FULL PAPER

Impact of DFAD density on tuna associative behavior and catchability in the Indian Ocean

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Funding information

Ecosystems and biodiversity across most of the world are being altered by human activities. Habitat modification and degradation is among the most important drivers of biodiversity loss. These modifications can have an impact on species behavior, which can in turn impact their mortality. The use of Drifting Fish Aggregating Devices (DFADs) by purse seine fisheries is a major concern and offers a good case study to assess the impact of habitat modifications on species behavior and mortality. Because several pelagic fish species, such as tuna, associate with floating objects, fishers have started deploying their own floating objects – DFADs – in the early 1990s to increase tuna catchability. The massive deployment of DFADs has modified tuna habitat, by increasing the density of floating objects, with potential consequences on tuna associative behavior. In this study we use an individual-based model, based on a correlated random walk calibrated on passive acoustic tagging data, to determine a general relationship between FAD density and the time tuna spend between two associations with a FAD. Using this general relationship and fisheries data in the Indian Ocean (IO), we predict that tuna spend a high percentage of their time (up to 85 %) associated to DFADs in the western IO, where purse seine fishing pressure on DFADs is highest. Hence, purse seine fisheries modify tuna habitat by increasing DFAD density which in turn impacts tuna mortality, through a modification of their associative behavior. As DFAD density is directly linked to tuna fishing mortality, there is an urgent need to continue regulation efforts on DFAD deployments.

KEYWORDS
global change, purse-seine fisheries, Fish Aggregating Device, individual-based model, associative behavior

1 | INTRODUCTION

In the context of global change, biodiversity and ecosystem functions are deteriorating under the pressure of several direct and indirect drivers (IPBES, 2019). In terrestrial and freshwater ecosystems, land-use increase, induced by agriculture, forestry and urbanization, is the driver with the largest relative impact, while direct exploitation of fish and seafood, alongside with increasing use of the sea and coastal land, have the largest relative impact in the oceans (IPBES, 2019). Land and sea increased exploitation modifies natural habitat, by reducing its surface (Hooke and Martín-Duque, 2012; Neumann et al., 2016) as well as degrading and fragmenting it (Haddad et al., 2015; IPBES, 2018).

Such habitat structural modifications can impact wild species distribution, reproduction, behavior and ultimately their fitness (Mullu, 2016; Vanbergen, 2014; Macura et al., 2019; Fischer and Lindenmayer, 2007). For example, a review by Mullu (2016) suggests that habitat fragmentation in terrestrial ecosystems, by inducing both a net loss of habitat and the formation of isolated habitat patches, leads to a long-term decrease of species survival. Hence, it is central to determine to what extent habitat modifications, driven by global change, can impact species fitness, both in terrestrial and marine ecosystems.

The impact of landscape modification and habitat fragmentation have been extensively studied in terrestrial ecosystems (Fischer and Lindenmayer, 2007). For example, evidence show that 82 % of endangered bird species are threatened by habitat loss (Temple, 1986; IPBES, 2018), as are most amphibian species, with some of them now only breeding in modified habitats (IPBES, 2018). Anthropogenic disturbances also impact terrestrial ecosystem functions, reducing plant production (Hooper et al., 2012), and the impact of terrestrial habitat fragmentation on population connectivity is regularly assessed (Li et al., 2015; Crosby et al., 2009; Ruell et al., 2012; Walkup et al., 2017).

However, the extent to which habitat modifications determine the behavior, survival and fitness of marine species is still largely unknown (Hays et al., 2016). Research on the topic mainly focuses on estuaries and coastal marine ecosystems. Habitat modifications in coastal areas come from fisheries and development of infrastructures and aquaculture (IPBES, 2019). Climate change is also an important driver, with most striking impacts in the poles and the tropics (Doney et al., 2012). Induced warming temperatures and ocean acidification are likely to drive the degradation of most warm-water coral reefs by 2040-2050 (Hoegh-Guldberg et al., 2017), and mangroves are predicted to move poleward (Alongi, 2015). Marine habitat modifications also impact benthic community composition and sensitivity (Neumann et al., 2016; Dupaix et al., 2021b), and could affect fish recruitment (Macura et al., 2019).

In pelagic environments, fewer studies have assessed habitat modifications (Dupaix et al., 2021a; Phillips et al., 2019; Swearer et al., 2021) and their impact on species behavior, condition and survival (Hallier and Gaertner, 2008). Detailed movement data can be more cumbersome to acquire for marine than for terrestrial species, due to the limitations of satelitte communication in the ocean. It is possible to record horizontal and vertical movements of pelagic species, but the deployment of such tracking devices is costly (Ogburn et al., 2017). For example, using active acoustic tagging, one can have a good estimation of an individual trajectory but needs to follow the individual by boat. Presence-absence data can be obtained through passive acoustic telemetry, by deploying networks of acoustic receivers allowing the detection of tagged individuals when they are in the vicinity (Reubens et al., 2019; Pérez et al., 2020).

Tropical tunas are of major commercial interest worldwide ($36.2 billion in 2018, Galland et al., 2016) and are subject to an important fishing pressure (5.3 million tons of tropical tuna caught globally in 2019, ISSF, 2021; FAO, 2022). Yellowfin tuna (*Thunnus albacares*, designated as YFT) is one of the three main targeted species, with the skipjack (*Katsuwonus pelamis*) and bigeye (*Thunnus obsesus*) tunas. The main fishing gear targeting tropical tunas is purse seining, which made around 65.7% of the global catch from 2015 to 2019 (ISSF, 2021). In the 1990s, tuna purse seine vessels started exploiting tuna associative behavior. Many pelagic species, like tunas, are known to associate with floating objects (designated as FOBs, Freon and Dagorn, 2000; Castro et al., 2002), such as tree logs which are a natural component of pelagic species habitat (Thiel and Gutow, 2005). Taking advantage of this behavior, tuna purse seine vessels started deploying their own artificial FOBs, called Drifting Fish Aggregating Devices (designated as DFADs).

