



Aggregation dynamics of tropical tunas around drifting floating objects based on large-scale echo-sounder data

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ABSTRACT: Based on data gathered by echo-sounder buoys attached to drifting fish-aggregating devices (dFADs) across tropical oceans, we applied a machine learning protocol to examine the temporal trends of tuna-school associations with drifting objects both in comparison to previous studies, and in the context of the 'ecological trap' theory. Using a binary output, metrics typically used in the literature were adapted to account for the fact that the entire tuna aggregation under the dFAD was considered. The median time it took tuna to colonize the dFADs for the first time varied between 25 and 43 d, depending on the ocean, and the longest soak and colonization times were registered in the Pacific Ocean. The continuous residence times of tuna schools were generally shorter than continuous absence times (median values: 5–7 and 9–11 d, respectively), in line with the results found by previous studies. Using a regression output, 2 novel metrics, namely aggregation time and disaggregation time, were estimated to obtain further insight into the symmetry of the aggregation process. Across all oceans, the time it took for tuna aggregations to depart from individual dFADs was not significantly longer than the time it took for the aggregations to form. This does not align with what would be expected if the association were 'strong and long-lasting' as proposed by one of the aspects of the 'ecological trap' theory. The value of these results in the context of the reasons driving the aggregation process is discussed, and further analyses to enrich and make use of this data source are proposed.

KEY WORDS: Tropical tunas · Echo-sounder buoys · Fish-aggregating devices · FADs · Associative behavior · Ecological trap

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1. INTRODUCTION

For centuries, floating objects drifting on the ocean's surface have been known to attract a number of fish species, including tropical tunas such as skipjack tuna *Katsuwonus pelamis*, yellowfin tuna *Thunnus albacares*, and bigeye tuna *T. obesus* (Castro et al. 2002, Maufoy et al. 2015). As fishermen have noticed this behavior, they have used both natural and man-made floating objects, or drifting fish-aggregating

devices (dFADs), as a tool for finding and catching tropical tunas. The use of dFADs in tuna purse-seine fisheries has gradually increased since the 1980s to the present time, where vessels using dFADs now contribute to 36% of the world's total tropical tuna catch (Fauvel et al. 2009, Davies et al. 2014, ISSF 2021, Wain et al. 2021). These widespread changes in fishing tactics have highlighted the need to better understand the potential ecological effects of dFADs on tuna ecology and the marine environment in

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order to ensure adequate management of fish stocks and dFAD usage.

Indeed, the dynamics of how and why tuna associate with dFADs are still poorly understood. Regarding the reasons behind tuna aggregation at dFADs, a number of hypotheses have been suggested (Fréon & Dagorn 2000, Castro et al. 2002, Dempster & Taquet 2004). Of these, 2 have gained traction: the 'meeting-point' hypothesis, which considers that dFADs facilitate the encounter between individuals or schools, thus constituting larger schools that could benefit survival rates (Fréon & Dagorn 2000), and the 'indicator-log' hypothesis, by which tunas may be safeguarding the survival of their eggs, larvae, and juvenile stages by using drifting objects as indicators of areas where plankton and food are readily available (Hall et al. 1992). This second hypothesis has led some authors to postulate that man-made dFADs could have detrimental effects on tuna populations by creating a so-called 'ecological trap' (Marsac et al. 2000, Hallier & Gaertner 2008, Dupaix et al. 2023), which is based on 3 main premises (Marsac et al. 2000):

- (1) the association of tuna with dFADs is fast, strong, and long-lasting;
- (2) dFADs modify the natural movements of tuna schools;
- (3) dFADs affect the growth and natural mortality of tuna.

Whether or not an ecological trap is occurring at dFADs has been subject to debate, and several authors have explored this issue by investigating different aspects of the 3 premises presented by Marsac et al. (2000). For example, Hallier & Gaertner (2008) found that fish around dFADs were generally in less healthy condition than those found unassociated with floating objects, thus supporting the third premise of Marsac et al. (2000). However, Robert et al. (2014a) later suggested that this difference in condition may not be a consequence of aggregating at the dFAD, but rather a strategy to improve their body condition, whereby the tuna actually obtain some benefit from aggregating near the floating object. Although many studies have continued to investigate the existence of ecological traps in general (Robertson & Hutto 2006), and in reference to tuna and dFADs (Dagorn et al. 2013), conclusive evidence is yet to be found. In fact, most authors generally agree that either, or both, the indicator-log hypothesis and the meeting-point hypothesis are at play when tuna aggregate at dFADs (Castro et al. 2002, Girard et al. 2004, Robert et al. 2012, 2013a,b).

To provide further insight into the reasons driving tuna aggregations around dFADs, several studies have

focused on the temporal aspect of school behavior around dFADs (Ohta & Kakuma 2005, Dagorn et al. 2007, Matsumoto et al. 2016, Tolotti et al. 2020). Authors have examined the continuous residence time (CRT) of tunas at dFADs, defined as the duration for which tuna were present at the dFAD without day-scale absences; continuous absence time (CAT), i.e. the time between 2 consecutive associations with dFADs (Ohta & Kakuma 2005); or colonization time (CT), the time it takes for tuna to first appear at a dFAD (Lopez et al. 2017, Orue et al. 2019b), among other indices. In general, results have been highly variable. For example, CRT has been found to range from <1 to 55 d (Baidai et al. 2020b). Likewise, the values of CAT range from 2 to >100 d (Robert et al. 2012). Marsac et al. (2000) also referred to the temporal aspect of aggregations in the first premise of the ecological trap theory, so it stands to reason that studies focused on this issue could shed light on the reasons driving tuna behavior around dFADs. Given the inherent difficulties of conducting experiments in the open ocean, most research on this subject is based on small-scale studies using electronic or acoustic tags to monitor individual tunas at a small number of dFADs, which might explain the variability in these results.

However, the dFADs used by tropical tuna purse-seine fisheries today are generally deployed with satellite-linked instrumented buoys equipped with one or more echo-sounders, which provide fishermen with accurate dFAD positioning as well as estimates of aggregated tuna biomass (Davies et al. 2014, Wain et al. 2021). Data collected by these buoys provide invaluable information for fishermen, but have also attracted the attention of the scientific community, who have highlighted their potential to provide insights in tuna migration and behavior on a global scale (Lopez et al. 2016, Moreno et al. 2016, Santiago et al. 2016, Orue et al. 2019a, Baidai et al. 2020a). As such, recent studies have begun to model and process the echo-sounder data provided by these buoys to remotely map tuna distribution or investigate patterns in tuna aggregation around dFADs (Baidai et al. 2019, 2020b, Orue et al. 2019b, Precioso et al. 2022). It has been suggested that dFAD data could even be used to test the ecological trap hypothesis (Dagorn et al. 2010), precisely by providing large-scale data on the biomass present under the dFAD at any given time.

