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Abstract :

We investigated the associative behavior of skipjack (Katsuwonus pelamis), yellowfin (Thunnus albacares), and bigeye (T. obsesus) tuna within multi-species aggregations associated with drifting fish aggregating devices (dFADs) in two different regions of the western Indian Ocean: the Mozambique Channel and the Seychelles, using acoustic telemetry. We documented the residence and absence times of tunas at two temporal scales (coarse and fine scale) and made comparisons between regions. A total of 56 tunas were tagged and released at 7 different dFADs (4 in the Mozambique Channel and 3 in the Seychelles) during four research cruises. We recorded the first observations of skipjack tuna making excursions of more than 24 hours away from dFADs before returning and confirmed findings of other studies showing that yellowfin tuna can make long excursions (4.07 days) before returning to their home dFADs. Combining both studied regions, average residence times were 7.59 days (min 0.03; max 16.49), 6.64 days (min 0.01; max 26.72), and 4.58 days (min 0.09; max 18.33) for bigeye, yellowfin, and skipjack tuna, respectively. Exponential models best fitted the residence times for all three tuna species, indicating time-independent probabilities of departure from dFADs. For yellowfin tuna, at a coarse temporal scale, no regional differences were observed in the residence times. However, at a fine temporal scale, regional differences were apparent in both residence and absence times. This study provides new information on the associative behavior of tunas at dFADs in the Indian Ocean which is key to improving the science-based management of dFADs.

Keywords : acoustic telemetry, associative behavior, bigeye tuna, fish aggregating devices, Indian Ocean, skipjack tuna, yellowfin tuna

Introduction

For centuries fishers have made use of floating objects to enhance the capture of fish (Freon and Dagorn, 2000; Dempster and Taquet, 2004). While floating objects have always been an important component of the strategy of purse seine fleets targeting tropical tunas (skipjack *Katsuwonus pelamis*, yellowfin *Thunnus albacares* and bigeye *Thunnus obesus*), fish aggregating devices (FADs) have become the main fishing mode for these fleets in the last three decades. Each year FAD fishing by purse seiners contributes nearly 2.5 million tons of the global tropical tuna catch (Dagorn *et al*., 2013; Fonteneau *et al*., 2013; ISSF, 2018). The increase in the deployment of large numbers of drifting FADs (dFADs) in the ocean has impacts in terms of catchability, but also on the habitat (Dagorn *et al*., 2013; Maufroy *et al*., 2015) and potentially on the ecology of the species that associate with such objects, by possibly acting as ecological traps (Marsac *et al*., 2000; Hallier and Gaertner, 2008; Dagorn *et al*., 2013). Although FADs have played a key role in the strategy of purse seiner fleets, monitoring and controlling their numbers has only recently occurred on the agenda of tuna Regional Fisheries Management Organizations (RFMO). FAD management plans are now a priority for all RFMO, but the lack of knowledge on the role of floating objects in the ecology of tunas complicates the work of policy makers. Knowing the amount of time tunas spend in association with dFADs and in unassociated free-swimming schools, and whether such variables change with local densities of dFADs, represents one of the key pieces of knowledge required to improve the science-based management of FADs.

The majority of studies investigating the behavior of tunas at FADs, primarily using acoustic telemetry, have been conducted on anchored FADs (e.g. Holland *et al*., 1990; Cayré, 1991; Ohta and Kakuma, 2005; Schaefer and Fuller, 2005; Dagorn *et al*., 2007a; Robert *et al*., 2013; Govinden *et al*., 2013; Rodriguez-Tress *et al*., 2017). Despite the rapid expansion in the use of dFADs across the world's oceans and the recognition that dFADs may impact the behavior of tunas, there have been very few studies examining the behavioral ecology of tuna species that aggregate around such drifting floating objects. The majority of these have been carried out in the Pacific Ocean (Matsumoto *et al*., 2005; Schaefer and Fuller, 2005; Muir *et al*., 2012; Schaefer and Fuller, 2013; Matsumoto *et al*., 2014, 2016), while only two have been conducted in the Indian Ocean (Dagorn *et al*., 2007b; Forget *et al*., 2015) and one in the Atlantic Ocean (Tolotti *et al*. 2020).

Knowledge on the associative patterns of tunas at FADs are necessary to develop models and assess the potential effects of changing densities of FADs and other habitat variables on their behavior (primarily through comparisons of associative patterns in different oceanic regions). Furthermore, such information is needed to improve our understanding of the catchability and the catch per unit effort (CPUE) of purse seiners fishing with dFADs (Katara *et al*., 2016; Capello *et al*., 2016; Gaertner *et al*., 2016). In this study, we used acoustic telemetry to investigate the associative behavior of skipjack, yellowfin and bigeye tuna within multi-species aggregations associated with dFADs in two regions of the western Indian Ocean: the Mozambique Channel and the Seychelles. Specifically, we aimed to document the residence and absence times of three species of tunas at a coarse and fine temporal scale, and compare their associative patterns between species and regions.

Materials and methods

Acoustic telemetry experiment

Four research cruises were carried out between March 2010 and April 2012 in the Mozambique Channel and the Seychelles area (Fig. 1; Table 1). During the cruises, dFADs were located through collaboration with European purse seine vessels. Once a dFAD was located and if there were enough tunas aggregated under the FAD, fishing operations were carried out to catch and tag fish. Tunas were caught using hand-line gear or rod and reel. Captured tunas were carefully brought onboard and placed in a V-shaped tagging cradle where a hose supplying sea water was inserted into the mouth to oxygenate the fish's gills. The fork length of the tunas was measured to the nearest centimeter using calipers.

Tunas were fitted with either a V13, V13P (pressure-sensitive) or V13TP (temperature and pressure-sensitive) (90s nominal delay, 69kHz, 1H) coded acoustic tag following standard internal tagging procedures as described in Dagorn *et al.* (2007b). All tagged tunas were released within close proximity of the dFAD where captured. Tagging took place around seven dFAD and passive monitoring of fish was carried out using Vemco VR4-Global satellite-linked acoustic receivers (VEMCO, a division of Innovasea, Canada) attached to the dFAD (Table 1). These receivers remotely relay the acoustic detection logs on a daily basis using the Iridium satellite system. Due to the threat of piracy, range testing could not be carried out to determine the exact detection range

of the receivers. We have therefore assumed a similar detection range of 460 – 686 m as Schaefer and Fuller (2013) who carried out range tests in the equatorial eastern Pacific Ocean using similar tags, in similar environmental conditions.

