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Quantifying the impact of habitat modifications on species behavior and mortality: A case study of tropical tuna

Amaël Dupaix[1] | **Laurent Dagorn**[1] | **Jean-Louis Deneubourg**[2] | **Manuela Capello**[1]

[1]MARBEC, Univ. Montpellier, CNRS, Ifremer, INRAE, IRD, Sète, France

[2]CENOLI, Université Libre de Bruxelles, Bruxelles, Belgium

Correspondence
Amaël Dupaix
Email: amael.dupaix@ens-lyon.fr

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Abstract

Ecosystems and biodiversity across the world are being altered by human activities. Habitat modification and degradation are among the most important drivers of biodiversity loss. These modifications can have an impact on species behavior, which can, in turn, impact their mortality. While several studies have investigated the impacts of habitat degradation and fragmentation on terrestrial species, the extent to which habitat modifications affect the behavior and fitness of marine species is still largely unknown, particularly for pelagic species. Since the early 1990s, industrial purse seine vessels targeting tuna have started deploying artificial floating objects—Drifting Fish Aggregating Devices (DFADs)—in all oceans to increase tuna catchability. Since then, the massive deployment of DFADs has modified tuna surface habitat, by increasing the density of floating objects, with potential impacts on tuna associative behavior and mortality. In this study, we investigate these impacts for yellowfin tuna in the Indian Ocean. Using an individual-based model based on a correlated random walk and newly available data on DFAD densities, we quantify for the first time how the increase in floating object density, due to DFAD use, affects the percentage of time that yellowfin tuna spend associated, which, in turn, directly impacts their availability to fishers and fishing mortality. This modification of tuna associative behavior could also have indirect impacts on their fitness, by retaining tuna in areas detrimental to them or disrupting schooling behavior. Hence, there is an urgent need to further investigate DFAD impacts on tuna behavior, in particular, taking social behavior into account, and to continue regulation efforts on DFAD use and monitoring.

KEYWORDS
associative behavior, correlated random walk, exploited species, Fish Aggregating Device, global change, individual-based model, purse seine fisheries, tropical tuna

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 has the largest relative impact in the oceans (IPBES, 2019). Increased exploitation of land and sea not only directly impacts populations but also modifies natural habitat, for example, by reducing its surface (Hooke & Martín-Duque, 2012; Neumann et al., 2016) or degrading and fragmenting it (IPBES, 2018). Such habitat modifications can impact wild species distribution, reproduction, behavior, and ultimately their fitness (Fischer & Lindenmayer, 2007; Macura et al., 2019; Mullu, 2016). Hence, it is central to determine to what extent these modifications, driven by global change or direct exploitation of animals, can impact species fitness, both in terrestrial and marine ecosystems.

The impact of landscape modification and habitat fragmentation has been extensively studied in terrestrial ecosystems (Fischer & Lindenmayer, 2007). For example, evidence shows that 82% of endangered bird species are threatened by habitat loss, 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 (IPBES, 2018).

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). Pollution is also a driver of marine habitat modification, through acidification, oil spills, or plastics, which can lead to changes in population dynamics (IPBES, 2022, p. 4.2.1.6.5). Marine habitat modifications also impact benthic community composition and sensitivity (Neumann et al., 2016), and could affect fish recruitment (Macura et al., 2019).

In pelagic environments, fewer studies have assessed habitat modifications (Dupaix et al., 2021) and their impact on species behavior, condition, and survival (Hallier & Gaertner, 2008). Detailed movement data can be more cumbersome to acquire for marine than for terrestrial species (Hussey et al., 2015). Currently, it is possible to record the horizontal and vertical movements of pelagic species, but the deployment of tracking devices is costly and operationally challenging (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. Pop-up satellite archival tags are also increasingly used and allow to record the movement and depth of marine animals without having to follow them. However, these tags using light-level data for geolocation (Global Location Sensors [GLS]) only allow to track movement at large geographical scales. Finally, 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. Recently, such data have been used to demonstrate the impacts of habitat modifications on the behavior of tropical tuna (Pérez et al., 2020).

Tropical tunas are of major commercial interest worldwide ($40.8 billion in 2018, McKinney et al., 2020) and are subject to an important fishing pressure (5 million tons of tuna caught annually in 2017–2021, ISSF, 2023). Yellowfin tuna (*Thunnus albacares*, designated as YFT) is one of the three main targeted species, with the skipjack (*Katsuwonus pelamis*) and bigeye (*Thunnus obesus*) tunas. The main fishing gear targeting tropical tunas is purse seining, which accounted for around 66% of the global catch from 2017 to 2021 (ISSF, 2023). Many pelagic species, like tunas, are known to associate with floating objects (noted FOBs, Castro et al., 2002; Fréon & Dagorn, 2000), such as tree logs which are a natural component of their habitat. In the 1990s, tuna purse seine vessels started to deploy their own artificial FOBs, called Fish Aggregating Devices (FADs), to exploit this associative behavior.

Since then, the deployment and use of drifting FADs (DFADs) has increased, and the last global estimate is between 81,000 and 121,000 DFAD deployed in 2013 (Gershman et al., 2015). In the beginning of the 2010s, fishers started equipping DFADs with echosounder buoys, transmitting the position of the DFAD and an estimation of the tuna biomass under it (and designated as operational buoys when transmitting), further increasing their efficiency (Wain et al., 2021). In 2017–2021, around 56% of global purse seine catch was performed on FOBs, representing around 1.8 million tons per year (ISSF, 2023), and this proportion can be much higher in some regions, for example, with more than 85% of purse seine catch around FOBs in the Indian Ocean (IOTC, 2022e). The use of DFADs directly impacts tuna populations, by increasing the proportion of juvenile yellowfin and bigeye tuna compared with free-swimming schools (Dagorn, Holland, et al., 2013). Furthermore, the massive deployment of DFADs can also have indirect impacts, affecting the behavior and natural mortality of tuna (Hallier & Gaertner, 2008; Marsac et al., 2000). Pérez et al. (2020) demonstrated, on arrays of anchored fish aggregating devices (AFADs), that a decrease in inter-AFAD 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-AFAD distances, the authors found that when the distance between AFADs decreases, tuna both spent more time associated with a given AFAD and less time between two associations. If an increase in 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 AFADs, both through active (Girard et al., 2004) and passive tagging (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 and species, 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., 2016). 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, nor can the consequences of an increase in DFAD density on tuna.

