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Tuna aggregation dynamics at Drifting Fish Aggregating Devices: a view through the eyes of commercial echosounder buoys

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Abstract :

This study addresses novel questions on the dynamics of tuna aggregations around floating objects, using echosounder buoys data collected throughout the drifts of newly deployed Drifting Fish Aggregating Devices (DFADs) in the Atlantic Ocean (AO) and Indian Ocean (IO). Time series of presence/absence of tunas were obtained by supervised classification of acoustic data. To avoid biases related to the variability in individual DFAD soak times, a new approach was developed to estimate the average colonization time of new DFADs by tuna aggregations. We showed that tunas colonize DFADs after an average of 16 days in the AO, and 40 days in the IO. Moreover, the analysis indicated that the time span during which tuna aggregations occupy DFADs is driven by a time-independent process with short- and long-term residence modes. On average, DFADs were continuously occupied by tuna aggregations for 6 and 9 days in the IO and AO, respectively. The time between two consecutive aggregations at the same DFAD averaged 9 days in the IO and 5 days in the AO. Throughout their soak time after being colonized, DFADs remained occupied for a larger proportion of time in the AO (63%) than in the IO (45%).

Keywords : absence times, associative behaviour, colonization times, Drifting Fish Aggregating Devices (DFADs), echosounder buoys, residence times, tropical tunas

Introduction

Substantial development in the tropical tuna purse-seine fishery has occurred over recent decades and it now accounts for the majority of the world's tropical tuna catch (ISSF, 2019). The increasing trend in catches has been accompanied by regular technological developments of vessels and fishing tools (Gaertner and Pallarés, 2002; Fonteneau *et al.*, 2000; Torres-Irineo *et al.*, 2014). Since the early 1990s, these developments have included the deployment of artificial floating objects, known as drifting Fish Aggregating Devices (DFADs) used to increase fishery efficiency. This fishing mode exploits the behavioural trait of the target tuna species, skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*), to naturally aggregate around floating objects (see Fréon and Dagorn, 2000 and Castro *et al.*, 2002). Thousands of DFADs specifically designed to attract tunas, are deployed by purse seine fleets in all of the world's oceans to enhance their catches. Initial estimates put the number of DFADs operated annually across the three major oceans in the range of 50,000 and 100,000 (Baske *et al.*, 2012; Scott and Lopez, 2014; Gershman *et al.*, 2015). Furthermore, the scale at which this fishing gear is used has quadrupled in less than a decade, in both the Atlantic and Indian oceans (Fonteneau *et al.*, 2015; Maufroy *et al.*, 2017). Over the past 30 years, this fishing mode has been significantly improved through the sequential introduction of new technologies (radio, GPS and echosounder buoys), with the latter now providing skippers and fleet managers with detailed information on the location and biomass associated with DFADs (Lopez *et al.*, 2014). In recent years, more than half of the world's purse seine catch of tropical tunas has come from DFAD fishing (Dagorn *et al.*, 2013; Fonteneau *et al.*, 2013).

The mechanisms underlying the associative behaviour of tropical tunas with floating objects remain poorly understood, despite the proposal of numerous hypotheses (see Fréon and Dagorn, 2000 and Castro *et al.*, 2002). As a consequence of the massive increase in the use of DFADs in the recent years, improving knowledge on the associative behaviour of tropical tunas with floating objects has become a key research priority. Primary areas of concern include the concomitant changes in catchability of tunas at floating objects as well as the understanding of the impact of DFADs on their ecology and that of other associated fauna. To date, most research efforts have focused on describing the associative dynamics of individual fish, primarily through electronic tagging studies, at both coastal anchored FADs (e.g. Holland *et al.*, 1990; Ohta and Kakuma, 2005; Dagorn *et al.*, 2007a; Mitsunaga *et al.*, 2012; Robert *et al.*, 2013; Rodriguez-Tress *et al.*, 2017), and drifting FADs (e.g. Schaefer and Fuller, 2013; Matsumoto *et al.*, 2014, 2016; Tolotti *et al.*, 2020). In contrast, behavioural patterns of FAD-associated aggregations (i.e. entire tuna schools under a DFAD) have received considerably less research attention. When investigated, studies were primarily focused on the spatial or temporal characterization of aggregations at fine timescales, using acoustic equipment on board research vessels (Josse and Bertrand, 2000; Doray *et al.*, 2006; Moreno *et al.*, 2007a; Trygonis *et al.*, 2016). The instrumentation of DFADs with satellite-linked echosounder buoys began in the late 2000's. Since then, their use has become widespread in many fleets. Currently, almost all deployed DFADs are equipped with these devices which provide remote and near real-time information on the DFAD location and aggregated biomass (Lopez *et al.*, 2014; Moreno *et al.*, 2019). Echosounder buoys generate a considerable stream of data that can be used to characterize DFAD aggregations (Lopez *et al.*, 2016; Orue *et al.*, 2019a; Baidai *et al.*, 2020). The availability of such data, which is continuously being collected, represents an unprecedented opportunity to observe fish aggregations associated with floating objects over long time scales. To date, only one study has provided characteristics of tuna aggregations at DFADs over the scale of weeks and months, using data from fisher's echosounder buoys (Orue *et al.*, 2019b).

This work aims to characterize how tunas occupy DFADs, in order to improve the understanding of their aggregation dynamics around these objects. Using data from commercial echosounder buoys attached to DFADs deployed in the Western Indian Ocean and Eastern Atlantic Ocean, we assessed several parameters related to the association of tuna aggregations with DFADs. These include the elapsed time between deployment of a new DFAD and its colonization by tunas; the average duration of association of tuna aggregations with DFADs and the length of time that DFADs remains vacant between consecutive tuna aggregations.

1. Material and methods

1.1. Echosounder Data

The echosounder data used in this study were collected using M3I buoys[1] attached to DFADs from the French tropical tuna purse seiner fleet operating in the Western Indian Ocean and Eastern Atlantic Ocean, from 2016 to 2018. The M3I buoy is equipped with a GPS positioning device and an echosounder powered by solar panels, operating at a frequency of 50 kHz, with

[1] Marine Instruments, Nigrán, Spain, www.marineinstruments.es

a power of 500 W, and a beam angle of 36°. The data output of the buoy is simplified acoustic information, designed for easy visual interpretation by fishers. The M3I buoy samples the water column in 3-meter layers covering a total depth of 150 m (50 layers, with the first two corresponding to the transducer near-field). An acoustic sample consists of 50 ordered categorical scores (ranging from 0 to 7), resulting from the automatic conversion of the acoustic backscatter signal recorded per 3-meter layer, with an inbuilt algorithm. In the default-operating mode, 12 samples collected at about 2 hour intervals, are transmitted daily via satellite by the buoy.

1.2. Data cleaning process

The raw data provided by the echosounder buoys were cleaned using the following protocol (see Baidai *et al.*, 2017 for details on the procedure):

(1) Duplicated rows, inconsistent positions, data recorded on land, at shallow positions (depth less than 150 meter), or under low voltage conditions (poor reliability of acoustic data collected below 11.5V) were omitted from the database.

(2) A rule-based algorithm, which uses buoy speed and its variations as main classifiers, was applied to discriminate acoustic data recorded when the buoy is on board a vessel from those actually recorded when the buoy is deployed at sea.

1.3. Classification of tuna presence/absence

The presence or absence of tuna at a DFAD was assessed from acoustic data collected by echosounder buoys, following the methodology described in Baidai *et al.*, (2020). This approach involves preliminary processing of the acoustic data, followed by a classification using random forest algorithms applied separately to each ocean. The learning datasets were constructed by cross-referencing the acoustic data with the activities of fishers at DFADs (namely sets with associated tuna catches, DFAD deployments and DFAD visits) recorded in logbooks and by on-board observers. A detailed description of the classification procedure can be found in Supplementary Material S1. The minimum catch value representing tuna presence in the learning dataset was 1 ton. Thus, in this work, the term “tuna aggregation” refers to a fish aggregation whose tuna biomass is at least equal to this value.