In this context, here we used data from echo-sounder buoys deployed on dFADs across the Atlantic, Indian, and Pacific Oceans to explore global temporal patterns in aggregation. To do this, we

applied machine learning based models from TUN-AI (Precioso et al. 2022) to echo-sounder data to provide accurate tuna biomass estimates below dFADs over time. We then adapted metrics already present in the literature to account for the fact that our study focuses on the entire tuna aggregation around the dFAD, as opposed to individual fish. Finally, given that TUN-AI can deliver estimated amounts of tuna biomass aggregated at the dFAD, not just presence–absence data, we examined the processes of aggregation and disaggregation in more detail, analyzing the symmetry of these processes. With particular reference to the first premise of the ecological trap (a fast, strong, and long-lasting association; Marsac et al. 2000), we specifically tested whether the time it takes for the tuna school to depart from a dFAD is significantly longer than the time it takes for the aggregation to form in the first place.

2. MATERIALS AND METHODS

2.1. Database description

The work presented in this paper makes use of an extensive amount of data arranged in 3 large databases, classified according to the source from which they were obtained.

2.1.1. Activity data on dFADs

The first database contains the activities performed by the Spanish tropical tuna purse seine fleet on dFADs drifting in the 3 major oceans (Atlantic, Indian,

and Pacific). These data were provided by the ship owners' association, Asociación de Grandes Atuneros Congeladores (AGAC), and contains 120 707 events spanning 11 April 2017 to 1 January 2021, out of which 35 813 happened in the Atlantic Ocean, 55 819 in the Indian Ocean, and the remaining 29 075 in the Pacific Ocean. Every entry in this database contains information on the type of interaction with the dFAD, the unique identification number and model of the echo-sounder buoy attached to the dFAD, the time-stamp and geographical coordinates where the activity took place, and other relevant details (for a complete description of the interaction types, see Ramos et al. 2017). The buoy identification number allowed us to establish a connection between the human interactions associated with a particular dFAD and the acoustic measurements recorded by the echo-sounder (see Section 2.1.2). Fig. 1 displays the spatial distribution, at a global scale, of the tuna catch events carried out by the Spanish fleet over the reference period used to train the biomass estimation model.

2.1.2. Echo-sounder buoy data

The echo-sounder buoy database assembles the data collected from Satlink (www.satlink.es) buoys deployed by the Spanish tropical tuna purse seine fleet. Altogether, this data set includes information from 16 419 different buoys distributed over the 3 major oceans and spanning the same time frame as the events in the activity database (see Section 2.1.1). The data set comprises over 70 million observations, generally sampled at hourly frequency.

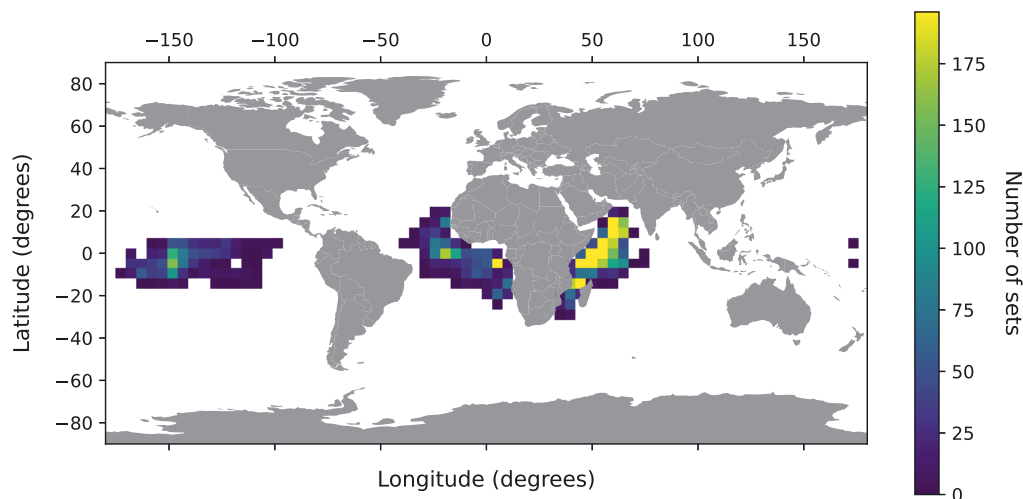


Fig. 1. Distribution of sets used to train the TUN-AI model, reported by the Asociación de Grandes Atuneros Congeladores between 11 April 2017 and 1 January 2021

Each entry in the database contains the unique buoy identification number, the timestamp of when the reading was taken, and an estimate of tuna biomass (in t) under the dFAD. These biomass estimates are obtained from acoustic samples taken periodically throughout the day, and the average back-scattered acoustic response is converted into estimated tonnage based on the target strength of skipjack tuna. See Lopez et al. (2016) for detailed explanations of the process within the buoy and Boyra et al. (2018) for the value of the target strength. For each reading, the biomass estimates are provided across 10 equally spaced depth layers, and values can range from 0 to 63 t per layer. The resolution of the information sent by the echo-sounder is 1 t, which means that tuna aggregations below this threshold are not considered.

The data set also includes all of the position information transmitted by the buoy. These GPS coordinates of the buoy are generally transmitted every 24 h, although transmission frequency can be modified by the buoy owner. Besides that, buoys are programmed to only send biomass estimates when the total measurement delivers values above 1 t. Hence, if a given buoy sent GPS coordinates but no biomass estimates over a certain period, the biomass estimates for that period were imputed to 0 t. Further information about the buoy models and the biomass estimation process is available in Section 2.1.2 in Precioso et al. (2022).

2.1.3. Oceanography data

The TUN-AI models are trained to provide accurate biomass estimates from echo-sounder data (Precioso et al. 2022), but they also need to be fed with several oceanographic variables at surface level (depth = 0.494 m). These data are provided at daily frequency by the EU Copernicus Marine Environment Monitoring Service (CMEMS) (Global Monitoring and Forecasting Center 2018) (products GLOBAL-ANALYSIS-FORECAST-PHY-001-024, 1/12° resolution; and GLOBAL-ANALYSIS-FORECAST-BIO-001-028, 1/4° resolution). Each record of the echo-sounder buoy database (see Section 2.1.2) is enriched with oceanographic variables for the location and time of the measurement. The variables used in this study are: temperature (°C), chlorophyll *a* concentration (mg m^{-3}), dissolved oxygen concentration (mmol m^{-3}), salinity (psu), thermocline depth (m, calculated as the depth where water temperature is 2°C lower than surface temperature), current velocity (m s^{-1}), and

sea surface height anomaly (SSHa) (m, deviation of the sea surface height from the long-term mean).

2.2. Data processing

2.2.1. Data cleaning

Prior to analysis, it is necessary to clean the data of any records that might pollute or obscure our study. To do this, a set of procedures have been established to remove potential errors:

- Duplicate rows and samples with missing buoy identification number are dropped from both the activity and the echo-sounder databases.
- Echo-sounder records corresponding to positions with less than 200 m depth are removed, as the echo-sounder signal could be affected by the sea floor. This filter also removes all acoustic records reported on land.
- Acoustic readings from buoys on board vessels are removed by calculating the mean buoy velocity over a day and discarding rows where the buoy velocity exceeds 3 knots, following the same criterion as Orue et al. (2019a).