Since the 1990s, the deployment of DFADs has increased, and the last global estimate is between 81,000 and 121,000 DFAD deployed in 2013 (Gershman et al., 2015). Using data from observers onboard tuna purse seine vessels, Dupaix et al. (2021a) highlighted the habitat modifications provoked by the drastic increase of DFAD use in the Western Indian Ocean (WIO) from 2006 to 2018. DFADs multiplied the densities of FOBs by at least 2 and represented more than 85 % of the overall FOBs. Phillips et al. (2019) also found much higher densities of DFADs than of natural FOBs in the Western Pacific Ocean.

This massive DFAD deployment is a major concern and offers an interesting case study to assess the impact of habitat modifications on pelagic species behavior and mortality (Marsac et al., 2000; Hallier and Gaertner, 2008). Pérez et al. (2020) demonstrated, on arrays of anchored FADs (designated as AFADs), that a decrease of inter-FAD distance leads to an increase in the percentage of time tuna spend associated. By comparing passive acoustic tagging data from three arrays with different inter-FAD distances, the authors found that when the distance decreases, tuna both spent more time associated to a given AFAD and less time between two associations. If an increase of DFAD density also increases the percentage of time tunas spend associated, it would strongly impact their catchability and therefore their mortality.

Several acoustic tagging studies characterized the behavior of tuna around anchored FADs, both through active (Girard et al., 2004) and passive tagging (Dagorn et al., 2007; Pérez et al., 2020; Robert et al., 2012). These studies allowed to determine both residence times and duration between two associations. On DFADs, residence times were measured and showed important variations between oceans, ranging from 1.0 to 6.6 days, 0.2 to 4.6 days and 1.4 to 7.6 days for yellowfin, skipjack and bigeye tuna respectively (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2014, 2016). Longer associations were also observed on rare occasions, 27 and 28 days for YFT in the IO for example (Govinden et al., 2021). However, times between two DFAD associations are not known because neighbor DFADs are difficult to locate and exhaustively instrument with acoustic receivers. Without these measures, the percentage of time tuna spend associated with DFADs cannot be assessed.

This study focuses on the impact of pelagic habitat modifications, driven by fisheries, on a pelagic species, the YFT. We use an individual-based model, based on a Correlated Random Walk (Pérez et al., 2022), to predict the percentage of time tuna spend associated in the IO in 2020 and specifically in the area where the purse seine fishing pressure on FOBs is highest. This allows us to determine how a modification of the pelagic habitat – DFAD density increase – impacts YFT associative behavior, which has a direct impact on its catchability.

2 | MATERIAL AND METHODS

2.1 | Simulations

Simulations were performed using the FAT albaCoRaW model v1.4 (Dupaix et al., 2022), an individual-based model simulating tuna trajectories in an array of FADs based on a Correlated Random Walk (Pérez et al., 2022). The model allows the simulation of a tuna trajectory based on three parameters: the speed v, the orientation radius R_0 and the sinuosity coefficient c. These parameters were fitted on passive acoustic tagging data of 70 cm long YFT in arrays of anchored FADs, in Pérez et al. (2022) (Table 1). We considered twelve different FAD densities (noted ρ), ranging from 1.00×10^{-4} to 4.44×10^{-3} FAD.km^{-2}. These densities correspond to a distance to the nearest neighbor in a regular square lattice ranging from 100 to 15 km respectively (Table 1). For each of these densities, 100 different random arrays were generated, with FAD longitude and latitude being randomly picked. A thousand individual tunas were released from a random FAD in each of these arrays. As in Pérez et al. (2020), we define a Continuous Absence Time (CAT) as the time spent between two associations to a FAD. A tuna was considered associated when it was located at less than 500 m from a FAD. CATs were separated into two categories: (i) CAT$_{diff}$ when the movement occurred between two different FADs and (ii) CAT$_{return}$ when the tuna returned to its departure FAD after more than 24 h. Studies processing experimental acoustic tagging data of tropical tuna relied on a Maximum Blanking Period of 24 h, *i.e.* bellow a temporal separation of 24 h between two subsequent acoustic detections at the same FAD, the fish is considered to be still associated (Capello et al., 2015; Pérez et al., 2022). Hence, each time a CAT_{return} of less than 24 h was recorded after a CRT, this movement was discarded and the simulation time was reset to the beginning. The simulation was stopped when the individual either performed a CAT$_{diff}$, a CAT$_{return}$ or after 1,500 days of simulation. The obtained Continuous Absence Time (CAT) was saved. A total of 100,000 CATs were simulated per FAD density, totaling 1,200,000 simulated CATs.

2.2 | CAT trends for different FAD densities

For each FAD density, the mean Continuous Absence Time (noted $\overline{CAT}$) was considered, based on the individual CAT values simulated above. Because the CAT_{diff} and CAT_{return} were demonstrated to follow different processes (Pérez et al., 2020), we assessed the relationship between these two metrics and FAD density separately. The $\overline{CAT_{diff}}$ was related to FAD density (ρ) as follow:

$$\overline{CAT_{diff}}(\rho) = \frac{a_d}{\rho^{b_d}} \tag{1}$$

with $(a_d, b_d) \in \mathbb{R}_+^2$. By construction, a CAT_{return} cannot be shorter than 24h (Pérez et al., 2022; Capello et al., 2015). Hence, $\overline{CAT_{return}}$ was related to ρ as follow:

$$\overline{CAT_{return}}(\rho) = 1 + \frac{a_r}{\rho^{b_r}} \tag{2}$$

with $(a_r, b_r) \in \mathbb{R}_+^2$. We note $R = \frac{A}{B}$, the ratio between the number of CAT_{diff} (A) and that of CAT_{return} (B).The ratio R as a function of FAD density was fitted based on the following equation:

$$R(\rho) = a\rho^c \exp(b \times \rho) \quad (3)$$

with $(a, b, c) \in \mathbb{R}_+^3$. The values of a_d, b_d, a_r, b_r, a, b and c were determined using the *nls* function of the R package *stats* v3.6.3. We then determined $\overline{CAT}(\rho)$ based on the fitted values of equations 1, 2 and 3, and on the following equation (see Supplementary Materials 1 for more details):

$$\overline{CAT}(\rho) = \frac{R(\rho)\overline{CAT_{diff}}(\rho) + \overline{CAT_{return}}(\rho)}{R(\rho) + 1} \quad (4)$$