An additional post-processing step was applied to improve the predictions made by the classification algorithm during the course of DFAD trajectories. Prediction results with short durations (i.e. an isolated event of presence or absence lasting a single day) were considered unlikely, attributed rather to misclassification, and corrected using the previous or following day's predicted values. This step allowed for the correction of 9 and 7% of the initial predictions made by the classification model, in the Atlantic Ocean (AO) and the Indian Ocean (IO) respectively.

1.4. Newly deployed DFADs

Only newly deployed DFADs (i.e. DFADs used for the very first time) equipped with echosounder buoys were considered. Natural floating objects (e.g. logs), reinforced old DFADs found at sea, relocated DFAD and buoy transfers were all excluded. Deployments of new DFADs were identified from fishing logbooks and observer data collected from 2016 to 2018 in the AO and IO. The 2016-2018 period was selected to provide a relatively homogeneous study period, while maintaining sufficient data in both oceans. Observer data were collected by the IRD-Ob7 observatory under the EU Data Collection Framework (DCF) and the French OCUP program (Observateur Commun Unique et Permanent). Trajectories and time series of tuna presence/absence associated with newly deployed DFADs were then identified by cross-referencing the logbook and observer databases with the echosounder buoy database, using the unique identification code of the buoy and the deployment date. To ensure that the subset correctly identified newly deployed DFADs (and not potentially misreported reinforcement activities), records for which fishing sets were reported during the week following the deployment were removed from the dataset. An additional cleaning step was applied to the dataset in order to omit data with inconsistent positions between the location of the DFAD deployment recorded in the logbook or observer database, and the actual position recorded by the buoy (0.3% and 0.8% of the dataset in Atlantic and Indian Oceans respectively). The cleaned dataset of newly deployed DFADs included 9118 trajectories with 498,276 presence/absence data points for the IO and 285 trajectories with 18,102 presence/absence data points for the AO (Figure 1).

1.5. Soak time and colonization time

Soak time was defined as the number of days between the deployment of a DFAD equipped with a buoy and the first reported operation on it (i.e., either a fishing set or the retrieval of the buoy). Tuna colonization time refers to the number of days between the deployment of a DFAD and the first day when a tuna aggregation is detected by the echosounder buoy (Figure 2). The term "colonized DFAD" thus refers to a DFAD that has aggregated tuna at least once (for longer than one day).

Due to fishing and buoy retrievals, the number of buoys at sea available for the analysis declined for increasing soak times. This can induce bias in the estimate of tuna colonization times obtained from simple averages (Figure 3). Specifically, the lower the number of DFADs with long soak times, the lower the chances of observing long colonization times, which leads to an underestimate of colonization times from simple arithmetic averages. To overcome this bias, colonization times were estimated from daily colonization rates, considering the daily fraction r_i of colonized DFADs relative to the total available DFADs, for each day i after deployment, see (Eq.1):

$$r_i = \frac{N_{colonized_i}}{N_{colonized_i} + N_{uncolonized_i}} \qquad \text{(Eq.1)}$$

Where, $Ncolonized_i$ indicates the number of DFADs colonized during day i after deployment and $Nuncolonized_i$ denote not-yet-colonized DFADs on day i after deployment. The denominator of (Eq.1) corresponds to the total number of DFADs available for colonization on day i, namely, the total number of DFADs in the water that at day i-1 after deployment were not yet colonized.

Mann-Whitney U tests, were used to compare daily colonization rates between the IO and the AO. The unbiased mean colonization time (T_{col}) (in days) was then estimated as the inverse value of the average of daily colonization rates ($\bar{r}$):

$$T_{col} = \frac{1}{\bar{r}} \qquad \text{(Eq.2)}$$

where $\bar{r}$ denotes the average daily colonization rate:

$$\bar{r} = \frac{1}{D}\sum_{i=1}^{D} r_i \qquad \text{(Eq.3)}$$

where D represents the total number of days during which the daily colonization rates r_i were calculated. When numbers of available DFADs were too low (i.e., the denominator in (Eq.1)), the daily colonization rate becomes less reliable. A preliminary sensitivity analysis, included in the Supplementary Material S1 (Figure S1.2), showed that *D* corresponds to the number of days after deployment when at least 30 DFADs remained available for colonization.

1.6. Aggregation stability

The continuous residence time (CRT) is commonly used to represent the amount of time spent by acoustically-tagged individual tunas around a FAD without a day scale (>24h) absence (Ohta and Kakuma, 2005; Capello *et al.*, 2015). Alternatively, the continuous absence time (CAT) refers to the time interval between two consecutive associations for an individual tuna (Robert *et al.*, 2012; Rodriguez-Tress *et al.*, 2017). In this work, the concepts of CRT and CAT were adapted and applied to DFAD aggregations rather than to individual fish. Accordingly, the *aggregation's continuous residence time at a floating object* (FOB-aCRT) was considered as the time span within which a tuna aggregation was continuously detected at a DFAD without a day scale (>24h) absence. Similarly, the *continuous absence time of aggregation at a floating object* (FOB-aCAT) was defined as the period between two consecutive detections of tuna aggregations at the same DFAD. Values occurring directly before an operation on the DFAD (fishing event or retrieval of the buoy) were excluded from the analysis as they were artificially truncated. Finally, the overall proportion of time that a tuna aggregation remained at a colonized DFAD (named *DFAD occupancy rate*), expressed as the ratio of the sum of all FOB-aCRTs against its soak time after the colonization period, was assessed and compared between oceans using Mann-Whitney *U* tests.

1.7. Survival analyses of FOB-aCRT and FOB-aCAT

Survival analyses (e.g. Capello *et al.*, 2015) were used to characterize the distribution of FOB-aCATs and FOB-aCRTs. Survival curves were constructed using the fraction of FOB-aCATs and FOB-aCRTs shorter than a given time, and compared between oceans using the logrank statistical test (Harrington and Fleming, 1982), implemented in the "*survival*" package in R (Therneau, 2015).

Survival curves were also fitted using three models: (*i*) single exponential, (*ii*) double exponential and (*iii*) power law (Supplementary Material S1: Table S1.3), by adapting the methodology of Robert *et al.*, (2013) to the DFAD aggregation metrics. Exponential models assume association dynamics (presence or absence of an aggregation at a DFAD) to be independent of time. Double exponential models imply the existence of two distinct time-scales occurring within aggregation presence or absence at a DFAD. Power law models indicates a time-dependent probability of presence and absence of tuna aggregations, meaning the longer the time a DFAD is occupied or vacant, the smaller the probability that a change in state will occur. Models were discarded if one or more parameters were not significant ($p > 0.05$ based on the t-statistics). The best-fitting models were chosen based on the Akaike Information Criterion (AIC) and q-q plots.

3. Results

3.1. Daily colonization rates and colonization times

No significant difference was found between DFAD soak times from the AO and the IO (Mann-Whitney U tests, $p = 0.76$) with mean values of 63.28 days (SD 65.08 days), and 54.24 days (SD 45.52 days) respectively. Approximately 22% DFADs in the AO (62 DFADs) and 34% (3,122 DFADs) in the IO did not show any sign of colonization by tunas during their soak time. The soak time of vacant DFADs (averages of 18.66 and 28.52 days for AO and IO, respectively) was significantly lower than that of colonized DFADs (averages of 75.68 and 67.63 for AO and IO respectively), with a p-values (Mann-Whitney U tests) lower than 0.001 in both oceans (Supplementary Material S1: Figure S1.4).

For colonized DFADs, the time before the echosounder buoy detected the first aggregation of tunas averaged 13.17 days (SD 12.37 days) in the AO and 20.22 days (SD 20.83 days) in the IO. Stable trends in daily colonization rates were observed in both oceans (see Figure 3). The average daily colonization rates were significantly higher (Mann-Whitney U test, $p < 0.001$) in the AO ($\bar{r}$ = 0.062, SD 0.037) than in the IO ($\bar{r}$ = 0.025, SD 0.011). Calculating the unbiased average colonization times following Eqs. (1-3) resulted in colonization times that were 2.5 times shorter in the AO (T_{col} = 16.10 days, SD 9.66 days – see Table 1) than in the IO (T_{col} = 40.46 days, SD 17.31 days – see Table 2).

