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## ► To cite this version:

Amaël Dupaix, Laurent Dagorn, Jean-Louis Deneubourg, Manuela Capello. Quantifying the impact of habitat modifications on species behavior and mortality: the case-study of tropical tuna. 2023. hal-04094705v3

**HAL Id: hal-04094705**

**<https://hal.science/hal-04094705v3>**

Preprint submitted on 20 Dec 2023 (v3), last revised 6 Jun 2024 (v4)

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

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## Open Research 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](https://github.com/adupaix/Quantif_impact_FAD)).

IOTC instrumented buoy data can be downloaded from the following URL: <https://iotc.org/WGFAD/02/Data/04-BU>. French observers data are not yet provided. Upon acceptance, the data will be provided via IRD's Ob7 at <https://www.ob7.ird.fr/en/pages/datacall.html>

Ecosystems and biodiversity across 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. **While several studies 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 of floating object density, due to DFAD use, affects the percentage of time that yellowfin tuna spend as-**

sociated, 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

tropical tuna, global change, purse-seine fisheries, Fish Aggregating Device, individual-based model, associative behavior, Correlated Random Walk, exploited species

## 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 has the largest relative impact in the oceans (IPBES, 2019). Increased exploitation of land and sea directly impacts populations but also modifies natural habitat, *e.g.* by reducing its surface (Hooke and 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 (Mullu, 2016; Macura et al., 2019; Fischer and Lindenmayer, 2007). 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 have been extensively studied in terrestrial ecosystems (Fischer and 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, 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).

61 In pelagic environments, fewer studies have assessed habitat modifications (Dupaix et al., 2021) and their impact  
62 on species behavior, condition and survival (Hallier and Gaertner, 2008). Detailed movement data can be more cum-  
63 bersome to acquire for marine than for terrestrial species, due to the limitations of satellite communication in the  
64 ocean. **Currently**, it is possible to record horizontal and vertical movements of pelagic species, but the deployment of  
65 such tracking devices is costly and operationally challenging (Ogburn et al., 2017). For example, using active acoustic  
66 tagging, one can have a good estimation of an individual trajectory but needs to follow the individual by boat. Pop-up  
67 satellite archival tags are also increasingly used and allow to record the movement and depth of marine animals with-  
68 out having to follow them. However, these tags, based on Global Location Sensors (GLS) only allow to track movement  
69 at a large geographical scale. Finally, presence-absence data can be obtained through passive acoustic telemetry, by  
70 deploying networks of acoustic receivers allowing the detection of tagged individuals when they are in the vicinity.  
71 **Recently, such data has been used to demonstrate the impacts of habitat modifications on the behavior of tropical**  
72 **tuna** (Pérez et al., 2020).

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

81 Since then, the deployment and use of drifting FADs (DFADs) has increased, and the last global estimate is be-  
82 tween 81,000 and 121,000 DFAD deployed in 2013 (Gershman et al., 2015). In the beginning of the 2010s, fishers  
83 started equipping DFADs with echosounder buoys, transmitting the position of the DFAD and an estimation of the  
84 tuna biomass under it (and designated as operational buoys when transmitting), further increasing their efficiency  
85 (Wain et al., 2021). In 2017-2021, around 56 % of global purse seine catch was performed on FOBs, representing  
86 around 1.8 million tons per year (ISSF, 2023), and this proportion can be much higher in some regions, *e.g.* with more  
87 than 85 % of purse seine catch around FOBs in the Indian Ocean (IOTC, 2022e). The use of DFADs directly impacts  
88 tuna populations, by increasing **the proportion of juvenile yellowfin and bigeye tuna compared to free-swimming**  
89 **schools** (Dagorn et al., 2013b). **Furthermore, the massive deployment of DFADs can also have indirect impacts, affect-**  
90 **ing the behavior and natural mortality of tuna** (Marsac et al., 2000; Hallier and Gaertner, 2008). Pérez et al. (2020)  
91 demonstrated, on arrays of anchored fish aggregating devices (AFADs), that a decrease of inter-AFAD distance leads  
92 to an increase in the percentage of time tuna spend associated. By comparing passive acoustic tagging data from three  
93 arrays with different inter-AFAD distances, the authors found that when the distance **between AFADs** decreases, tuna  
94 both spent more time associated to a given AFAD and less time between two associations. If an increase of DFAD  
95 density also increases the percentage of time tunas spend associated, it would strongly impact their catchability and  
96 therefore their mortality.