This study investigates the impacts of pelagic habitat modifications, driven by industrial purse seine fisheries, on the behavior and mortality of YFT in the Western Indian Ocean (IO). In the IO, both the bigeye and YFT stocks are currently overfished and subject to overfishing (IOTC, 2022a, 2022b, 2022c). One of the possible causes explaining the decline of these stocks is the important fishing pressure in the area. Tuna fisheries in the IO represent 1.2 Mt of tuna caught in 2021, 44% of which are caught by PS fisheries (percentage over 2017–2021), followed by gillnet and baitboat (IOTC, 2022d; ISSF, 2023). Industrial purse seiners substantially rely on the use of DFADs, with the percentage of tuna caught at FOBs having increased from around 60% (mainly on natural FOBs) in the 1980s, to more than 85% lately (IOTC, 2022e). The massive use of DFADs observed in recent years increases the fishing mortality of juvenile yellowfin and bigeye tuna and could also induce other indirect impacts, by modifying their habitat and thus increasing their natural mortality (Hallier & Gaertner, 2008; Marsac et al., 2000). Recent studies investigated habitat modifications induced by the use of DFADs by industrial purse seine fleets in the Western IO (Dagorn, Bez, et al., 2013; Dupaix et al., 2021). Using data from observers onboard tuna purse seine vessels from 2006 to 2018, Dupaix et al. (2021) highlighted that DFADs multiplied the densities of FOBs by at least 2 and represented more than 85% of the overall FOBs. This study aims at quantifying how such habitat changes have affected the behavior of tropical tuna and its availability to the fisheries. Since 2020, detailed information on the total number of DFADs equipped with echosounder buoys has been made available to scientists (IOTC, 2019) at a 1°/monthly scale. This new data allow, for the first time, to have quantitative estimates of the density of DFADs in the IO. Furthermore, a recent study (Pérez et al., 2022) developed an individual-based model fitting the movement behavior of YFT in an array of AFADs measured from acoustic telemetry data. In the following, we used this newly available dataset, combined with observers' data and the outputs of the individual-based model from Pérez et al. (2022), to predict the time that YFT spend between two DFAD associations in the Western IO. Using these predictions, we assess the impact of the modification of the pelagic habitat—FOB density increase due to the introduction of DFADs—on the percentage of their time YFT spend associated. This percentage of time spent associated has a direct impact on tuna availability to fishers and can thus affect their mortality due to fishing. Furthermore, we discuss how this habitat modifications can have other potential indirect impacts on tuna's fitness.

MATERIALS AND METHODS

In order to compare tuna behavior in modified habitats (due to the introduction of DFADs) relative to an unmodified environment (where only FOBs other than DFADs, either of natural or anthropic origin, noted LOGs, are present), we estimated the percentage of time tuna spend associated with FOBs (P_a) in FOB arrays characterized by different FOB densities. Simulations were run to model tuna movements in arrays of FOBs, using an individual-based model calibrated on passive acoustic data recorded for YFT (Pérez et al., 2022). These simulations allowed estimating a theoretical relation between the time spent by tuna between two consecutive FOB associations (named Continuous Absence Time [CAT]) and the density of FOBs. Observer data, combined with data on the density of DFADs at a 1°/monthly scale, were used to estimate the total density of FOBs (DFADs and LOGs) and the density of FOBs in the environment not modified by DFAD use (LOGs only).

Predictions of CATs obtained in the pristine and modified habitat, combined with acoustic telemetry data informing on the amount of time spent by tuna associated with FOBs (named Continuous Residence Time [CRT]), were used to estimate changes in P_a. A schematic view of the methodology developed is presented in Figure 1 and details of the model, methods, and data are provided below.

Model of tuna movements in an array of FOBs

Simulations were performed using the FAT albaCoRaW model v1.4 (Dupaix, Pérez, & Capello, 2023), an individual-based model simulating tuna trajectories in an array of FOBs based on a Correlated Random Walk (Pérez et al., 2022). This model is built upon three behavioral rules: (i) tuna display a random search behavior between two associations to FOBs, (ii) at a certain distance from FOBs (the orientation radius R_0) tuna show oriented movements toward FOBs, and (iii) the tuna association dynamics follow a diel rhythm. The random search between two associations is based on three parameters: the time-step Δt, determining the time interval between two positions; the speed v, determining the length of each displacement at each time step; and the sinuosity coefficient c, determining the sinuosity of the path, from straight to a simple random walk. These parameters were

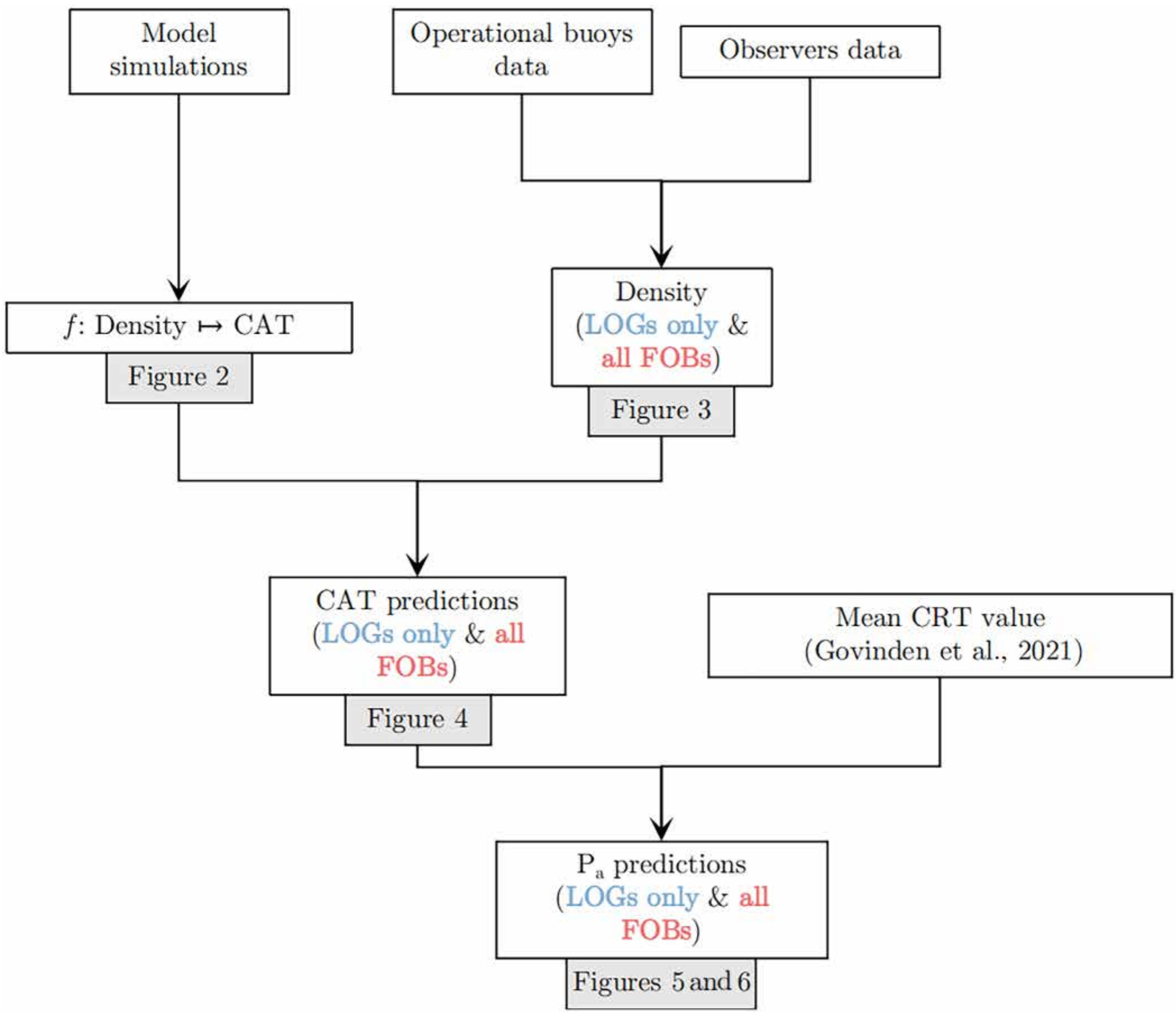

FIGURE 1 Schematic representation of the methodology used in the study, which allowed the calculation of P_a both for the densities of all floating objects (all floating objects [FOBs], habitat modified by Drifting Fish Aggregating Devices [DFADs]) and for floating objects other than DFADs (LOGs only, habitat not modified). Figure numbers illustrating different steps of the study are indicated on the scheme. CAT, Continuous Absence Time; CRT, Continuous Residence Time. P_a, percentage of time spent associated.