3.2. Aggregation continuous residence (FOB-aCRT) and absence times (FOB-aCAT)

A total of 15,415 FOB-aCRTs and 13,328 FOB-aCATs events were recorded during the course of the trajectories of newly deployed DFADs in the IO. In the AO, 723 FOB-aCATs and 779 FOB-aCRTs were recorded. Distributions of FOB-aCATs and FOB-aCRTs in both oceans are shown in Figure 4. The average duration of tuna aggregations was 8.96 days (SD 11.52) around DFADs in the AO and 6.20 days (SD 6.86) in the IO. It should be noted that very long continuous residence times of tuna aggregations under the same DFAD were also observed in both oceans (96 and 109 days, in the AO and IO respectively). The average time that DFADs remained vacant between two consecutive tuna aggregations (FOB-aCAT), was 5.38 days (SD 6.01 days), with a maximum duration of 86 days in the AO, and at 8.84 days (SD 10.93 days), with a maximum of 119 days in the IO (Table 1 and Table 2).

Inter-ocean comparisons of FOB-aCAT and FOB-aCRT survival curves indicated significant differences in the associative dynamics of tuna aggregations (logrank test, $p < 0.001$ for both FOB-aCAT and FOB-aCRT ocean-comparisons – Figure 5).

In the IO double exponential models were the best fitting for survival curves of both FOB-aCATs and FOB-aCRT. Short-term residences represented 94% of the FOB-aCRTs with a mean duration of 4.58 days, while long-term residences represented 6% with a mean duration of 20.18 days. Short-term absences lasted an average of 4.43 days (representing 66% of FOB-aCATs), while long-term absences had a mean duration of 15.45 days (34% of FOB-aCATs).

In the AO, a double exponential model was the best fit for the survival curve of FOB-aCRTs with averages of 3.75 days (62% of FOB-aCRTs) and 15.70 days (38% of FOB-aCRTs) for short and long-term residence times, respectively. Conversely, a single exponential model was the best fit for absence times of tuna aggregations at DFADs with a mean duration of 4.30 days (see Table 3 and Figure 6).

3.3. DFAD occupancy rate

Significant differences in the proportion of time that colonized DFADs were occupied by tuna were observed between the two oceans (Mann-Whitney *U* tests $p < 0.001$). After colonizing DFADs, in the AO tuna aggregations were detected for an average of 63.27% (SD 19.86%) of the soak time (Figure 7A), while in the IO, this figure was 45.45% (SD 21.73%) (Figure 7B).

4. Discussion

This work aimed at characterizing the dynamics of the tuna aggregation processes around DFADs, using acoustic data collected by commercial echosounder buoys on newly deployed DFADs in the IO and AO. To date, very few studies have designed scientific protocols to quantify the time that pelagic species take to colonize newly deployed DFADs. The only previous documented observations in the Atlantic Ocean come from Bard *et al.* (1985), who reported rapid colonization by tunas, ranging from 1 hour to 6 days, through the monitoring of a dozen newly deployed DFADs and detecting tuna presence by visual observations, on-board echosounders, or by fishing sets. Their estimates are significantly shorter than ours for the same ocean (average of 16 days); however, interpretation of these discrepancies is complicated by the large differences in methods and the time when the studies were conducted. The Bard *et al.* study was performed before the development of the FAD-fishery, when tropical tuna stocks were only moderately exploited. Furthermore, their observation protocol could not identify whether observed individuals only visited or remained associated with the DFAD. Taquet *et al.*, (2007) observed that dolphinfish (*Corypheana hippurus*) could arrive a few hours after the deployment of a new floating object, but did not necessarily associate with it. In the Indian Ocean, using Local Ecological Knowledge (LEK), Moreno *et al.*, (2007b) suggested that it typically takes one month before tunas aggregate under a newly deployed DFAD. Although aggregation dynamics at anchored FADs may differ from those at drifting FADs, it is worth noting that Macusi *et al.*, (2017) reported that fishers typically wait approximately 22 days for tuna aggregations to form at anchored FADs in the Philippines, based on interview data. In a recent study using echosounder buoys produced by a different manufacturer, Orue *et al.*, (2019b) examined acoustic data from over 900 newly deployed DFADs in the Western Indian Ocean and suggested that tunas begin to aggregate approximately 13 days after deployment. At three times longer, the findings of the current study (an average of about 40 days in the IO) appear to be more aligned with the knowledge of purse seine skippers (Moreno *et al.*, 2007b). The discrepancy between these acoustic studies may be related to (*i*) differences in methodological approaches applied in the conversion of acoustic data into indicators of presence or absence of tuna, (*ii*) the method used in the current study to estimate colonization times, which avoids possible underestimation biases linked to the large variability in DFAD soak times, or (*iii*) from the differences in the specificities of the buoy models used in each study. Since their introduction into the fishery, echosounder buoys have evolved rapidly, through continuous technological innovations in both hardware and software (Lopez *et al.*, 2014). Thus, the intrinsic performance of buoys for detecting tuna aggregations may differ by model and/or manufacturer. Hardware and software differences in the design of buoys may lead to variable thresholds for the detection of aggregations, which could ultimately result in biases in the detection of small aggregations for some models. Such disparities highlight the critical need for a detailed assessment of the reliability of outputs from the different models of buoys and the accuracy of the data processing methods they use to estimate fish abundance. This is especially important when considering the growing use of echosounder buoy data for scientific purposes (Moreno *et al.*, 2016).

Until now, most scientific knowledge on the behaviour of tunas around floating objects stems from observations of individuals, using electronic tags, with the majority of studies focused on anchored FADs (e.g. Holland *et al.*, 1990; Ohta and Kakuma, 2005; Dagorn *et al.*, 2007a; Mitsunaga *et al.*, 2012; Robert *et al.*, 2013; Rodriguez-Tress *et al.*, 2017). By exploiting the potentially massive data source that echosounder buoys on DFADs represent, this work introduces two novel metrics (FOB-aCAT and FOB-aCRT), providing descriptive elements of DFAD use by entire tuna aggregations. It is particularly interesting to note that, in both oceans, the time taken for tunas to colonize new DFADs was significantly longer than durations between consecutive tuna aggregations (average FOB-aCATs: 9 and 6 days in AO and IO respectively). This result is consistent with previous assertions regarding the role of non-tuna species in the tuna colonization process. Several authors have suggested that the colonization of FADs is a sequential process starting with the arrival of non-tuna species, which may play a key role in the attraction or retention processes of tunas (Deudero *et al.*, 1999; Castro *et al.*, 2002; Nelson, 2003; Moreno *et al.*, 2007b; Taquet *et al.*, 2007; Macusi *et al.*, 2017). The duration of the settlement stage of these pioneer communities could be one of the major factors driving the colonization time of tunas at a new DFAD. As such, colonization time may be viewed as a unique type FOB-aCAT with an extended duration due to the requisite maturation phase of the DFAD. Further studies on interspecific relationships would be of major benefit for improving our understanding of the role played by non-tuna species in the aggregative processes of tunas with DFADs.

A review of the main findings from electronic tagging studies on the associative behaviour of tunas under DFADs reveals that the continuous residence time of individual tuna (CRT) is subject to a degree of variability related to the species or the oceanic region under consideration (see Table 4). Off the coast of Guinea in the Atlantic Ocean, Tolotti *et al.*, (2020) estimated average CRT values of 9 and 19 days, for skipjack and yellowfin tuna respectively. For bigeye tuna the reported CRTs were up to 25 days, which is longer than observations from other oceans. Shorter CRTs (about 1 day on average) were observed for the same three species by Dagorn *et al.*, (2007b) in the Western Indian Ocean. However, these results are likely to be underestimated due to artificial truncation of the observation experiments. Govinden *et al.*, (2010) reported residence times ranging from 4 to 10 days (median values) depending on the tuna species, at DFADs monitored in the Mozambique Channel. In Eastern Pacific Ocean, studies carried out by Matsumoto *et al.,* (2014) and Matsumoto *et al.* (2016), both indicated that individual tunas remain associated with DFADs for less than 7 days. Despite this variability, tuna CRTs reported by this limited number of tagging studies appear to be lower or equal to the average FOB-aCRTs obtained in this work (9 and 6 days in the AO and the IO, respectively), especially for skipjack tuna which is the dominant species in DFAD-associated catches (Dagorn *et al.*, 2013).

