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Mariana Tolotti, Fabien Forget, Manuela Capello, John David Filmalter, Melanie Hutchinson, David Itano, Kim Holland, Laurent Dagorn

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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

Tolotti Mariana Travassos [1,*], Forget Fabien [1], Capello Manuela [1], Filmalter John David [2], Hutchinson Melanie [3], Itano David [4], Holland Kim [5], Dagorn Laurent [1]

[1] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France
[2] South African Institute for Aquatic Biodiversity, Grahamstown, South Africa
[3] Joint Institute for Marine and Atmospheric Research, University of Hawaii, Honolulu, HI, USA
[4] 689 Kaumakani Street, Honolulu, HI, USA
[5] Hawaii Institute of Marine Biology, University of Hawaii at Manoa, Kaneohe, HI, USA

* Corresponding author : Mariana Travassos Tolotti, email address : mariana.travassos@ird.fr

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

1. Introduction

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

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

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

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

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

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

[2] Resolution by the Indian Ocean Tuna Commission (IOTC) to establish procedures on a FAD management plan.

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

2. Material and methods

2.1. Data collection

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

Once captured, each fish was carefully brought onboard in a scoop net and placed in a V-shaped tagging cradle where a hose supplying seawater was inserted into the buccal cavity to oxygenate the gills. Through a small surgical incision, a Vemco coded acoustic tag (120seconds nominal delay, 69kHz, 1H) was inserted in the peritoneal cavity of the fish. Pressure sensitive tagsV9P and V13P were used depending on the size and species of fish. All tagged fish were released within close proximity (300 m) of the FAD and VR4 of capture.

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

2.2. Data analysis

The association of pelagic species with drifting FADs was studied based on the concept of continuous residence times (CRTs) and continuous absence times (CATs). The CRT is defined as the amount of time during which a tagged fish is continuously detected by the receiver without absences of a pre-determined duration (Capello et al., 2015). Conversely, the CAT is defined as the period of time between two consecutive CRTs. The total residence time (TRT) is the period of time between the first and last detections, including absence periods, i.e. the sum of all CRTs and CATs. Fine-scale residence and absence times (FCRTs and FCATs) were calculated by considering absence periods of at least 1 hour to evaluate the fine-scale associative behavior (Capello et al., 2015; Govinden et al., 2013). For the long-term associative behavior, the CRTs and CATs were calculated using absence periods of at least 24 hours (Ohta and Kakuma, 2005). In this latter case, solely acoustic telemetry experiments lasting a minimum of 30 days were considered. For these long-lasting experiments, the total drifting distance of each FAD was calculated by the cumulative sum of the distance between every consecutive point of the FAD's transmitted track. FAD's position is transmitted daily.

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

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

The FCRT and FCAT data were used to assess whether the short excursions performed by the tagged fish began or ended at regular times. Thus, the relative frequencies of departures and arrivals were calculated for each hour of the 24-hour cycle. The time data are expressed in GMT, which also corresponds to local times. As a reference point, sunset times were estimated based on the NOAA Solar Calculator (https://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html). To test if departures and arrivals were uniformly distributed throughout the day, Rao's spacing tests were performed using the "circular" package in R (Agostinelli and Lund, 2013). All statistical analyses were performed with a0.05significance level using the statistical computing software R (R Core Team, 2013).

3. Results

A total of 107 fish were tagged, consisting of23 bigeye, 20 yellowfin and 7 skipjack tunas and 18 silky sharks, 19 rainbow runner and 20 oceanic triggerfish (Table 1). Only 1 bigeye tuna, 7 silky sharks and 2 oceanic triggerfish were never detected by the receivers. All fish were exclusively detected at the FAD of release. All four experiments were interrupted due to equipment malfunctions before all fish had left the FAD. The duration of each experiment ranged from 3 to 55 days (Fig.1).

3.1. Fine-scale association dynamics

The FCRTs for bigeye, yellowfin and skipjack tuna averaged 18.82, 24.11 and 24.74 hours respectively (Table 2). Rainbow runner and triggerfish had considerably higher average values of 98.81 and 80.40 hours respectively, whereas silky sharks produced the lowest average of 8.91 hours (Table 2). An overview of the FCRTs recorded for all species at each drifting FAD is shown on Fig.2. The survival curves constructed from the FCRTs evidenced the behavioral similarities between rainbow runners and triggerfish (logrank test, $p=0.624$), as well as between all tuna species (logrank test, $p=0.66$) (Fig.3b). For the silky shark, the survival curve of FCRTs differed significantly from the other species (logrank test, $p<0.05$) and decreased more rapidly, indicating shorter fine-scale residence times in line with the trends observed for the mean FCRT (Table 2).