fitted on passive acoustic tagging data of 70-cm-long YFT in arrays of AFADs, in Pérez et al. (2022) (Table 1). We considered 12 different FOB densities (noted ρ), ranging from 1.00×10^{-4} to 4.44×10^{-3} FOB.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 FOB longitude and latitude being randomly picked. A thousand individual tunas were released from a random FOB in each of these arrays. As in Pérez et al. (2020), we define a CAT as the time spent between two associations to a FOB. A tuna was considered associated when it was located at less than 500 m from a FOB, which corresponds to the distance at which a tagged tuna can be detected by an acoustic receiver. CATs were separated into two categories: (i) CAT_{diff} when the movement occurred between two different FOBs and (ii) $\text{CAT}_{\text{return}}$ when the tuna returned to its departure FOB after more than 24 h. Studies processing experimental acoustic tagging data of tropical tuna relied on a Maximum Blanking Period of 24 h, that is, below a temporal separation of 24 h between two subsequent acoustic detections at the same FOB, the fish is considered to be still associated (Capello et al., 2015; Pérez et al., 2022). Hence, each time a $\text{CAT}_{\text{return}}$ of less than 24 h was recorded, 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 $\text{CAT}_{\text{return}}$ or after 1500 days of simulation. The obtained CAT was saved. A total of 100,000 CATs were simulated per FOB density, totaling 1,200,000 simulated CATs.

CAT trends for different FOB densities

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

$$\overline{\text{CAT}_{\text{diff}}}(\rho) = \frac{a_d}{\rho^{b_d}}, \tag{1}$$

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

$$\overline{\text{CAT}_{\text{return}}}(\rho) = 1 + \frac{a_r}{\rho^{b_r}}, \tag{2}$$

with $(a_r, b_r) \in \mathbb{R}^2_+$. Then, the mean $\overline{\text{CAT}}(\rho)$ can be expressed as follows (see Appendix S1 for more details):

$$\overline{\text{CAT}}(\rho) = \frac{R(\rho)\overline{\text{CAT}_{\text{diff}}}(\rho) + \overline{\text{CAT}_{\text{return}}}(\rho)}{R(\rho) + 1}, \tag{3}$$

where $R = \frac{A}{B}$ is the ratio between the number of CAT_{diff} (A) and that of $\text{CAT}_{\text{return}}$ (B). The ratio R as a function of ρ was fitted based on the following Equation (4):

$$R(\rho) = a\rho^c \exp(b \times \rho), \tag{4}$$

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.

TABLE 1 Parameters used in the simulations, performed using Dupaix, Pérez, and Capello (2023) and based on the calibration in Pérez et al. (2022).

Parameter	Definition	Value
Δt	Time-step	100 s
v	Speed	0.7 m.s^{-1}
R_0	Orientation radius	5 km
c	Sinuosity coefficient	0.99
D	Mean inter-FOB distance	15, 20, 25, 30, 35, 40, 50, 60, 70, 80, 90, 100 km

Abbreviation: FOB, floating object.

FOB density calculation in the IO

Echosounder buoy density data from January to December 2020, provided by the Indian Ocean Tuna Commission (IOTC, the regional fisheries management organization managing tuna fishing in the IO), was used as a proxy for DFAD data (IOTC, 2021b). This dataset contains the monthly mean of the number of *operational buoys*, that is, the echosounder buoys whose GPS position is remotely transmitted to one or several fishing vessels, for each 1° × 1° cell of the IO. This value was divided by the sea area of each cell, to obtain a mean monthly DFAD density (ρ_{DFAD}). Densities were then averaged over 5° cells to predict CATs (for more elements on the spatial and temporal resolution choice, see Appendix S2).

FOB and LOG densities were calculated combining DFAD densities with data recorded by scientific observers on board French purse seine vessels (2014–2019). Observer data include the date, time, and location of the main activities of the fishing vessel (e.g., fishing sets, installation or modification of FOBs, searching for FOBs). For every activity occurring on a FOB, the type of operation (e.g., deployment, removal, and observation of a FOB) and the type of FOB (DFAD or LOG) are recorded. Using the methodology developed in Dupaix et al. (2021) applied to these observations, we calculated a mean monthly ratio $m=\frac{n_{\mathrm{LOG}}}{n_{\mathrm{DFAD}}}$ (with n_{LOG} and n_{DFAD} the number of LOG and DFAD observations, respectively) per 5° cell which was used to calculate the density of FOBs ($\rho_{\mathrm{FOB}}=(1+m)\rho_{\mathrm{DFAD}}$) and the density of LOGs ($\rho_{\mathrm{LOG}}=m\rho_{\mathrm{DFAD}}$). Because observer data are only available in areas where purse seine vessels are actively fishing, the calculation of the m ratio restricted the study area to the purse seine fishing zones.

Prediction of mean CAT and percentage of time associated in the IO

Using the density values calculated above and the fitted models' coefficients, monthly $\overline{\mathrm{CAT}}$ values were predicted for each 5° cell in 2020.

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

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

with $\overline{\mathrm{CRT}}$ the mean CRT, 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 $\overline{\mathrm{CRT}}$ depends on AFAD density but to a lesser extent than $\overline{\mathrm{CAT}}$. Hence, $\overline{\mathrm{CRT}}$ was considered constant and estimated to be 6.64 days, as measured on YFT at DFADs in the Western IO by Govinden et al. (2021). Using this value and the predicted $\overline{\mathrm{CAT}}(\rho)$, we predicted the monthly values of $P_a(\rho)$ in each 5° cell in 2020, for each FOB category (DFAD, FOB, LOG). Because the calculation of the m ratio reduced greatly the study area, we first predicted $\overline{\mathrm{CAT}}$ and P_a values based on the density of DFADs (ρ_{DFAD}). However, to determine the impact of DFADs on the predicted associative behavior, we compared the predicted values of $\overline{\mathrm{CAT}}$ and P_a obtained with ρ_{FOB} and ρ_{LOG}. This comparison allows to determine the impact of the DFAD-induced habitat modification on tuna availability to fishers.