2.2.2. TUN-AI estimates

A simple approach for estimating tuna biomass is to use only raw acoustic records, like the baseline model defined by Precioso et al. (2022). This baseline model uses the 72 h echo-sounder window prior to the date of the prediction. The window contains 1 acoustic record per hour, and each is composed of 1 value for each of the 10 layer depths, thus defining a matrix of size 72×10 . As the output of the model (i.e. the overall biomass estimation) is a single number, it is necessary to apply a set of aggregation rules on the echo-sounder window matrix. The rules that performed best in terms of accuracy were the maximum of all the hours for every layer and then the mean of all layers. However, there are models that can perform better than this baseline, as we explain below.

The biomass estimates provided by the echo-sounder may present variations when compared to real tuna tonnage under the dFAD (Lopez et al. 2016, Escalle et al. 2019a, Orue et al. 2019a). This could be due to multiple causes, including the influence of oceanographic conditions or the diverse species composition under the dFAD. To mitigate this issue, we estimated tuna biomass using TUN-AI (Precioso et al. 2022), which has proven to be more accurate than

simply considering the raw acoustic signal provided by the echo-sounder (i.e. the baseline model). TUN-AI, based on a gradient boosting (GB) algorithm (Friedman 2001) and trained using set and deployment events from the dFAD logbook, uses information from the acoustic records, buoy location, and oceanographic variables to estimate the tuna biomass under dFADs. This pipeline includes:

(1) a binary classification model trained to estimate whether the tuna biomass under a dFAD is higher or lower than 10 t. This model attained an F1-score of 0.925, compared to the 0.763 reported by the baseline model over sets.

(2) a regression model trained to give a direct estimate of the quantity of tuna biomass under a dFAD. This model has a mean absolute error (MAE) of 21.6 t and a symmetric mean absolute percentage error (SMAPE) of 29.5% when evaluated over sets (see Steurer et al. 2021 for detailed definitions of these metrics). In comparison, the MAE of the baseline model over sets was 30.0 t.

Both models require a 72 h echo-sounder window, containing 1 acoustic record per hour. TUN-AI also includes a 3-class classification model that was not used in this study. For a detailed explanation of TUN-AI, we refer the reader to the original paper (Precioso et al. 2022). One of the novelties of our analysis with respect to previous studies is the fact that using a regression model allows us to examine both the aggregation and disaggregation processes to dFADs, which would not be possible with a binary classification model.

It is worth noting that 2 strong assumptions are considered when building these models: first, the

total catch captured by the vessel and later recorded in the dFAD logbooks corresponds to the entire tuna aggregation present at the dFAD; and second, the whole tuna school is sampled by the echo-sounder beam at any moment of the echo-sounder window. Hypotheses of this kind are unavoidable in these large-scale studies, and we expect that no significant changes in the relative variation of the biomass are observed due to these issues after the smoothing procedures described in Section 2.2.4 are carried out.

TUN-AI models can provide hourly biomass estimates for each buoy, but this frequency was not adequate for our study due to the noise generated by the day–night oscillations in tuna biomass (Escalle et al. 2019a). To circumvent this problem, we generated daily biomass estimates for each buoy, producing 3 873 531 outputs in total, after the cleaning process described in Section 2.2.1 was carried out. Fig. 2 shows the spatial distribution of these biomass estimates given by TUN-AI. Note that the geographical positions of most biomass estimates correspond to the areas with high numbers of training data (see Fig. 1), so we believe the coverage of the model to be sufficient to obtain good estimates across all 3 oceans.

2.2.3. Generating unaltered segments

To avoid the effects of potential human interactions when studying tuna aggregation dynamics under dFADs, the time series of each buoy was broken into smaller segments in which such processes were not altered by any external action, which we call ‘unaltered segments’.

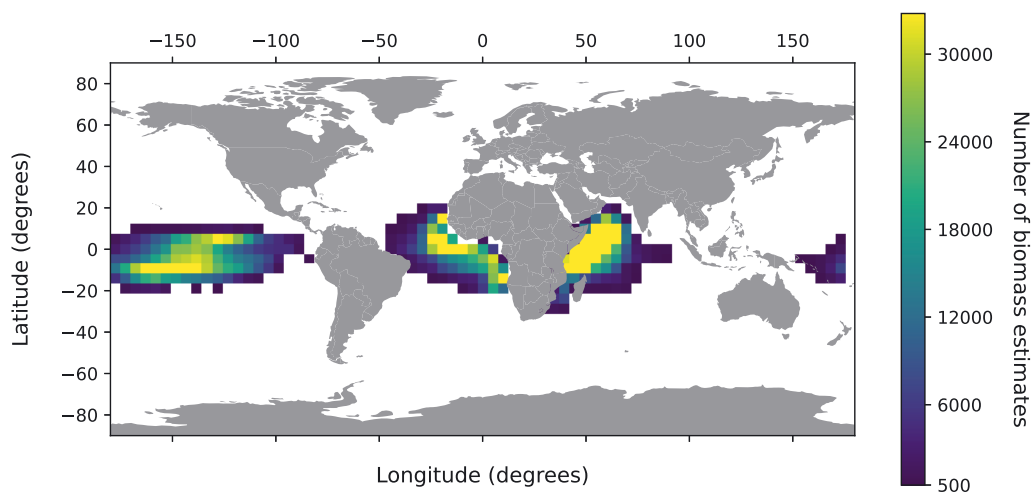


Fig. 2. Heat map of the number of biomass predictions at a global scale for the 16 419 drifting fish-aggregating devices (dFADs) employed in this study, where only the regions in which more than 500 buoy biomass estimates were tracked over the reference period are depicted

To generate the unaltered segments for any particular echo-sounder buoy, we first merged the TUN-AI estimates (for both the binary classification and the regression models) with the activity database, using the buoy identification number as the primary key. Of the activities recorded in the dFAD logbook, only deployments, sets, retrievals at sea, recoveries at port, and losses were considered to be ‘segment-generating’, that is, they could directly affect the echo-sounder readings and the biomass dynamics under the dFAD. Visits and modifications were assumed to have no effect on aggregated tuna biomass or on the echo-sounder readings, so they were not considered in this study. Lastly, a period of more than 24 h with no information reported by the buoy, which we refer to as an ‘empty period’, would also generate an unaltered segment, as this could indicate that the buoy was switched off or otherwise inoperable.

We only considered segments longer than 72 h, as that is the minimum length of the window that TUN-AI needs to estimate biomass. We also omitted segments where TUN-AI failed to output an estimate for more than 80 % of the total segment length. This may happen for very short segments (not discarded previously because they are longer than 72 h) or if the oceanographic data are not available (for example, due to issues on the CMEMS platform or with data resolution). Otherwise, missing values from TUN-AI were interpolated, in the case of the regression model, or propagated based on the last valid estimate, in the case of the binary classification model. Finally, after the pre-processing outlined in Section

2.2.1, and the steps described here, a total of 43 334 unaltered segments were generated. The process of generating the unaltered segments is illustrated in Fig. 3.