Survival analyses of the FOB-aCRTs indicated the coexistence of two distinct modes of DFAD association by tuna aggregations: a dominant mode consisting of short durations, and a longer residence mode. Nearly all of the FOB-aCRTs measured in the IO belonged to the short-term residence mode, whereas the two modes occurred in more similar proportions in the AO. There are several possible explanations for the occurrence of these different modes and their inter-ocean variation. Individually, bigeye and yellowfin tuna generally exhibit longer residence times than skipjack tuna, as indicated by the tagging studies mentioned above. Long-term residence modes may therefore reflect aggregations with a large proportion of the two former species. Furthermore, this study was conducted at a broad spatial and temporal scale. As such, it is possible that the observed differences in modes could be a result of behavioural patterns of tuna that are driven by local environmental differences (such as prey or conspecific abundance, or densities of floating objects) between seasons or oceanic regions. The long-term residence mode could also be indicative of the occurrence of turnover processes of schools at the same DFADs as reported by Weng *et al.,* (2013). Further spatially constrained analyses combined with electronic tagging studies, conducted on DFADs equipped with echosounder buoys, will be crucial to relate the individual and the collective dynamics of tuna around DFADs.

The associative behaviour of the tuna population implies that, at any given time, the overall abundance in an area is the sum of the abundance of two permanently interacting components: the associated and the free-swimming (or unassociated) populations. At present, the underlying reasons driving the association or departure of tunas from floating objects remain unclear. Nevertheless, an improved understanding of the interactions between the two population components can be achieved through the study of the relationships between the association metrics assessed at the scale of the individual (i.e. CAT and CRT) and at the scale of aggregations (FOB-aCAT and FOB-aCRT). Rodriguez-Tress *et al.,* (2017) suggested that high FAD densities tend to reduce the time that tuna spend in an un-associated state (CAT). While these findings may need to be interpreted with caution as they stem from observations at anchored FADs, this could suggest that the underlying trend may occurs irrespective of the FAD type. Logically, higher FAD densities would increase the probability of an individual encountering and associating with a FAD, hence reducing the time individual tuna spend in a free-swimming state (CAT). Similarly, FAD vacancy (FOB-aCATs) should be related to the abundance of the un-associated tuna population. Long FOB-aCATs would result when the un-associated population is small, either due to a low overall tuna population or a large density of FADs drawing them in to aggregate. Following this reasoning, the longer FOB-aCAT and colonization time observed in the IO may thus be indicative of a smaller size of the tuna population and/or higher densities of DFADs in this ocean than in the AO. Furthermore, the double exponential curve for FOB-aCATs observed in the IO, could be a result of regions/periods where at least one of these two factors differ. Previous work by Capello *et al.*, (2016) demonstrated that indicators of abundance for tropical tuna populations could be derived from their individual associative dynamics (CRT and CAT). Combining our current understanding of the individual associative behaviour of tunas with the metrics describing tuna aggregation dynamics provided by this work could aid in developing new methods for obtaining direct abundance estimates of tuna populations. Such methods will depend upon the availability of estimates of the total number of DFADs at sea (more specifically the total number of floating objects). Currently, obtaining these statistics is a challenge in all oceans despite the recent data reporting requirements for DFAD activities by Tuna Regional Fisheries Management Organisations (t-RFMOs).

Conclusion

Using data from the echosounder buoys of French purse seiner fleets, this study characterized key parameters of tuna aggregations at DFADs: colonization times, aggregation lifetimes and time span between aggregations. In both oceans, lifespan of tuna aggregations at DFAD followed a time-independent process with two modes. This suggests that the species composition and/or the local conditions (e.g. prey, conspecifics or density of floating objects) could play key roles in aggregation dynamics. However, opposing trends also existed between the two oceans, with shorter residence time of aggregations and longer periods of DFAD vacancy in the IO than in the AO. Further spatially restricted analyses assessing these behavioural metrics at smaller spatial and temporal scales could help in understanding the dynamics of aggregations at a local scale, as well as the role played by various environmental factors. The integration of these new findings into population assessment models which account for the associative behaviour of tunas present an opportunity for the development of alternative abundance indices (independent from catch and effort data) for tropical tunas and the construction of reliable scenarios on the impacts that DFADs have on tuna populations.

Data availability statement

The data underlying this article were provided by Ob7 – "Observatoire des Ecosystèmes Pélagiques Tropicaux exploités" from IRD/MARBEC under data exchange agreement with fishing companies. Data will be shared on request to Ob7 with permission of the owners.

Supplementary Material

The following supplementary material is available at ICESJMS online version of the manuscript

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References

Baidai, Y., Capello, M., Billet, N., Floch, L., Simier, M., Sabarros, P., and Dagorn, L. 2017. Towards the derivation of fisheries-independent abundance indices for tropical tunas: Progress in the echosounders buoys data analysis. IOTC-2017-WPTT19-22. https://www.iotc.org/sites/default/files/documents/2017/10/IOTC-2017-WPTT19-22_Rev1.pdf. (Last accessed 15 September 2020).

Baidai, Y., Dagorn, L., Amande, M.J., Gaertner, D., and Capello, M. 2020. Machine learning for characterizing tropical tuna aggregations under Drifting Fish Aggregating Devices (DFADs) from commercial echosounder buoys data. Fisheries Research 229:105613 https://doi.org/:10.1016/j.fishres.2020.105613

Bard, F.-X., Stretta, J.-M., and Slepoukha, M. 1985. Les épaves artificielles comme auxiliaires de la pêche thonière en océan Atlantique : quel avenir ? Pêche Maritime, 1291, 655–659.

Baske, A., Gibbon, J., Benn, J., and Nickson, A. 2012. Estimating the use of drifting Fish Aggregation Devices (FADs) around the globe. Pew Environ. Gr. https://www.pewtrusts.org/-/media/legacy/uploadedfiles/peg/publications/report/fadreport1212pdf.pdf (last accessed 15 September 2020).

Capello, M., Robert, M., Soria, M., Potin, G.G., Itano, D., Holland, K., Deneubourg, J.L., and Dagorn, L. 2015. A methodological framework to estimate the site fidelity of tagged animals using passive acoustic telemetry. PLoS One 10, e0134002. https://doi.org/10.1371/journal.pone.0134002

Capello, M., Deneubourg, J. L., Robert, M., Holland, K. N., Schaefer, K. M., and Dagorn, L. 2016. Population assessment of tropical tuna based on their associative behavior around floating objects. Scientific Reports, 6: 1–14. http://dx.doi.org/10.1038/srep36415

Castro, J., Santiago, J., and Santana-Ortega, A. 2002. A general theory on fish aggregation to floating objects: An alternative to the meeting point hypothesis. Reviews in Fish Biology and Fisheries, 11, 255–277. https://doi.org/10.1023/A:1020302414472a

Dagorn, L., Holland, K.N., and Itano, D.G. 2007a. Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). Marine Biology, 151, 595–606. https://doi.org/10.1007/s00227-006-0511-1

Dagorn, L., Pincock, D., Girard, C., Holland, K., Taquet, M., Sancho, G., Itano, D., *et al.* 2007b. Satellite-linked acoustic receivers to observe behavior of fish in remote areas. Aquatic Living Resources, 20: 307–312. http://doi.org/10.1051/alr:2008001

Dagorn, L., Holland, K.N., Restrepo, V., and Moreno, G. 2013. Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? Fish and Fisheries, 14, 391–415. https://doi.org/10.1111/j.1467-2979.2012.00478.x

Davies, T.K., Mees, C.C., and Milner-Gulland, E.J. 2014. The past, present and future use of drifting fish aggregating devices (FADs) in the Indian Ocean. Marine Policy, 45, 163–170. https://doi.org/10.1016/j.marpol.2013.12.014

Deudero, S., Merella, P., Massutí, E., and Alemany, F. 1999. Fish communities associated with FADs. Scientia Marina, 63, 199–207.