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

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

3.2. Large-scale association dynamics

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

The longest total association periods (maximum TRTs) were recorded for bigeye and yellowfin tuna at 55 days, which corresponded to the duration of the experiment on FAD 92. Considering this association period, these tunas followed the FAD for at least 607 km (Fig.6). Unlike the other tuna species, skipjack exhibited the shortest maximum TRT at 15 days and 104 km traveled. For the bycatch species, maximum TRT and corresponding traveled distance were 28 days and 229 km for silky shark, 41 days and 363 km for rainbow runner and 33 days and 273 km for triggerfish (Fig.6).

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

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

4. Discussion

4.1. Fine-scale association dynamics

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

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

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

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

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

4.2. Large-scale association dynamics

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

Furthermore, our study shows that during the 55 days associated to the same FAD, these yellowfin and bigeye tuna travelled about 600 km when the experiment was prematurely ended due to equipment failure. The other species did not remain associated for so long and over such distances with a same FAD. These long association periods and travelled distances exhibited by yellowfin and bigeye tuna can lead to interrogations concerning the possibility of an ecological trap, as suggested by some authors (Dagorn et al., 2013b; Hallier and Gaertner, 2008; Marsac et al., 2000). This hypothesis states that tunas could be "trapped" by drifting FADs and consequently be entrained to areas that could be less favorable to their biology. Until this study, the TRTs measured at single drifting FADs for tunas were relatively short (a few days), suggesting that if an ecological trap were to happen, it would have to be at the scale of large clusters of floating objects, and not at single floating objects. The long TRT and traveled distance measured for yellowfin and bigeye tuna clearly show a strong residence of these individuals to the FAD. However, without information on their physiological condition and a proxy for habitat quality, in particular in terms of prey availability, it is difficult to ascertain if such prolonged associations could have negatively impacted their biology. Dedicated studies with simultaneous observations of local habitat conditions and physiology are required to determine whether the seeding of thousands of drifting FADs can impact the biology of tuna. Nonetheless, observation tools required for such challenging investigations have not yet been developed, but technological innovation should allow scientists to address this issue in the near future.

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

The three tuna species displayed considerably longer residence in the Atlantic Ocean compared to other studies conducted both on anchored and drifting FADs in the Indian and Pacific Ocean. The substantial difference observed between ocean basins is difficult to explain because the factors influencing residence times of tunas around FADs remain unknown. It is conceivable that factors such as physiological condition, presence of conspecifics, density of predators and prey availability could have an effect. Residence times could as well be influenced by oceanographic conditions, albeit Ohta and Kakuma (2005) did not observe any relationship between tuna CRTs at FADs and abiotic oceanographic conditions. In other words, Ohta and Kakuma (2005) concluded that the biological environment (prey availability, predators, and productivity) and the internal state of the individual might be more influential than the abiotic environmental cues for inducing changes in associative behavior. No other studies have attempted to investigate the effects of biotic or abiotic factors on the residence of tuna at FADs. As suggested by Dagorn et al. (2007b), the association dynamics should be considered within the context of the larger environment in which they occur (abiotic, geographic, biotic).

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

5. Conclusion

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

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

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

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Table

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	18.45	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	15.75	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	15.56	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	46.41	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	35.30	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	-	-	-	-	-	-

Table 4. Summary results of the modeled survival curves of continuous residence times (CRTs) obtained for each species. BET= bigeye tuna, YFT= yellowfin tuna, SKJ= skipjack tuna, FAL= silky shark, ELA= rainbow runner and TRI= oceanic triggerfish. N= number of observed points, Est = parameter estimate, SE = standard error, Pr(>|t|) = p-value of the significance test and AIC = Akaike Information Criterion, ΔAIC= delta-AIC values in reference to the lowest AIC. The best fitted models are highlighted in bold. Significance codes: ***=0; **= 0.001; *=0.01; .=0.05