Data analysis

Residence and absence times

The amount of time tunas spent associated with a dFAD was investigated at two temporal scales. Firstly, the continuous residence time (CRT), defined by Ohta and Kakuma (2005) as "the duration in which a tagged tuna was continuously monitored without day-scale (>24 h) absences" was calculated. The continuous absence time (CAT), which is the time between two consecutive CRT, also known as an excursion, was calculated (Capello *et al*., 2015). Secondly, the fine-scale residence time (FCRT), defined by Govinden *et al*. (2013) as "the duration over which a tagged tuna was monitored without a one-hour absence" was calculated. Using the FCRT, the fine-scale continuous absence time (FCAT) was calculated.

Similar to the study conducted by Robert *et al*. (2013), survival curves of CRT data were fitted using three different models (single exponential, double exponential and power law). The single and double exponential models imply that the probability of a fish joining/leaving a dFAD is independent of the time spent away from or at the dFAD. In contrast, the power law model indicates a functional dependence between the probability of a fish joining/leaving a dFAD and the time the fish spends away from or at the dFAD. The best-fit model was identified using the Akaike Information Criterion (AIC) (Akaike, 1973) and by examining the quantile-quantile plots. The models were fitted for each species by grouping the two regions to represent the Indian Ocean (IO) and by separate regions for species where there were enough data points in each region. Table 2 provides a summary of the models fitted in this study.

Survival curves of CRTs were compared using the logrank statistical test, using the 'survival' package in R (Therneau, 2015; R Core Team, 2016) to examine whether differences exist between species in the IO and between the two regions. The significance threshold was set at $p<0.05$. Comparisons were carried out for species where the sample size (number of data points) was larger than five. Consequently, comparisons between regions could only be carried out for yellowfin

tuna. Similarly, the logrank statistical test was used to compare the different survival curves of FCRT and FCAT and regional comparisons were conducted for bigeye and yellowfin tuna. The average FCRT and FCAT were calculated for each species in each region.

Index of residence

The degree of association with dFAD displayed by each species was investigated by calculating an index of residence (IR). For each tagged individual j, the index of residence (IR) was defined as follows:

$$IR_j = \frac{\sum_{i=1}^{N_j} FCRT_{ij}}{TRT_j}$$

where $FCRT_{ij}$ is the ith fine-scale continuous residence time recorded for individual j, Σ denotes the sum running over all the N_j FCRT recorded, and TRT_j is the total residence time calculated as the elapsed time between the first and last detection recorded for individual j. For each species, the above index was averaged for all individuals and the standard error was calculated.

Diel periodicity

To examine the diel periodicity in the presence of tunas in each region, the daily acoustic detection data was compiled in hourly bins and a fast fourier transformation (FFT) was carried out using the 'stats' package in R (R Core Team, 2016). Only tunas with TRTs of over five days were included in this analysis.

To elucidate any pattern in the arrival and departure time of tunas at dFAD between the two regions, we used the FCRT data to calculate the percentage number of arrival and departure events in each hour bin for all dFAD combined for each region. Rao's spacing tests were carried out to determine whether arrival and departure events were uniformly distributed throughout the day (Batschelet, 1981). The analysis was carried out using the 'circular' package in R (Agostinelli and Lund, 2013; R Core Team, 2016). The arrival and departure events were separated into daytime and nighttime. Nighttime was the period from 6 pm to 6 am. Day-night differences in the arrival and departure events were investigated for each species in the two different region using Kruskal-Wallis tests ('stats' R package; R Core Team, 2016). All statistical analysis was carried out using software package R (R version 3.3.1) (R Core Team, 2016).

Results

The acoustic tagging experiment was performed at 7 different dFADs (4 in the Mozambique Channel and 3 in the Seychelles), see Table 2. A total of 56 tunas were tagged and released at the dFADs, of which 46 individuals were detected and monitored with the VR4-Global acoustic receivers. The numbers of tunas tagged and detected from each species at each dFAD is provided in Table 2. All fish were monitored until they left the dFAD except at dFAD MOZ31 where the experiment was interrupted after 12 days due to a fishing event. The sizes of bigeye tuna tagged in the Mozambique Channel and Seychelles ranged from 54 to 56 cm FL (mean ± SD: 55 ± 1, n=4) and 43 to 59 cm FL (mean ± SD: 52 ± 8, n=4) respectively. Tagged skipjack tuna ranged in size from 47 to 57 cm FL (mean ± SD: 50 ± 3, n=13) and 42 to 56 cm FL (mean ± SD: 48 ± 6, n=4) respectively, whilst yellowfin tuna ranged from 29 to 111 cm FL (mean ± SD: 65 ± 22, n=16) and 42 to 66 cm FL (mean ± SD: 59 ± 9, n=15) respectively.

Residence times

Continuous residence times (CRT) and continuous absence times (CAT)

Of the 46 tunas detected at the dFADs, a total of 8 yellowfin and 3 skipjack tunas made excursions away from the dFAD which lasted more than 24 hours (Fig. 2). However, the majority of the excursions occurred approximately 2 hours after the fish were released, which may reflect an effect of capture and tagging. Only two skipjack and one yellowfin tuna in the Mozambique Channel made excursions 3 to 18 days after being released. The average duration of these excursions was 1.56 days for skipjack tuna and ranged from 1.10 days to 2.27 days (n=3). In contrast, the duration of the only excursion observed for yellowfin tuna was 4.07 days.