RESULTS

Simulated CAT trends

Simulated $\overline{\mathrm{CAT}}$, $\overline{\mathrm{CAT}_{\mathrm{diff}}}$, and $\overline{\mathrm{CAT}_{\mathrm{return}}}$ 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 2 and Table 2). The ratio R between the number of $\mathrm{CAT}_{\mathrm{diff}}$ and that of $\mathrm{CAT}_{\mathrm{return}}$ was always above 1, meaning that the majority of CATs were performed between two different FOBs ($\mathrm{CAT}_{\mathrm{diff}}$). It varied from 2.82, for the lowest density ($\rho=1.00\times10^{-4}$ km^{-2}), with $\mathrm{CAT}_{\mathrm{return}}$ representing 26.18% of the number of CAT, to 87.11 for the highest density ($\rho=4.44\times10^{-3}$ km^{-2}), with $\mathrm{CAT}_{\mathrm{return}}$ representing 1.13% of the total number of simulated CAT. Hence, when ρ decreases, tuna tend to return to the FOB of departure more often. Consequently, $\overline{\mathrm{CAT}}$ values were shorter than $\overline{\mathrm{CAT}_{\mathrm{diff}}}$ for lower densities due to the higher proportion of $\overline{\mathrm{CAT}_{\mathrm{return}}}$, but were almost exclusively driven by $\overline{\mathrm{CAT}_{\mathrm{diff}}}$ for high densities (Figure 2 and Table 2). The parameters of the fits of $\overline{\mathrm{CAT}_{\mathrm{diff}}}(\rho)$, $\overline{\mathrm{CAT}_{\mathrm{return}}}(\rho)$, and $R(\rho)$ are presented in Table 3.

DFAD densities

Buoy densities obtained from the IOTC data, considered as DFAD densities (ρ_{DFAD}), are presented in Figure 3. The maximum observed density in a 1° cell was $\rho=8.39\times10^{-3}$ km^{-2}, in August, which corresponds to 84 operational buoys in a 100 × 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 $\rho=2.8\times10^{-3}$ km^{-2}, corresponding to 28 operational buoys in a 100 × 100 km square. Mean density over the whole area was $\overline{\rho}=3.45\times10^{-4}$ km^{-2}, corresponding to 3.45 buoys per 100 × 100 km square. Areas with the highest buoy densities were different according to the month, moving from the west to the east of the Seychelles from January to April. Highest buoy 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. Finally, a high number of buoys around the Maldives was present in May and December, suggesting a high number of DFADs drifting toward the eastern IO during this period (Figure 3E,L).

Predictions of CAT and percentage of time associated

Predicted $\overline{\mathrm{CAT}}(\rho_{\mathrm{DFAD}})$ values in 5° cells are presented in Figure 4 (see Appendix S3 for predictions of $\overline{\mathrm{CAT}_{\mathrm{diff}}}$, $\overline{\mathrm{CAT}_{\mathrm{return}}}$, and R, and Appendix S4 for predictions on ρ_{FOB} and ρ_{LOG}). Minimum $\overline{\mathrm{CAT}}(\rho_{\mathrm{DFAD}})$ predicted value was 1.06 days in February 2020. The area with the shortest predicted $\overline{\mathrm{CAT}}(\rho_{\mathrm{DFAD}})$ 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 $\overline{\mathrm{CAT}}(\rho_{\mathrm{DFAD}})$ was observed and moved from the south of the area to the north, from January to June (Figure 4A–F), and back to the south of the area from June to December (Figure 4F–L). The percentage of time spent by tuna associated with a DFAD ($P_a(\rho_{\mathrm{DFAD}})$) displayed similar spatial patterns as $\overline{\mathrm{CAT}}(\rho_{\mathrm{DFAD}})$ (Figure 5).

Impact of DFAD on tuna availability

The comparison of the predictions obtained with FOB and LOG densities is presented in Figure 6 and

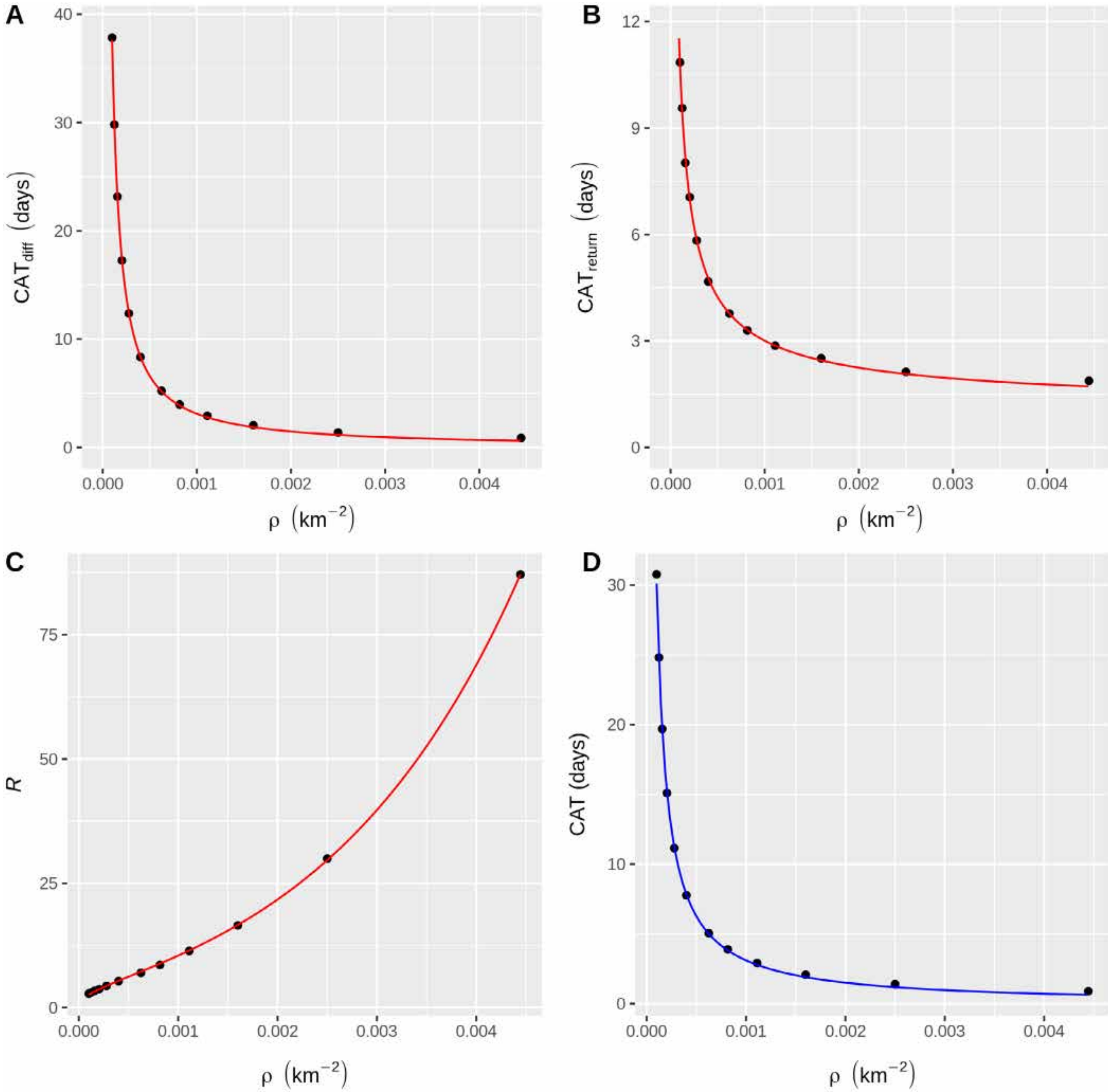

FIGURE 2 Continuous Absence Time (CAT) trends as a function of floating object (FOB) density, obtained from the simulations. (A) $\overline{\mathrm{CAT}_{\mathrm{diff}}}$ fitted according to Equation (1). (B) $\overline{\mathrm{CAT}_{\mathrm{return}}}$ fitted according to Equation (2). (C) Ratio between the number of $\mathrm{CAT_{diff}}$ and the number of $\mathrm{CAT_{return}}$ (R) fitted according to Equation (4). Parameter values are available in Table 3. (D) Mean $\overline{\mathrm{CAT}}$. The blue line is obtained from the fits in panels A–C and from Equation (3). ρ, FOB density.

