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Associative behavior of yellowfin *Thunnus albacares*, skipjack *Katsuwonus pelamis*, and bigeye tuna *T. obesus* at anchored fish aggregating devices (FADs) off the coast of Mauritius

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ABSTRACT: Anchored fish aggregating devices (FADs) are deployed by fishermen worldwide to facilitate the capture of pelagic fish. We investigated the associative behavior of yellowfin *Thunnus albacares*, skipjack *Katsuwonus pelamis*, and bigeye tuna *T. obesus* in an array of anchored FADs off the coast of Mauritius (southwestern Indian Ocean) using passive acoustic telemetry. Our results suggest that yellowfin and bigeye tuna have longer FAD residence times than skipjack tuna. The survival curves based on the continuous residence times for bigeye and skipjack tuna were best explained by single exponential models, indicating time-independent associative processes and characteristic timescales of 4.3 and 0.9 d, respectively. Continuous residence times of yellowfin tuna were best explained by time-dependent power law models, but the single exponential model (characteristic timescale of 6.5 d) also fit the data well. The analysis of absence times (time between 2 FAD associations) revealed that single exponential models fit the data for all 3 species (characteristic timescales of 1.3, 5, and 2.7 d for yellowfin, skipjack, and bigeye, respectively), with a time-dependent sigmoidal component at short timescales for skipjack and bigeye tuna, ascribed to diel behavior and the short inter-FAD distances of the array. Our results are consistent with those of previous studies but also reveal common behavioral patterns among species and suggest that inter-FAD distances affect absence times but not residence times. In other words, high densities of FADs tend to decrease the amount of time tuna spend unassociated with FADs.

KEY WORDS: Fish-aggregating device · Tropical tunas · Behavioral variability · Acoustic tagging · Residence time · Survival analysis

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INTRODUCTION

Floating objects aggregate tropical tunas, including yellowfin *Thunnus albacares*, skipjack *Katsuwonus pelamis*, and bigeye *T. obesus*, which explains why

both artisanal and large-scale commercial vessels have been using floating objects to enhance their catches (Fonteneau et al. 2000). Depending on the fishery, fish aggregating devices (FADs) are either free to drift with currents and equipped with buoys to

locate them (Lopez et al. 2014) or anchored near shore (Dempster & Taquet 2004). Observing the behavior of tuna around FADs has become a priority for scientists to gain a better understanding of this striking associative behavior (Holland et al. 1990) and to assess the impacts of FAD-based fisheries on tuna populations, as drifting FADs have begun to be used in large numbers in all oceans (Dagorn et al. 2013). Four main techniques have been used to study the behavior of tuna around FADs: acoustic telemetry with active tracking (Yuen 1970, Holland et al. 1990, Cayré 1991, Dagorn et al. 2000), passive acoustic telemetry (Klimley & Holloway 1999, Ohta & Kakuma 2005, Dagorn et al. 2007, Mitsunaga et al. 2012, Robert et al. 2012, Matsumoto et al. 2014), acoustic surveys (Doray et al. 2006, Moreno et al. 2007, Trygonis et al. 2016), and archival tags (Schaefer & Fuller 2010). These studies were conducted in different years, seasons, and oceanic regions, with different FAD types.

Only a few studies have characterized the associative behavior of the 3 main exploited tropical tuna species (yellowfin, skipjack, and bigeye) simultaneously to discern species-specific behavioral traits (Leroy et al. 2009, Schaefer & Fuller 2013, Forget et al. 2015). The latter 2 studies focused on the vertical and horizontal behavior of tuna on a diel timescale and did not investigate the associative dynamics on larger timescales. Moreover, as only few individual drifting FADs were equipped with receivers (neighboring FADs were not instrumented), these studies could not investigate the inter-FAD movements of fish. Only Leroy et al. (2009) monitored the associative behavior of the 3 species in an instrumented FAD array for several weeks. However, that study could not provide information on the absence times (i.e. the time between 2 consecutive FAD associations), since very few excursions and FAD exchanges were observed. Comparing the species-specific associative behavior of the 3 main tropical tuna species in the same FAD array on large timescales (omitting the diel excursions out of the FAD) is essential for determining the main mechanisms that drive their associative dynamics. For this purpose, both residence and absence times need to be measured.

Using survival analysis, Robert et al. (2013) observed that the FAD-associative dynamics of yellowfin tuna in Hawaii (USA) could be best explained by time-independent exponential models, and they provided characteristic timescales for the residence and absence times of this species in this area. Such analyses, conducted on a species-specific basis, are key to parameterizing the behavioral models and construct-

ing scenarios on the impact of FADs on tuna populations (Sempo et al. 2013, Capello et al. 2015, 2016).

In this study, we employed similar approaches as Robert et al. (2013) to simultaneously investigate the associative behavior of 3 tuna species (yellowfin, skipjack, and bigeye) in an anchored FAD array using acoustic telemetry off the coast of Mauritius in the southwestern Indian Ocean. The objective of this study was to analyze both residence and absence times to characterize the species-specific associative dynamics. More specifically, we tested the null hypothesis that the 3 tuna species exhibited the same behavioral traits, in terms of the time spent at FADs (i.e. residence time), and the time spent in between 2 FAD associations (i.e. absence time). Finally, through model fitting, we investigated the mechanisms that underlie the FAD-associated fish dynamics for the 3 species.