In the Mozambique Channel, the average CRT of yellowfin tuna (7.56 days) was longer than the two other species, whereas in the Seychelles, bigeye tuna had a longer average CRT of 8.77 days. However, a wide degree of inter-individual variability was observed in both areas (Table 3, Fig. 2). Moreover, only two skipjack and two bigeye tuna were detected in the Seychelles and in the Mozambique Channel, respectively, rendering any interspecific comparisons between regions of limited use. For both areas combined, the average CRT was 7.59 d for bigeye, 6.64 days for yellowfin and 4.58 d for skipjack (Table 3).

The survival curves of CRTs obtained for the three tuna species for the IO region are shown in Figure 3. The logrank statistical test showed that there were no significant differences among species (p=0.44). Based on the AIC values, the double exponential model provided the best fit for the survival curve of CRTs of yellowfin and skipjack tuna (Table 4). Using the optimized parameters from the model (*a* and *b* in Table 4), for yellowfin tuna, the short associations were characterized by mean stays (1/*a*) of 4.73 hours, whilst the mean duration of the long periods (1/*b*) of CRT was 16.67 days. For skipjack tuna, the mean duration of the short associations was 3.42 hours whilst the average duration of the long associations was 7.14 days. However, for both species, the p-value of the parameters associated to the shorter timescale was not significant. In contrast, for bigeye tuna the double exponential model did not converge and the single exponential model provided the best AIC, with a mean CRT duration of 11.11 days.

Yellowfin tuna was the only species for which a comparison between survival curves of CRTs recorded in the two regions could be conducted. The logrank test of comparison run between survival curves of CRTs recorded in the Mozambique Channel and in the Seychelles area showed no significant differences between the two regions (p=0.58), see Figure 1S in the Supplementary Material.

Fine scale continuous residence time (FCRT) and fine-scale continuous absence time (FCAT)

The survival curves of FCRTs and FCATs for the three tuna species in the Mozambique Channel and Seychelles area are shown in Figure 4. For yellowfin tuna, a significant difference was observed in the survival curves of FCRT between the two regions (logrank test, p<0.01). The average FCRT in the Mozambique Channel (16.6 hours) was nearly three times longer than in Seychelles (5.8 hours) (Table 5). In contrast, no difference was observed in the FCRT of bigeye tuna between the two regions (logrank test, p=0.15). The average FCRT was 10.1 hours and 17.6 hours in the Mozambique Channel and the Seychelles respectively (Table 5). For skipjack tuna, only the data recorded in the Mozambique Channel could be analyzed, since the two individuals tagged in the Seychelles area remained associated for a short period of time. The average duration FCRT for skipjack tuna in the Mozambique Channel was 6.5 hours.

Regional comparisons of survival curves of FCATs showed that there was a significant difference in the FCAT of yellowfin tuna between the Mozambique Channel and Seychelles (logrank test,

p=0.01), whilst no significant difference was observed for bigeye tuna between the two areas (logrank test, p=0.97). The average FCAT showed little variability between species and regions and ranged between 3.1 and 4.1 hours (Table 5).

Index of Residence

The index of residence indicates that all tuna were strongly associated with the dFADs (Fig. 5). All indices were comparable, indicating a certain homogeneity of associative behavior among species and regions. Yellowfin tuna in the Mozambique Channel exhibited stronger associations, spending in average 90% of their time within the reception range of the receiver, while the same species in the Seychelles area, as well as other species in the Mozambique Channel or the Seychelles area, showed average indices of residence between 69 and 76% (Fig. 5).

Diel patterns in detection

The FFT results showed clear 24-hour peaks in the detection for the majority of tunas (Fig. 2S in Supplement 1). However, the amplitude of the peaks varied between individuals of the same species and between regions with some fish showing a stronger diel pattern than others.

Arrival and departure events

The percentage number of arrival and departure events was not uniform over 24 hours (Rao's spacing test; p<0.05) for all three species in both regions (Fig. 6). In the Mozambique Channel, arrival events were significantly more common at night than during the day for all three species (Kruskal-Wallis test; p<0.05) with a percentage of nighttime arrivals of 77%, 83%, and 90% for skipjack, bigeye and yellowfin tuna respectively. Similarly, nighttime departure events were significantly higher for bigeye and yellowfin tuna (Kruskal-Wallis test; p<0.05) and corresponded to 100% and 81%, respectively, of all departures. In contrast, there was no significant difference between the nighttime and daytime departure events of skipjack tuna (Kruskal-Wallis test; p>0.05), where departures started at noon and only 63% of departures occurred at night (Fig. 6).

In Seychelles, the diel pattern of arrivals and departures was less clear. For bigeye tuna departures and arrivals were spread between noon and early night and there were no significant differences between the nighttime and daytime arrival and departure events (Kruskal-Wallis test; p>0.05).

Indeed, only 62% of arrivals and 41% of departures occurred at night (Fig. 6). In contrast, for yellowfin tuna, the frequency of nighttime arrival events was significantly higher than in the day (Kruskal-Wallis test; p<0.05). Sixty-nine percent of arrival events took place at night compared to 31% during daytime. However, departure events were distributed throughout the whole day and there was no significant daytime (47%) or nighttime (53%) difference (Kruskal-Wallis test; p>0.05) (Fig. 6).

Discussion

Following upon the first measures of residence times of tunas at dFAD in the Indian Ocean (Dagorn *et al*., 2007b), this study provides a more comprehensive insight into the associative behavior of the three major tuna species at dFAD in this ocean.

Large-scale dynamics

The Mozambique Channel is a region rich in meso-scale features (De Ruijter *et al*., 2002) and an area where natural logs form a large proportion of the available floating object habitats (Dagorn *et al*., 2013). In contrast, the Seychelles area is considered to be oceanographically more uniform and the majority of floating objects are artificial dFADs. Remarkably, despite these potential differences in the environment, we found that yellowfin tuna (the only species where a comparison between areas was possible) manifested the same continuous residence times across both areas. This result justifies the combined analysis of CRTs recorded in different areas for yellowfin tuna. It is important to note that sample size could potentially affect the statistical power of the test, therefore a much larger sample size would be required to potentially detect any geographical differences. The smaller sample size available for bigeye and skipjack tuna constrained the comparative analysis of CRT for these species at the level of the Indian Ocean.

