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Behavior of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye (*T. obsesus*) tunas associated with drifting fish aggregating devices (dFADs) in the Indian Ocean, assessed through acoustic telemetry

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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

1 | INTRODUCTION

For centuries, fishers have made use of floating objects to enhance the capture of fish (Dempster & Taquet, 2004; Freon & Dagorn, 2000). 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 (Dagorn et al., 2013; Hallier & Gaertner, 2008; Marsac et al., 2000). 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 policymakers. 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., Cayré, 1991; Dagorn et al., 2007; Govinden et al., 2013; Holland et al., 1990; Ohta & Kakuma, 2005; Robert et al., 2013; Rodriguez-Tress et al., 2017; Schaefer & Fuller, 2005). 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, 2014, 2016; Muir et al., 2012; Schaefer & Fuller, 2005, 2013), while only two have been conducted in the Indian Ocean (Dagorn, Pincock, et al., 2007; Forget et al., 2015) and one in the Atlantic Ocean (Tolotti et al., 2020). So far, very few studies have investigated the behavior of tunas between different regions within the same ocean.

Knowledge on the associative patterns of tunas at FADs is 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 (Capello et al., 2016; Gaertner et al., 2016; Katara 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. The two regions have distinct oceanographic characteristics and distributions of floating objects, which represents an opportunity to compare the behavior of tunas between the two regions. The Mozambique Channel is characterized by many meso-scale features such as anticyclonic eddies that propagate southwards (De Ruijter et al., 2002) and natural logs comprise a much larger proportion of the available floating objects in that area (Dagorn et al., 2013). In contrast, the Seychelles region is considered to be oceanographically more uniform and artificial dFADs contribute significantly to increasing the number of floating objects in this area (Dagorn et al., 2013). 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.

2 | MATERIALS AND METHODS

2.1 | Acoustic telemetry experiment

Four research cruises were carried out between March 2010 and April 2012 in the Mozambique Channel and the Seychelles area (Figure 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 seawater 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) (90 s nominal delay, 69 kHz, 1H) coded acoustic tag following standard internal tagging procedures as described in Dagorn, Pincock, et al., (2007). All tagged tunas were released within close proximity of the dFAD where captured. Tagging took place around seven dFADs 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 dFADs (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.

2.2 | Data analysis

2.2.1 | Residence and absence times

The amount of time tunas spent associated with a dFAD was investigated at two temporal scales. Firstly, the continuous