97 Several acoustic tagging studies characterized the behavior of tuna around AFADs, both through active (Girard  
98 et al., 2004) and passive tagging (Pérez et al., 2020; Robert et al., 2012). These studies allowed to determine both  
99 residence times and duration between two associations. On DFADs, residence times were measured and showed  
100 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  
101 for yellowfin, skipjack and bigeye tuna respectively (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al.,  
102 2016). However, times between two DFAD associations are not known because neighbor DFADs are difficult to  
103 locate and exhaustively instrument with acoustic receivers. Without these measures, the percentage of time tuna

104 spend associated with DFADs cannot be assessed, nor can the consequences of an increase of DFAD density on  
105 tuna.

106 This study **investigates the impacts** of pelagic habitat modifications, driven by industrial purse seine fisheries, on  
107 the behavior and mortality of **yellowfin tuna in the Western Indian Ocean**. In the Indian Ocean (IO), both the bigeye  
108 and yellowfin tuna stocks are currently overfished and subject to overfishing (IOTC, 2022a,b,c). One of the possible  
109 causes explaining the decline of these stocks is the important fishing pressure in the area. Tuna fisheries in the IO  
110 represent 1.2 Mt of tuna caught in 2021, 44 % of which are caught by PS fisheries (percentage over 2017-2021),  
111 followed by gillnet and baitboat (IOTC, 2022d; ISSF, 2023). Industrial purse seiners substantially rely on the use of  
112 DFADs, with the percentage of tuna caught at floating objects having increased from around 60 % (mainly on natural  
113 floating objects) in the 1980s, to more than 85 % lately (IOTC, 2022e). The massive use of DFADs observed in recent  
114 years increases the fishing mortality of juvenile yellowfin and bigeye tuna and could also induce other indirect impacts,  
115 by modifying their habitat and thus increasing their natural mortality (Marsac et al., 2000; Hallier and Gaertner, 2008).  
116 Recent studies investigated habitat modifications induced by the use of DFADs by industrial purse seine fleets in the  
117 Western IO (Dagorn et al., 2013a; Dupaix et al., 2021). Using data from observers onboard tuna purse seine vessels  
118 from 2006 to 2018, Dupaix et al. (2021) highlighted that DFADs multiplied the densities of FOBs by at least 2 and  
119 represented more than 85 % of the overall FOBs. On the other hand, quantitative estimates of how such habitat  
120 changes have affected the behavior of tuna and its availability to the fisheries were not possible, because of the  
121 high uncertainties on the total number of DFADs present in the open ocean and the lack of data on the movement  
122 behavior of tuna in arrays of DFADs. Since 2020, detailed information on the total number of DFADs equipped with  
123 echosounder buoys has been made available to scientists (IOTC, 2019) at a 1°/monthly scale. This new data allows  
124 for the first time to have quantitative estimates of the density of DFADs in the Indian Ocean. Furthermore, a recent  
125 study (Pérez et al., 2022) developed an individual-based model fitting the movement behavior of yellowfin tuna in  
126 an array of AFADs measured from acoustic telemetry data. In the following, we used this newly available dataset,  
127 combined with observers' data and the outputs of the individual-based model from (Pérez et al., 2022), to predict the  
128 time that yellowfin tuna spend between two DFAD associations in the Western IO. Using these predictions, we assess  
129 the impact of the modification of the pelagic habitat – **FOB density increase due to the introduction of DFADs** – on  
130 the percentage of their time YFT spend associated. This percentage of time spent associated has a direct impact on  
131 tuna availability to fishers and can **thus affect their mortality due to fishing**. Furthermore, we discuss how this habitat  
132 **modifications can** have other potential indirect impacts on tuna's fitness.