2.3 | Predictions in the Indian Ocean

Predictions of the $\overline{CAT}(\rho)$ in 2020 in the Indian Ocean were performed based on buoy density data (IOTC, 2021b). Buoy density data provided by the IOTC contains the monthly mean of the number of operational buoys for each 1°×1° cell of the Indian Ocean in 2020. This value was divided by the sea area of each cell, to obtain a mean monthly DFAD density (designated as $\overline{\rho}$). Densities were then averaged over 5° cells to predict CATs (Supplementary Materials 2). Using these density values and the coefficients of the models fitted in the previous section, monthly $\overline{CAT}$ values were predicted for each 5° cells in 2020.

The percentage of time a tuna spends associated with a FAD (noted P_a) can be expressed as follow :

$$P_a(\rho) = \frac{\overline{CRT}}{\overline{CRT} + \overline{CAT}(\rho)} \times 100 \quad (5)$$

with $\overline{CRT}$ the mean Continuous Residence Time, defined as continuous bouts of time spent at the same FAD without any day-scale absence (>24 h, Capello et al., 2015). Pérez et al. (2020) showed that $\overline{CRT}$ depends on AFAD density but to a lesser extent than $\overline{CAT}$. Hence, $\overline{CRT}$ was considered constant and estimated to be 6.64 days, as measured on YFT in the Indian Ocean by Govinden et al. (2021). Using this value and the predicted $\overline{CAT}(\rho)$, we predicted the monthly values of $P_a(\rho)$ in each 5° cells in 2020.

2.4 | Fishing pressure

To determine if the predicted associative behavior could influence tuna fishing mortality, we used FAD activity data from the IOTC (IOTC, 2021a). This dataset provides the 1°×1° cell, the month and the year of each set performed on a FOB by a purse seine fishing vessel in the IO. From this dataset we determined the number of sets on FOB per month per cell in 2020. Each FOB set was attributed a random position inside the 1° cell where it was performed and a kernel density estimation was obtained using the function *kde* from the package *ks* v1.13.5. The obtained density estimation was used to determine a fished area, defined as the area where 95 % of the FOB sets occurred. We then determined the 5° cells used for $\overline{CAT}$ and P_a predictions which were in the fished area. A cell was considered in the fished area when its center was in it.

3 | RESULTS

3.1 | CAT trends

$\overline{CAT}$, $\overline{CAT_{diff}}$ and $\overline{CAT_{return}}$ values varied from 0.89 to 30.77 days, from 0.88 to 37.84 days, and from 1.88 to 10.85 days respectively. Shorter values were obtained for higher densities (Figure 1 & Table 2). R was always above 1, meaning that the majority of CATs were performed between two different FADs. It varied from 2.82, for the lowest density ($\rho = 1.00 \times 10^{-4}$ km^{-2}), to 87.11 for the highest density ($\rho = 4.44 \times 10^{-3}$ km^{-2}). Hence, when ρ decreases, tuna tend to return to the departure FAD more often. CAT_{return} represented 1.13 % of the total number of simulated CAT for the maximum simulated FAD density ($\rho = 4.44 \times 10^{-3}$ km^{-2}) and 26.18 % of the number of CAT for the minimum FAD density ($\rho = 1.00 \times 10^{-4}$ km^{-2}). Consequently, $\overline{CAT}$ values were almost exclusively driven by $\overline{CAT_{diff}}$ for low densities but were shorter than $\overline{CAT_{diff}}$ for higher densities, due to the higher proportion of $\overline{CAT_{return}}$ (*i.e* lower R values; Figure 1 & Table 2).

3.2 | Operational buoy densities

Buoy densities obtained from the IOTC data are presented in Figure 2. The maximum observed density in a 1° cell was $\rho = 8.39 \times 10^{-3}$, in August, which corresponds to 84 operational buoys in a 100 km × 100 km square and a mean distance to the nearest neighbor (in a regular square lattice) of 10.9 km. After averaging the densities on a 5° grid, highest observed density was $\rho = 2.76 \times 10^{-3}$. Mean density over the whole area was $\overline{\rho} = 3.45 \times 10^{-4}$, corresponding to 3.5 buoys per 100 km × 100 km square. Areas with highest buoys densities showed strong monthly variations, moving from the West to the East of the Seychelles from January to April. A second area with high buoys densities could then be observed in the Arabian Sea, from May to July. In September and forward, highest densities were observed around the Seychelles and East of the Somalian EEZ. The obtained maps showed a high number of buoys around the Maldives in May and December, suggesting a high number of buoys drifting towards the Eastern IO (Figure 2E&L).