MATERIALS AND METHODS

Acoustic tagging experiment

The anchored FAD array in Mauritius consists of 23 FADs, with the majority deployed off the west coast of the island. A group of 9 neighboring FADs on the western side of the island were successfully equipped with VR2W acoustic receivers (Vemco) (Fig. 1). Two range tests were performed on 28 and 29 September 2010, showing 93% of the emissions recorded up to 300 m from the receivers (maximum distance tested). Distances between neighboring equipped FADs varied between 2.5 and 14.5 km, and the total extent of the instrumented FAD array was 34.7 km in latitude and 31.6 km in longitude. The acoustic receivers were fixed to the main mooring line of the FADs using stainless steel U-bolts and heavy duty cable ties at a depth of 10 m below the FAD. The receivers were deployed between 28 September and 8 October 2010 and data were recovered the first time between 11 and 15 November 2010. FAD X2 (see Fig. 1) broke on an unknown date and was recovered with its acoustic receiver on 19 October 2010. Data from this receiver were not considered in this study due to the short time window for data collection. The acoustic receiver on FAD X1 was lost during retrieval; therefore, no data were available for this FAD. Ultimately, 7 FADs were successfully monitored throughout the first study period. A second recovery operation was carried out 6 mo after the first one but did not provide valuable data since most of the FADs were broken and lost after tropical

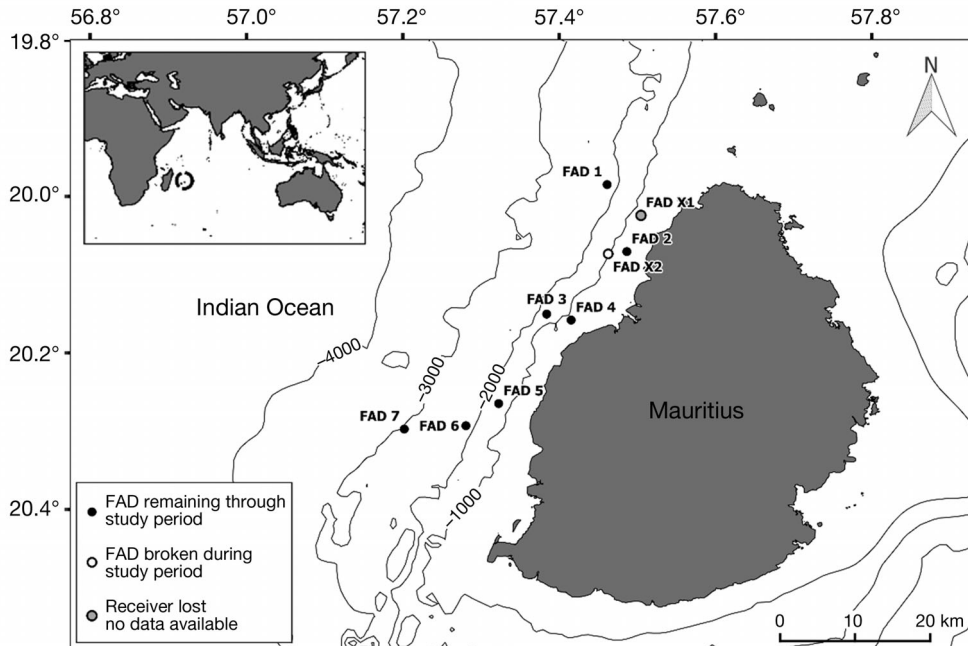


Fig. 1. Instrumented fish aggregating device (FAD) array off the coast of Mauritius. Coastal line and bathymetry sources: Openstreetmap (PGS) (<http://openstreetmapdata.com/>) and Gebco gridded global bathymetry data from the British Oceanographic Data Centre

storms during the austral summer. Our dataset is thus limited to the first monitoring period. Acoustic tagging operations were conducted between 1 and 8 October 2010. Yellowfin, skipjack, and bigeye tuna were caught around the instrumented FADs using rods and reels with artificial lures. Acoustic transmitters (V13 and V13P 1H at 69 kHz with a 50 to 130 s delay and V9 1L at 69 kHz with a 50 to 130 s delay) were surgically implanted into the peritoneal cavities of 52 healthy individuals of the 3 tuna species (26 yellowfin, 19 skipjack, 7 bigeye) following procedures described by Dagorn et al. (2007). Fish were tagged opportunistically through the FAD array (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m570p213_supp1.pdf). Mean \pm SD fork length (FL) per species was 60.9 ± 9.7 cm for yellowfin (min = 46 cm, max = 81 cm), 47.9 ± 5.2 cm for skipjack (min = 41 cm, max = 59 cm), and 53.0 ± 3.7 cm for bigeye tuna (min = 48 cm, max = 60 cm).

Fishing and tagging operations were performed by scientists trained in animal experimentation and experimental fish surgery under the authority of the National Veterinary School of Nantes (France).