## 133 2 | MATERIAL AND METHODS

134 In order to compare tuna behavior in modified habitats (due to the introduction of DFADs) relative to an unmodified  
135 environment (where only FOBs other than DFADs, either of natural or anthropic origin, noted LOGs, are present),  
136 we estimated the percentage of time tuna spend associated with floating objects ( $P_a$ ) in FOB arrays characterized by  
137 different FOB densities. Simulations were run to model tuna movements in arrays of FOBs, using an individual-based  
138 model calibrated on passive acoustic data recorded for yellowfin tuna (Pérez et al., 2022). These simulations allowed  
139 estimating a theoretical relation between the time spent by tuna between two consecutive FOB associations (named  
140 CAT, Continuous Absence Time) and the density of FOBs. Observers data, combined with data on the density of  
141 DFADs at a 1°/monthly scale, were used to estimate the total density of FOBs (DFADs and LOGs) and the density of  
142 FOBs in the environment not modified by DFAD use (LOGs only). Predictions of CATs obtained in the pristine and  
143 modified habitat, combined with acoustic telemetry data informing on the amount of time spent by tuna associated

144 with FOBs (named CRT, Continuous Residence Time) were used to estimate changes in  $P_d$ . A schematic view of the  
 145 methodology developed is presented in Figure 1 and details of the model, methods and data are provided below.

## 146 2.1 | Model of tuna movements in an array of FOBs

147 Simulations were performed using the FAT albaCoRaW model v1.4 (Dupaix et al., 2023b), an individual-based model  
 148 simulating tuna trajectories in an array of FOBs based on a Correlated Random Walk (Pérez et al., 2022). This model is  
 149 built upon three behavioral rules: (i) tuna display a random search behavior between two associations to FOBs, (ii) at a  
 150 certain distance from FOBs (the orientation radius  $R_0$ ) tuna show oriented movements towards FOBs and (iii) the tuna  
 151 association dynamics follow a diel rhythm. The random search between two associations is based on three parameters:  
 152 the time-step  $\Delta t$ , determining the time interval between two positions, the speed  $v$ , determining the length of each  
 153 displacement at each time step, and the sinuosity coefficient  $c$ , determining the sinuosity of the path, from strait to a  
 154 simple random walk. These parameters were fitted on passive acoustic tagging data of 70 cm long YFT in arrays of  
 155 AFADs, in Pérez et al. (2022) (Table 1). We considered twelve different FOB densities (noted  $\rho$ ), ranging from  $1.00 \times 10^{-4}$   
 156 to  $4.44 \times 10^{-3}$  FOB.km $^{-2}$ . These densities correspond to a distance to the nearest neighbor in a regular square lattice  
 157 ranging from 100 to 15 km respectively (Table 1). For each of these densities, 100 different random arrays were  
 158 generated, with FOB longitude and latitude being randomly picked. A thousand individual tunas were released from  
 159 a random FOB in each of these arrays. As in Pérez et al. (2020), we define a Continuous Absence Time (CAT) as the  
 160 time spent between two associations to a FOB. A tuna was considered associated when it was located at less than  
 161 500 m from a FOB, which corresponds to the distance at which a tagged tuna can be detected by an acoustic receiver.  
 162 CATs were separated into two categories: (i)  $CAT_{diff}$  when the movement occurred between two different FOBs and  
 163 (ii)  $CAT_{return}$  when the tuna returned to its departure FOB after more than 24 h. Studies processing experimental  
 164 acoustic tagging data of tropical tuna relied on a Maximum Blanking Period of 24 h, i.e. below a temporal separation  
 165 of 24 h between two subsequent acoustic detections at the same FOB, the fish is considered to be still associated  
 166 (Capello et al., 2015; Pérez et al., 2022). Hence, each time a  $CAT_{return}$  of less than 24 h was recorded, this movement  
 167 was discarded and the simulation time was reset to the beginning. The simulation was stopped when the individual  
 168 either performed a  $CAT_{diff}$ , a  $CAT_{return}$  or after 1,500 days of simulation. The obtained Continuous Absence Time  
 169 (CAT) was saved. A total of 100,000 CATs were simulated per FOB density, totaling 1,200,000 simulated CATs.