3.3 | CAT predictions

Obtained parameters of the models fitting $\overline{CAT_{diff}}(\rho)$, $\overline{CAT_{return}}(\rho)$ and $R(\rho)$ are presented in Table 3 and predicted $\overline{CAT}$ values in 5° cells are presented in Figure 3. Minimum predicted value was 1.06 days in February 2020. Predicted $\overline{CAT}$ values in the fished area (*i.e.* the area where 95 % of the FOB sets occurred) varied from 1.06 to 11.34 days, with a mean value of 2.88 days (SD: 1.49 d). The area with shortest predicted $\overline{CAT}$ was spatially conserved through time: low values were observed from the North of the Mozambique Channel to the Arabian Sea, and from the African coast to 65°E. However, for each month, a peak of short $\overline{CAT}$ was observed and moved from the South of the area to the North, from January to June (Figure 3A-F), and back to the South of the area from June to December (Figure 3F-L).

The percentage of time spent by tuna associated with a FAD (P_a) displayed similar spatial patterns as $\overline{CAT}$ (Figure 4). In the fished area predicted P_a values were comprised between 36.9 and 86.2 %, with a mean of 71.1 % (SD: 9.1 %).

4 | DISCUSSION

Human induced habitat modifications can impact species behavior (Swearer et al., 2021). Continuous Absence Times (noted CATs) and Continuous Residence Times (noted CRTs) are two behavioral metrics allowing to assess the impact of the modification of one habitat component – the density of floating objects – on pelagic species. Several studies measured CATs (Robert et al., 2012, 2013; Rodriguez-Tress et al., 2017) or CRTs (Mitsunaga et al., 2012; Robert et al., 2013, 2012; Govinden et al., 2013; Weng et al., 2013) in arrays of anchored FADs. CRTs were also measured at drifting FADs (Matsumoto et al., 2014, 2016; Tolotti et al., 2020; Govinden et al., 2021). However, experimentally measuring CATs in an array of FADs requires the equipment of the whole array with acoustic receivers. When these FADs are drifting, finding, equipping and recovering them is cumbersome and has never been achieved. This study is, to our knowledge, the first to give estimates of CATs of YFT in arrays of drifting FADs. These estimates show a strong influence of fisheries induced habitat modifications on tuna associative behavior in the Western Indian Ocean (WIO). By increasing FAD density, purse seine fisheries increase the time tunas spend associated, which also has a direct influence on YFT catchability and fishing mortality.

DFAD density also influences the propensity of tunas to return to the same DFAD: as FAD density decreases tunas return more often to the departure FAD (see Figure 1 & Supplementary Materials 3). Hence, at high densities, a higher inter-FAD connectivity can be observed. However, as tunas would associate very shortly to a DFAD close to the departure one, there is a risk that high DFAD densities would retain them in unsuitable areas, further increasing the impact of this habitat modification on tuna survival. This risk was already pointed out by Marsac et al. (2000) as part of the ecological trap hypothesis. Pérez et al. (2020) assessed the Total Residence Time (TRT) to determine the total time tuna would stay in an array of AFADs. However, drifting FOBs span the entire ocean, hence an array of DFADs is not clearly bounded and the TRT cannot be defined. Further studies determining the distance travelled by an individual tuna at different FAD densities could be performed to assess the risk of DFADs retaining individuals in some areas.

The predicted percentages of time spent associated (P_a) by individuals were very high in the WIO, with a mean of more than 70 % in the fished area. This strongly influences YFT catchability and fishing mortality. In the IO, from 2015 to 2019, the main fishing gear targeting YFT were purse seine with 35% of the catch (*i.e.* around 150,000 tons in 2019; ISSF, 2021). Around 80% and 70% of purse seine catch on YFT was made on floating objects in 2018 and 2019 respectively (IOTC, 2020). If YFT spend a high percentage of their time associated with floating objects, for increasing DFAD densities, it increases their vulnerability to purse seine sets. In the IO, the YFT stock is currently overfished (*i.e.* the biomass is bellow the biomass reference point corresponding to the maximum sustainable yield) and subject to overfishing (*i.e.* the fishing mortality is above the reference point corresponding to the maximum sustainable yield; IOTC, 2020). The Indian Ocean Tuna Commission (IOTC) limited the number of operational buoys to 300 per vessel at any one time, and no more than 500 new buoys can be acquired per vessel annually (IOTC, 2019a). The present results show that limiting the number of operational buoys directly affects tuna catchability by purse seine vessels. Added to existing measures, these limits could be an effective management tool and should be further reduced if tuna stocks were to remain overfished.

Numerous factors could affect the obtained $\overline{CAT}$ and P_a predictions. First, several uncertainties are inherent to the data used for the predictions. Predictions were made based on operational buoys densities (IOTC, 2021b), which is a proxy of the actual floating objects (FOBs) density in the ocean. Most natural FOBs and FOBs from pollution, which represented 11% of the total FOBs encountered by purse seine vessels in 2018 (Dupaix et al., 2021a), are not equipped with a buoy. Also, among equipped FOBs, those for which the buoy was turned-off are not present in the data. Moreover, if most Contracting Parties provided their buoys' positions to the IOTC, some countries did not share their data (IOTC, 2021b). It suggests that the P_a predicted in this study is likely to be slightly underestimated.

The other data used for the predictions are measurement of CRTs. Only the mean value for the Indian Ocean was used in our study (measured in Govinden et al., 2021) and we considered CRT as constant. This approximation could influence the predictions, as it was demonstrated that CRTs also depend on FAD density, even if to a lesser extent than CATs (Pérez et al., 2020). CRT measurements on DFADs also showed a variability between oceans as well as strong inter-individual variations (Tolotti et al., 2020; Govinden et al., 2013, 2021; Matsumoto et al., 2016). Further measurements of CRTs at DFADs and some modelling approach would then be needed to take this variability into account. However, Pérez et al. (2020) found that, as AFAD density increases, CRT also increases, suggesting that the increase in catchability observed in this study should be conserved.