Data analysis

Calculating continuous residence and absence times

To estimate the amount of time spent by tuna at FADs, we calculated the continuous residence times (CRTs), which were originally developed by Ohta &

Kakuma (2005). CRTs allowed for the conversion of the discrete pattern of acoustic detections into a continuous estimator of fish presence or absence around FADs. In this manner, the detections per individual recorded at the same FAD separated by less than a predefined period, called the maximum blanking period (MBP, see Capello et al. 2015), were grouped into 1 CRT. Furthermore, each time a tagged fish was detected at a different FAD, the CRT recorded at the FAD of origin was stopped at the last detection, even if the interval between subsequent detections was smaller than the MBP. The choice of the MBP duration depends on the aim of the study and on the empirical knowledge of fish behavior. To avoid the effect of fine-scale movements related to diel behavior patterns (Schaefer & Fuller 2013, Forget et al. 2015), a 24 h MBP was chosen. This empirical choice, common to many studies (e.g. Ohta & Kakuma 2005, Dagorn et al. 2007, Robert et al. 2013), was recently supported by quantitative arguments (Capello et al. 2015). Consequently, our study focused on temporal scales of days and weeks. The R code used for the CRT calculation is available as supplementary material at www.int-res.com/articles/suppl/m570p213_supp2.zip. Analogous to the CRT construction detailed above, periods between 2 consecutive CRTs represented the continuous absence times (CATs), namely the estimated amount of time spent by fish out of the acoustic receiver's detection range around the FAD. Finally, total residence time (TRT) in the array was calculated for each fish as the time difference between the beginning of the first CRT and the end of the last CRT.

Survival analyses of CRT and CAT

For each species, survival curves were constructed for both CRTs and CATs from the fraction of CRTs/CATs that were shorter than a given time, t (Robert et al. 2013, Capello et al. 2015). The survival curves were fitted according to various models to examine the evolution of departures and association rates through time. Following the methodology of Robert et al. (2013), 3 different survival models were considered: (1) simple exponential, (2) double exponential, and (3) power law. The exponential model assumes a constant rate of failure events over time and as such, expresses a memoryless process for the departure and arrival of the tagged fish from and to the FAD. In addition, a double exponential model allows for 2 subpopulations of CRT or CAT, with each one characterized by its own probability of departure and arrival. This model assumes that 2 behavioral modes are manifested by either 2 populations of tagged fish or a unique population. On the other hand, a power law survival model involves a time-dependent probability of failure events. In the case of CRTs (CATs), this model assumes that the probability of departing from (arriving at) the FAD decreases with time. Table 1 provides a summary of all the models employed in this study. For all models, the analytical formula for survival curves $S(t)$ was constrained by the normalization condition $S(0) = 1$.

The fit of the survival curves of CRTs was conducted with data collected from a specific FAD (FAD 6), where each of the 3 species manifested at least 10 CRTs, a sufficient number to run a consistent survival analysis (Robert et al. 2013). For CATs, despite having more than 10 data points for each species, the above-mentioned models could not fit the data well at short timescales (particularly for bigeye tuna). Therefore, we also considered time-dependent sigmoidal models. Sigmoidal models incorporate the presence of a characteristic timescale where the majority of the events takes place (e.g. see Capello et al. 2015). For CATs, this translates to an increased probability of reaching a FAD when the duration of the excursions attains a characteristic value. In our analysis, sigmoidal models were combined with exponential models to accurately fit the survival curves of CATs on both short and long timescales.

The best model was selected by the significance of parameters, comparison of Akaike's information criterion (AIC; Akaike 1973) values, and quantile-quantile plots (Robert et al. 2013). As a rule, models were

Table 1. Models used to fit the survival curves of continuous residence times and continuous absence times as a function of time, t

Model type	Analytic formula
Single exponential	$\exp(-at)$
Double exponential	$p \exp(-at) + (1 - p) \exp(-bt)$
Power law	$(b/(b + t))^a$
Sigmoidal	$(1 + c)/(c + \exp(dt))$
Sigmoidal + exponential	$1/(1 + c \exp(dt)) + (1 - 1/(1 + c)) \exp(-at)$

discarded if one or more parameters were not significantly different from 0 at the 0.05 threshold based on the p-value of the t-statistic. The overall analysis was performed using R (CRAN, R version 3.2.1). Model fitting was conducted with the R package 'minpack.lm' (version 1.2-0) using the 'nlsLM' function. The survival curves were compared through the logrank statistical test, using the R package 'survival' (version 2.38-3), with the null hypothesis of similarity between curves. The null hypothesis was rejected at the 0.05 threshold, and the Bonferroni correction was applied in the case of multiple pairwise tests.

RESULTS

In total, 49 tagged tuna were detected in the instrumented FAD array, including 26 yellowfin, 16 skipjack, and 7 bigeye (Fig. 2, and see Table S1 in Supplement 1). One of the skipjack only had a single detection and was thus removed from subsequent analysis. The total number of CRTs (CATs) recorded in the array was 61 (35) for yellowfin, 44 (29) for skipjack, and 38 (31) for bigeye tuna (Table S2 in Supplement 1). On average, yellowfin and bigeye tuna exhibited longer residency in the FAD array (Table 2). The mean TRT was 30.1 d for yellowfin, 17.6 d for skipjack, and 35.3 d for bigeye (Table 2). Maximum TRT for each species was 45.1, 40.9, and 42 d, respec-

Table 2. Average continuous residence time (CRT), continuous absence time (CAT), and total residence time (TRT) in days, recorded for each species of tuna (YFT: yellowfin *Thunnus albacares*, SKJ: skipjack *Katsuwonus pelamis*, BET: bigeye *T. obesus*). Values in parentheses indicate the standard deviation