TABLE 2 Values of Continuous Absence Times (CATs) for each of the simulated floating object (FOB) density.

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

Note: *D*, mean inter-FOB distance in a regular square lattice (in km); ρ, FOB density (in square kilometers); $\overline{CAT}$, mean Continuous Absence Time (in days); $\overline{CAT}_{diff}$, mean Continuous Absence Time when the movement occurred between two different FOBs (in days); $\overline{CAT}_{return}$, mean CAT when the individual returned to the departure FOB (in days); *R*, ratio between the number of CAT_{diff} and the number of CAT_{return}.

TABLE 3 Summary of the fitted parameter values.

Metric	Formula	Fitted values	SE
$\overline{CAT}_{diff}$	$a_d\times\rho^{-b_d}$	$a_d=1.8\times10^{-3}$	1.10×10^{-4}
		$b_d=1.08$	1.40×10^{-2}
$\overline{CAT}_{return}$	$1+a_r\times\rho^{-b_r}$	$a_r=1.7\times10^{-2}$	1.35×10^{-3}
		$b_r=6.9\times10^{-1}$	1.78×10^{-2}
R	$a\rho^c\exp(b\times\rho)$	$a=150$	16
		$b=422$	7
		$c=4.5\times10^{-1}$	1.5×10^{-2}

Table 4. The mean density of all types of FOBs ($\overline{\rho_{FOB}}=1.32\times10^{-3}$ km^{-2}) was 6.6 times higher than the mean LOG density ($\overline{\rho_{LOG}}=2.00\times10^{-4}$ km^{-2}), resulting in much shorter $\overline{CAT}$ with mean values, averaged over cells and months, of 5 and 46 days predicted from FOB and LOG densities, respectively. The strong density increase induced by DFADs resulted in an increase in the predicted proportion of time tuna spent associated (P_a), from $\overline{P_a(\rho_{LOG})}=20\%$ for the environment without DFADs, to $\overline{P_a(\rho_{FOB})}=68\%$ for the environment modified by the introduction of DFADs.

DISCUSSION

Human-induced habitat modifications can impact species behavior and ultimately their fitness (Swearer et al., 2021). CATs and CRTs are two behavioral metrics that allow one to assess the impact of the modification of one habitat component—the density of FOBs—on pelagic species. Several studies measured CATs (Robert et al., 2012, 2013; Rodriguez-Tress et al., 2017) or CRTs (Govinden et al., 2013; Robert et al., 2012, 2013) in arrays of anchored FADs. CRTs were also measured at DFADs (Govinden et al., 2021; Matsumoto et al., 2016; Tolotti et al., 2020). 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 difficult and has never been achieved. Another challenge is related to the availability of reliable data on DFAD densities. In the IO, this data deficiency could only be overcome recently, with the provision of the number of operational buoys by the IOTC secretariat. This study is, to our knowledge, the first to give estimates of CATs of YFT in arrays of DFADs. These estimates show a strong influence of fisheries-induced habitat modifications on tuna associative behavior in the Western IO. By modifying tuna habitat, purse seine fisheries increase the percentage of time tuna spend associated (P_a), which has a direct influence on YFT availability to fishers, which can impact fishing mortality and tuna fitness.

Numerous factors could affect the obtained $\overline{CAT}$ and P_a predictions. Predictions were made based on operational buoy densities deployed on FOBs (IOTC, 2021b), which is a proxy of the actual DFAD density in the ocean. Among the instrumented FOBs, those for which the buoy was remotely deactivated (and thus could not transmit its position anymore) 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), so densities could be underestimated.

The other datasets used for the predictions are French observer data and measurement of CRTs. The use of French observer data restricted the study area, highlighting the need to better share these data among countries, as is done for instrumented buoys, and to increase observer coverage. Only the mean CRT value for the Western IO 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