Species	N	**Single exponential**								**Double exponential**								**Power law**							
			Est	SE	t-value	Pr(>Itl)		AIC	ΔAIC		Est	SE	t-value	Pr(>Itl)		AIC	ΔAIC		Est	SE	t-value	Pr(>Itl)		AIC	ΔAIC
BET	16	L	0.04	0.01	6.17	1.80E-05	***	-12.52	-14.32	P	0.31	0.13	2.40	-14.32	*	**-26.84**	**0.00**	α	0.51	0.13	0.00	1.49E-03	**	-22.55	-4.29
										L1	0.65	0.50	1.28	0.22				β	2.70	1.48	3.94	0.09	.		
										L2	**0.02**	**0.01**	**4.20**	**1.03E-03**	**										
YFT	11	L	0.19	0.08	2.29	0.05	*	-1.52	-22.13	P	0.35	0.04	7.97	4.50E-05	***	**-23.64**	**0.00**	α	0.29	0.09	3.17	0.01	*	-11.76	-11.89
										L1	23.08	10.62	2.17	0.06	.			β	0.20	0.22	0.92	0.38			
										L2	**0.03**	**0.01**	**6.37**	**2.16E-04**	**-*** **										
SKJ	6	**L**	**0.11**	**0.02**	**6.13**	**1.68E-03**	**	**-5.46**	**0.00**	Didn't converge								Didn't converge							
FAL	10	L	0.24	0.04	6.05	1.90E-04	***	-12.45	-9.52	P	0.29	0.15	1.94	0.09	.	**-21.97**	**0.00**	α	0.83	0.30	2.78	0.02	*	-18.08	-3.88
										L1	2.56	3.06	0.84	0.43				β	1.43	0.88	1.62	0.14			
										L2	**0.15**	**0.04**	**3.74**	**0.01**	**										
ELA	11	**L**	**0.06**	**0.01**	**8.82**	**4.96E-06**	***	**-13.11**	**0.00**	Didn't converge								Didn't converge							
TRI	9	L	0.15	0.02	7.04	1.08E-04	***	-12.53	-12.53	P	0.21	0.04	5.13	2.15E-03	**	**-25.45**	**0.00**	α	0.18	0.07	2.46	0.04	*	-3.18	-22.27
										L1	427	290	1.47	0.19				β	0.01	0.02	0.47	0.65			
										L2	**0.11**	**0.01**	**9.37**	**8.38E-05**	***										