2.2.4. Smoothing the signal

The outputs of both the binary and regression models of TUN-AI are more representative of real tuna biomass than the raw estimates provided by the buoy. However, some noise is still present in the data, likely due to the small-scale changes in tuna aggregations or to the influence of other fish species around the dFAD. Since the aim of the current study was to identify general trends in the tuna aggregation processes, we smoothed the resulting series to capture general trends while discarding small oscillations.

For the binary series, isolated estimates of one class or another were smoothed according to the values recorded for the previous day (Fig. 4). Altogether, 2.7 % of the total binary data were modified by this smoothing procedure.

In the regression model, we applied a constrained P-splines approach developed by Navarro-García et al. (2023), which captures the trend of the data without overfitting the signal while forcing the response to be non-negative (as the nature of the data requires). To smooth the series following this methodology, the open-source Python package ‘cpsplines’ was used (Navarro-García 2021). Fig. 5 shows the

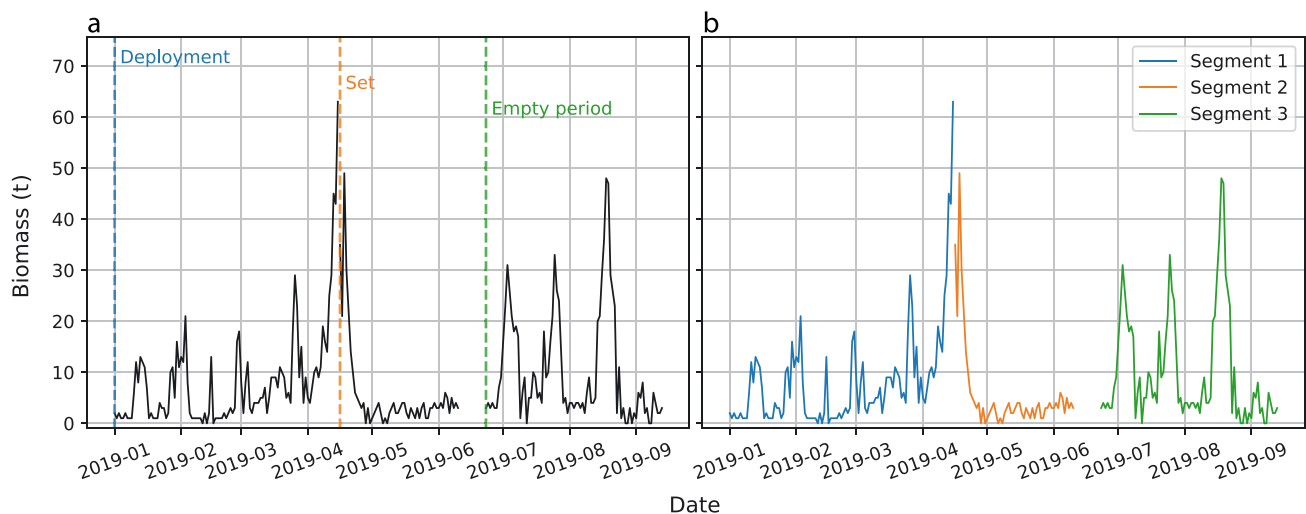


Fig. 3. Process of generating unaltered segments from the biomass estimates and registered dFAD logbook activities on a sample echo-sounder buoy over time. (a) A sample buoy’s biomass estimates over time, together with registered activities from the dFAD logbook depicted as dashed lines. (b) Generation of the unaltered segments from the activities registered in the dFAD logbook, and from a period with no buoy records. Each color represents the resulting individual unaltered segments

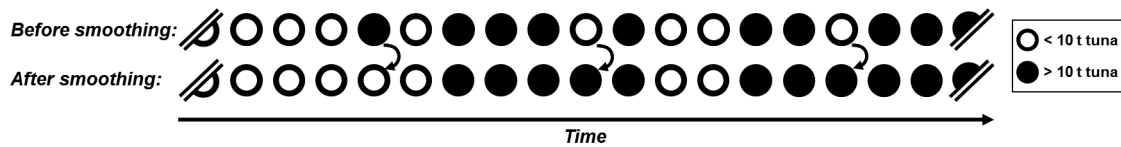


Fig. 4. Smoothing procedure for the binary series. Isolated estimates are modified according to neighboring values

rightmost unaltered segment from Fig. 3b together with its smoothed version.

2.2.5. Characterization of tuna dynamics

To characterize the temporal patterns of tuna aggregations to newly deployed dFADs, we estimated a number of metrics using the binary classification results and unaltered segments beginning with a deployment (7368 segments):

- Soak time (ST): reflects the amount of time a given dFAD has been drifting at sea. Thus, it was calculated here as the time elapsed between the initial deployment of the dFAD and the end of the unaltered segment (Fig. 6).

- Colonization time (CT): captures the time between the initial deployment of the dFAD and the first detection of tuna (Orue et al. 2019b). Here, we estimated it as the time between the initial deployment of the dFAD and the first day where the binary model of TUN-AI predicted a positive output, i.e. tuna biomass was greater than 10 t (Fig. 6).

- Aggregation continuous residence time (aCRT): first defined as CRT by Ohta & Kakuma (2005) for individually tagged tunas at dFADs, and adapted here to consider the entire aggregation, aCRT reflects how long a tuna aggregation is continuously detected by the echo-sounder buoy on a given dFAD without day-scale (>24 h) absences. That is, aCRT was calculated here as the number of days where TUN-AI continuously estimated tuna biomass greater than 10 t (Fig. 6).

- Aggregation continuous absence time (aCAT): adapted here to consider the entire aggregation, this metric also draws from Ohta & Kakuma (2005). In a similar way, aCAT reflects how long the tuna aggregation is continuously absent from a given dFAD without day-scale (>24 h) presences, and was calculated here as the number of days where TUN-AI continuously estimated tuna biomass ≤ 10 t (Fig. 6).

- Occupancy rate (OR): defined as the proportion of time that the tuna school remains at the dFAD after it has been colonized, and it can be estimated by means of the previous metrics.

- Percentage of dFADs that are never colonized: proportion of dFADs where the presence of tuna has never been observed. This metric is useful to contextualize the colonization time statistics.