Secondly, the model used for the predictions was fitted on passive acoustic tagging data from YFT of FL 70±10 cm, tagged in an array of AFADs (Pérez et al., 2022). At drifting FADs, two main size classes of YFT are found: individuals around 50 cm and individuals around 120 cm (IOTC, 2019b, p. 52). The size of an individual can change its speed, hence the model parameter used in this study (one body-length per second, *i.e.* $v = 0.7$ m.s^{-1}) may not be the most appropriate. Also, as tuna orient themselves towards FADs several kilometers away (4 to 17 km, Girard et al., 2004), it was suggested that they could detect FADs using acoustic stimuli (Pérez et al., 2022). Although FAD design has not been identified as influencing the attractiveness of FADs (Freon and Dagorn, 2000), there might be a difference in detectability between anchored, which are composed of a bigger structure containing a metal chain, and drifting FADs. Hence, the type of FAD (anchored or drifting) could also change some model parameters, such as the orientation radius (R_0, fitted value of 5 km). To account for these uncertainties, we also performed predictions using other parameters ($v = 0.5$ m.s^{-1} and $R_0 = 2$ km). The obtained $\overline{CAT}$ were longer, resulting in smaller P_a values (see Supplementary Materials 4). The obtained P_a values decreased, with a mean value of 44.7 % and predicted values in the main fishing ground comprised between 15.6 and 65.4 %. However, changing the parameters did not change the observed trend, and as DFAD density increases, YFT catchability was still predicted to increase.

Capello et al. (2022) developed a model to study school behavior in a heterogeneous habitat, using tuna and FADs as a case study. They demonstrated that social behavior has an influence on how the fraction of schools which are associated varies with FAD density. Tuna associative behavior can also be influenced by climate change, which modifies prey abundance and physical characteristics of the environment (Arrizabalaga et al., 2015; Druon et al., 2015, 2017). All deployed DFADs in the IO are to be equipped with an echosounder buoy, allowing to locate them and determine the presence or absence of tuna school at the DFAD (Baidai et al., 2020a). These data can be used to determine tuna aggregation dynamics (Baidai et al., 2020b), and could be used to assess the impact of the environment on tuna association to DFADs, taking their social behavior into account.

4.1 | Conclusion and perspectives

Climate change impacts species habitat, potentially impacting their fitness (IPBES, 2019). Several studies assessed the direct impact of habitat modifications on species fitness, or on fitness proxies (Mullu, 2016; Mac Nally et al., 2000; IPBES, 2018). These impacts on fitness can also be behaviorally mediated, *e.g.* through ecological traps (Swearer et al., 2021; Gilroy and Sutherland, 2007; Dwernychuk and Boag, 1972). Hence, there's a need to assess the impact of habitat modifications on species behavior and mortality. In the case of exploited species, such as tuna, behavioral change can have even greater impacts on fitness because it can increase their catchability. Yellowfin tuna and Fish Aggregating Devices are a important case-study, as it allows to assess the impact of the modification of one habitat component, floating object density, on the associative behavior of a commercially important species, this behavior being strongly linked to survival. The simple modelling framework used here could predict such impacts and can be used as a tool to take into account indirect impacts of fisheries on tuna's mortality. This framework can also be used as a base to assess how more complex processes such as social behavior and environmental changes could impact species survival and their vulnerability to human activities.

Authors' Contribution

A.D. performed the simulations, analysed the data and wrote the paper with major contributions of M.C., L.D. and J-L.D. All authors read and approved the final manuscript.

Data Availability Statement

Simulations were performed with the model FAT albaCoRaW v1.4. (doi: 10.5281/zenodo.5834056). All the scripts used in the study can be found on GitHub (`https://github.com/adupaix/Quantif_impact_FAD`).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Q.Schull for his insights on the redaction of the paper. We also acknowledge the anonymous reviewers for their extensive and constructive feedback.