Figure

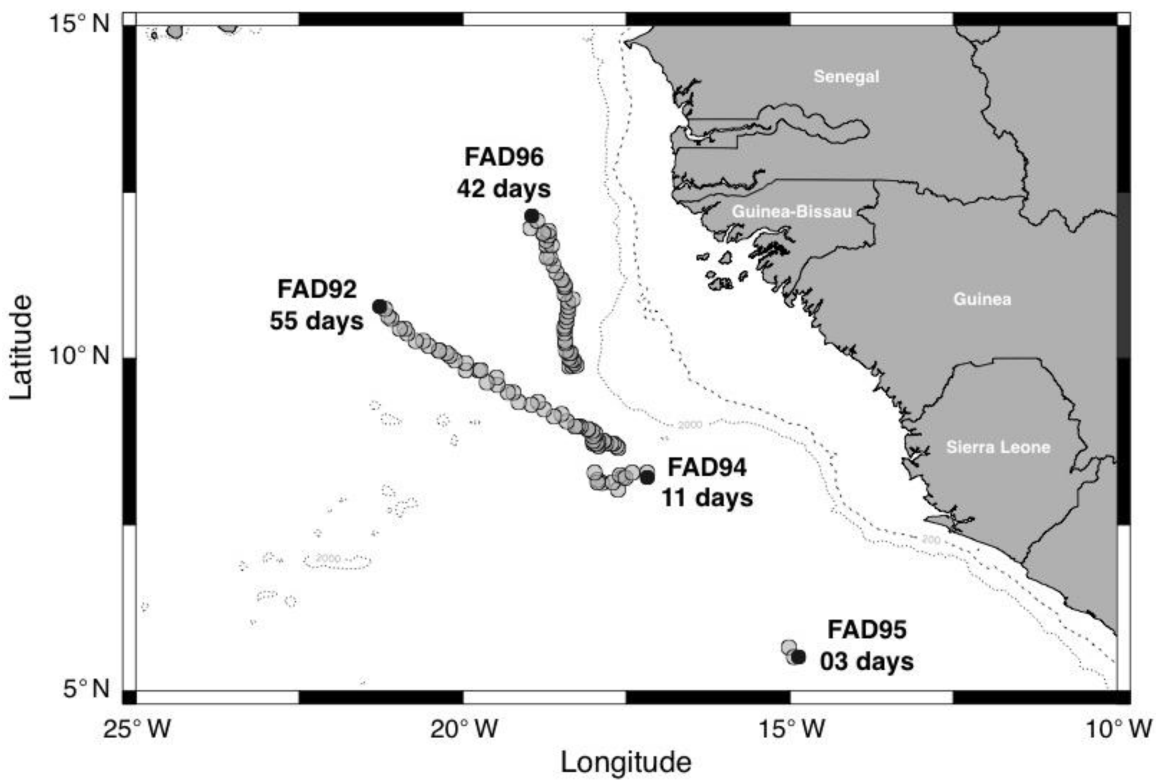

Figure 1. FAD drifts and corresponding duration of the acoustic telemetry experiments conducted from October to December 2015 in the eastern Atlantic Ocean. The black circles mark the time and location of equipment failures and the end of the experiments.

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.

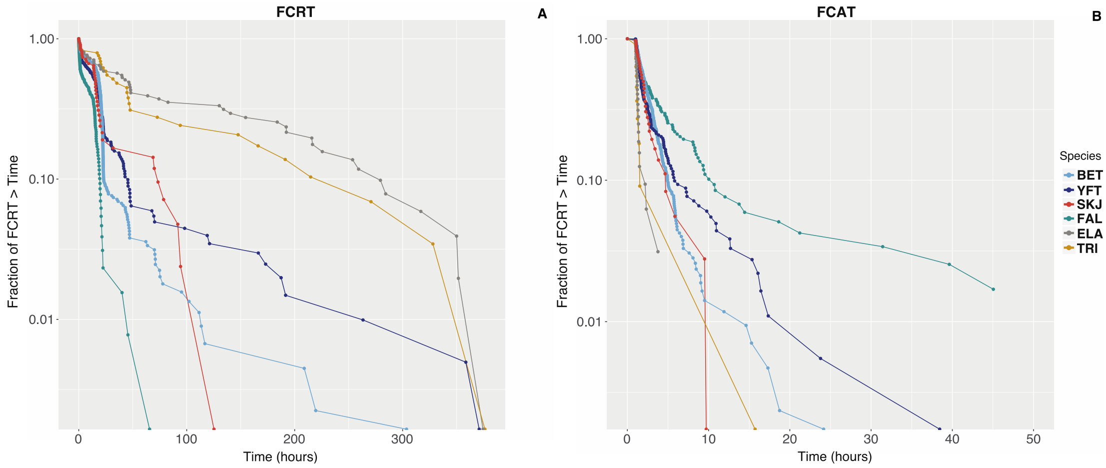

Figure 3. Survival curves of fine-scale continuous residence and absence times (FCRTs – panel A and FCATs – panel B) for tunas and bycatch species associated with drifting FADs off the coast of Guinea from October to December 2015. The y-axis is in logarithmic scale.