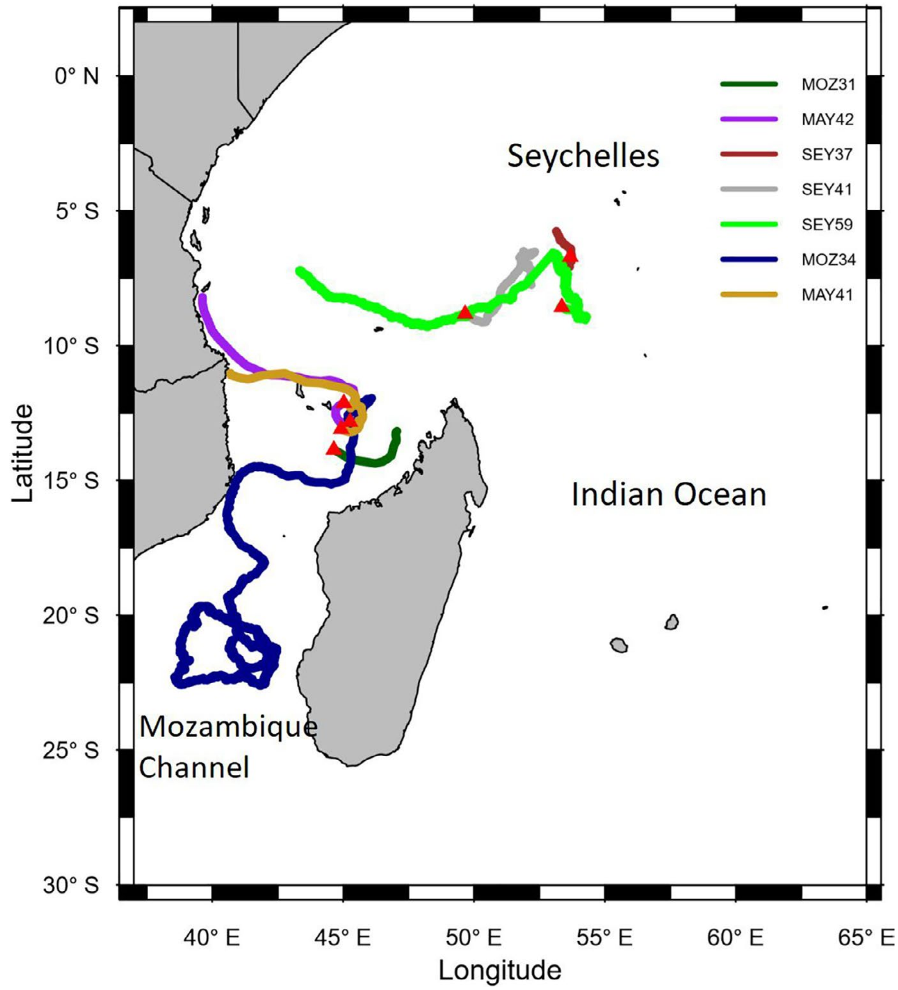


FIGURE 1 Map of western Indian Ocean indicating the study area. The red triangles indicate the location of drifting fish aggregating devices (FADs) where acoustic telemetry experiments were conducted. The colored lines indicates the FAD drifts

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

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) to identify which behavioral process best explains the data. 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 (R Core Team, 2016; Therneau, 2015) 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.

2.2.2 | Index of residence

The degree of association with dFADs 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.

2.2.3 | Diel periodicity

To examine the diel periodicity in the presence of tunas in each region, the daily acoustic detection data were 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.

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	$(b/(b + t))^{a}$

To elucidate any pattern in the arrival and departure time of tunas at dFADs 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 dFADs 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 & 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). The non-parametric Kruskal–Wallis test was used as the data did not meet the normality assumptions for a parametric test. All statistical analysis was carried out using software package R (R version 3.3.1) (R Core Team, 2016).

3 | RESULTS

The acoustic tagging experiment was performed at 7 different dFADs (4 in the Mozambique Channel and 3 in the Seychelles), see Table 1. 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 are provided in Table 1. All fish were monitored until they left the dFADs 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, while 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.

3.1 | Residence times

3.1.1 | 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 dFADs which lasted more than 24 hours (Figure 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

FIGURE 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

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, Figure 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, while 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 with 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 S1.

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

				Continuous Residence Time (Days)			
Area	**Species**	***N***	***n***	**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

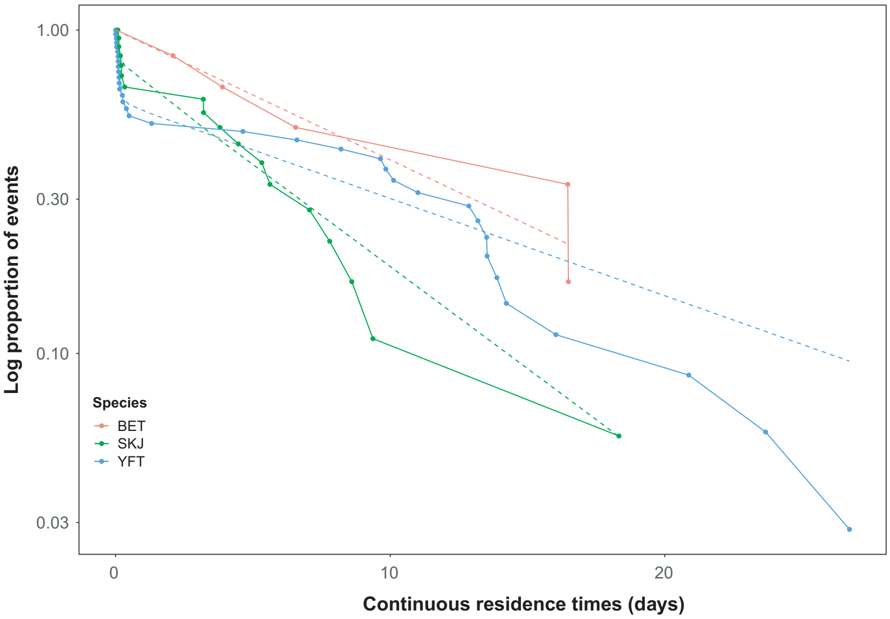


FIGURE 3 Survival curves of CRTs for tunas tagged in the Indian Ocean. Dashed lines represent the best model fit

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	

3.2 | 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 (16.7 hours) was nearly three times longer than in Seychelles (5.7 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 17.4 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, $p = 0.01$), while 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 4.7 hours (Table 5).