Doray, M., Josse, E., Gervain, P., Reynal, L., and Chantrel, J. 2006. Acoustic characterisation of pelagic fish aggregations around moored fish aggregating devices in Martinique (Lesser Antilles). Fisheries Research , 82, 162–175. https://doi.org/10.1016/j.fishres.2006.06.025

Fonteneau, A., Pallarés, P., and Pianet, R. 2000. A worldwide review of purse seine fisheries on FADs, *In*: Pêche Thonière et Dispositifs de Concentration de Poissons, p 15-35. J.Y., Le Gall, P., Cayré, and M., Taquet, Editions Ifremer, Plouzané, France.

Fonteneau, A., Chassot, E., and Bodin, N. 2013. Global spatio-temporal patterns in tropical tuna purse seine fisheries on drifting fish aggregating devices (DFADs): Taking a historical perspective to inform current challenges. Aquatic Living Resources, 26, 37–48. https://doi.org/10.1051/alr/2013046

Fonteneau, A., Chassot, E., and Gaertner, D. 2015. Managing tropical tuna purse seine fisheries through limiting the number of drifting fish aggregating devices in the Atlantic: food for thought. Collective Volume Scientific Papers ICCAT, 71: 460–475.

Fréon, P., and Dagorn, L. 2000. Review of fish associative behaviour toward a generalisation of the meeting point hypothesis. Reviews in Fish Biology and Fisheries, 10, 183–207.

Gaertner, D., and Pallarés, P. 2002. The European Union Research Project, Efficiency of Tuna Purse-Seiners and Effective Effort (ESTHER): Scientific report of project. Doc.

SCTB15-FTWG-3. https://www.spc.int/digitallibrary/doc/fame/meetings/sctb/15/ftwg_3.pdf (last accessed 15 September 2020)

Gershman, D., Nickson, A., and O'Toole, M. 2015. Estimating the use of FADS Around the World, The Pew Charitable Trusts. Available at: https://www.pewtrusts.org/-/media/assets/2015/11/global_fad_report.pdf (last accessed 15 September 2020)

Govinden, R., Dagorn, L., Soria, M., and Filmalter, J. 2010. Behaviour of tuna associated with Drifting Fish Aggregating Devices (FADs) in the Mozambique Channel, IOTC-2010-WPTT-25. https://iotc.org/sites/default/files/documents/proceedings/2010/wptt/IOTC-2010-WPTT-25.pdf (last accessed 15 September 2020).

Harrington, D.P. and Fleming, T.R. 1982. A class of rank test procedures for censored survival data. Biometrika 69, 553–566.

Holland, K. N., Brill, R. W., and Chang, R. K. C. 1990. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fishery Bulletin, 88: 493–507.

ISSF, 2019. Status of the world fisheries for tuna 2013 – October 2019. ISSF Technical Report 2019-12: 113. Available at http://iss-foundation.org/resources/downloads/?did=512

Josse, E., and Bertrand, A. 2000. In situ acoustic target strength measurements of tuna associated with a fish aggregating device. ICES Journal of Marine Science, 57: 911–918. https://doi.org/10.1006/jmsc.2000.0578

Lopez, J., Moreno, G., Sancristobal, I., and Murua, J. 2014. Evolution and current state of the technology of echo-sounder buoys used by Spanish tropical tuna purse seiners in the Atlantic, Indian and Pacific Oceans. Fisheries Research, 155: 127–137. http://dx.doi.org/10.1016/j.fishres.2014.02.033

Lopez, J., Moreno, G., Boyra, G., and Dagorn, L. 2016. A model based on data from echosounder buoys to estimate biomass of fish species associated with fish aggregating devices. Fishery Bulletin, 114: 166–178. https://doi.org/10.7755/FB.114.2.4

Macusi, E.D., Abreo, N.A., and Babaran, R.P. 2017. Local Ecological Knowledge (LEK) on fish behavior around anchored FADs: the case of tuna purse seine and ringnet fishers from Southern Philippines. Frontiers in Marine Science 4, 1–13. https://doi.org/10.3389/fmars.2017.00188

Matsumoto, T., Satoh, K., and Toyonaga, M. 2014. Behavior of skipjack tuna (*Katsuwonus pelamis*) associated with a drifting FAD monitored with ultrasonic transmitters in the equatorial central Pacific Ocean. Fisheries Research, 157, 78–85. https://doi.org/10.1016/j.fishres.2014.03.023

Matsumoto, T., Satoh, K., Semba, Y., and Toyonaga, M. 2016. Comparison of the behavior of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna associated with drifting FADs in the equatorial central Pacific Ocean. Fisheries Oceanography, 25, 565–581. https://doi.org/10.1111/fog.12173

Maufroy, A., Kaplan, D.M., Bez, N., De Molina, A.D., Murua, H., Floch, L., and Chassot, E. 2017. Massive increase in the use of drifting Fish Aggregating Devices (dFADs) by tropical tuna purse seine fisheries in the Atlantic and Indian oceans. ICES Journal of Marine Science, 74, 215–225. https://doi.org/10.1093/icesjms/fsw175

Mitsunaga, Y., Endo, C., Anraku, K., Selorio, C.M., and Babaran, R.P. 2012. Association of early juvenile yellowfin tuna *Thunnus albacares* with a network of payaos in the Philippines. . Fisheries Science , 78, 15–22. https://doi.org/10.1007/s12562-011-0431-y

Moreno, G., Josse, E., Brehmer, P., Nøttestad, L. 2007a. Echotrace classification and spatial distribution of pelagic fish aggregations around drifting fish aggregating devices (DFAD). Aquatic Living Resources, 20, 343–356. https://doi.org/10.1051/alr:2008015

Moreno, G., Dagorn, L., Sancho, G., and Itano, D. 2007b. Fish behaviour from fishers' knowledge: the case study of tropical tuna around drifting fish aggregating devices (DFADs). Canadian Journal of Fisheries and Aquatic Sciences, 64, 1517–1528. https://doi.org/10.1139/f07-113

Moreno, G., Dagorn, L., Capello, M., Lopez, J., Filmalter, J., Forget, F., Sancristobal, I., and Holland, K. 2016. Fish aggregating devices (FADs) as scientific platforms. Fisheries Research, 178, 122–129. https://doi:10.1016/j.fishres.2015.09.021

Moreno, G., Boyra, G., Sancristobal, I., Itano, D., and Restrepo, V. 2019. Towards acoustic discrimination of tropical tuna associated with Fish Aggregating Devices. PLoS One 14, e0216353. https://doi.org/10.1371/journal.pone.0216353

Nelson, P.A. 2003. Marine fish assemblages associated with fish aggregating devices (FADs): Effects of fish removal, FAD size, fouling communities, and prior recruits. Fishery Bulletin, 101, 835–850.

Ohta, I., Kakuma, S., 2005. Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. Marine Biology, 146, 581–594. https://doi.org/10.1007/s00227-004-1456-x

Orue, B., Lopez, J., Moreno, G., Santiago, J., Boyra, G., Soto, M., and Murua, H. 2019a. Using fishers' echo-sounder buoys to estimate biomass of fish species associated with drifting fish aggregating devices in the Indian Ocean. Revista de Investigación Marina, AZTI, 26: 1–13.