The fit of the survival curves of CRTs demonstrated that exponential models best fitted the residence times for the three tuna species, indicating time-independent probabilities of departure from dFADs (Robert *et al*., 2013). The double exponential model was the best fit for yellowfin and skipjack tuna, revealing two behavioral modes characterized by either very short (of the order of a few hours) or long residence times (about two weeks). However, the p-value associated with the short timescales were not significant, indicating that the short residence times were not

significantly different from zero. Similar short residence times for tunas at FADs were previously observed (e.g. Dagorn *et al*., 2007b at drifting FADs, Robert *et al*., 2013 and Govinden *et al*., 2013 at anchored FADs). The authors interpreted these short residence times as a result of local environmental conditions, which can still be valid in our study. However, as these very short residence times were mainly recorded immediately after tagging, occurring for nearly half of the tagged individuals, it could also be attributed to a tagging induced stress response (Scutt Phillips *et al*., 2017). In a similar experiment on silky sharks, Filmalter *et al*. (2015) observed that 90% of tagged silky sharks (*Carcharhinus falciformis*) left the monitored dFAD after they were released. The authors attributed this behavior to stress associated with capture, handling and tagging. Without further information on the local conditions, it is not possible to explain whether these short residence times are natural or due to stress caused by the catching and tagging events. For bigeye tuna, the single exponential model provided the best fit indicating a single behavioral mode. However, bigeye tuna was also the species with the smallest number of individuals tagged, therefore the absence of very short residence times may be an artefact of the small sample size.

In a similar study conducted on yellowfin tuna at anchored FADs in Hawaii, Robert *et al*. (2013) found that only exponential models fitted the survival curves of CRTs. Similarly, in the Atlantic Ocean, single exponential models provided the best fit for skipjack tuna, whilst the double exponential model provided the best fit for bigeye and yellowfin tuna (Tolotti *et al.*, 2020). Similarly, Rodriguez-Tress *et al*. (2017) observed that the skipjack and bigeye tuna CRTs at anchored FADs were best fitted by single exponential model. In contrast, the CRTs for yellowfin tuna were best fitted by a power law model, however, they argued that the single exponential model provided a good alternative fit to the data based on the significance of the model parameter and the behavior of the quantile-quantile plot. Our observations therefore support the findings of the previous studies that the three tuna species exhibit similar mechanisms that describe their behavioral dynamics i.e, the behavioral processes are time independent.

For both regions combined we observed mean CRTs of 7.59 days for bigeye, 6.64 days for yellowfin and 4.58 days for skipjack. In comparison to other studies carried out in the Indian Ocean, Dagorn *et al*. (2007b) observed much shorter mean residence times of 1.43, 1.04 and 0.91 days for bigeye, yellowfin and skipjack tuna respectively. These data, however, were collected with classic acoustic receivers (which need to be recovered to download the data) or with new

prototypes of satellite-linked acoustic receivers, which did not allow for long observations. Most of these data were therefore interrupted. In the equatorial central Pacific Ocean, Matsumoto *et al.* (2014) observed short mean CRT of 2.3 days for skipjack tuna, whilst Matsumoto *et al.* (2016) recorded mean CRTs of 2.2 and 5.1 days for bigeye, 2.2 and 6.1 days for yellowfin and 0.2 and 2.4 days for skipjack tuna at two different dFADs. In contrast, in the Atlantic Ocean, Tolotti *et al.* (2020) observed much longer mean CRTs of 25.31, 19.15 and 9.19 days for bigeye, yellowfin nd skipjack tuna respectively. At anchored FADs in the Maldives, Govinden *et al.* (2013) recorded shorter mean CRTs of 0.2 and 3.5 days for skipjack and 0.66 days for yellowfin tuna. In contrast, Ohta and Kakuma (2005) reported median CRTs of 7.0 and 7.9 days for bigeye and yellowfin tuna, respectively, around anchored FADs near Okinawa Island, whilst Dagorn *et al.* (2007b) reported that mean CRTs for bigeye and yellowfin tuna around anchored FADs near Hawaii was 4.8 and 8.0 days, respectively. From these comparisons, it appears that CRTs are of the same order of magnitude, independent of FAD type and region. However, it can be observed that the CRT of yellowfin and bigeye tuna are generally longer than that of skipjack tuna. Several authors have also noted this observation from previous studies (e.g. Schaefer and Fuller, 2013; Matsumoto *et al.*, 2014, 2016; Rodriguez-Tress *et al.*, 2017; Tolotti *et al.*, 2020). Variability in the residence times of tunas at FADs is likely to be species specific and related to different factors that influence the local conditions around the FAD, such as food availability, the environmental conditions, presence of predators or the proximity of other floating objects in the vicinity (Ohta and Kakuma, 2005; Robert *et al.*, 2013).

We observed a total of eight yellowfin and three skipjack tuna that returned to the dFADs after making prolonged excursions lasting more than 24 hours. However, of these 11 tunas, seven yellowfin and one skipjack made these excursions within 2 hours after being released, similarly to the excursions observed for silky sharks (Filmalter *et al.*, 2015), and could be interpreted as a reaction to the stress of capture and tagging. In contrast, one yellowfin tuna made an excursion lasting 4.07 days, 12 days after it was tagged. Moreover, two skipjack tuna undertook excursions lasting more than a day (1.10 and 2.27 days) after prolonged CRTs (4 and 18 days respectively). Similar observations of tuna returning to a dFAD after a long excursion (> 24 h) comes from Matsumoto et al. (2016) who observed one yellowfin and one bigeye tuna returning to the dFAD after an absence of more than 24 hours. However, the duration of the absence time was not