3.2.1 | Index of residence

The index of residence indicates that all tuna were strongly associated with the dFADs (Figure 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 on 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% (Figure 5).

3.2.2 | Diel patterns in detection

The FFT results showed clear 24-hour peaks in the detection for the majority of tunas (Figure S2). 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.

3.2.3 | Arrival and departure events

The percentage 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 (Figure 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 (Figure 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

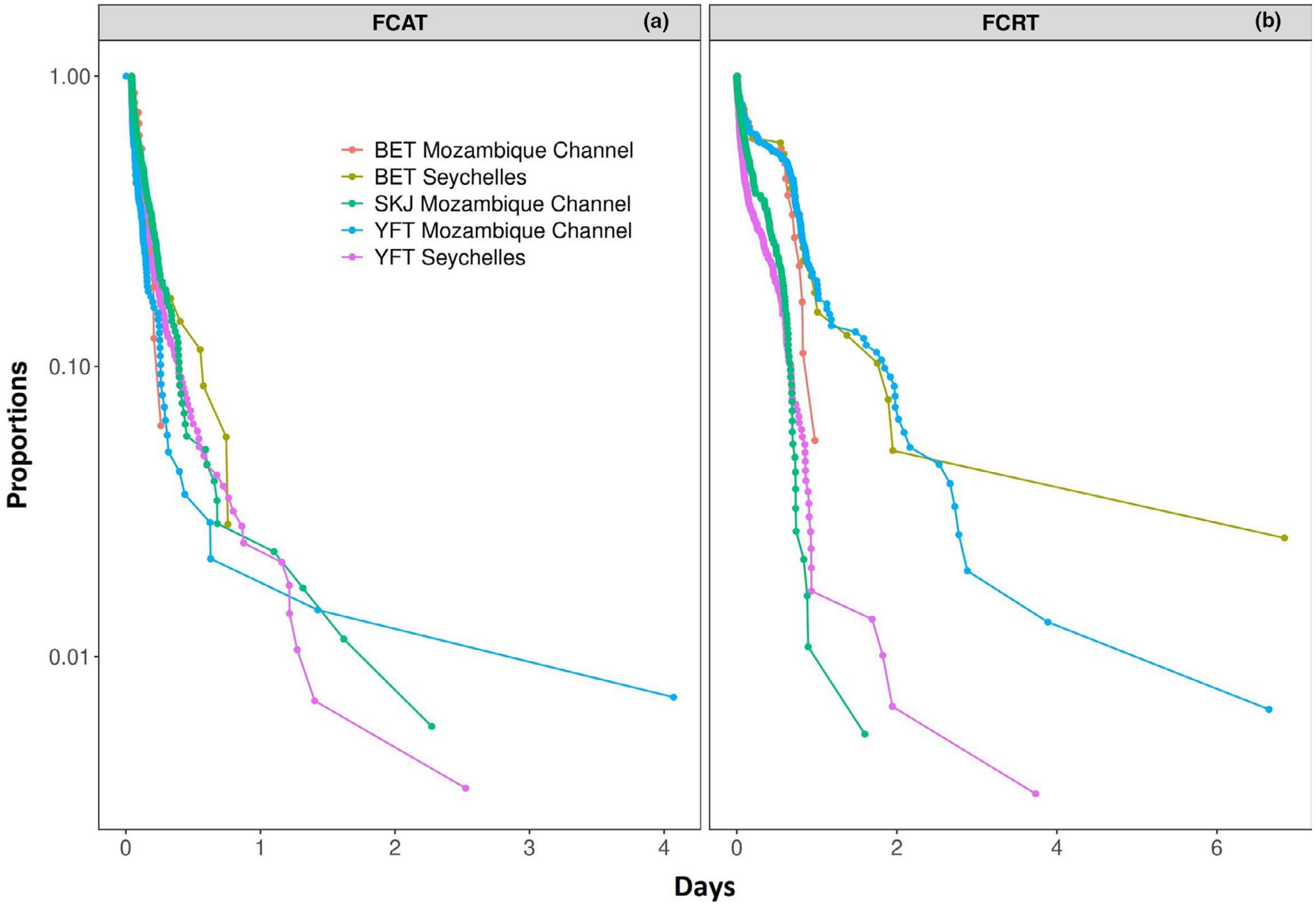


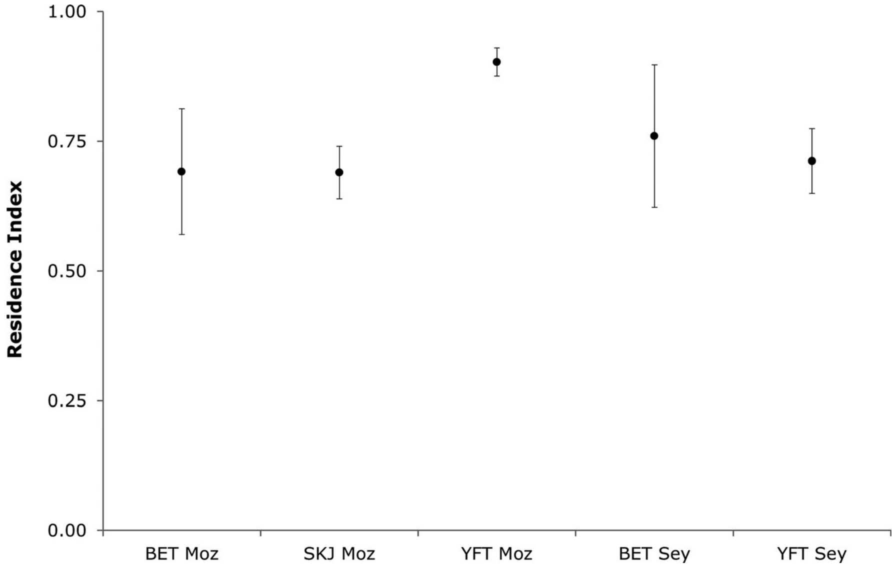
FIGURE 4 Survival curves of FCATs (a) and FCRTs (b) for tunas tagged in the Mozambique Channel and Seychelles

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)	-

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 (Figure 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 with 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; $p > 0.05$) (Figure 6).

FIGURE 5 Average index of residence for tunas tagged in the Mozambique Channel and Seychelles. Error bars indicate standard errors