## 170 2.2 | CAT trends for different FOB densities

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

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

175 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).  
 176 Hence,  $\overline{CAT_{return}}$  (in days) was related to  $\rho$  as follow:

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

177 with  $(a_r, b_r) \in \mathbb{R}_+^2$ . Then, the mean Continuous Absence Time  $\overline{CAT}(\rho)$  can be expressed as follow (see Supplementary  
178 Materials 1 for more details):

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

179 where  $R = \frac{A}{B}$ , the ratio between the number of  $CAT_{diff}$  ( $A$ ) and that of  $CAT_{return}$  ( $B$ ). The ratio  $R$  as a function of  $\rho$   
180 was fitted based on the following equation:

$$R(\rho) = a\rho^c \exp(b \times \rho) \quad (4)$$

181 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  
182 *stats* v3.6.3.

## 183 2.3 | FOB density calculation in the IO

184 Echosounder buoy density data from January to December 2020, provided by the Indian Ocean Tuna Commission  
185 (IOTC, [the regional fisheries management organisation managing tuna fishing in the Indian Ocean](#)), was used as a proxy  
186 for DFAD data (IOTC, 2021b). This dataset contains the monthly mean of the number of [textitoperational buoys, i.e.,](#)  
187 [the echosounder buoys whose GPS position is remotely transmitted to one or several fishing vessels](#), for each  $1^\circ \times 1^\circ$   
188 cell of the Indian Ocean. This value was divided by the sea area of each cell, to obtain a mean monthly DFAD density  
189 ( $\rho_{DFAD}$ ). Densities were then averaged over  $5^\circ$  cells to predict CATs (for more elements on the spatial and temporal  
190 resolution choice see Supplementary Materials 2).

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

## 2.4 | Prediction of mean Continuous Absence Time and Percentage of time associated in the IO

Using the density values calculated above and the coefficients of the models fitted in section 2.3, 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 at DFADs in the Western 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, for each floating objects categories (DFAD, FOB, LOG). Because the calculation of the  $m$  ratio reduced greatly the study area, we first predicted  $\overline{CAT}$  and  $P_a$  values based on the density of DFADs ( $\rho_{DFAD}$ ). However, to determine the impact of DFADs on the predicted associative behavior, we compared the predicted values of  $\overline{CAT}$  and  $P_a$  obtained with  $\rho_{FOB}$  and  $\rho_{LOG}$ . This comparison allows to determine the impact of the DFADs induced habitat modification on tuna availability to fishers.

## 3 | RESULTS

### 3.1 | Simulated Continuous Absence Time trends

Simulated  $\overline{CAT}$ ,  $\overline{CAT}_{diff}$  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 2 & Table 2). The ratio  $R$  between the number of  $CAT_{diff}$  and that of  $CAT_{return}$  was always above 1, meaning that the majority of CATs were performed between two different **FOBs** ( $CAT_{diff}$ ). It varied from 2.82, for the lowest density ( $\rho = 1.00 \times 10^{-4} \text{ km}^{-2}$ ), with  $CAT_{return}$  representing 26.18 % of the number of  $CAT$ , to 87.11 for the highest density ( $\rho = 4.44 \times 10^{-3} \text{ km}^{-2}$ ), with  $CAT_{return}$  representing 1.13 % of the total number of simulated  $CAT$ . Hence, when  $\rho$  decreases, tuna tend to return to the **FOB** of departure more often. Consequently,  $\overline{CAT}$  values were shorter than  $\overline{CAT}_{diff}$  for lower densities, due to the higher proportion of  $\overline{CAT}_{return}$ , but were almost exclusively driven by  $\overline{CAT}_{diff}$  for high densities (Figure 2 & Table 2). The parameters of the fits of  $\overline{CAT}_{diff}(\rho)$ ,  $\overline{CAT}_{return}(\rho)$  and  $R(\rho)$  are presented in Table 3