Orue, B., Lopez, J., Moreno, G., Santiago, J., Soto, M., and Murua, H. 2019b. Aggregation process of drifting fish aggregating devices (DFADs) in the Western Indian Ocean: Who arrives first, tuna or non-tuna species? PLoS One 14, e0210435. https://doi.org/10.1371/journal.pone.0210435

Robert, M., Dagorn, L., Deneubourg, J.L., Itano, D., and Holland, K. 2012. Size-dependent behavior of tuna in an array of fish aggregating devices (FADs). Marine Biology, 159, 907–914. https://doi.org/10.1007/s00227-011-1868-3

Robert, M., Dagorn, L., Filmalter, J.D., Deneubourg, J.L., Itano, D., and Holland, K. 2013. Intra-individual behavioral variability displayed by tuna at fish aggregating devices (FADs). Marine Ecology Progress Series, 484, 239–247. https://doi.org/10.3354/meps10303

Rodriguez-Tress, P., Capello, M., Forget, F., Soria, M., Beeharry, S., Dussooa, N., and Dagorn, L. 2017. 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. Marine Ecology Progress Series 570, 213–222. https://doi.org/10.3354/meps12101

Schaefer, K.M., and Fuller, D.W., 2013. Simultaneous behavior of skipjack (*Katsuwonus pelamis*), bigeye (*Thunnus obsesus*), and yellowfin (*T. albacares*) tunas, within large multi-species aggregations associated with drifting fish aggregating devices (FADs) in the equatorial eastern Pacific Ocean. Marine Biology, 160, 3005–3014.

https://doi.org/10.1007/s00227-013-2290-9

Scott, G. P., and Lopez, J. 2014. The use of FADs in Tuna Fisheries. 71 pp.https://www.europarl.europa.eu/RegData/etudes/note/join/2014/514002/IPOL-PECH_NT(2014)514002_EN.pdf (last accessed 15 September 2020)

Scutt P., J., Leroy, B., Peatman, T., Escalle, L., and Smith, N. 2019. Electronic tagging for the mitigation of bigeye and yellowfin tuna juveniles by purse seine fisheries. WCPFC Scientific Committee WCPFC-SC15-2019/EB-WP-08. https://www.wcpfc.int/file/302866/download?token=5nmVHVYt (last accessed 15 September 2020).

Taquet, M., Dagorn, L., Gaertner, J.-C., Girard, C., Aumerruddy, R., Sancho, G., and Itano, D. 2007. Behavior of dolphinfish (*Coryphaena hippurus*) around drifting FADs as observed from automated acoustic receivers. Aquatic Living Resources, 20: 323–330. http://www.alr-journal.org/10.1051/alr:2008008

Therneau T. 2015. A Package for Survival Analysis in S. Version 2.38. URL: https://CRAN.R-project.org/package=survival (last accessed 15 September 2020)

Tolotti, M.T., Forget, F., Capello, M., Filmalter, J.D., Hutchinson, M., Itano, D., Holland, K., and Dagorn, L. 2020. Association dynamics of tuna and purse seine bycatch species with drifting fish aggregating devices (FADs) in the tropical eastern Atlantic Ocean. Fish. Res. 226, 105521. https://doi.org/10.1016/j.fishres.2020.105521

Torres-Irineo, E., Gaertner, D., Chassot, E., and Dreyfus-León, M. 2014. Changes in fishing power and fishing strategies driven by new technologies: The case of tropical tuna purse seiners in the eastern Atlantic Ocean. Fisheries Research, 155: 10–19. http://dx.doi.org/10.1016/j.fishres.2014.02.017

Trygonis, V., Georgakarakos, S., Dagorn, L., and Brehmer, P. 2016. Spatiotemporal distribution of fish schools around drifting fish aggregating devices. Fisheries Research, 177, 39–49. https://doi.org/10.1016/j.fishres.2016.01.013

Weng, J.-S., Hung, M.-K., Lai, C.-C., Wu, L.-J., Lee, M.-A., and Liu, K.-M. 2013. Fine-scale vertical and horizontal movements of juvenile yellowfin tuna (*Thunnus albacares*) associated with a subsurface fish aggregating device (FAD) off South-western Taiwan. Journal of Applied Ichthyology, 29, 990–1000. https://doi.org/10.1111/jai.12265

Tables

Table 1. Summary of tuna aggregation metrics measured in the Atlantic Ocean.

	Min.	Max.	Median	Mean	Standard deviation
DFAD Soak time (days)	1	305	44	63.28	65.08
Daily colonization rate (days^{-1})	0	0.15	0.06	0.06	0.04
Tuna colonization time (days)	-	-	-	16.10	9.66
FOB-aCAT (days)	2	86	4	5.38	6.01
FOB-aCRT (days)	2	96	4	8.96	11.52
Occupancy rate (%)	5.13	97.59	60.49	63.27	19.86

Table 2. Summary of tuna aggregations metrics measured in the Indian Ocean.

	Min.	Max.	Median	Mean	Standard deviation
DFAD Soak time (days)	1	363	43	54.24	45.52
Daily colonization rate (days^{-1})	0	0.07	0.02	0.02	0.01
Tuna colonization time (days)	-	-	-	40.46	17.31
FOB-aCAT (days)	2	119	5	8.84	10.93
FOB-aCRT (days)	2	109	4	6.20	6.86
Occupancy rate (%)	2.83	98.08	46.16	45.45	21.73

Table 3: Summary of the model fits of the survival curves of aggregation continuous residence and absence times (FOB-aCRTs and FOB-aCATs) obtained in Atlantic and Indian Oceans. , Est = parameter estimate, Std. Error = standard error, t-value = value of t-statistic, Pr(> |t|) = *p*-value at t-tests and AIC = Akaike Information Criterion. AIC values of the best-fitted models are highlighted in bold.
*Significance codes: *** = 0; ** = 0.001; * = 0.01; .= 0.05*

Ocean	Metric	Fitting law	Parameter	Estimate	Std. Error	t-value	Pr(>|t|)		AIC
Atlantic Ocean	FOB-aCRT	Single exponential	a	0.14	3.61E-03	38.35	6.92E-42	***	-217.80
		Double exponential	a	0.27	8.51E-03	31.29	2.75E-36	***	**-416.09**
			b	0.06	2.13E-03	29.95	2.58E-35	***	
			p	0.62	1.89E-02	33.03	1.71E-37	***	
		Power law	a	2.29	7.19E-02	31.87	3.87E-37	***	-389.71
			b	11.73	5.11E-01	22.94	7.76E-30	***	
	FOB-aCAT	Single exponential	a	0.23	5.03E-03	46.16	7.42E-31	***	**-154.98**
		Double exponential	a	0.24	1.24E-02	19.59	1.20E-18	***	-155.22
			b	0.03	6.18E-02	0.43	6.68E-01		
			p	0.98	3.24E-02	30.26	4.86E-24	***	
		Power law	a	22.04	2.51E+01	0.88	3.87E-01		-153.74
			b	91.78	1.08E+02	0.85	4.03E-01		
Indian Ocean	FOB-aCRT	Single exponential	a	0.20	2.84E-03	69.54	3.63E-69	***	-404.29
		Double exponential	a	0.22	8.71E-03	25.04	2.85E-37	***	**-426.38**
			b	0.05	1.94E-02	2.56	1.27E-02	*	
			p	0.94	3.37E-02	27.90	2.42E-40	***	
		Power law	a	8.49	2.17E+00	3.92	2.00E-04	***	-415.36
			b	39.48	1.10E+01	3.58	6.24E-04	*	
	FOB-aCAT	Single exponential	a	0.14	2.12E-03	64.29	1.01E-80	***	-471.48
		Double exponential	a	0.23	3.10E-03	72.73	1.98E-84	***	**-875.29**
			b	0.06	1.11E-03	58.30	1.34E-75	***	
			p	0.66	1.02E-02	64.71	9.41E-80	***	
		Power law	a	3.06	5.51E-02	55.51	3.31E-74	***	-806.27
			b	17.36	4.04E-01	43.01	4,41E-64	***	

Table 4 : Summary of main findings from previous studies on continuous residence time of individual tunas at drifting FADs. (FL: fork length, YFT: *Thunnus albacares*, SKJ: *Katsuwonus pelamis*, BET: *Thunnus obesus*)