	YFT	SKJ	BET
CRT	9.6 (11.4)	2.5 (4.4)	5.2 (5.9)
CAT	1.4 (1.9)	2.9 (6.7)	0.8 (0.58)
TRT	30.1 (13.2)	17.6 (14.3)	35.3 (7.0)

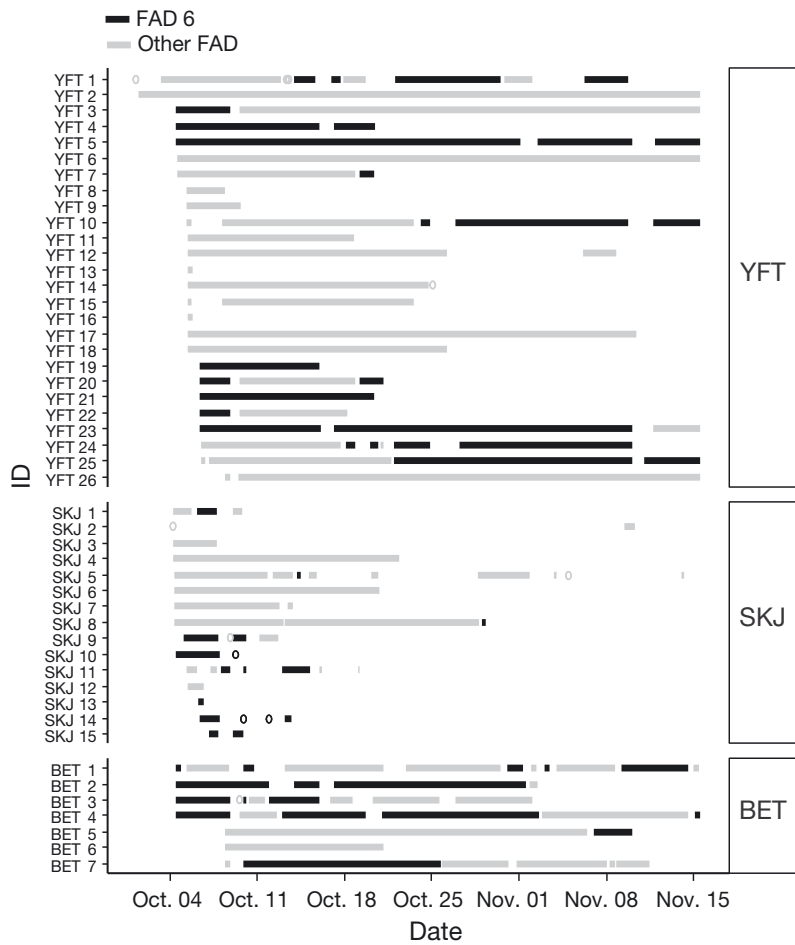


Fig. 2. Schematic representation of the pattern of continuous residence times (CRTs) obtained for the tagged tuna that were detected within the FAD array. Each line corresponds to one individual (species abbreviations as in Table 2; also see Table S1), and each bar corresponds to one CRT, with the length of the bar indicating the CRT duration. The points represent short CRTs that would not be visible otherwise. Black bars and points denote the CRTs recorded at fish aggregating device (FAD) 6; grey bars and points denote all the other FADs

tively, which is similar to the receiver deployment time. On average, yellowfin and bigeye tuna exhibited longer CRTs than skipjack, while skipjack had higher average CATs (Table 2).

The FAD array was heterogeneously occupied by the 3 tuna species, with yellowfin being associated with both the southern (FADs 5 and 6) and the northern FADs (FAD 1), skipjack spending the majority of their association time at the center of the array (FAD 3), and bigeye essentially localized in the southern FADs (FADs 6 and 7; Fig. 3). Similarly, the number of CRTs per FAD varied by species, and one FAD (FAD 6) recorded the highest number of CRTs for all species (Table S2).

The survival analysis of CRTs recorded over the entire FAD array confirmed species-dependent residence times, with yellowfin tuna spending the longest time associated to the FADs, and skipjack spending the shortest amount of time (Fig. 4a). All p-values of the logrank test of the pairwise comparison among species were below the 5% threshold (Table S3 in Supplement 1); however, when the Bonferroni correction was applied (significance threshold lowered to 0.016), only the comparison between yellowfin and skipjack tuna resulted in significantly different residence times ($p < 0.001$). The survival curves of the CRTs recorded from fish detected at FAD 6 highlighted the distinct associative patterns of skipjack (Fig. 4b and Table S3).