### 3.2 | DFAD densities

Buoy densities obtained from the IOTC data, considered as DFAD densities ( $\rho_{DFAD}$ ) are presented in Figure 3. The maximum observed density in a 1° cell was  $\rho = 8.39 \times 10^{-3} \text{ km}^{-2}$ , 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  $\rho = 2.8 \times 10^{-3} \text{ km}^{-2}$ , corresponding to 28 operational buoys in a 100 km × 100 km square. Mean density over the whole area was  $\bar{\rho} = 3.45 \times 10^{-4} \text{ km}^{-2}$ , corresponding to 3.45 buoys per 100 km × 100 km square. Areas with highest buoys densities were different according to the month, moving from the West to the East of the Seychelles from January to April. Highest buoys



233 densities could then be observed in the Arabian Sea, from May to July. In September and forward, highest densities  
 234 were observed around the Seychelles and East of the Somalian EEZ. Finally, a high number of buoys around the  
 235 Maldives was present in May and December, suggesting a high number of DFADs drifting towards the Eastern IO  
 236 during this period (Figure 3E&L).

### 237 3.3 | Predictions of Continuous Absence Time and Percentage of time associated

238 Predicted  $\overline{CAT(\rho_{DFAD})}$  values in 5° cells are presented in Figure 4 (see Supplementary Materials 3 for predictions  
 239 of  $\overline{CAT_{diff}(\rho_{DFAD})}$ ,  $\overline{CAT_{return}(\rho_{DFAD})}$  and  $R(\rho_{DFAD})$ , and Supplementary Materials 4 for predictions on  $\rho_{FOB}$   
 240 and  $\rho_{LOG}$ ). Minimum  $\overline{CAT(\rho_{DFAD})}$  predicted value was 1.06 days in February 2020. The area with shortest pre-  
 241 dicted  $\overline{CAT(\rho_{DFAD})}$  was spatially conserved through time: low values were observed from the North of the Mozam-  
 242 bique Channel to the Arabian Sea, and from the African coast to 65°E. However, for each month, a peak of short  
 243  $\overline{CAT(\rho_{DFAD})}$  was observed and moved from the South of the area to the North, from January to June (Figure 4A-  
 244 F), and back to the South of the area from June to December (Figure 4F-L). The percentage of time spent by tuna  
 245 associated with a DFAD ( $P_a(\rho_{DFAD})$ ) displayed similar spatial patterns as  $\overline{CAT(\rho_{DFAD})}$  (Figure 5).

### 246 3.4 | Impact of DFAD on tuna availability

247 The comparison of the predictions obtained with FOB and LOG densities is presented in Figure 6 and Table 4. The  
 248 mean density of all types of FOBs ( $\overline{\rho_{FOB}} = 1.32 \times 10^{-3} \text{ km}^{-2}$ ) was 6.6 times higher than the mean LOG density  
 249 ( $\overline{\rho_{LOG}} = 2.00 \times 10^{-4} \text{ km}^{-2}$ ), resulting in much shorter  $\overline{CAT}$  with mean values, averaged over cells and months, of 5  
 250 and 46 days predicted from FOB and LOG densities, respectively. The strong density increase induced by DFADs  
 251 resulted in a increase of the predicted proportion of time tuna spent associated ( $P_a$ ), from  $\overline{P_a(\rho_{LOG})} = 20\%$  for the  
 252 environment without DFADs, to  $\overline{P_a(\rho_{FOB})} = 68\%$  for the environment modified by the introduction of DFADs.