Study	Location	Species	FL range (cm)	CRT
Dagorn *et al.*, (2007b)	Western Indian Ocean	SKJ	*Not provided*	Average at 0.91 days (maximum: 7.03 days)
		BET		Average at 1.43 days (maximum: 3.06 days)
		YFT		Average at 1.04 days (maximum: 15.22 days)
Govinden *et al.*, (2010)	Mozambique Chanel, (Western Indian Ocean)	SKJ	47 – 57	Median at 4.47 days (maximum: 18.33 days)
		BET	54 – 56	Median at 3.89 days (maximum: 6.56 days)
		YFT	29 – 60	Median at 9.98 days (maximum: 26.72 days)
Matsumoto *et al.*, (2014)	Equatorial central Pacific Ocean	SKJ	36 – 65	Average at 2.3 days (maximum: 6.4 days)
Matsumoto *et al.*, (2016)	Equatorial central Pacific Ocean	SKJ	34.5 – 65.0	Average at 1.3 days
		BET	33.5 – 85.5	Average at 3.8 days (maximum: about 11 days)
		YFT	31.6 – 93.5	Average at 4.1 days (maximum 14.5 days)
Scutt *et al.*, (2019)	Western Central Pacific Ocean	SKJ	46 – 60	Median at 1 day (maximum: 18 days)
		BET	37 – 90	Median at 10 days (maximum: 30 days)
		YFT	36 – 98	Median at 2 days (maximum: 50 days)
Tolotti *et al.*, (2020)	Eastern Atlantic Ocean	SKJ	39 – 61	Average at 9.19 days (maximum value to 15 days)
		BET	45 – 61	Average at 25.31 days (maximum value to 55 days)
		YFT	34 – 82	Average at 19.15 days (maximum value to 55 days)

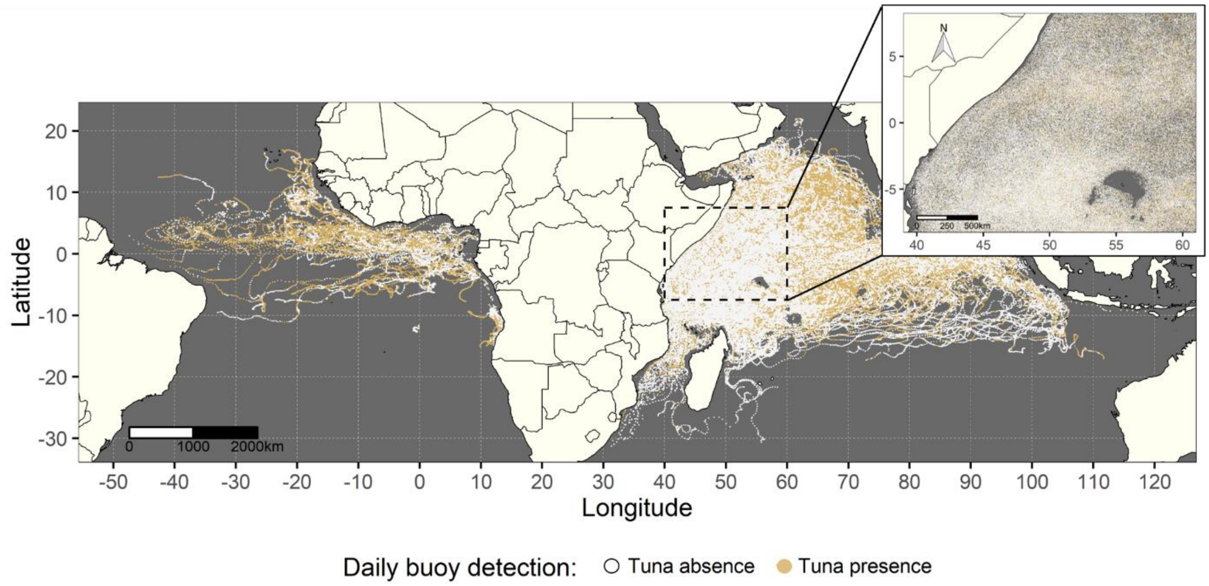

Figure 1: Presence/absence of tuna aggregations along the course of the trajectories of newly deployed DFADS monitored in Western Indian Ocean and Eastern Atlantic Ocean from 2016 to 2018. Orange dots indicate days when tuna aggregations were present, white dots represent days with no tuna aggregations.

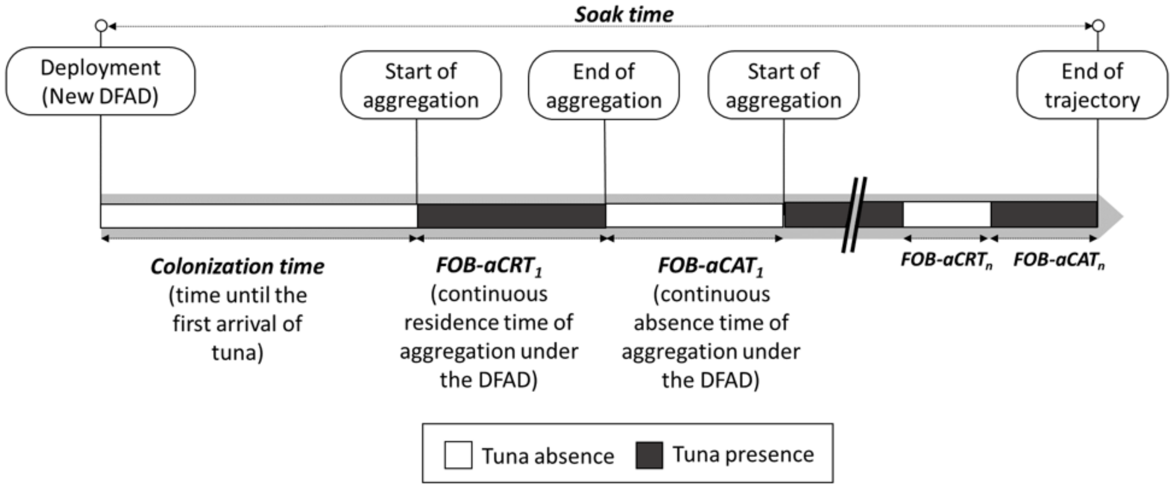

Figure 2: Schematic representation of the timeline of tuna aggregation dynamics at a DFAD. The term “end of trajectory” denotes here the first operation carried out on FADs likely to affect the aggregation (e.g. either a fishing set or the retrieval of the buoy).

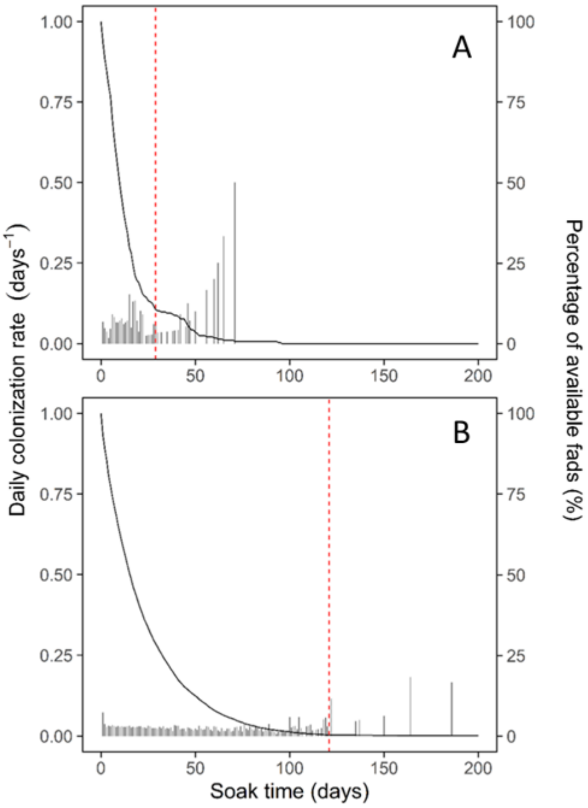

Figure 3 : Daily colonization rates (bars) and percentage of equipped DFADs available (solid lines) over time in the Atlantic Ocean (Panel A) and the Indian Ocean (Panel B). Red dashed lines indicate the number of days after deployment at which 30 DFADs were still available.