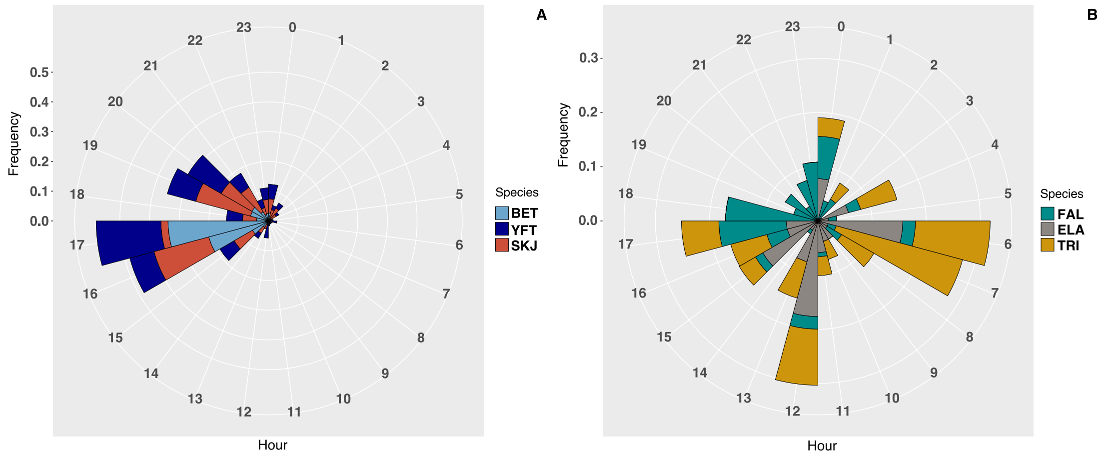

Figure 4. Frequency of departures by hour of the day of tunas (panel A) and bycatch species (panel B) associated with drifting FADs off the coast of Guinea from October to December 2015.

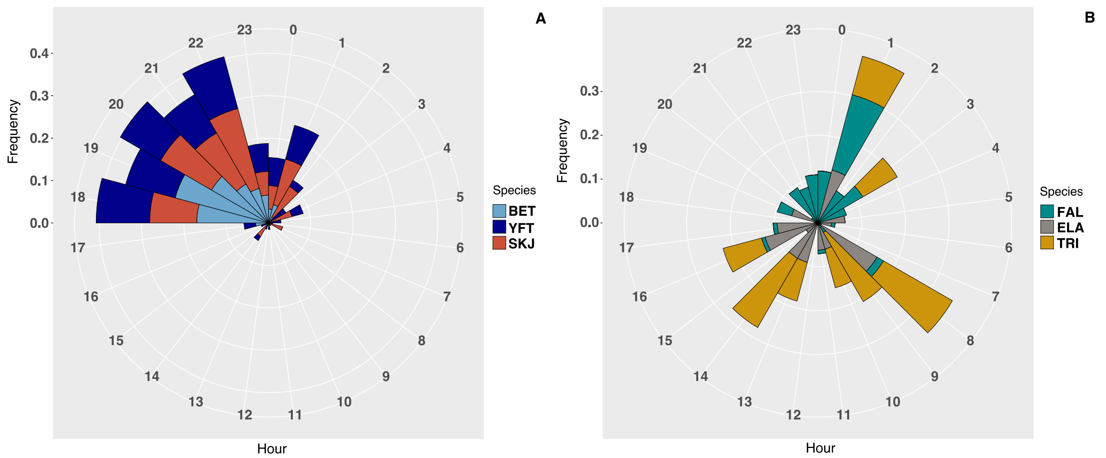

Figure 5. Frequency of arrivals by hour of the day of tunas (panel A) and bycatch species (panel B) associated with drifting FADs off the coast of Guinea from October to December 2015.

