency of departures by hour of the day of tunas (panel A) and bycatch species (panel B) associated with drifting FADs off the coast of Guinea from October to December 2015.



**Figure 5.** Frequency of arrivals by hour of the day of tunas (panel A) and bycatch species (panel B) associated with drifting FADs off the coast of Guinea from October to December 2015.

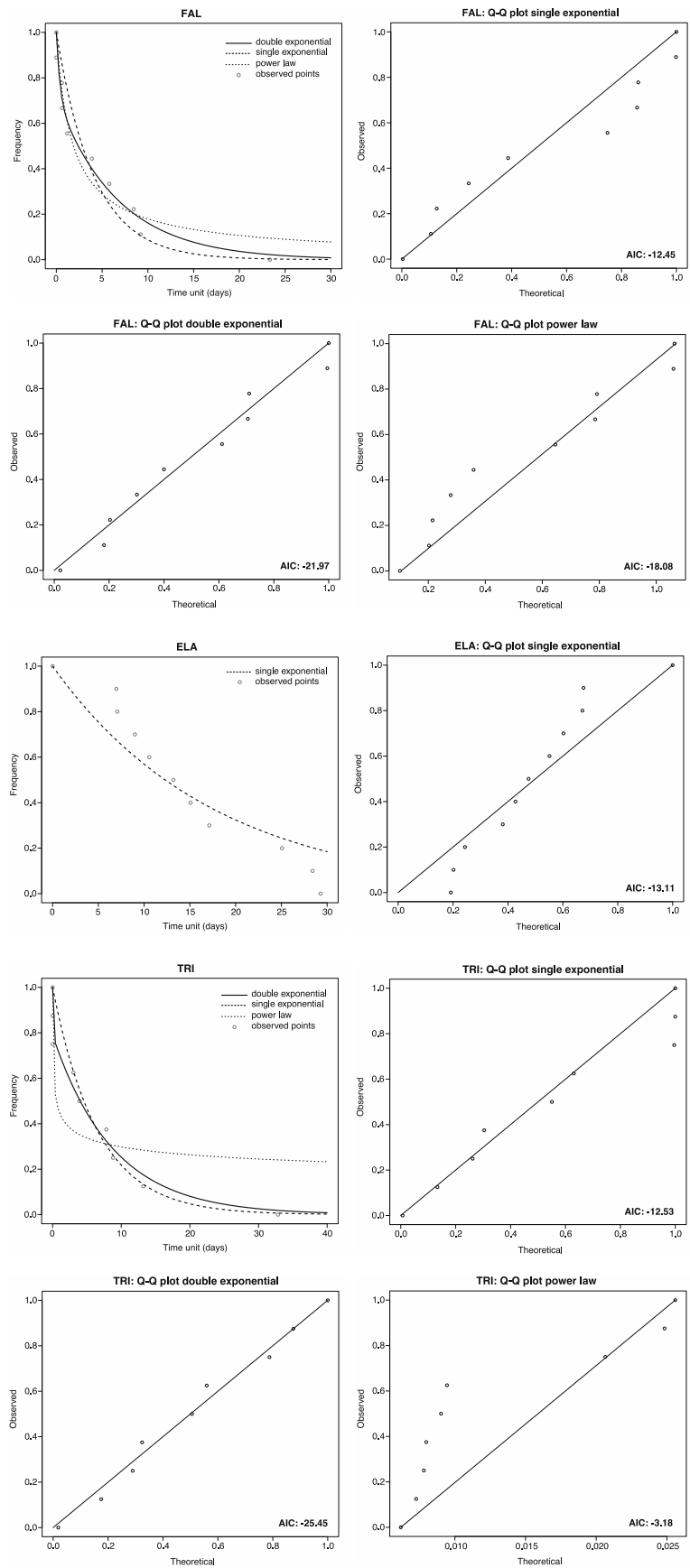


**Figure 6.** Boxplots of total residence times (TRTs) and traveled distance at maximum TRT of tuna and bycatch species associated with drifting FADs off the coast of Guinea from October to December 2015.



**Figure 7.** Fits of exponential and power law models, with corresponding Q-Q plots, to the survival curves of continuous residence times (CRTs) obtained for tuna species associated with drifting FADs.





**Figure 8.** Fits of exponential and power law models, with corresponding Q-Q plots, to the survival curves of CRTs obtained for bycatch species associated with drifting FADs.

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.