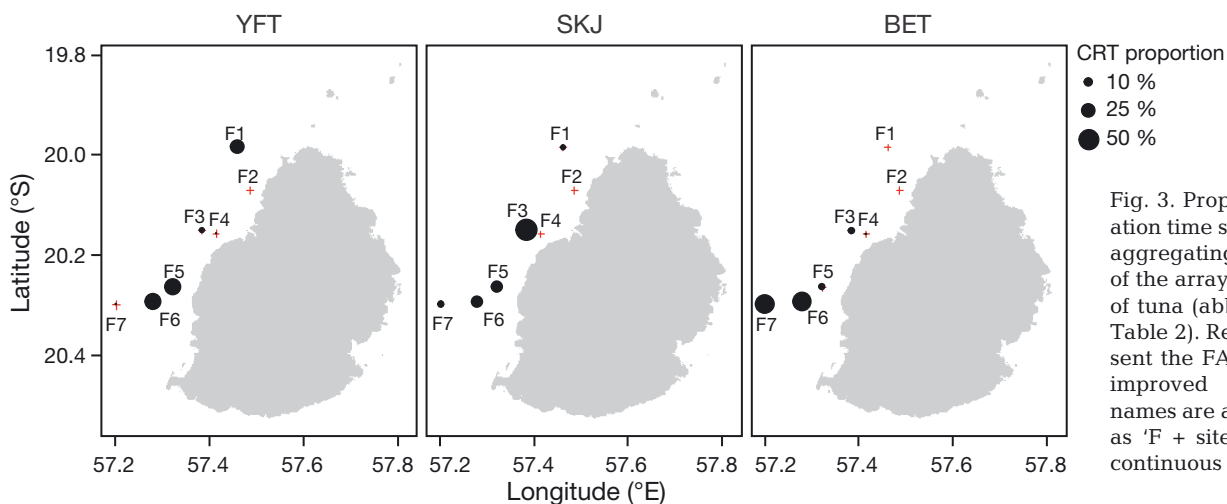


Fig. 3. Proportion of association time spent at each fish aggregating device (FAD) of the array by each species of tuna (abbreviations as in Table 2). Red crosses represent the FAD positions. For improved visibility, FAD names are abbreviated here as 'F + site number'; CRT: continuous residence time

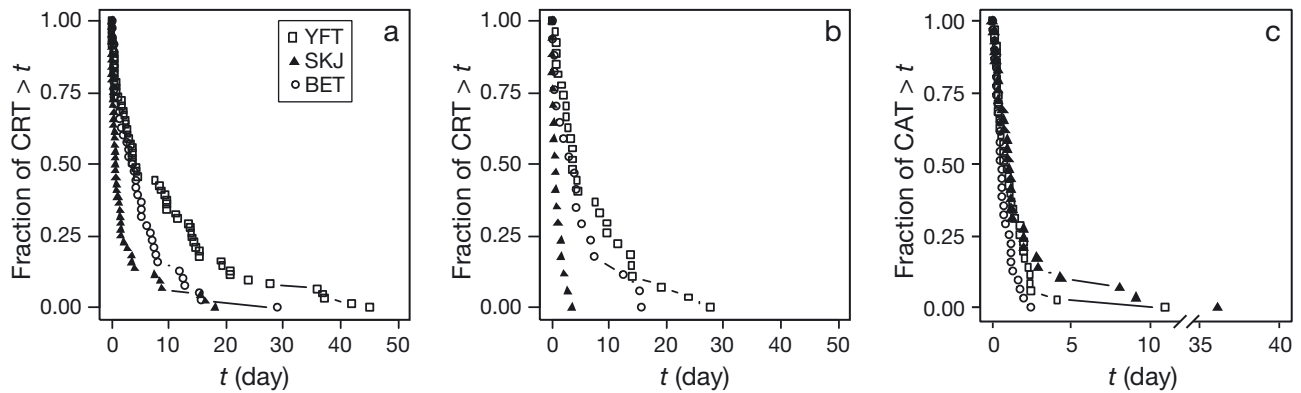


Fig. 4. Survival curves of continuous residence times (CRT) recorded for (a) the entire fish aggregating device (FAD) array and (b) FAD 6, and (c) continuous absence times (CAT) recorded for yellowfin *Thunnus albacares* (squares), skipjack *Katsuwonus pelamis* (triangles), and bigeye tuna *T. obesus* (circles). Species abbreviations as in Table 2

Bigeye and yellowfin tuna both displayed longer and similar FAD residence times ($p = 0.242$) compared to the shorter residence times of skipjack, which were significantly different from both species at FAD 6 ($p < 0.001$ for the comparison with bigeye and $p < 0.001$ with yellowfin). The logrank test of comparison conducted on the survival curves of CATs (Fig. 4c and Table S3) revealed a similarity between yellowfin and skipjack tuna ($p = 0.4$), which both displayed longer absence times. A significant difference was found between the CATs of bigeye and skipjack tuna ($p = 0.01$), while a marginally significant difference was found between yellowfin and bigeye tuna ($p = 0.033$).

The survival curves of CRTs recorded at FAD 6 were best explained by a single exponential model for both bigeye and skipjack tuna (Table 3, Figs. S1 & S2 in Supplement 1). For all species, the double exponential model was rejected because the fitted parameter related to the shortest timescale (a in Table 3) was not significantly different from 0 ($p > 0.05$). Similarly, the fitted parameters of the power law models for bigeye and skipjack tuna were not significant. Alternatively, for yellowfin tuna, both the single exponential and the power law models showed significant fit parameters. Despite AIC values favoring the power law model, the quantile-quantile plots (Fig. S2) demonstrated the proximity of the exponential and the power law fits.

Considering the optimized exponents of the single exponential model (a in Table 3) for all species, the characteristic residence timescales ($1/a$) were 6.5, 0.9,

and 4.3 d for yellowfin, skipjack, and bigeye tuna, respectively.