Figures

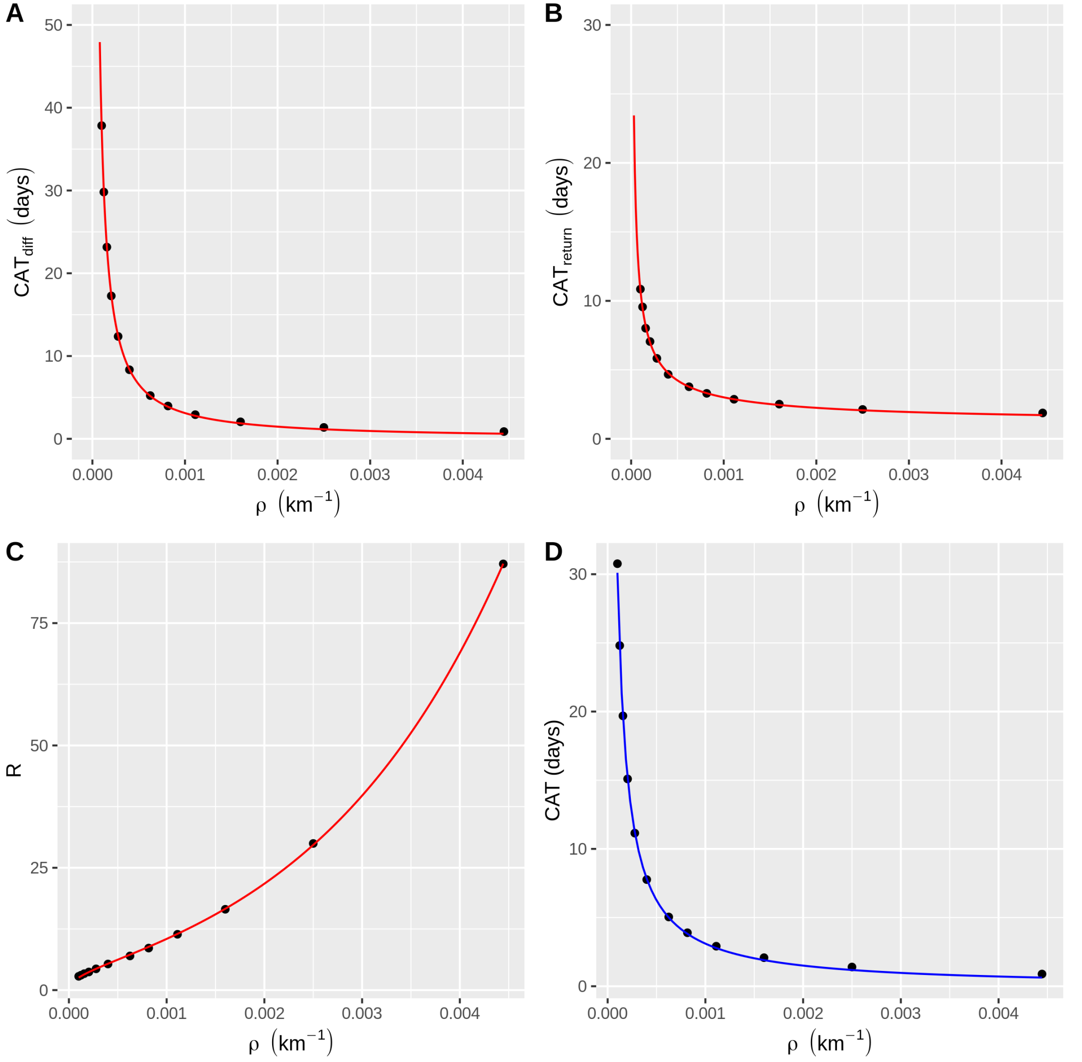

FIGURE 1 Continuous Absence Times (CATs) trends as a function of FAD density, obtained from the simulations. (A) $\overline{CAT_{diff}}$ fitted according to Equation 1; parameter values: $a_d = 1.76 \times 10^{-3}$; $b_d = 1.08$. (B) $\overline{CAT_{return}}$ fitted according to Equation 2; parameter values: $a_r = 1.73 \times 10^{-2}$; $b_r = 6.88 \times 10^{-1}$. (C) Ratio between the number of CAT_{diff} and the number of CAT_{return} (R) fitted according to Equation 3; parameter values: $a = 149.49$; $b = 422.19$ and $c = 4.46 \times 10^{-1}$. (D) Mean $\overline{CAT}$. The blue line is obtained from the fits in panels A,B and C and from Equation (4). ρ: FAD density.

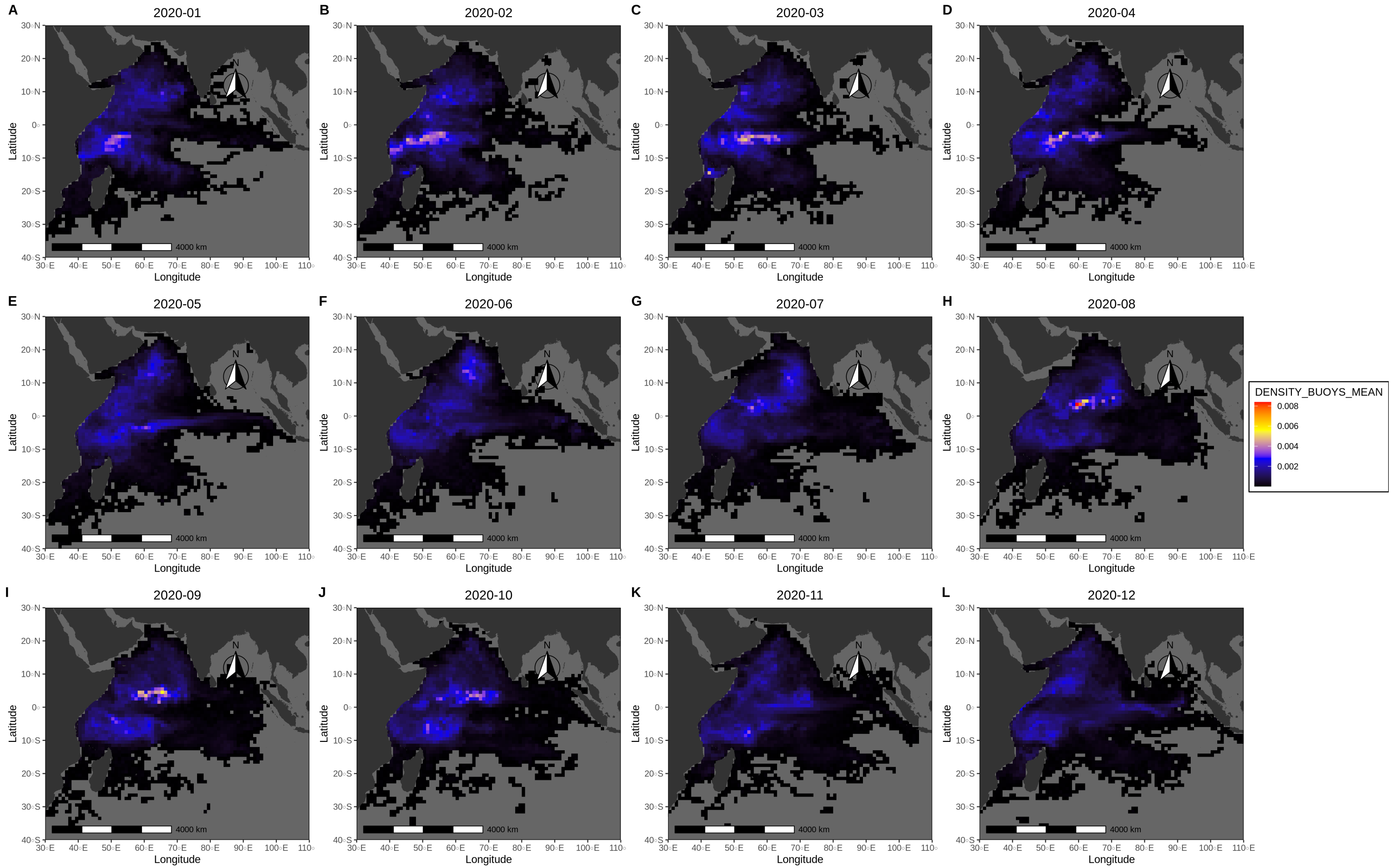

FIGURE 2 Mean monthly buoy densities per 1° cells in the western Indian Ocean, expressed in buoys.km^{-2}.