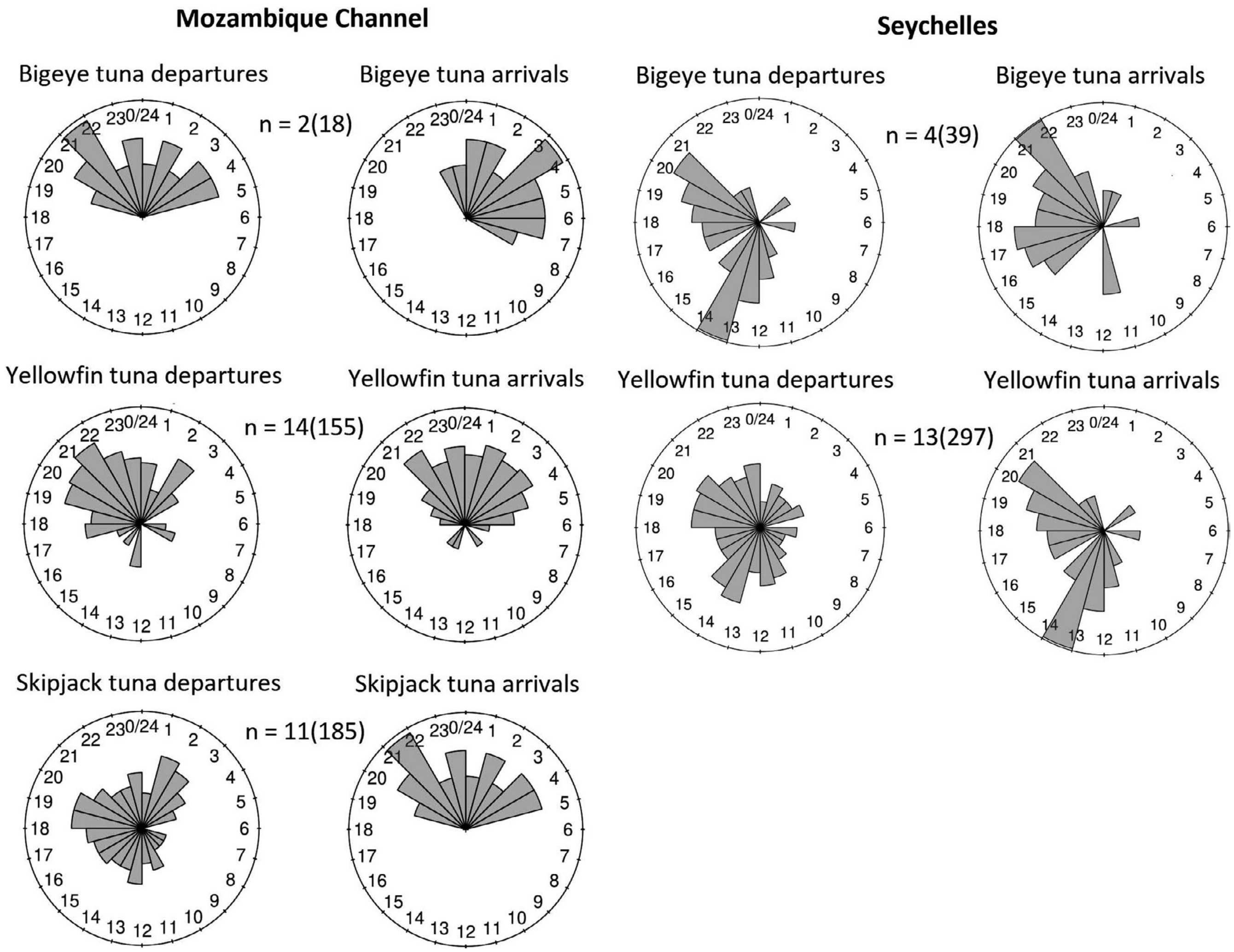


FIGURE 6 Percentage number of departures and arrivals in each hour bin for tunas tagged in the Mozambique Channel (left) and Seychelles (right), *n* = number of fish. The numbers in parenthesis () indicate the number of arrival and departure events

4 | DISCUSSION

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

4.1 | 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 comprise 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 was not significant. Similar short residence times for tunas at FADs were previously observed (e.g., Dagorn, Pincock, et al., 2007 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 dFADs 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 artifact 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, while 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, that is the behavioral processes are time independent, which infers that the probability for tunas to leave/join a dFAD does not depend on the time they have spent at or away from the dFAD.

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 with other studies carried out in the Indian Ocean, Dagorn, Pincock, et al., (2007) 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, while 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, and 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, while Dagorn, Pincock, et al., (2007) 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., Matsumoto et al., 2014, 2016; Rodriguez-Tress et al., 2017; Schaefer & Fuller, 2013; 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, and presence of predators

(Ohta & Kakuma, 2005; Robert et al., 2013). The proximity/density of other floating objects in the vicinity of a dFAD could potentially influence the residence times. In a recent study investigating the impacts of FAD densities on the behavior of tunas, Pérez et al., (2020) observed a significant decrease in residence times of tunas at FADs with increasing inter-FAD distances. The authors concluded that observed trend could be driven by complex processes involving inter-individual interactions at FADs (meeting point hypothesis) or due to prey availability (Pérez et al., 2020).