Finally, the fits of the survival curves of CATs revealed an exponential model for yellowfin tuna, with a characteristic absence timescale ($1/a$ in Table 4) of 1.3 d. For skipjack and bigeye tuna, the best-fit model was an exponential model with a sigmoidal component on short timescales (Figs. S3 & S4 in Supplement 1 and Table 4). The sigmoidal component manifested a characteristic timescale of approximately 12 h for skipjack and 6 h for bigeye tuna. The

Table 3. Results of the fits of continuous residence times recorded at fish aggregating device (FAD) 6 for the 3 species of tuna (abbreviations as in Table 2). The models and corresponding parameters optimized in the fits are summarized in Table 1 (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$). AIC: Akaike's information criterion

Survival curve	Model	Parameter	Estimate (SE)	Pr(> t)	AIC
YFT	Single exp.	a	0.153 (0.005)	$< 2 \times 10^{-16}$ ***	-92.3
		b	0.350 (0.249)	0.17262	-98.8
	Power law	p	0.109 (0.034)	0.00368**	
		a	0.307 (0.346)	0.38333	
		b	3.728 (1.286)	0.00754**	-99.4
		b	21.187 (8.314)	0.01707*	
SKJ	Single exp.	a	1.147 (0.057)	2.73×10^{-13} ***	-52.1
		b	169.086 (93.583)	0.0909+	-77.4
	Power law	p	0.955 (0.038)	9.45×10^{-14} ***	
		a	0.116 (0.017)	7.35×10^{-6} ***	
		b	3.537 (1.977)	0.0925+	-53.7
		b	2.641 (1.701)	0.1401	
BET	Single exp.	a	0.231 (0.014)	6.5×10^{-12} ***	-45.4
		b	2.628 (1.753)	0.1545	-59.4
	Power law	p	0.180 (0.018)	4.99×10^{-8} ***	
		a	0.160 (0.060)	0.0173*	
		b	2.043 (0.850)	0.0286*	-48.5
		b	6.620 (3.517)	0.0781+	

Table 4. Results of the fits of continuous absence times for the 3 species of tuna (abbreviations as in Table 2). The models and corresponding parameters optimized in the fits are summarized in Table 1 (** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$). AIC: Akaike's information criterion

Survival curve	Model	Parameter	Estimate (SE)	Pr(> t)	AIC	
YFT	Single exp.	<i>a</i>	0.800 (0.020)	$< 2 \times 10^{-16}$ ***	-123.4	
		Sigmoid	<i>c</i>	0.389 (0.209)	0.0716 ⁺	-125.9
			<i>d</i>	0.985 (0.092)	2.04×10^{-12} ***	
	Sigmoid + exp.	<i>a</i>	0.706 (0.264)	0.0116*	-123.7	
		<i>c</i>	1.060 (0.524)	0.0512 ⁺		
		<i>d</i>	1.350 (0.558)	0.0212*		
SKJ	Single exp.	<i>a</i>	0.686 (0.021)	$< 2 \times 10^{-16}$ ***	-97.9	
		Sigmoid	<i>c</i>	0.430 (0.320)	0.19	-97.8
			<i>d</i>	0.871 (0.124)	1.27×10^{-7} ***	
	Sigmoid + exp.	<i>a</i>	0.201 (0.057)	0.00146**	-111.0	
		<i>c</i>	0.352 (0.070)	2.73×10^{-5} ***		
		<i>d</i>	1.978 (0.113)	2.94×10^{-16} ***		
BET	Single exp.	<i>a</i>	1.214 (0.050)	$< 2 \times 10^{-16}$ ***	-77.2	
		Sigmoid	<i>c</i>	2.791 (0.656)	0.000189***	-106.7
			<i>d</i>	2.635 (0.225)	1.01×10^{-12} ***	
	Sigmoid + exp.	<i>a</i>	0.365 (0.177)	0.0485*	-115.8	
		<i>c</i>	0.167 (0.032)	1.60×10^{-5} ***		
		<i>d</i>	3.907 (0.283)	2.82×10^{-14} ***		

exponential component indicated a longer timescale for absence times of 5.0 and 2.7 d for skipjack and bigeye, respectively. Alternatively, for all species, the power law and double exponential models either did not converge, or they led to values of the fitting parameters that were not significantly different from 0. Table 5 summarizes the characteristic timescales found from the model fits for all species.

DISCUSSION

Few studies have simultaneously monitored the associative behavior of yellowfin, skipjack, and bigeye tuna in the same experimental conditions. Schaefer & Fuller (2013) and Forget et al. (2015) compared the diel behavior of the 3 species at drifting FADs, and Leroy et al. (2009) compared the vertical and horizontal behavior of the 3 species at anchored FADs with few observations of absence times that did not lead to further analysis. However, a large amount of literature is available detailing acoustic tagging experiments that were conducted within an anchored FAD array on a single tuna species (Klimely & Holloway 1999, Mitsunaga et al. 2012, Robert et al. 2012, 2013, Matsumoto et al. 2014) or 2 species (yellowfin and bigeye: Ohta & Kakuma 2005, Dagorn et al. 2007; yellowfin and skipjack: Govinden et al. 2013).