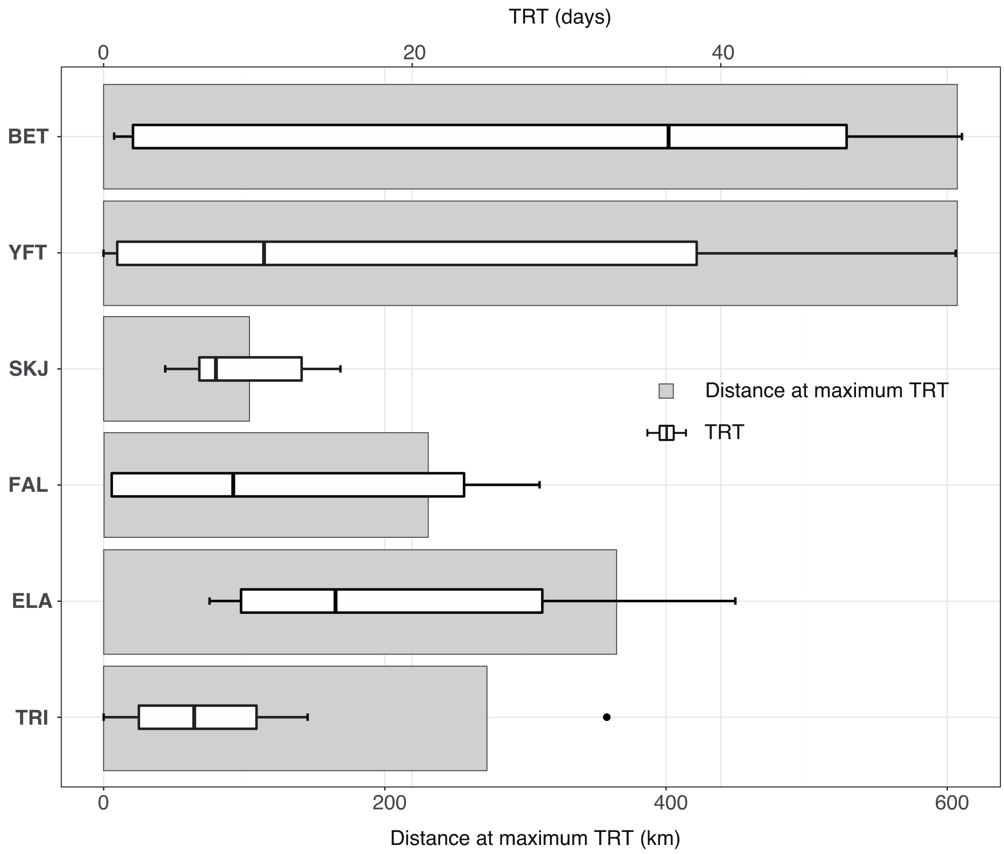

Figure 6. Boxplots of total residence times (TRTs) and traveled distance at maximum TRT of tuna and bycatch species associated with drifting FADs off the coast of Guinea from October to December 2015.

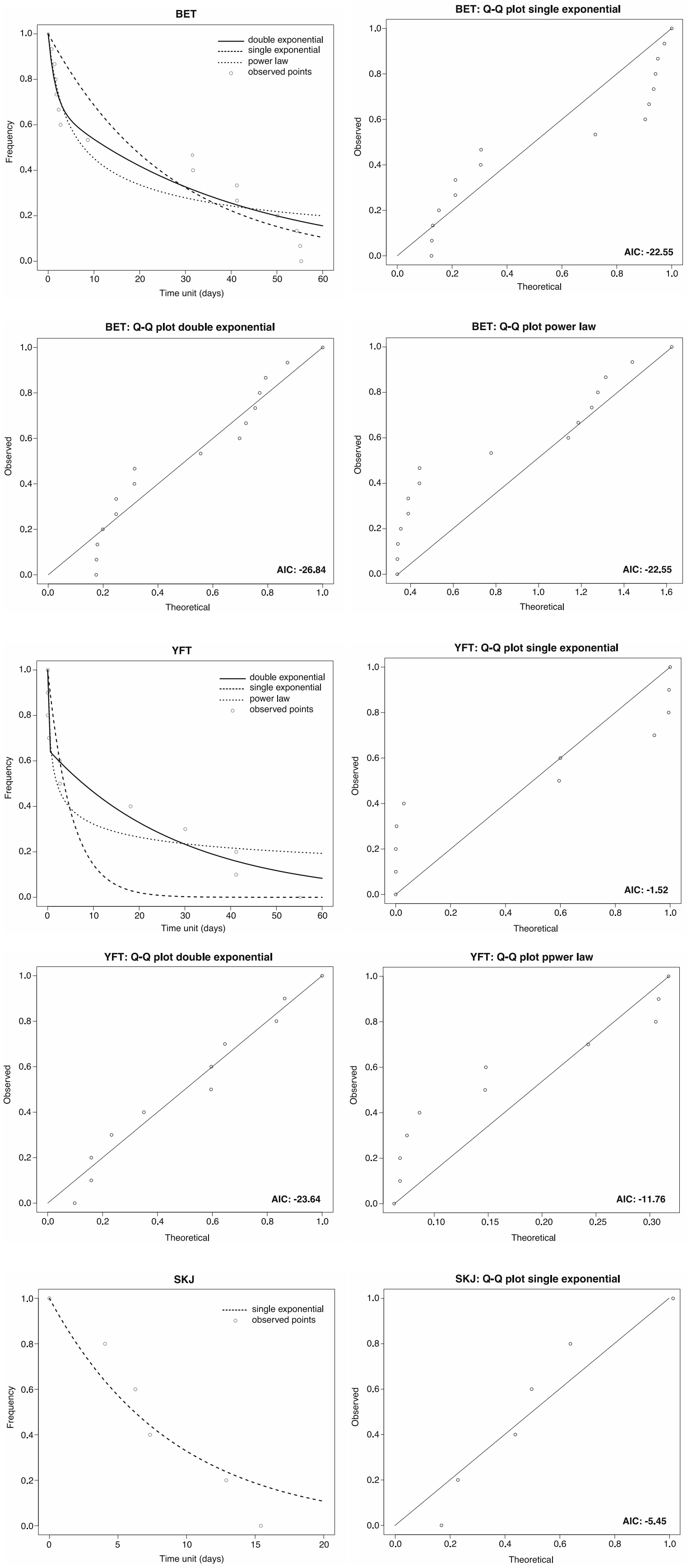

Figure 7. Fits of exponential and power law models, with corresponding Q-Q plots, to the survival curves of continuous residence times (CRTs) obtained for tuna species associated with drifting FADs.