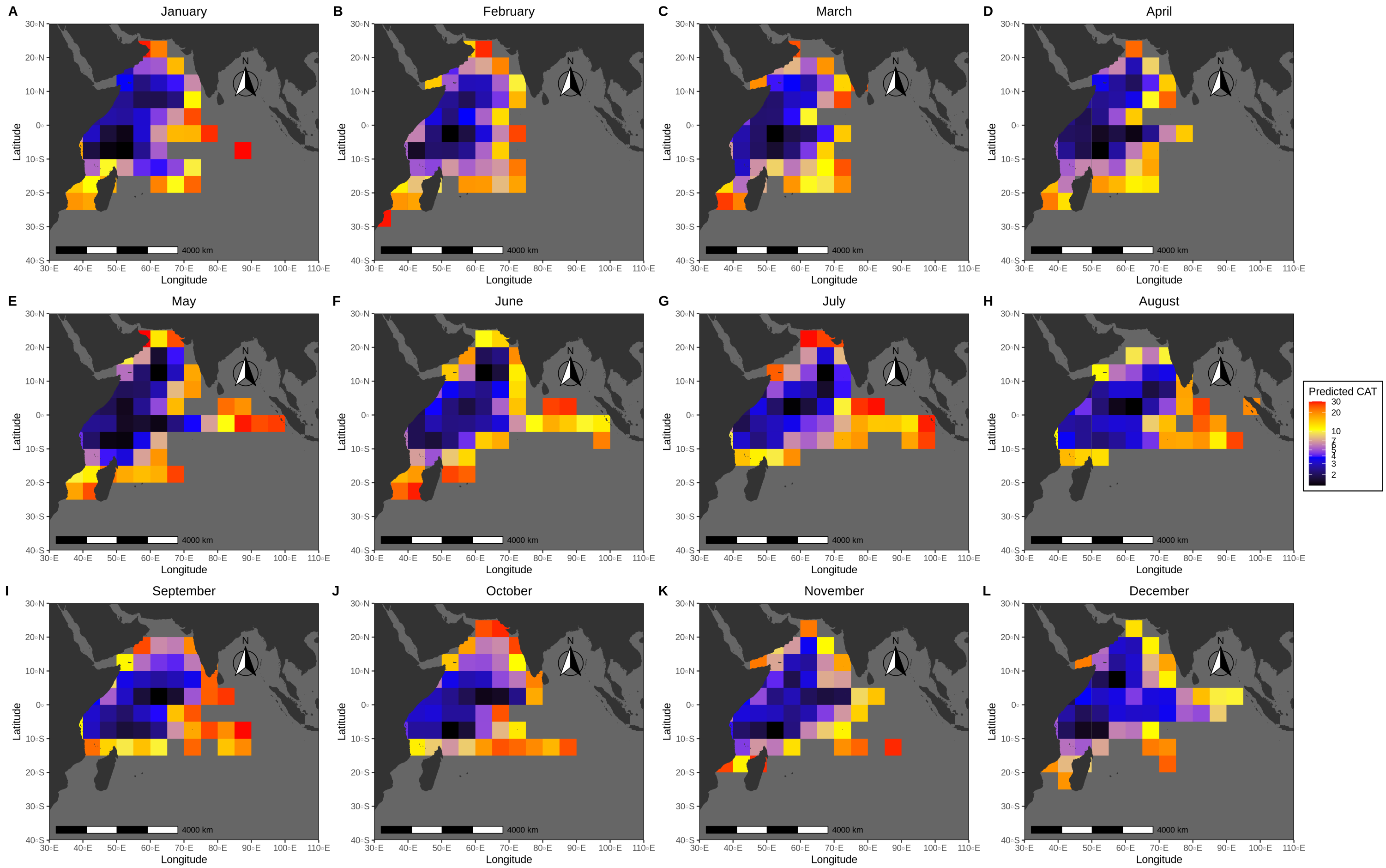

FIGURE 3 Predicted monthly mean Continuous Absence Times of individual yellowfin tunas ($\overline{CAT}$, in days) per 5° cells in the western Indian Ocean in 2020. The color scale is log transformed. $\overline{CAT}$ longer than 30 days, out of the main fishing grounds, were not represented.