specified in that study. In the Atlantic Ocean, Tolotti *et al.* (2020) observed a single bigeye tuna that made an excursion lasting 1.01 days. Studies on anchored FADs did show long scale CATs. Returns to the same FAD and visits to other FADs were both observed (Dagorn *et al.*, 2007a, Robert *et al.*, 2012, 2013). The latter type of CATs was possible because several FADs in the same array were instrumented with acoustic receivers, a protocol that is quite difficult to replicate for dFAD as the array is constantly changing. Observing long-scale returns to the same dFAD, could in theory, depend on the local densities of floating objects, e.g. the distance between floating objects. Data reported in Fauvel *et al.* (2009) showed that FADs contributed to a greater increase in the number of floating objects in the Seychelles area compared to the Mozambique Channel and found that FADs contributes to decreasing the average distance between two floating objects. In areas where floating objects are close to each other, it is logic to consider that tunas could find another FAD during their excursions. In contrast, in areas where floating objects are further apart, encountering another floating object might take longer, and therefore the probability of returning to the same FAD could be higher. Of the 8 yellowfin tuna which were observed returning to the same FAD, 6 were tagged in the Seychelles and 2 in the Mozambique Channel, while the 3 skipjack exhibiting a return movement to the same FAD were all tagged in the Mozambique Channel. The behavior of these few tagged tunas can only be interpreted in regards to the actual local floating object environment where these fish were swimming, which is not known. Monitoring the local densities of floating objects during tagging experiments would considerably help interpreting the data. Our study provides the first observation of long scale excursions (> 24 h) for skipjack tuna and highlights the importance of long-term monitoring of tunas associated with dFADs in order to obtain a comprehensive understanding of their associative behavior.

Fine-scale dynamics

When inspecting the associative behavior of tuna at a fine scale, we showed that there were regional and species-specific differences. The analysis of FCRT revealed that the residence times of yellowfin tuna were about three times higher in the Mozambique Channel compared to the Seychelles region. The index of residence shows that all tuna are strongly associated with FADs, with fish spending in average between 69 and 90% of their time in the vicinity of FADs. It is noteworthy that the highest values were measured for yellowfin tuna in the Mozambique Channel. This could be due to a particular behavior of this species under the specific oceanographic

dynamics of the Mozambique Channel, where drifting objects could frequently encounter features such as eddies and fronts, which are known for their increased productivity. As a result, foraging excursions away from a floating object could be shorter, but understanding why skipjack tuna did not also show higher indices of residence in this region deserves more behavioral investigations, in particular better characterization of possible different foraging strategies of these species under these conditions.

For bigeye tuna, the comparison of FCRT between regions did not reveal significant differences, nor did the index of residence. However, the patterns of arrivals and departures were different between regions, with a higher activity at nighttime in the Mozambique Channel than in the Seychelles for both bigeye and yellowfin tuna. The small-scale behavior of skipjack tuna in the Mozambique showed an index of residence similar to that of bigeye tuna, but a less marked diel pattern in the activity.

In the equatorial central Pacific Ocean, Matsumoto *et al*. (2016) observed significantly higher detection rates during the daytime compared to nighttime. In contrast, in the eastern equatorial Pacific Ocean, Schaefer and Fuller (2013) found that there were no significant differences between the day and night percentages of time that the three tuna species spent within the detection range of the receiver at the FAD. However, they observed that skipjack tuna spent more time during the day and less time at night in close proximity of FADs compared to bigeye and yellowfin tuna. Around anchored FADs near Okinawa Islands, Ohta and Kakuma (2005) found that 72 % of the CRT logs of yellowfin and 100 % of those of bigeye tuna showed a periodicity of approximately 24 h. Moreover, they classified the fluctuations in detection rates into five simple patterns. One of the patterns was characterized by a detection rate that was significantly higher in the nighttime than in the daytime. This was the most common pattern observed for yellowfin tuna. In addition, in Hawaii, Holland *et al.* (1990) observed yellowfin and bigeye tunas making diurnal movements on and off FADs. The tunas stayed close to the FADs during daytime and left between late afternoon and nighttime to make extensive nighttime excursions.

We observed some differences in the nighttime and daytime activity of tunas associated with dFADs in the two regions. In the Mozambique Channel, for all three species, the nighttime arrival events were significantly higher compared to the daytime. In addition, the nighttime departure

events of yellowfin and bigeye tuna were significantly higher, whilst for skipjack there was no difference between daytime and nighttime. This suggests that all three species are more mobile and active during nighttime. This is coherent with the current knowledge which considers that nighttime excursions could correspond to foraging behavior (Jaquemet *et al.,* 2011; Schaefer and Fuller, 2010) (see below). However, during the day, skipjack tuna is more active than yellowfin and bigeye tuna, which tends to show that this species also have considerable foraging activity during daylight hours. In Seychelles, the arrival events of yellowfin tuna were significantly higher during nighttime compared to during the day. However, there was no difference between the nighttime and daytime departure events. In contrast, for bigeye tuna there was no difference between the nighttime and daytime arrival and departure events. This indicates that both species were more active throughout the day and night in Seychelles compared to the Mozambique Channel. It could be hypothesized that these differences between regions correspond to different foraging strategy or different prey availability at night and day in these regions (see below). As a consequence, in Seychelles, the daily residence times for yellowfin tuna were much lower compared to the Mozambique Channel.

The exact causes for the differences in fine-scale association patterns are still poorly understood. Movements away from FADs can possibly be associated with feeding habits. In the equatorial eastern Pacific Ocean, Alatorre-Ramirez *et al.* (2017) observed that although both yellowfin and skipjack tuna employed similar predation strategy, their diet composition was significantly different indicating that they occupy different trophic levels and that there is no competition for food between the two species. Jaquemet *et al*. (2011) deduced that patterns in the dietary habits of tunas around dFADs are complex and related to the prey availability in their vicinity and the productivity of the pelagic waters where the dFADs and tunas drift to. Moreover, Schaefer and Fuller (2010) suggested that the nighttime occurrence or absence of deep scattering layer (DSL) prey organisms may influence the behavior of tunas, therefore influencing their associative patterns with dFADs. The presence of predators can potentially influence the associative patterns of tunas around FADs. Ohta and Kakuma (2005) observed cases where the presence of predators coincided with the short-term absences of monitored tuna.