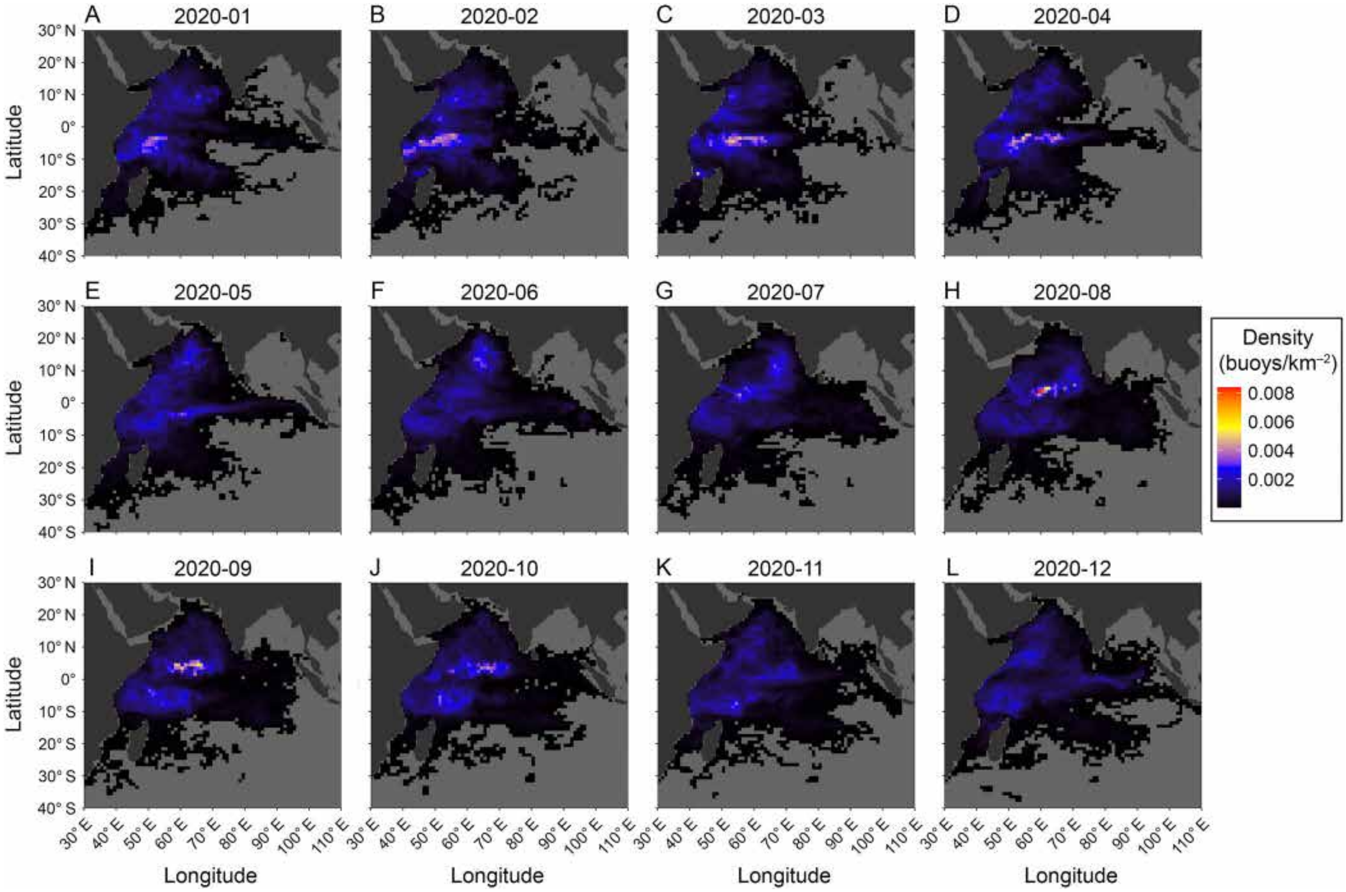

FIGURE 3 Mean monthly buoy densities per 1° cell in the Western Indian Ocean calculated from IOTC (2021b), expressed in buoys per square kilometer. Buoy densities are considered as Drifting Fish Aggregating Device (DFAD) densities.

as well as strong inter-individual variations (Govinden et al., 2013, 2021; Matsumoto et al., 2016; Tolotti et al., 2020). Further measurements of CRTs at DFADs and some modeling 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 or even intensified.

The model used for the predictions was fitted on passive acoustic tagging data from YFT of fork length 70 ± 10 cm, tagged in an array of AFADs (Pérez et al., 2022). At DFADs, two main-size classes of YFT are found: individuals around 50 cm and individuals around 120 cm (IOTC, 2022e, p. 52). Fitting the model on bigger individuals (70 cm instead of 50 cm) should not change drastically the obtained parameters, but could change slightly individual speed (fitted value $v = 0.7 \mathrm{m.s}^{-1}$ in Pérez et al., 2022). Also, as tuna orient themselves toward FADs several kilometers away (4–17 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 to influence the attractiveness of FADs (Fréon & Dagorn, 2000), there might be a difference in detectability between AFADs, which are composed of a bigger structure containing a metal chain, and DFADs. Hence, both the type of FAD (anchored or drifting) and tuna size class could change some model parameters, such as the orientation radius (R_0, fitted value of 5 km) and swimming speed (v, fitted value of 0.7 $\mathrm{m.s}^{-1}$). To account for these uncertainties, we also performed predictions using other parameters ($v = 0.5$ $\mathrm{m.s}^{-1}$ and $R_0 = 2$ km). The obtained $\overline{CAT}$ were longer, resulting in smaller P_a values (see Appendix S5). However, it should be noted that changing the parameters does not change the observed trend: the habitat modification induced by increasing DFADs increases YFT catchability, regardless of the parameter set considered.

Since 2016, in the IO, more than 80% of purse seine catch on tropical tuna was made on FOBs, reaching a

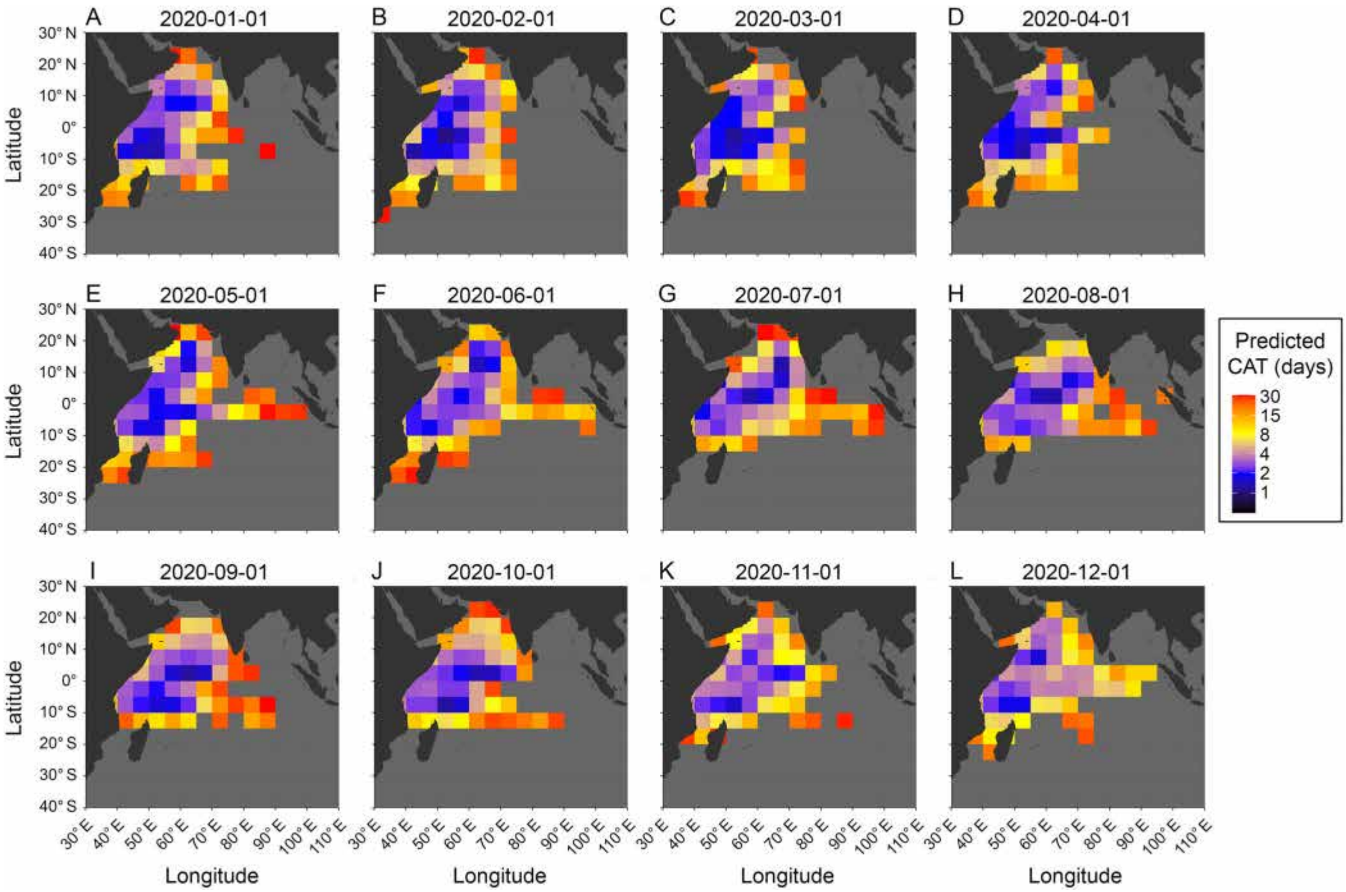

FIGURE 4 Mean monthly Continuous Absence Times (CATs) of individual yellowfin tunas predicted using Drifting Fish Aggregating Device (DFAD) density ($\overline{\text{CAT}}(\rho_{\text{DFAD}})$, in days) per 5° cell in the Western Indian Ocean in 2020. The color scale is log-transformed. $\overline{\text{CAT}}(\rho_{\text{DFAD}})$ longer than 30 days were not represented.