Globally, the characteristic timescales found in this study are close to previous findings. The mean TRT calculated here for yellowfin (30.1 d) is comparable to times reported by Dagorn et al. (2007) and Robert et al. (2012), with 28.7 d and approximately 37 d, respectively. However, it is apparent that some TRTs for some yellowfin and bigeye were truncated in our study by the receiver retrieval (see Fig. 2). Robert et al. (2012) found a maximum TRT of 220.5 d for yellowfin, which indicates that this species has the potential to stay in a FAD array for longer periods than what we observed here. Alternatively, Dagorn et al. (2007) calculated a lower mean TRT for bigeye tuna (6.2 d, SD = 3.3 d) than was observed here (35.3 d, see Table 2). Despite the limited duration of our experiment, our monitoring timeframe allowed observation of several absence times longer than 24 h and also included several inter-FAD movements for all 3 spe-

cies. Therefore, the experimental duration is appropriate to address the objective of our study, i.e. comparing the association dynamics (residence and absence times) of the 3 tuna species. The mean CRT of 9.6 d for yellowfin (Table 2) is comparable with the 8 d reported by Dagorn et al. (2007) in Hawaii and is within the range of 6.4 to 12.8 d reported by Ohta & Kakuma (2005) in Okinawa, Japan. However, Govinden et al. (2013) reported 1 order of magnitude lower CRT for smaller yellowfin (33–53 cm FL) in the Maldives, with a mean of 0.66 d and a maximum of 2.8 d. Robert et al. (2012) found a mean CRT for small yellowfin tuna (<50 cm FL) of 4.05 d. If this CRT is similar to the results in our study, their 'large class' of yellowfin (>50 cm FL) showed a lower mean CRT that was nearly 6 times shorter (1.65 d) than that of our

Table 5. Characteristic timescales found from the fits of continuous residence times (CRT) and continuous absence times (CAT) for each species of tuna (abbreviations as in Table 2). The exponential timescale is obtained from the inverse of the parameter *a* of the single exponential model in Tables 3 & 4. The sigmoidal timescale is obtained from the inverse of the *d* parameter in Table 4

	YFT	SKJ	BET
Exponential timescale for CRT (d)	6.5	0.9	4.3
Sigmoidal timescale for CAT (h)	–	12	6
Exponential timescale for CAT (d)	1.3	5.0	2.7

study. The results of Mitsunaga et al. (2012), collected from a FAD array in the Philippines, observed CRTs of early juvenile yellowfin tuna (19–31 cm FL) of less than 6 d, were also comparable to those that we observed in this study. For bigeye tuna, the average CRT estimated in this study is very similar to that observed by Dagorn et al. (2007) near Hawaii, with 5.2 versus 4.8 d, respectively. The average skipjack CRT found in this study (2.5 d) was between the mean CRTs of 0.2 and 3.55 d, which were recorded during different months in the Maldives by Govinden et al. (2013). Matsumoto et al. (2014) recorded skipjack tuna CRTs from drifting FADs, with a mean of 2.3 d, which is consistent with those found from anchored FADs here.

As of yet, the observed differences in the residence times between species have not provided strong arguments toward species-specific behavioral traits because of the heterogeneous conditions of each experiment (e.g. different FAD-array locations and different environmental conditions), and the multiple (and still unknown) causative factors that may affect the associative behavior of tuna. Our study provides a robust frame for comparative analysis of the 3 main tuna species that associate with FADs. It is true that on the scale of a single FAD array, one may still have heterogeneous conditions, such as variable local biotic and abiotic factors influencing the environment surrounding each FAD (Capello et al. 2012). If each species occupies a different sub-portion of the array as observed in this study (Fig. 3), this might bias the interpretation of the results. For this reason, we conducted a comparative analysis by considering the residence times recorded at the same FAD (FAD 6) at the same time, thus ensuring the same spatio-temporal coverage for all species. The outcome of this analysis confirms the global patterns found in the entire FAD array and also those found in the previous literature, with skipjack displaying shorter residence times relative to bigeye and yellowfin tuna. Yellowfin and bigeye tuna exhibited similar residence times with FADs.

A possible source of variability in the associative behavior observed in this study compared to other studies may be ascribed to fish length and maturity. Graham et al. (2007) observed that yellowfin tuna experienced a rapid ontogenic shift in their diet during their growth, mainly at 45–50 cm FL. An increase in endothermic capability may allow them to feed in deeper, colder water masses compared to smaller individuals, which are likely more limited in their vertical movements by ambient temperature. Robert et al. (2012) argued that this shift could directly influence the associative behavior of yellowfin with FADs after

noting significantly shorter residence times in yellowfin tuna >50 cm FL, compared to individuals <50 cm FL. In our experiment, yellowfin size ranged from 46 to 81 cm FL. As only 4 individuals were under 50 cm and none were under the 45 cm threshold, it is unlikely that ontogenic shifts in the diet are a source of variability for this species in our experiment.