Given that the current study also draws from estimates of the total amount of tuna under the dFADs, the processes of both aggregation and disaggregation can be examined. Therefore, we defined 2 novel metrics: aggregation time (AT) and disaggregation time (DT). To estimate them, we considered the daily tuna biomass estimates provided by the TUN-AI regression model after smoothing (see Section 2.2.4). Using these data, we identified the moments where tuna biomass reached a local maximum above 10 t, since this is the amount of tuna we considered to be a significant aggregation. This was achieved using a modified version of the function 'scipy.signal.find_peaks' (Virtanen et al. 2020), and these peaks were determined by simple comparison of neighboring values of tuna biomass estimates. Any peaks found within the first or last 5 d of the unaltered segment were discarded, as an extra precaution to avoid the effects of any human activity on the biomass estimates. This resulted in all unaltered segments lasting less than 10 d to be discarded, so a total of 23 326

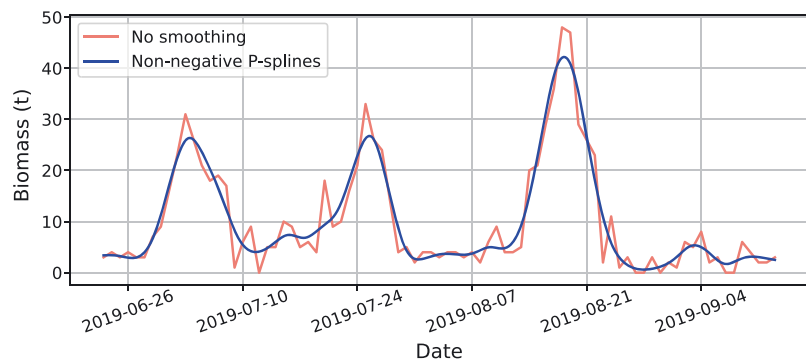


Fig. 5. Smoothing process for the regression series. Biomass estimates generated from the TUN-AI regression model (in pink) are smoothed to show general trends with the non-negative P-splines approach (in blue). The smoothed curve is less influenced by noise in the original data to better represent general trends while providing coherent estimates with the non-negative requirement

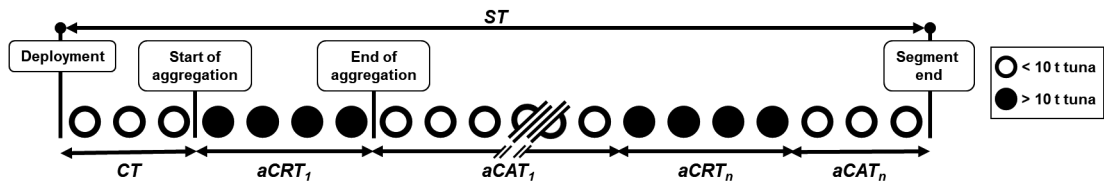


Fig. 6. Results obtained by the TUN-AI binary model for a given dFAD and the calculation of aggregation metrics based on unaltered segments starting with a deployment. ST: soak time; CT: colonization time; aCRT: aggregation continuous residence time; aCAT: aggregation continuous absence time

unaltered segments were considered. The final number of peaks was 71 644. For each peak, AT was then calculated as the time elapsed between the first biomass estimate larger than 10 t and the day maximum biomass was reached. Likewise, DT was calculated as the time between the maximum biomass to the next biomass estimate under 10 t. This process is illustrated in Fig. 7.

The binary classification TUN-AI model of Precioso et al. (2022) used a 10 t threshold for class discrimination, which we maintained in this study for several reasons. First, as the models were trained over sets and only 7.6% of them reported less than 10 t, no significant changes were expected. Second, smaller aggregations cannot be discerned due to the errors of the models, and hence reducing this threshold would not improve the quality of the estimates. Finally, to describe the tuna dynamics under dFADs, we were mainly interested in how the size of a tuna school varies over time and not in its absolute value.

Regarding the variables estimated from the binary TUN-AI biomass estimates and using newly deployed dFADs, a summary of statistical metrics, itemized by the ocean basin, is displayed, and their distributions are shown by means of box plots. To better

examine whether any of the previously mentioned metrics varied significantly across oceans, Kruskal-Wallis tests were carried out and followed by Dunn tests to confirm pairwise differences. Likewise, aggregation colonization and absence times (aCRT, aCAT), as well as aggregation and disaggregation times (AT, DT), were compared using Mann-Whitney tests.

3. RESULTS

3.1. General aggregation metrics

ST and CT both showed similar patterns between oceans (Fig. 8a,b): the longest CT and ST were reported in the Pacific Ocean, and the shortest in the Indian Ocean, while the Atlantic Ocean showed results somewhere in between. Median ST for the Pacific Ocean was more than double that of the Indian Ocean, while CT was nearly double. Concerning the variability of these variables, the lowest standard deviation occurred in the Indian Ocean (Table 1), while results were more variable for the other 2 oceans. The proportion of dFADs that were

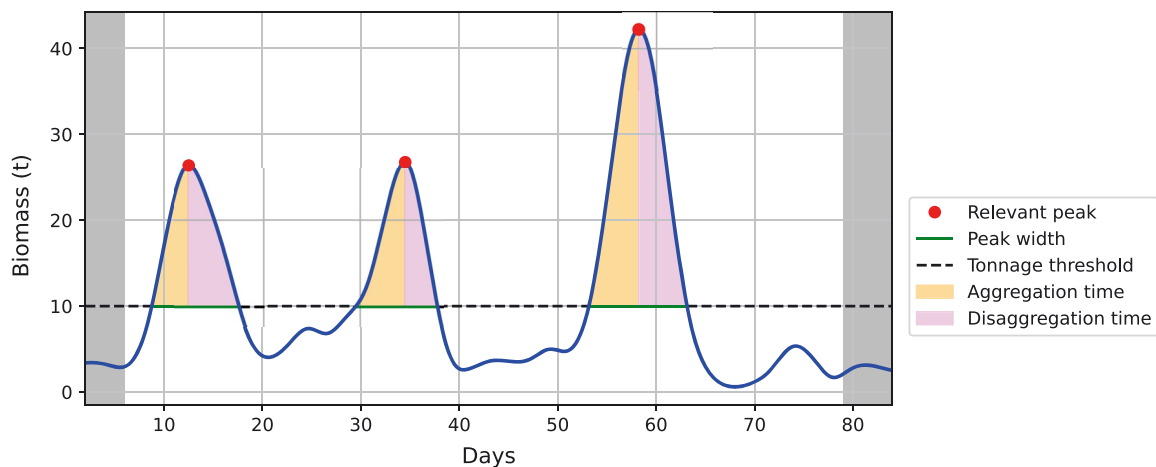


Fig. 7. Calculation of aggregation and disaggregation times from the smoothed biomass estimates delivered by the TUN-AI regression model for a representative unaltered segment. The gray-shaded areas represent the days where no peaks are considered, and the dashed line represents the 10 t threshold