maximum of almost 95% in 2018 (see fig. 5 in IOTC, 2022e). YFT caught by industrial purse seine vessels on FOBs in the IO has steadily increased since 2008 and represented around 22% of the total YFT catch, by all gear types, in 2021 (IOTC, 2022e; ISSF, 2023). The predicted P_a were very high in the Western IO, with a mean of 68% (calculated on all FOBs), mainly due to DFAD introduction (mean prediction without DFADs of 20%). As the habitat modification induced by DFADs strongly increases the percentage of their time YFT spend associated with FOBs, it increases their vulnerability to purse seine sets. In the IO, the YFT stock is currently overfished (i.e., the biomass is below 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, 2021a). The IOTC imposes limits on the number of operational buoys (buoys which transmit DFAD position and other information to fishers) at 300 per vessel at any one time (IOTC, 2019). The present results show that limiting the number of FOBs and of operational buoys directly affects tuna catchability by purse seine vessels. Therefore, if the YFT stock is to remain overfished, efforts should be made to further limit the number of FOBs in the ocean, through limits on operational buoy numbers and on DFAD deployments.

In addition to the increase in fishing availability to fishers, the observed increase in the percentage of time associated (P_a) could also have indirect impacts (i.e., not linked with fishing mortality) on YFT and other associated species. One of the main hypotheses to explain the association of tuna with FOBs is the *meeting-point* hypothesis (Fréon & Dagorn, 2000). Under this hypothesis, tuna would use FOBs as meeting-points to form larger schools. Fish schools can be viewed as an evolutionary trade-off: increasing school size would not only increase protection, mate choice, and information, but would also increase inter-individual competition and the propensity to be detected by predators (Maury, 2017). The increase in FOB density, inducing an increase in P_a, could result in a disruption of schooling behavior and

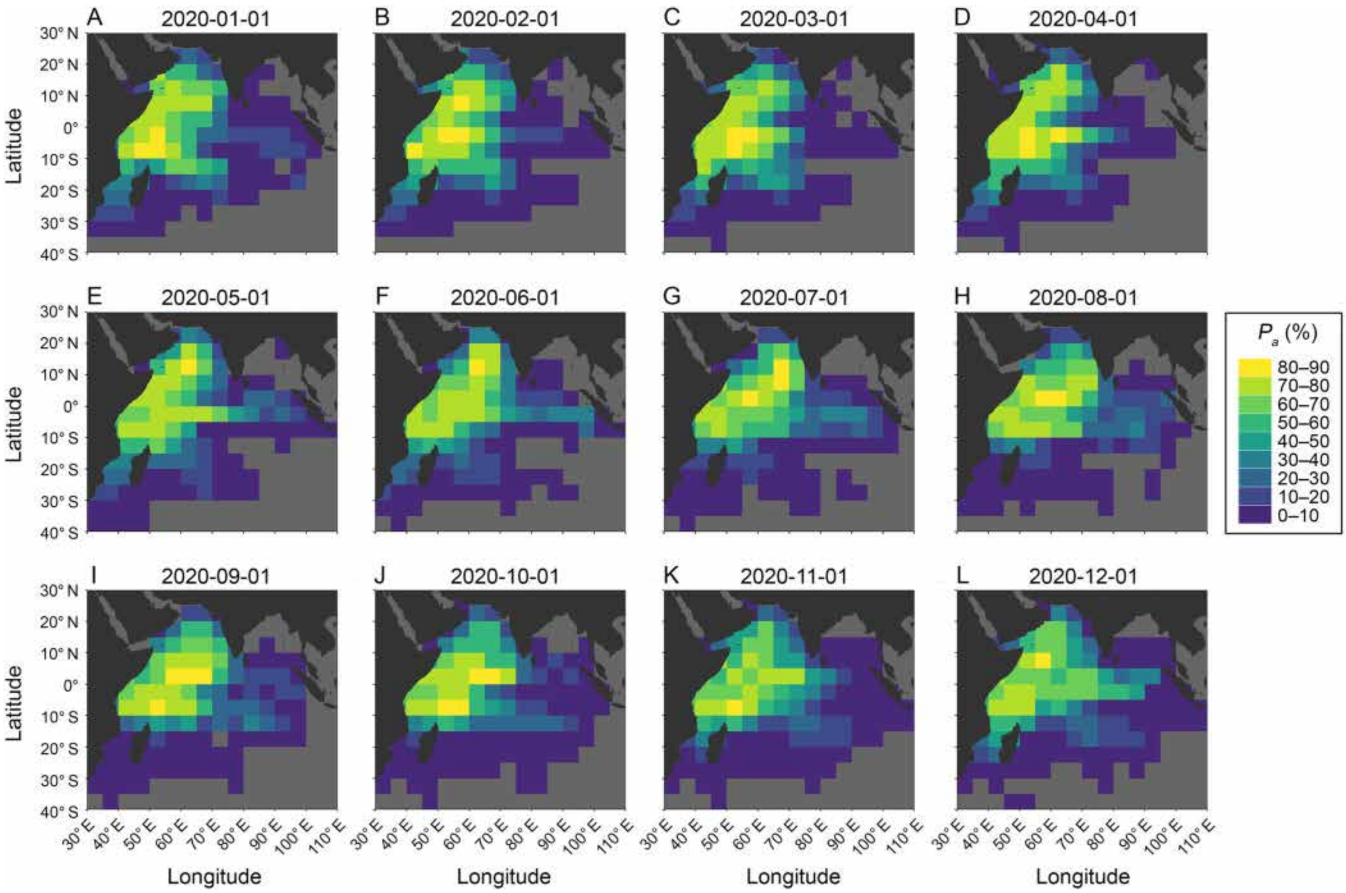

FIGURE 5 Mean monthly percentage of time spent associated by individual yellowfin tunas predicted using Drifting Fish Aggregating Device (DFAD) density ($P_a(\rho_{DFAD})$) per 5° cell in the Western Indian Ocean in 2020.

provoke the dispersion of individuals among FOBs. Capello et al. (2022) developed a model to study school behavior in a heterogenous habitat, using tuna and FADs as a case study. Using several social scenarios, they demonstrated that social behavior has an influence on how the fraction of schools which are associated varies with FAD density. Considering social behavior could help further understanding of tuna behavior and its link with fitness. Echosounder buoy data allow to determine tuna aggregation dynamics (Baidai et al., 2020), and could be used to assess the impact of DFADs on tuna association dynamics, taking their social behavior into account.