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, Holland, et al., 2007; 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 dFADs as the array is constantly changing. Observing long-scale returns to the same dFADs, could in theory, depend on the local densities of floating objects, for example, the distance between floating objects. This theory is supported by the Pérez et al., (2020) study whereby it was observed that tunas spent more time away from FADs as the inter-FAD distance increased. 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 with the Mozambique Channel and found that FADs contribute 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 regard 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.

4.2 | 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 with 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 with 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 with 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 with the daytime. In addition, the nighttime departure events of yellowfin and bigeye tuna were significantly higher, while 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 & 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 with 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 with 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 with 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.

4.3 | 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 dFADs 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, that is, 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 dFADs, which would depend on other factors operating over longer timescales.

5 | CONCLUSION

This study contributes toward a better understanding of the associative behavior of tropical tunas with dFADs 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 dFADs before returning and confirmed findings of other studies showing that yellowfin tuna can make long excursions and return to the same dFADs. In addition, we show that, in the case of yellowfin tuna, regional comparisons of the associative behavior are 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 dFADs. 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 modeling 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 dFADs.

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CONFLICT OF INTERESTS

The authors declare to have no conflict of interest.

AUTHOR CONTRIBUTIONS

LD, FF, and JDF designed the study; LD, FF, JDF, and 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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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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