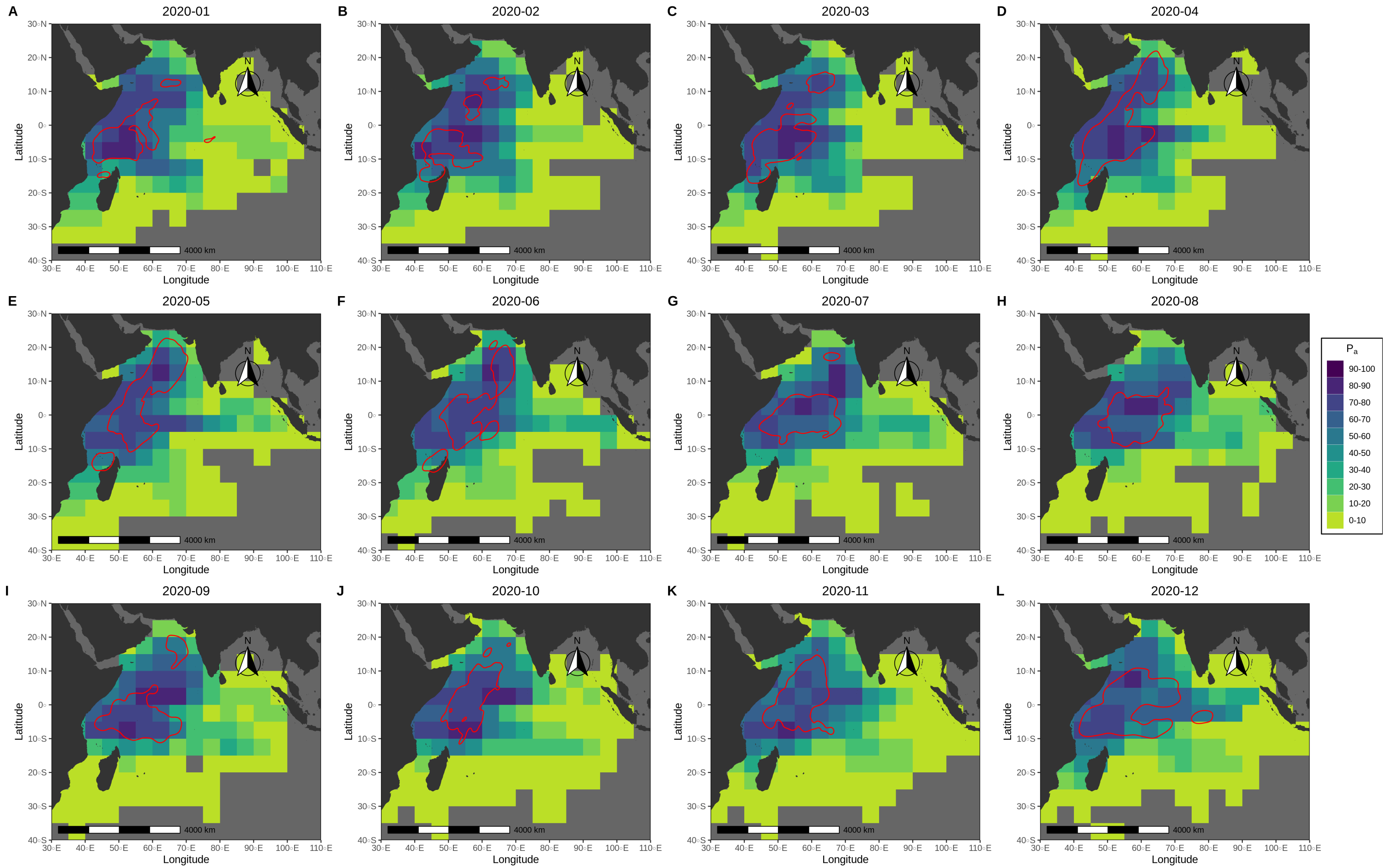

FIGURE 4 Predicted monthly percentage of time spent associated by individual yellowfin tunas (P_a) per 5° cells in the Western Indian Ocean in 2020. The red lines represent the boundaries of the fished area, where 95 % of the FOB sets were performed.

Tables

TABLE 1 Parameters used in the simulations. v: speed; R_0: orientation radius; c: sinuosity coefficient; D: mean inter-FAD distance.

v	R_0	c	D
0.7 $m.s^{-1}$	5 km	0.99	15, 20, 25, 30, 35, 40, 50, 60, 70, 80, 90, 100 km

TABLE 2 Values of CATs for each of the simulated FAD density. D: mean inter-FAD distance in a regular square lattice (in km); ρ: FAD density (in km^{-1}); $\overline{CAT}$: mean Continuous Absence Time (in days); $\overline{CAT_{diff}}$: mean Continuous Absence Time when the movement occurred between two different FADs (in days); $\overline{CAT_{return}}$: mean Continuous Absence Time when the individual returned to the departure FAD (in days); R: ratio between the number of CAT_{diff} and the number of CAT_{return}.

D	ρ	$\overline{CAT}$	$\overline{CAT_{diff}}$	$\overline{CAT_{return}}$	R
15	4.44×10^{-3}	0.89	0.88	1.88	87.11
20	2.50×10^{-3}	1.40	1.38	2.13	29.97
25	1.60×10^{-3}	2.08	2.05	2.51	16.52
30	1.11×10^{-3}	2.91	2.92	2.87	11.41
35	8.16×10^{-4}	3.89	3.96	3.30	8.59
40	6.25×10^{-4}	5.04	5.23	3.77	6.98
50	4.00×10^{-4}	7.77	8.35	4.67	5.33
60	2.78×10^{-4}	11.15	12.37	5.83	4.35
70	2.04×10^{-4}	15.09	17.26	7.05	3.71
80	1.56×10^{-4}	19.69	23.16	8.02	3.36
90	1.23×10^{-4}	24.81	29.81	9.56	3.04
100	1.00×10^{-4}	30.77	37.84	10.85	2.82

TABLE 3 Summary of the fitted parameter values.

Metric	Formula	Fitted values	Standard Error
$\overline{CAT_{diff}}$	$a_d \times \rho^{-b_d}$	$a_d = 1.76 \times 10^{-3}$	1.10×10^{-4}
		$b_d = 1.08$	1.40×10^{-2}
$\overline{CAT_{return}}$	$1 + a_r \times \rho^{-b_r}$	$a_r = 1.73 \times 10^{-2}$	1.35×10^{-3}
		$b_r = 6.88 \times 10^{-1}$	1.78×10^{-2}
R	$a\rho^c \exp(b \times \rho)$	$a = 149.49$	15.94
		$b = 422.19$	6.57
		$c = 4.46 \times 10^{-1}$	1.46×10^{-2}

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