Marsac et al. (2000) suggested that DFADs could act as ecological traps on tropical tuna. This hypothesis was based on another behavioral hypothesis, the *indicator-log*, which suggests that tuna associate with FOBs to select rich areas. Natural FOBs would be located mainly in rich areas because they originate from rivers and accumulate in rich frontal zones (Castro et al., 2002). By modifying the distribution of FOBs, DFADs could attract or retain individual tuna in areas that are detrimental to them and ultimately impact their fitness. Recent evidence, using a condition indicator as a proxy for tuna's fitness, tends to suggest that DFADs did not act as an ecological trap in the Western IO. However, DFAD impact could have been counteracted by other environmental effects or could have acted on other biological processes than condition (Dupaix, Dagorn, Duparc, et al., 2023). 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., 2017). Our study shows that the increase of FOB density impacts P_a and FOB array connectivity (increase in R, i.e., of the proportion of CAT_{diff}). Added to previous evidence suggesting that an increase in FAD density induces an increase in tuna residence times around FADs (Pérez et al., 2020), it suggests that DFAD use could retain tuna in some areas. Whether these areas can be considered poor for tropical tuna and the impact this retention can have on tuna fitness—through other biological parameters than condition—still needs to be investigated further.

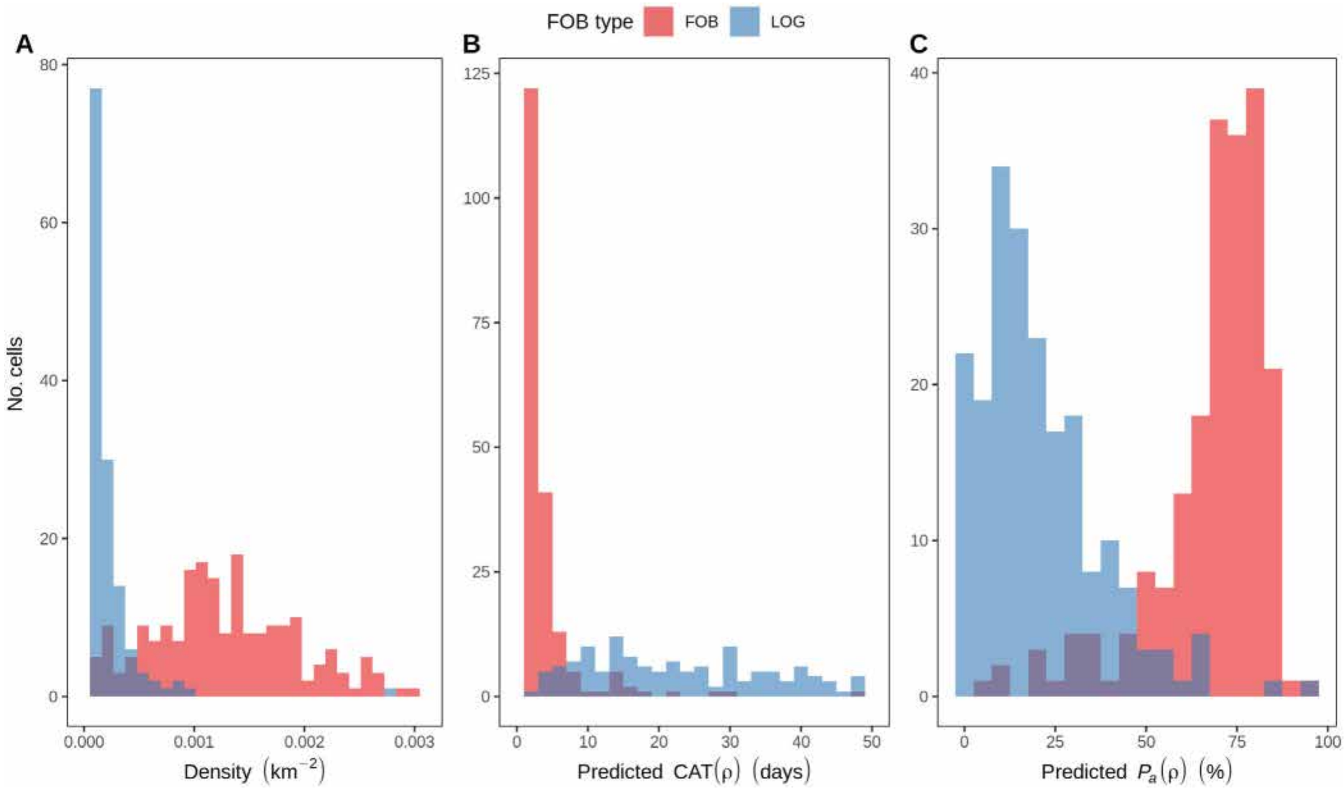

FIGURE 6 Comparison between predictions performed on the density of all floating objects (FOBs) (ρ_{FOB}, in red) and LOGs only (ρ_{LOG}, in blue) density. Monthly mean density of floating object (A), predicted mean monthly Continuous Absence Time ($\overline{CAT}(\rho)$) (B), and percentage of time spent associated ($P_a(\rho)$) (C), per 5° cell.

TABLE 4 Summary of monthly Continuous Absence Time (CAT) and P_a values per 5° cell in the Indian Ocean in 2020, predicted using floating object (FOB) and LOG densities (ρ_{FOB} and ρ_{LOG}).

	ρ (km^{-2})		CAT (days)		P_a (%)	
FOB type	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
FOB	1.32×10^{-3}	4.52×10^{-6}	4.97	6.30×10^{-2}	68.3	8.00×10^{-2}
LOG	2.00×10^{-4}	3.38×10^{-6}	46.3	3.43×10^{-1}	20.5	8.30×10^{-2}

CONCLUSION AND PERSPECTIVES

Human activities impact species habitat, potentially impacting their fitness (IPBES, 2019). Several studies assessed the direct impact of habitat modifications on species fitness, or on fitness proxies (IPBES, 2018; Mullu, 2016). These impacts on fitness can also be behaviorally mediated, for example, through ecological traps (Dwernychuk & Boag, 1972; Gilroy & Sutherland, 2007; Marsac et al., 2000; Swearer et al., 2021). Hence, there is 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 also increase their availability to fishers and, hence, their catchability and fishing mortality. YFT and DFADs are an important case study, as they allow to assess the impact of the modification of one habitat component, FOB density, on the associative behavior of a commercially important species, this behavior being strongly linked to survival. The modeling framework used here could predict such impacts and can be used as a tool to take into account the indirect impacts of fisheries on tuna mortality. This framework could also be used as a predictive tool for assessing the potential benefits of management measures, for example, DFAD number reductions, on the behavior and fishing mortality of tropical tuna.

AUTHOR CONTRIBUTIONS

AD performed the simulations, analyzed the data, and wrote the paper with major contributions from MC, LD, and J-LD. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Simulations were performed with the model FAT albaCoRaW v1.4 (Dupaix, Pérez, & Capello, 2023) which is available in Zenodo at https://doi.org/10.5281/zenodo.5834056. All scripts (Dupaix, Dagorn, Deneubourg, et al., 2023) used in this study are available in Zenodo at https://doi.org/10.5281/zenodo.7915851. Indian Ocean Tuna Commission (IOTC) instrumented buoy data (IOTC, 2021b) are available at https://iotc.org/WGFAD/02/Data/04-BU. French observers data used in this research was obtained from the French National Research Institute for Sustainable Development (IRD) and these data can be requested via IRD's Ob7 by specifying "all operations on floating objects and all vessel activities, in the Indian Ocean, 2013–2022" in the request form at https://ob7-ird.science/les-donnees.

ORCID

Amaël Dupaix https://orcid.org/0000-0001-9925-5756

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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