Comparison between regions at different temporal scales for yellowfin

Our results for yellowfin tuna showed that assessing the regional variability of the associative behavior of tuna at dFAD is a matter of timescales. While the large-scale residence times appeared to be zone-independent, the small-scale behavior appeared to vary between Seychelles and the Mozambique Channel. Even if the link between these short and long timescales remains unclear, we can advance some hypotheses on how this observation could be possible. One hypothesis may be that the two timescales are independent, i.e., the fine-scale behavior and the factors affecting it (e.g. local environment, prey availability, presence of predators and densities of floating objects) are not influencing the long-term residence of yellowfin tuna at dFAD, which would depend on other factors operating over longer timescales.

Conclusion

This study contributes towards a better understanding of the associative behavior of tropical tunas with dFAD in the Indian Ocean through the characterization of residence and absence times at two different temporal scales. In general, we observed that the CRT of yellowfin and bigeye tuna were longer than those of skipjack tuna. We recorded the first observations of skipjack tuna making excursions of more than 24 hours away from dFAD before returning, and confirmed findings of other studies showing that yellowfin tuna can make long excursions and return to the same dFAD. In addition, we show that, in the case of yellowfin tuna, regional comparisons of the associative behavior is dependent on time scale. Understanding the behavioral patterns of tunas around dFADs remains a complex issue. In order to get a comprehensive understanding of the associative patterns, there is clearly a need to carry out additional field experiments whereby potential factors driving the associative patterns are characterized or measured. This may include the collection of in situ data on environmental conditions, including densities of floating objects, tuna abundance, prey availability and predator presence in conjunction with passive acoustic tracking of tunas. In order to assess the links between the behavior at small and large timescales, there is a need to combine long-term passive tracking studies with short-term active tracking experiments to get a better understanding of the short-term movement of tunas both at and away from dFAD. Eventually, collecting residence and absence times at different dFADs under different conditions (abundance of tunas, prey, predators and densities of floating objects) will allow us to better understand the drivers of the associative behavior. These are key parameters needed for modelling

the behavior of tuna in order to assess the effects of densities of floating objects on their movement patterns, a key priority to develop science-based management of the number of dFAD.

Acknowledgments

Conflict of interests

The authors declare to have no conflict of interest.

Author contributions

LD, FF, JDF designed the study, LD, FF, JDF, RG performed the experiments, RG and MC carried out the data analysis, RG took the lead in writing the manuscript, RG, LD and MC contributed to the interpretation of the results. All authors provided critical feedback and helped shape the manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Tables

Table 1 Tagging summary: Drifting FAD of release, location of dFAD at start of experiment, tagging period and number of skipjack (SKJ), bigeye (BET) and yellowfin (YFT) tunas tagged and detected.

Area	FAD ID	Location Latitude, Longitude	Periods of tagging	Number of SKJ-YFT-BET tuna tagged	Number of SKJ-YFT-BET tuna detected
Mozambique channel	MOZ31†[1]	13° 51 S, 44° 38 E	15–16 Mar 10	6–6–2	5–5–0
	MOZ34	14° 55 S, 43° 30 E	08–09 Mar 10	7–6–2	6–6–2
	MAY41	9° 07 S, 50° 22 E	16 Apr 11	0–3–0	0–2–0
	MAY42	12° 21 S, 44° 42 E	21 Apr 11	0–1–0	0–1–0
Seychelles	SEY37	6° 42 S, 53° 40 E	22–23 Jun 11	2–6–0	1–5–0
	SEY41	8° 58 S, 49° 54 E	14 Apr 12	0–5–0	0–4–0
	SEY59	8° 38 S, 53° 32 E	26 Apr 12	2–4–4	1–4–4

Table 2 Models used to fit the survival curves of continuous residence times as a function of time, *t*. In the analytic formula *a*, *b* and *p* are model parameters.

Model type	Analytic formula
Single exponential	$\exp(-a\,t)$
Double exponential	$p\exp(-a\,t) + (1-p)\exp(-b\,t)$
Power law	$(b/(b+t))^a$

Table 3 Summary statistics for the continuous residence time (CRT) for tunas in the Mozambique Channel, Seychelles and for both areas combined (Indian Ocean). N= number of tunas, n= number of CRTs

Area	Species	N	n	Continuous Residence Time (Days)			
				Minimum	Maximum	Average	SD
Mozambique Channel	BET	2	2	3.89	6.56	5.22	1.88
	SKJ	11	15	0.09	18.33	5.16	4.81
	YFT	14	16	0.01	26.72	7.56	7.76
Seychelles	BET	4	4	0.03	16.49	8.77	8.94
	SKJ	2	2	0.12	0.33	0.23	0.15
	YFT	13	19	0.005	23.67	5.86	7.98
Indian Ocean	BET	6	6	0.03	16.49	7.59	7.21
	SKJ	13	17	0.09	18.33	4.58	4.78
	YFT	27	35	0.005	26.72	6.64	7.81

Table 4 Comparison of the goodness of fit between models. The parameter estimates and values of Akaike Information Criterion (AIC) are given for the three models tested on the survival curves of continuous residence time (CRT) obtained for each tuna species.

Species	Area	N	Model	Parameter estimates	p-value	AIC
BET	Indian Ocean	6	Double exponential	-	-	-
			Single exponential	$a = 0.09$	<0.001	−13.5
			Power law	$a = 2.84$	0.447	−12.69
				$b = 25.69$	0.512	
SKJ	Indian Ocean	18		$p = 0.21$	0.047	−40.43
			Double exponential	$a = 7.01$	0.296	
				$b = 0.14$	<0.001	
			Single exponential	$a = 0.19$	<0.001	−25.81
			Power law	-	-	-
YFT	Indian Ocean	35		$p = 0.36$	0.007	−28.91
			Double exponential	$a = 5.07$	0.186	
				$b = 0.06$	0.002	
			Single exponential	$L1 = 1.13$	0.037	2.12
			Power law	$a = 0.27$	<0.001	−21.84
				$b = 0.12$	0.105	

Table 5 Summary statistics for FCRT and FCAT in days (in hours) recorded for different species and regions. Last column is the p value of the logrank test of comparison.