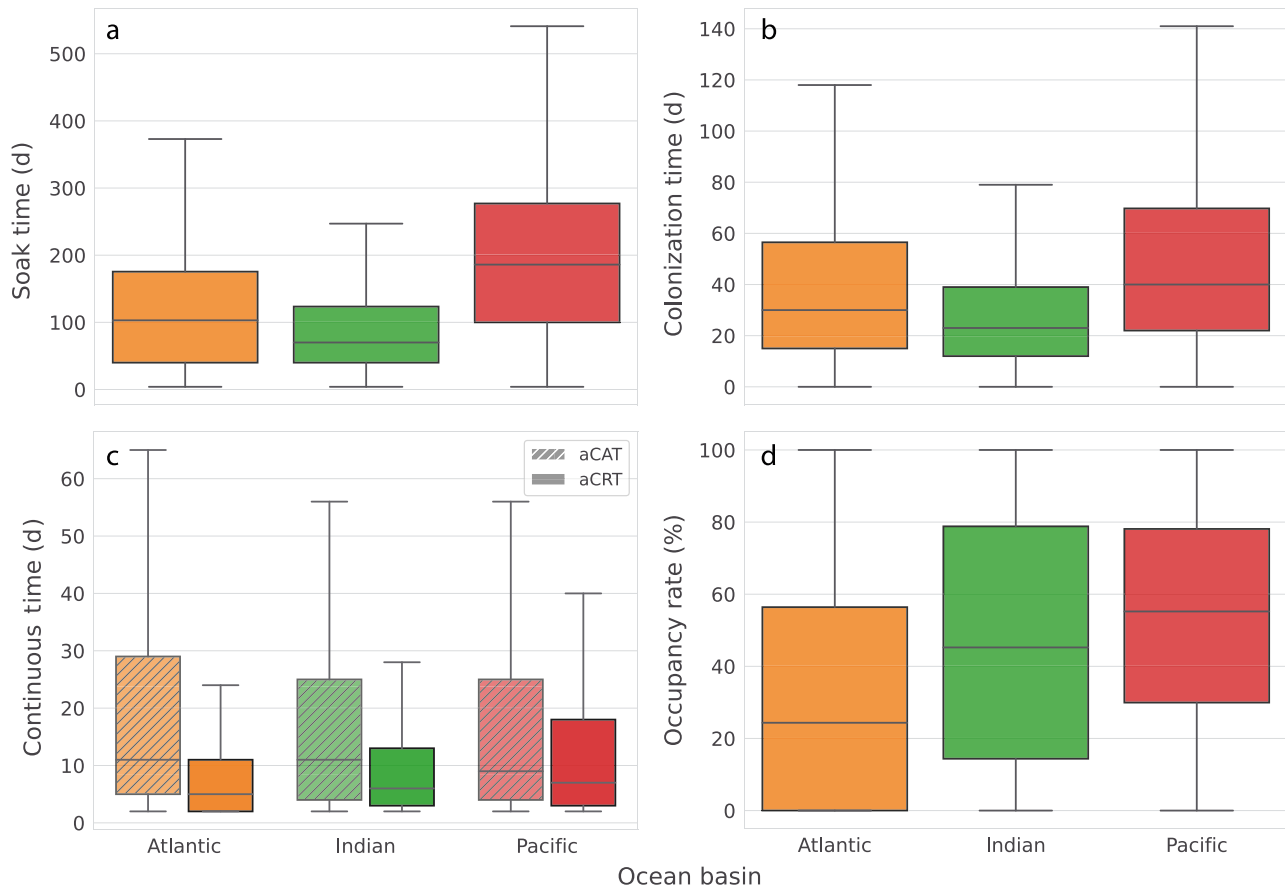


Fig. 8. Variables estimated from the binary model. Line: median; box: interquartile range [IQR]; whiskers: max./min. values $<1.5 \times$ IQR above/below box (outliers $\geq 1.5 \times$ IQR were removed from the figure). (a) Soak time (ST), (b) colonization time (CT), (c) aggregation continuous residence and absence times (aCRT and aCAT), (d) occupancy rate (OR)

not colonized throughout their soak time also presented considerable variations (27% in the Atlantic, 16% in the Indian, and 11% in the Pacific).

Regarding aCRT, aCAT, and OR, consistent patterns were again visible across oceans, although trends were different for both ST and CT (Fig. 8c,d). In this case, the Indian Ocean showed values for aCRT, aCAT, and OR that fell between those of the Atlantic and Pacific oceans. Concerning the aCRT, the Atlantic Ocean showed the shortest times, and the Pacific Ocean showed the longest, while the opposite was true for aCAT (Fig. 8c). Hypothesis tests showed significant differences for both aCRT and aCAT among oceans (Kruskal-Wallis test, $p < 0.01$), and these differences were confirmed in the pairwise comparisons between oceans (Dunn test, $p < 0.01$). Median values for both aCRT and aCAT across oceans were generally similar, 5–7 and 9–11 d, respectively (Table 1). Overall, global aCRT was significantly lower than the global aCAT (Mann-Whitney test, $p < 0.01$), and variability was also consistently higher for aCAT than for aCRT. Lastly, OR was

Table 1. Summary statistics, per ocean, for tuna aggregation metrics calculated from unaltered segments starting with a deployment using the binary model. ST: soak time; CT: colonization time; aCRT: aggregation continuous residence time; aCAT: aggregation continuous absence time; OR: occupancy rate; IQR: interquartile range

Metric	Ocean	Count	Mean	SD	Median	IQR
ST (d)	Atlantic	1015	124	101	103	136
	Indian	1591	92	73	70	84
	Pacific	4762	202	129	186	177
CT (d)	Atlantic	1015	44	43	30	42
	Indian	1591	29	25	23	27
	Pacific	4762	51	42	40	48
aCRT (d)	Atlantic	3201	10	16	5	9
	Indian	4389	11	16	6	10
	Pacific	24408	17	25	7	15
aCAT (d)	Atlantic	3875	24	33	11	24
	Indian	5088	19	23	11	21
	Pacific	26552	21	30	9	21
OR (%)	Atlantic	1015	33	32	24	56
	Indian	1591	48	35	45	64
	Pacific	4762	53	31	55	48

Table 2. Summary of tuna aggregation metrics for the continuous model and decoupled by ocean basin. IQR: interquartile range

Ocean	Count	Aggregation time (d)				Disaggregation time (d)			
		Mean	SD	Median	IQR	Mean	SD	Median	IQR
Atlantic	19581	7.60	13.51	3.02	5.64	6.36	10.47	3.00	4.67
Indian	26806	8.24	13.65	3.63	6.85	7.26	12.48	3.44	5.42
Pacific	25257	15.45	25.04	5.89	13.99	14.63	25.99	5.49	11.03

globally around 50%, with the lowest median OR registered in the Atlantic Ocean at 24% (Table 1).

3.2. Aggregation and disaggregation times

Using the TUN-AI regression model, we were able to examine tuna aggregation dynamics around dFADs in more detail, estimating both AT and DT. In general, AT and DT showed similar patterns across oceans, with the shortest median AT and DT being registered for the Indian Ocean, and the longest for the Pacific Ocean (Table 2, Fig. 9). Globally, DT was not significantly longer than AT (Mann-Whitney test, $p \gg 0.01$). In fact, it is worth noting that the first quartile for both AT and DT was generally similar, while more variation was seen for the third quartile, with AT generally longer than DT (Fig. 9). Significance tests found differences for both AT and DT among oceans (Kruskal-Wallis test, $p < 0.01$) and in the pairwise comparisons between oceans (Dunn test, $p < 0.01$). Lastly, the distributions for AT and DT were positively skewed (i.e. the mean was greater than the median), regardless of the ocean where the dFAD was deployed.

4. DISCUSSION

By using the data acquired by echo-sounder buoys attached to dFADs, over the course of several years and across all oceans, the current study aimed to capture the general trends in tuna aggregation dynamics at a global scale. This was achieved by means of a powerful machine learning pipeline, TUN-AI (Precioso et al. 2022), which processes echo-sounder information to deliver estimates of tuna tonnage under each dFAD either as a binary output (<10 or ≥ 10 t), or as a direct estimate of biomass. To our knowledge, this is the first analysis to exam-

ine typical metrics of tuna aggregation (namely ST, CT, aCRT, aCAT, and OR) across all oceans and in such detail, providing insight into the processes of both aggregation and disaggregation in the colonization of dFADs by tuna.