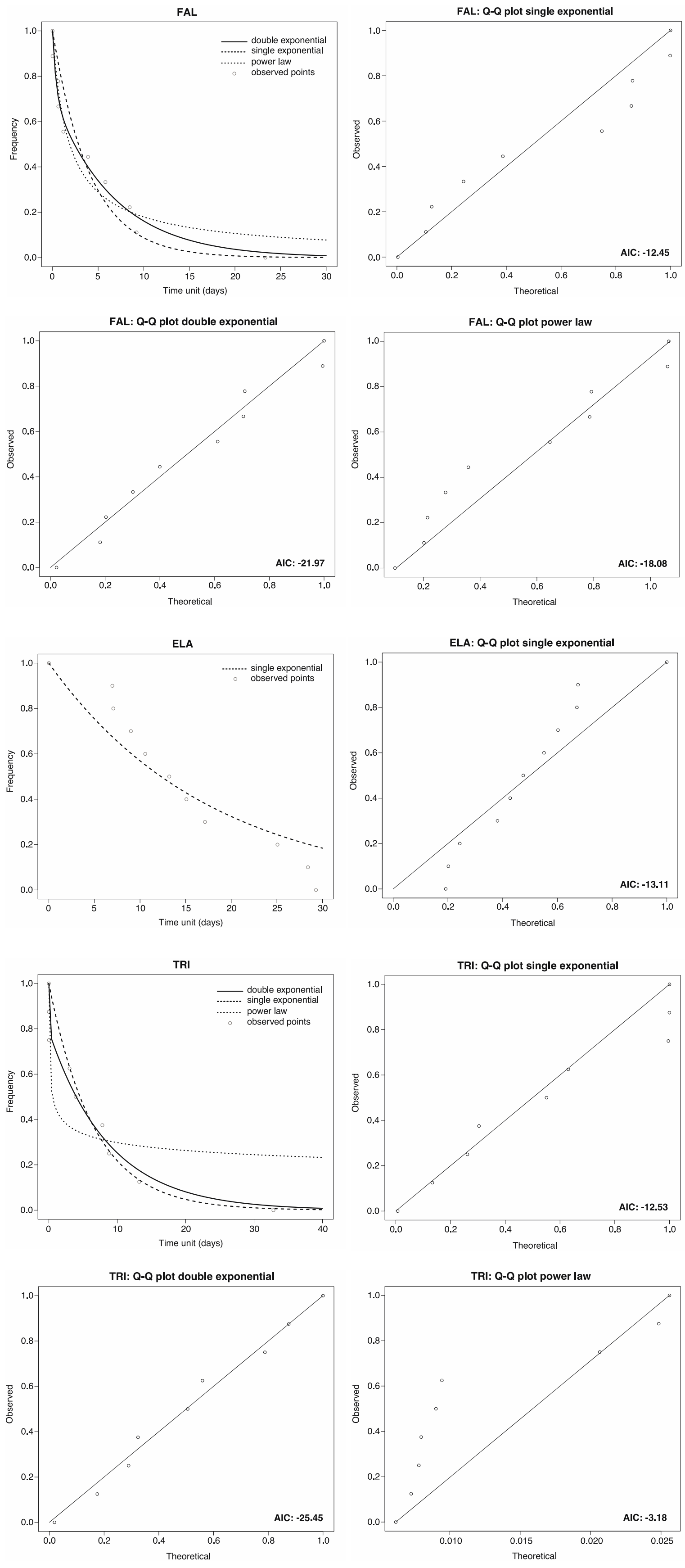

Figure 8. Fits of exponential and power law models, with corresponding Q-Q plots, to the survival curves of CRTs obtained for bycatch species associated with drifting FADs.

***Declaration of Interest Statement**

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.