Fine-scale continuous residence time (FCRT)	N	n	Minimum	Maximum	Average	SD	p-value
BET Mozambique Channel	2	18	0.01 (0.34)	0.98 (23.41)	0.42 (10.06)	0.36 (8.66)	0.15
BET Seychelles	4	39	0.01 (0.13)	6.84 (164.24)	0.73 (17.44)	1.14 (27.25)	
YFT Mozambique Channel	14	152	0.001 (0.03)	6.65 (159.61)	0.69 (16.66)	0.86 (20.62)	<0.01
YFT Seychelles	13	297	0.001 (0.02)	3.73 (89.63)	0.24 (5.69)	0.37 (8.79)	
SKJ Mozambique Channel	11	185	0.001 (0.02)	1.6 (38.40)	0.27 (6.45)	0.27 (6.51)	-
Fine-scale continuous absence time (FCAT)							
BET Mozambique Channel	2	16	0.05 (1.11)	0.26 (6.26)	0.13 (3.05)	0.06 (1.48)	0.97
BET Seychelles	3	35	0.04 (1.00)	0.76 (18.20)	0.16 (3.95)	0.2 (4.80)	
YFT Mozambique Channel	8	138	0.002 (4.07)	4.07 (97.70)	0.15 (3.61)	0.37 (8.85)	0.01
YFT Seychelles	9	284	0.04 (2.53)	2.53 (60.61)	0.17 (4.19)	0.25 (6.01)	
SKJ Mozambique Channel	9	174	0.04 (1.01)	2.27 (54.57)	0.20 (4.70)	0.26 (6.27)	-

Figures

Fig. 1 Map of western Indian Ocean indicating the study area. The red triangles indicate the location of drifting fish aggregating devices (FADs) where acoustic telemetry experiments were conducted. The colored lines indicates the FAD drifts.
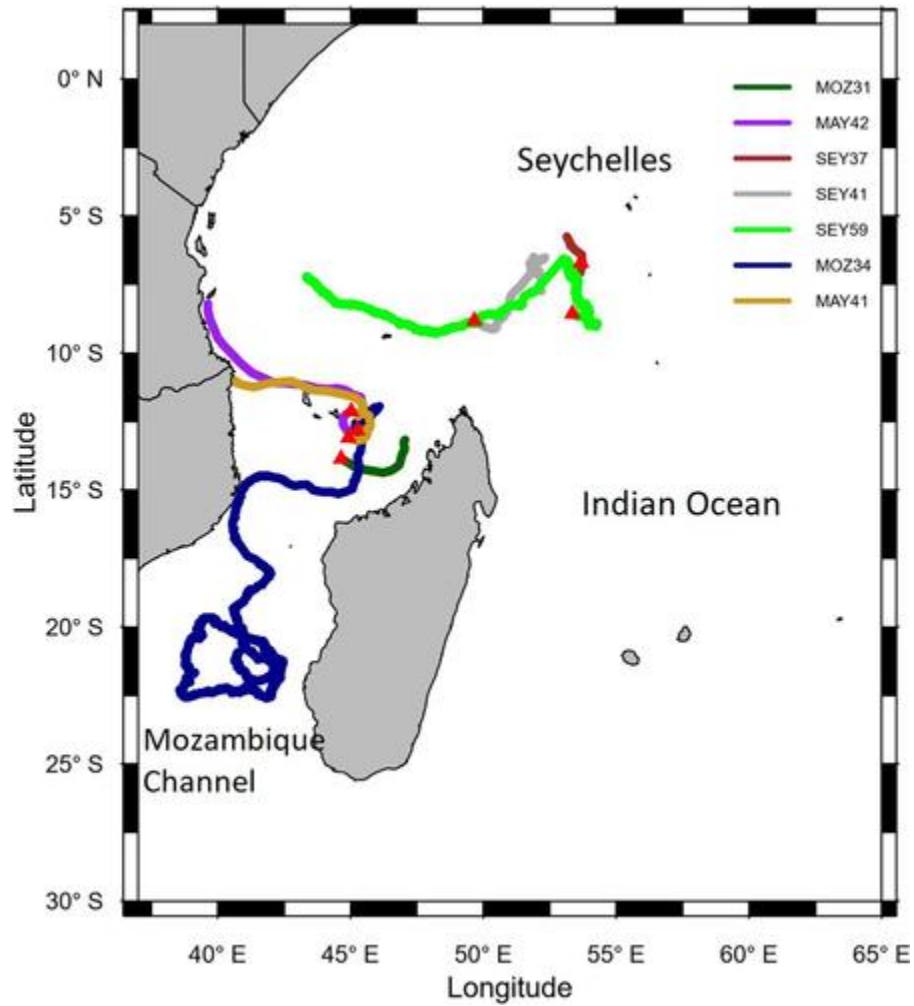
Fig. 2 Residence times for tagged tunas in the Mozambique Channel and Seychelles. Black bars correspond to the CRTs and white bars represent absences of 24 hours or more (CATs). The symbol ‡ marks CRTs which were interrupted due to fishing.