Concerning the modeling of residence times with exponential time-independent models and power law time-dependent models, only Robert et al. (2013) performed comparable survival analyses. In their study on acoustically tagged yellowfin tuna in Hawaii, the authors observed that the residence times were best fitted by time-independent, simple, and double exponential models. Here, we found that the skipjack and bigeye tuna CRTs were best fitted by single exponential models, whereas yellowfin tuna data were fitted by a power law model based on the AIC value alone. The simpler exponential model provided a good alternative, with significant parameters, and the quantile-quantile plot showed a good fit of the data. Single exponential models of the CRTs assumed a memoryless process, with constant probabilities of departure from the FADs. These models are the simplest and most parsimonious models that can be constructed to explain the observations. It is remarkable that, with only one fitting parameter and simple assumptions (time-independence), these models could fit the data with such high accuracies. On the other hand, in the literature of survival analysis, it is very common to have ambiguous results in the goodness of fits tests when discriminating exponential from power law models (Chu-Shore et al. 2010). Taking into account such ambiguity in the tests, the good fit of the data using the single exponential model as shown from the quantile-quantile plots and the principle of model parsimony, we cannot rule out the single exponential model for yellowfin tuna at this stage. For this reason, the null hypothesis that the 3 tuna species exhibit the same general mechanisms to describe their associative behaviors (i.e. a time-independent association dynamics) cannot be rejected based solely on our results.

Performing such survival analysis with model fitting is key in understanding the associative dynamics and the relevant temporal scales (Table 5). Simply considering the average CATs (Table 2) for skipjack and bigeye would be misleading, given that their dynamics follows 2 separate timescales, a sigmoidal diel excursion scale (of a few hours) and a longer exponential timescale (of several days). For the CRTs, in the presence of a single exponential model, the 2 methods (average and model fitting) should provide

the same characteristic scales. However, with few data points, the statistical average generally underestimates this timescale and has large variability. As such, the single exponential fits of CRTs (Table 5) allowed us to avoid this underestimation and better assess the timescale.

Finally, our study provides average values for absence times (Table 2) that are much shorter than those recorded for yellowfin tuna by Robert et al. (2012) (1.4 d for yellowfin tuna in our study versus 9.4 and 13.27 d for individuals above and below 50 cm in the study by Robert et al. 2012). Using survival analysis, Robert et al. (2013) found that an exponential type model could best fit their data of yellowfin tuna CATs. Despite having a short component timescale closer to the single exponential timescale that we found for yellowfin tuna in this study, it was still twice as high (2.8 versus 1.3 d, respectively; see Table 5). For skipjack and bigeye tuna, the performances of the exponential and power law models were very poor (or did not attain convergence), and for this reason, we had to consider a sigmoidal component in the fitting functions.

A possible and intuitive explanation for the sigmoidal component, which was not present in the survival curves analyzed by Robert et al. (2013), could be found in the FAD-array geometry of our experiment. Off the coast of Mauritius, FADs are closer to one another (distances ranging from 2.5 to 14.5 km between adjacent FADs) relative to those off the coast of Hawaii (7.3–31.1 km) or the Maldives (30–95 km). When a tagged individual departs from a FAD at night, due to the FAD array density and the proximity of the island limiting the swimming directions, it has a high probability of encountering another FAD within the array and associate with it. By construction (see 'Materials and methods' and Capello et al. 2015), this stops the CRT at the FAD of origin and generates a CAT corresponding to the duration of the diel excursion. This explanation is supported by the characteristic timescale of the sigmoidal component found to be approximately 12 h for skipjack and 6 h for bigeye tuna, which correspond to typical durations for diel excursions away from FADs found in other studies (Yuen 1970, Holland et al. 1990, Forget et al. 2015). When a tuna departs from a FAD, it has a higher probability of being detected at another FAD (i.e. higher probabilities to stop its absence time) when the inter-FAD distance is shorter, thus affecting the recorded CAT. The shorter CATs found in our study can be thus attributed to the inter-FAD distances of the FAD array in Mauritius, which are smaller than those found in previous studies.

Additional long-range exponential tails observed in the fits of the CAT survival curves (Table 4) were related to the random search of a fish for a FAD depending on initial departure orientation. This observation is supported by the fact that skipjack tuna, which were mostly located in the less dense part of the array (FAD 3), had the longest CATs and the longest exponential timescale (5 d). On the other hand, the calculated CRTs were mostly similar or longer than in previous studies despite the higher density of the FAD array in Mauritius. This would suggest that, all things being equal, an increase in the FAD density does not seem to lead to shorter CRTs, i.e. to a higher probability for a tuna to depart from a FAD, despite the smaller inter-FAD distance.

For tropical tuna purse seine fisheries, and in particular, fisheries in the Indian and Atlantic Oceans, scientists have noted a significant decrease in catches of free-swimming schools of tunas (Fonteneau et al. 2000). This is concomitant with the large increase in the numbers of FADs deployed by the fishing fleets (Guillotreau et al. 2011). The observed increase in the catches of tropical tuna at FADs relative to free-swimming schools can be explained in terms of a change in the fishing strategy (with fishermen being more oriented towards FAD sets), or in terms of a decrease in the number and/or size of free-swimming schools, or both. Our results suggest that the time a tuna spends away from a FAD (i.e. free-swimming) decreases with increased FAD density. Therefore, the possible effects of the FAD-array geometry observed in this study, as well as the species-specific behavioral traits outlined here, could have important implications for our understanding of the effects of FADs (in particular numbers of FADs) on tuna populations and on FAD management. More experiments are required to increase the size of our dataset, but we can already advance in the construction of behavioral models and scenarios based on the data and knowledge acquired here.

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