Using a binary model, and applying a similar approach with echo-sounder buoys from a different manufacturer, Baidai et al. (2020b) quantified several metrics related to tuna aggregations around dFADs in the Atlantic and Indian Oceans. In terms of soak time, their estimates are considerably shorter than ours for the same oceans (median values of 44 and 43 d in the Atlantic and Indian Oceans, respectively), likely due to slight differences in definition. While Baidai et al. (2020b, p. 2962) defined soak time as ‘the number of days between the deployment of a dFAD equipped with a buoy and the first reported operation on it’, our definition captures the length of the entire unaltered segment. Per our definition, this would likely be longer for buoys where no activities other than deployment were registered, which made up 27% of our dataset. In the Pacific Ocean, Escalle et al. (2021) reported mean drift times of 118 d for dFADs included in the Parties to the Nauru Agreement’s (PNA) dFAD tracking trial program, which is

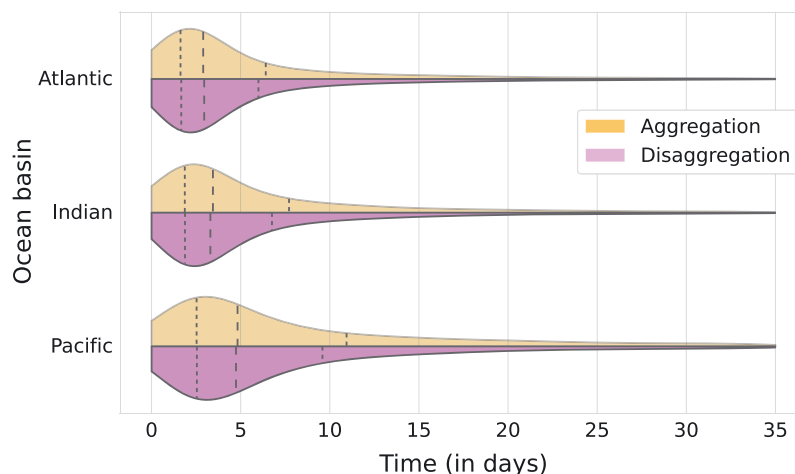


Fig. 9. Aggregation and disaggregation time distributions itemized by ocean basin. The vertical dashed lines depict the positions of the quartiles for each distribution

shorter than the median 202 d soak time we reported. However, Escalle et al. (2021) highlighted that due to data-sharing constraints, it is likely that these times are underestimated, as information outside of the PNA's Exclusive Economic Zones was not analyzed. Fishermen have mentioned that the average lifespan of an artificial dFAD is about 5–12 mo (Lopez et al. 2017), in line with the values registered here. The differences in soak time between oceans, while likely influenced by the ocean basin itself (with longer soak times in larger oceans simply due to the space the dFAD has to drift), may also be affected by how fleets operate in each ocean (Maufroy et al. 2015). In both the Atlantic and Indian Oceans, purse-seiners can be supported by supply vessels, whose primary activity is centered around dFADs. Among others, these supply vessels monitor and intercept dFADs as they drift out of regular fishing zones where the purse-seine vessels operate, often recovering and deactivating the buoys associated with these dFADs (Báez et al. 2022). The activity of these vessels may well have slightly shortened soak times, in comparison to what they would be if the dFADs were allowed to drift indefinitely.

Regarding colonization time, it appears that there is no general consensus among fishing masters. Moreno et al. (2007) interviewed fishing masters from the Indian Ocean, of which about one-third considered that it usually takes a minimum of 1 mo for a school to aggregate at a dFAD. Indeed, although there is considerable variation in the colonization times registered in our study for dFADs across all oceans, median values are around 20–40 d, in line with the observations of these fishing masters. However, about 45% of interviewed fishing masters believed that colonization of a dFAD by tuna was not dependent on time at all (Moreno et al. 2007), an observation which was also reflected by Lopez et al. (2017), where tuna abundance at dFADs was not positively correlated with soak time, and further evidenced in the large variability for colonization time in our own data. Small-scale tagging studies have found that local conditions may influence whether or not tuna decide to aggregate at a dFAD at all (Girard et al. 2004, Robert et al. 2013a), also in accordance with the view expressed by almost half of the fishing masters interviewed by Moreno et al. (2007), whereby the time to form an aggregation of tuna under a dFAD is influenced by environmental factors. Indeed, the basis of the 'indicator-log' hypothesis (Hall et al. 1992) is that tuna consider the dFAD to be representative of local conditions and may thus choose to aggregate when those conditions are favorable.

While we did not analyze the local conditions present around each dFAD at the time of colonization, instead establishing general trends across ocean basins, this should certainly be the focus of future studies.

In the same way that colonization time may be affected by local conditions, small-scale studies on the time tuna spend at a dFAD (continuous residence time) also evidence a number of factors at play (Ohta & Kakuma 2005, Schaefer & Fuller 2005, Dagorn et al. 2007, Matsumoto et al. 2014, 2016, Rodriguez-Tress et al. 2017, Tolotti et al. 2020, Chiang et al. 2021, Govinden et al. 2021). For example, Robert et al. (2012) found size-dependent differences in the time yellowfin tuna spent around an anchored FAD, with smaller individuals (<50 cm fork length) spending about 4 times as much time around the FAD than larger individuals. In a later study, they found different behavioral modes of tuna around anchored FADs depending on the local conditions (Robert et al. 2013a). Some tuna would pass by a FAD without associating with it, while others made short visits, or remained near it for several days in a row. Similarly, differences in the continuous residence time of skipjack, yellowfin, and bigeye tuna have been observed across oceans (Schaefer & Fuller 2005, Tolotti et al. 2020, Govinden et al. 2021). Some of these factors, such as size of individual fish in a school, or the exact species composition of the school, are currently overlooked when using echo-sounder buoy data and could help explain the large variability found in CRTs and CATs across oceans. Nonetheless, as buoy technology improves, it is possible that estimates of both size or species composition will become available, giving further insight into those factors influencing the associative behavior of tuna.