Fig. 3 Survival curves of CRTs for tunas tagged in the Indian Ocean. Dashed lines represents the best model fit.
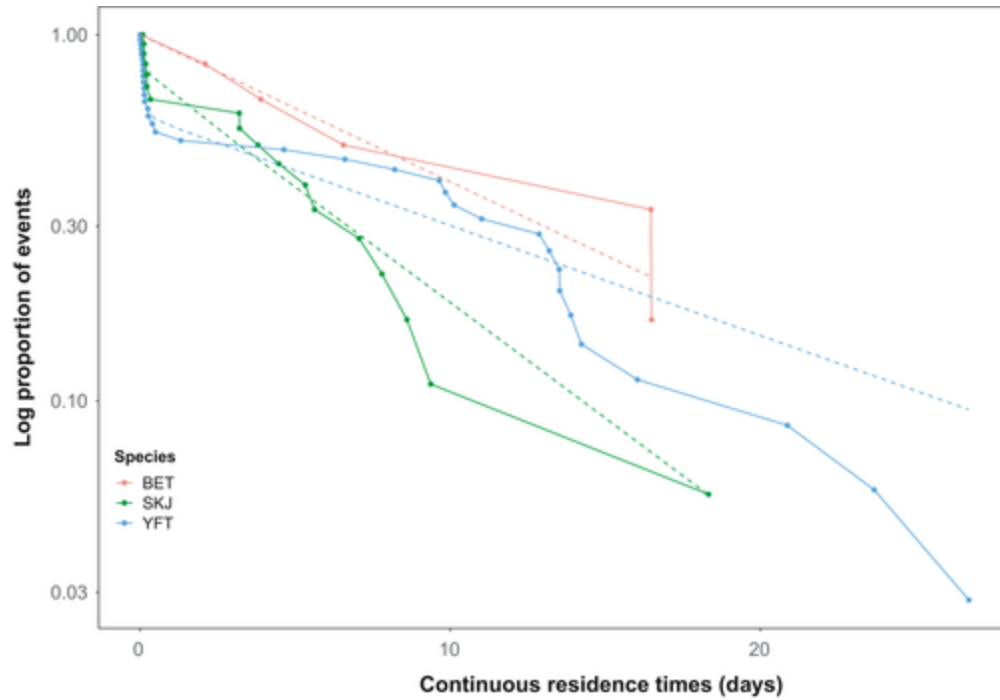
Fig. 4 Survival curves of FCATs (a) and FCRTs (b) for tunas tagged in the Mozambique Channel and Seychelles.
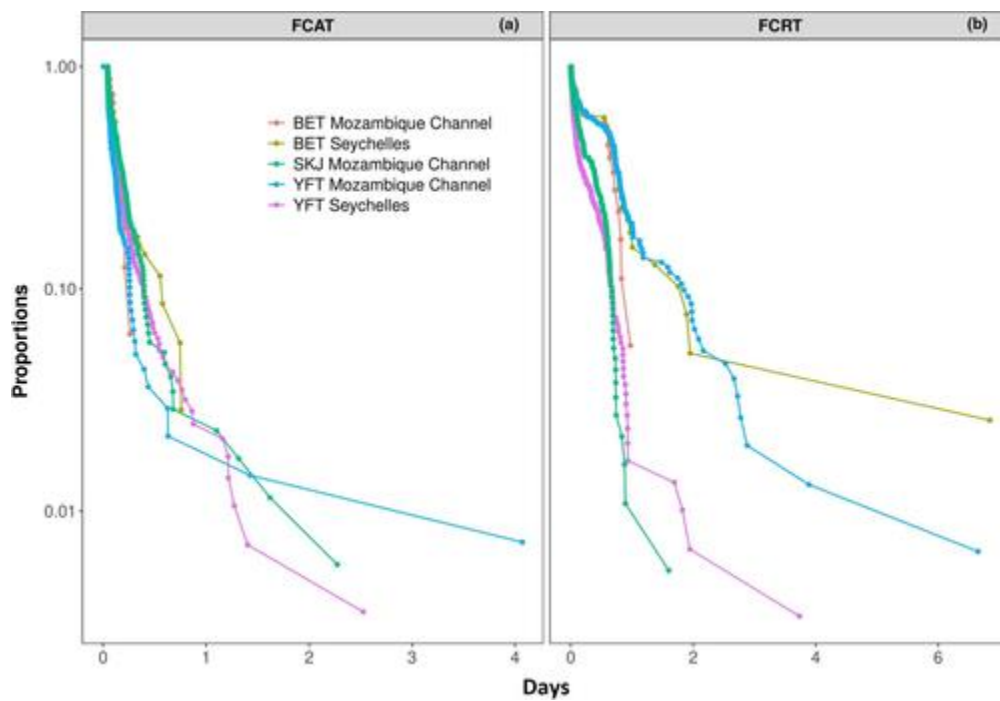
Fig. 5 Average index of residence for tunas tagged in the Mozambique Channel and Seychelles. Error bars indicate standard errors.
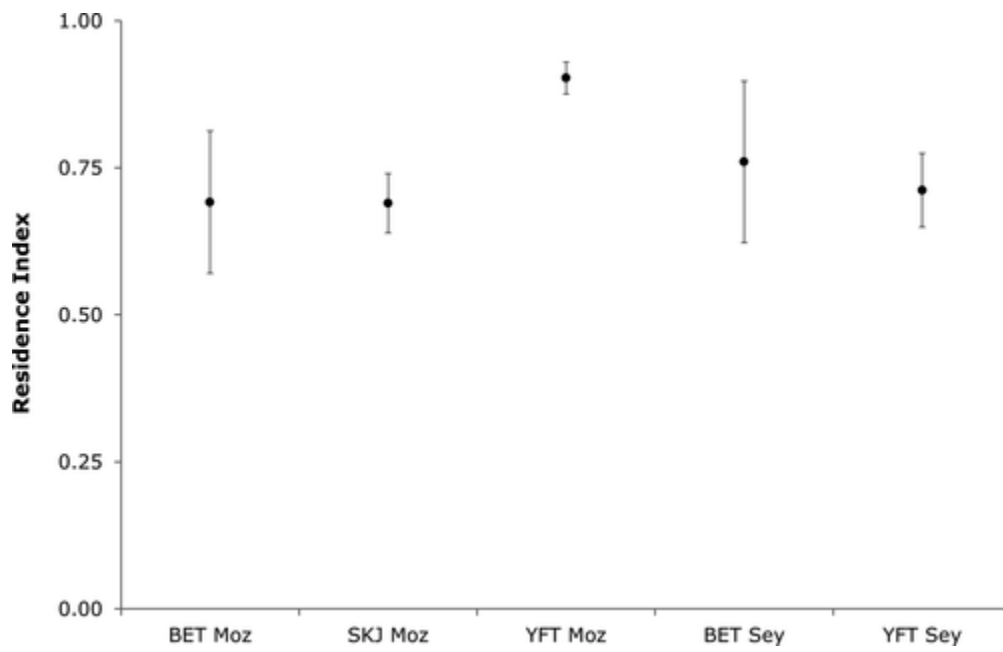
Fig. 6 Percentage number of departures and arrivals in each hour bin for tunas tagged in the Mozambique Channel (left) and Seychelles (right), n = number of fish. The numbers in parenthesis () indicates the number of arrival and departure events.