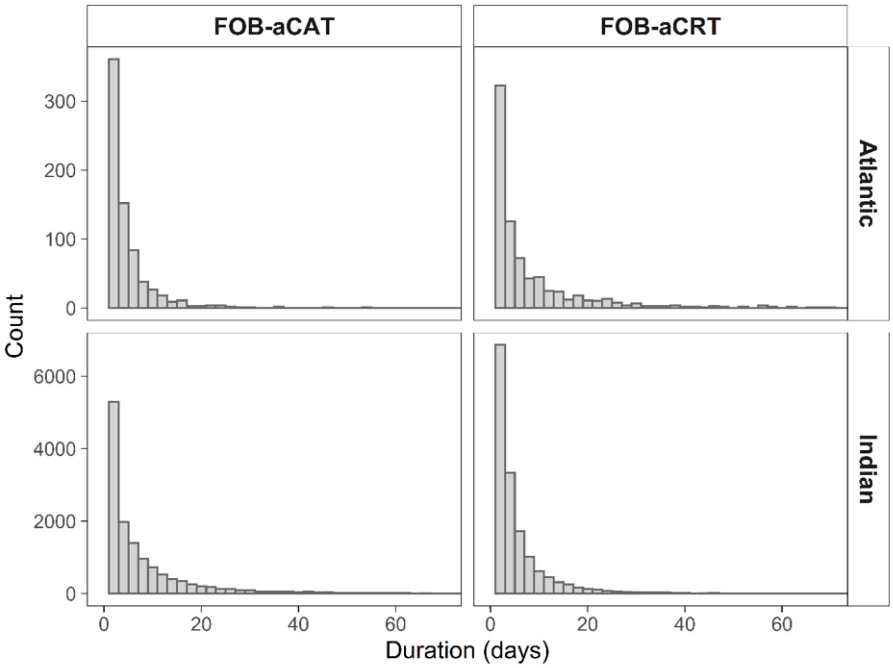

Figure 4: Distribution of FOB-aCATs (left) and FOB-aCRTs (right) in the Atlantic Ocean (top) and Indian Ocean (bottom). FOB-aCRT and FOB-aCAT denote the aggregation's continuous residence time at a floating object and the continuous absence time of aggregation at a floating object, respectively.

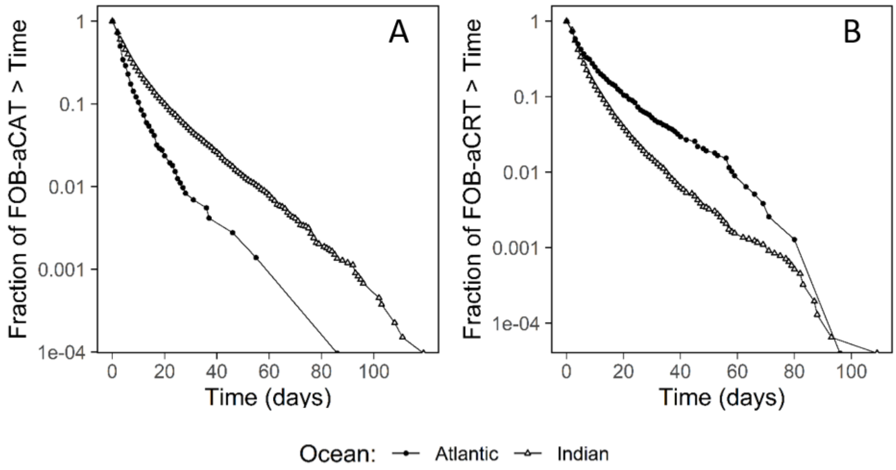

Figure 5: Survival curves of FOB-aCRTs (Panel A) and FOB-aCATs (Panel B) recorded on trajectories of newly deployed DFADs in Atlantic Ocean (black dots) and Indian Ocean (white dots). The y-axis is on a logarithmic scale. FOB-aCRT and FOB-aCAT denote the aggregation's continuous residence time at a floating object and the continuous absence time of aggregation at a floating object, respectively.

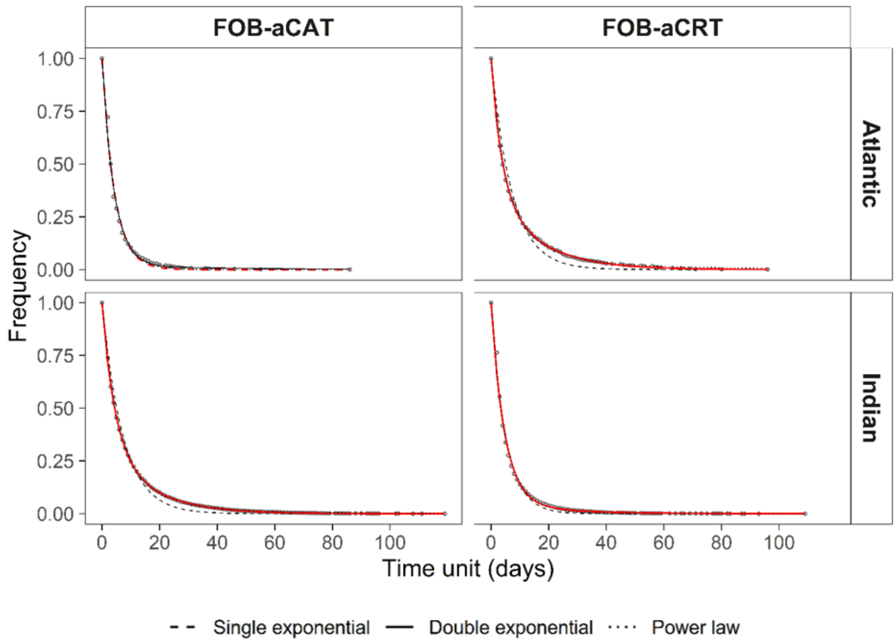

Figure 6: Survival curves of FOB-aCAT (left) and FOB-aCRT (right) the observed in Atlantic Ocean (top) and Indian Ocean (bottom) fitted with single exponential, double exponential and power law models. The red line indicates the best fit. FOB-aCRT and FOB-aCAT denote the aggregation's continuous residence time at a floating object and the continuous absence time of aggregation at a floating object, respectively.

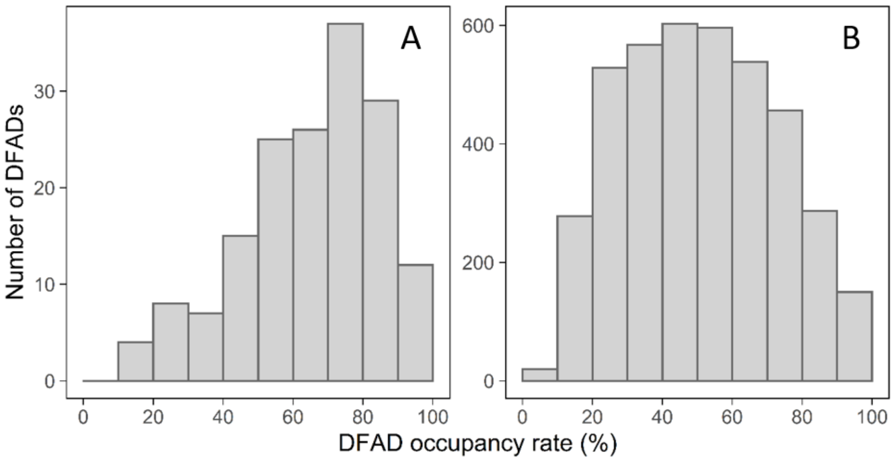

Figure 7: Distribution of the DFAD occupancy rates in the Atlantic Ocean (Panel A) and the Indian Ocean (Panel B).