Even though the massive amount of data that is available from echo-sounder buoys attached to dFADs may not provide such highly detailed information as small-scale studies, there is value in identifying general trends on how entire tuna aggregations behave. One of the specific objectives of the current study was to examine whether the first premise of the 'ecological-trap' theory, whereby the association of tuna with dFADs is fast, strong, and long-lasting (Marsac et al. 2000), was evident in our data. In the original study, Marsac et al. (2000) based the first premise of the ecological trap on a series of observations, namely tag and recapture events around the same dFAD, or reports of 'fast' associations, where tuna appeared under a dFAD after less than 7 d. While our data cannot show the movements of individual tuna around the dFADs, we do see that in

most cases, the time for tuna to colonize the dFAD is longer than the 7 d reported by Marsac et al. (2000). In our results, 75 % of colonization events took more than 15 d, and more than 50 % took over 20 d, across all oceans. Nonetheless, some cases in our data did show very short colonization times (minimum was 2 d), though these appear to be the exception rather than the norm. Secondly, the first premise states that the association of tuna to dFADs is 'strong'. To look into this, we applied a regression model to the echosounder buoy data, which allowed for direct estimates of tuna biomass aggregated to the dFAD (Precioso et al. 2022), and the calculation of 2 derived metrics, namely AT and DT. If the association of tuna to dFADs were strong, we would generally expect aggregation to occur more quickly than departure from the dFAD; however, this was not the case in our results. We found that DT was not significantly longer than AT. In fact, in some ocean basins, DT was slightly shorter than AT, although they were largely symmetrical. The third part of the first premise states that the association is 'long-lasting', although the length of time considered by the authors for this statement is not clear, it seems reasonable to believe they refer to at least month-long associations. Our results did show considerable variability in continuous residence time, reaching up to 40 d in length in the Pacific Ocean, though median values were substantially shorter: between 5 and 7 d across all oceans. Although we recognize that the nature of tuna associations with dFADs may not be restricted to a single object, as studied here, our results do not evidence a clear 'attraction' of tuna to dFADs in general terms, in line with previous studies (Girard et al. 2004), nor a potential trapping effect, at least in temporal terms and on individual dFADs. Although these findings do not yet provide a complete picture of whether dFADs represent an ecological trap, they have important implications for the management and regulation of dFAD usage. If dFADs do not act as ecological traps, management objectives can shift focus onto other issues around dFAD usage such as preventing impact on sensitive environments and reducing dFAD loss (Dagorn et al. 2013, Escalle et al. 2019b, Imzilen et al. 2021). Whether dFAD networks can exert a trapping effect on tuna should still be explored, however, for example by comparing temporal metrics of association in areas with higher or lower dFAD density, in order to fully understand the potential effects of dFADs on tuna populations, and fully inform policy and regulation.

Through the regression model analysis, we found that aggregations occur gradually. That is, arrival

and departure of tuna to the dFAD does not occur at the same time for the entire school: the amount of tuna aggregated around a specific dFAD slowly grows, reaching a peak after about 5 to 7 d, and then slowly decreases, in roughly the same amount of time. Gradual increases in biomass under dFADs were also noted by Orue et al. (2019b), where tuna biomass at dFADs in the Indian Ocean appeared to reach a peak after around 30 d at sea. Previous research does show synchronicity in departure and arrival at dFADs for some individuals, but not all (Dagorn et al. 2007), in line with the observations of fishing masters, who stated that multiple discrete schools of tuna are generally found around dFADs, segregated by species and size (Moreno et al. 2007). The observations of previous authors (Dagorn et al. 2007, Moreno et al. 2007, Robert et al. 2014b, Anderson et al. 2019) and our own results do appear to support some social dynamics at play when aggregation occurs, in line with the 'meeting-point' hypothesis (Fréon & Dagorn 2000), at least up until peak biomass is reached. However, it is worth noting that due to the smoothing procedures employed in our study, abrupt changes in biomass around the dFADs, such as those caused when smaller aggregations or 'sub-schools' arrive and depart, could have been overlooked. Future research could supplement echosounder buoy data with tagging data to provide further insight into how individuals and schools move around dFADs. Orue et al. (2019b) pointed out that there is a lack of research examining the reasons for departure of tuna around dFADs. Indeed, examining the oceanographic context of the dFAD at the moment of departure of tuna schools could provide a closer view of how and why these schools use the dFAD.

Although echo-sounder buoy data are undoubtedly a powerful tool for scientific research, providing huge amounts of information that would be otherwise impossible to procure, special care should be taken when using and interpreting data from different buoy models and brands. As in our study, Diallo et al. (2019) used echo-sounder data from 2 dFAD buoy models from a different manufacturer to estimate aCRTs and aCATs in the Indian Ocean. Both were shorter than ours, and significant differences were found between buoy models (6–8 and 8–9 d, respectively, depending on buoy model). This is an important factor to consider when comparing the results of different studies using echo-sounder buoys. Diallo et al. (2019) concluded that the higher sensitivity of the newer model could be driving the differences in these metrics, so it stands to reason that

buoys from different manufacturers would also register biomass differently. For example, the use of different frequency echo-sounders likely impacts the biomass estimates provided by different buoy brands (Lopez et al. 2014, Moreno et al. 2019). Indeed, fishing masters perceive differences in the biomass readings of different manufacturers (Lopez et al. 2014), so these differences should be handled with care. Fishing technology evolves quickly, and it is important for researchers to be in line with manufacturers when drawing conclusions from technology-derived data. This being true, echo-sounder buoys deployed with dFADs represent a crucial source of data, delivering huge amounts of information on vast areas of the ocean which are otherwise unfeasible to monitor and study using traditional methods. Although these data have drawbacks, and should be complemented by small-scale and *in situ* studies, analyses like the ones outlined here pave the way for identifying general trends and patterns that can inform and strengthen policy and regulations aimed at protecting and ensuring the health of tuna populations across all major oceans.

5. CONCLUSIONS

- Data from echo-sounder buoys attached to dFADs provide important insight into general trends and patterns of tuna aggregations to dFADs across oceans, though care should be taken when using different buoy brands and models.
- Across all oceans, the association of tuna with individual dFADs does not seem to be ‘fast, strong, and long-lasting’, as suggested by the first premise of the ‘ecological trap’ hypothesis, according to the large-scale echo-sounder data.
- Future research should test for differences in temporal metrics in areas of differing dFAD densities to assess the effects of dFAD networks on tuna populations.
- Echo-sounder buoy data should be supplemented with oceanographic context, or individual tagging studies, to provide further insight into whether dFADs act as ‘indicator-logs’ or ‘meeting-points’.

Acknowledgements. This study was conducted using EU Copernicus Marine Service Information. We thank AGAC for providing the logbook data used in the analysis and for helpful comments on the manuscript. We also thank Carlos Roa for rendering available the Satlink echosounder data set. The research of D.G.U. is supported in part by the Spanish Agencia Estatal de Investigación under grants PID2021-122154NB-I00, PGC2018-096504-B-C33, RTI2018-100754-

B-I00, and TED2021-129455B-I00, and by a 2021 BBVA Foundation project for research in Mathematics. D.G.U. also acknowledges support from the EU under the 2014–2020 ERDF Operational Programme and the Department of Economy, Knowledge, Business and University of the Regional Government of Andalusia (project FEDER-UCA18-108393). The research of M.N.G. was financed by the research project IND2020/TIC-17526 (Comunidad de Madrid). The research of A.T.B. was financed in part by a Torres Quevedo grant PTQ2019-010642 from the Agencia Estatal de Investigación (Spain). The research of D.P. was financed by an Industrial PhD grant from the University of Cádiz.

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Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA

Reviewed by: Y. Matsumoto, M. Cronin and 1 anonymous
referee

Submitted: December 13, 2022

Accepted: May 25, 2023

Proofs received from author(s): 24 July, 2023