## 253 4 | DISCUSSION

254 Human induced habitat modifications can impact species behavior and ultimately their fitness (Swearer et al., 2021).  
 255 Continuous Absence Times (CATs) and Continuous Residence Times (CRTs) are two behavioral metrics allowing to  
 256 assess the impact of the modification of one habitat component – the density of floating objects – on pelagic species.  
 257 Several studies measured CATs (Robert et al., 2012, 2013; Rodriguez-Tress et al., 2017) or CRTs (Robert et al., 2013,  
 258 2012; Govinden et al., 2013) in arrays of anchored FADs. CRTs were also measured at drifting FADs (Matsumoto  
 259 et al., 2016; Tolotti et al., 2020; Govinden et al., 2021). However, experimentally measuring CATs in an array of FADs  
 260 requires the equipment of the whole array with acoustic receivers. When these FADs are drifting, finding, equipping  
 261 and recovering them is difficult and has never been achieved. Another challenge is related to the availability of reliable  
 262 data on DFAD densities. In the Indian ocean, this data deficiency could only be overcome recently, with the provision  
 263 of the number of operational buoys by the IOTC secretariat. This study is, to our knowledge, the first to give estimates  
 264 of CATs of yellowfin tuna (YFT) in arrays of DFADs. These estimates show a strong influence of fisheries-induced  
 265 habitat modifications on tuna associative behavior in the Western Indian Ocean (WIO). By modifying tuna habitat,  
 266 purse seine fisheries increase the percentage of time tuna spend associated ( $P_a$ ), which has a direct influence on YFT  
 267 availability to fishers, which can impact fishing mortality and tuna's fitness.

268 Numerous factors could affect the obtained  $\overline{CAT}$  and  $P_a$  predictions. Predictions were made based on operational

269 buoys densities deployed on FOBs (IOTC, 2021b), which is a proxy of the actual DFAD density in the ocean. Among  
270 **the instrumented FOBs, those for which the buoy was remotely deactivated (and thus could not transmit its position**  
271 **anymore)**, are not present in the data. Moreover, if most Contracting Parties provided their buoys' positions to the  
272 IOTC, some countries did not share their data (IOTC, 2021b), so densities could be underestimated.

273 The other datasets used for the predictions are French observers data and measurement of CRTs. The use of  
274 French observers data restricted the study area, highlighting the need to better share this data among countries, as  
275 it is done for instrumented buoys, and to increase observers coverage. Only the mean CRT value for the WIO was  
276 used in our study (measured in Govinden et al., 2021) and we considered CRT as constant. This approximation could  
277 influence the predictions, as it was demonstrated that CRTs also depend on FAD density, even if to a lesser extent  
278 than CATs (Pérez et al., 2020). CRT measurements on DFADs also showed a variability between oceans as well as  
279 strong inter-individual variations (Tolotti et al., 2020; Govinden et al., 2013, 2021; Matsumoto et al., 2016). Further  
280 measurements of CRTs at DFADs and some modelling approach would then be needed to take this variability into  
281 account. However, Pérez et al. (2020) found that, as AFAD density increases, CRT also increases, suggesting that the  
282 increase in catchability observed in this study should be conserved or even intensified.

283 The model used for the predictions was fitted on passive acoustic tagging data from YFT of fork length  $70 \pm 10$  cm,  
284 tagged in an array of AFADs (Pérez et al., 2022). At DFADs, two main size classes of YFT are found: individuals around  
285 50 cm and individuals around 120 cm (IOTC, 2022e, p. 52). Fitting the model on bigger individuals (70 cm instead  
286 of 50 cm) should not change drastically the obtained parameters, but could change slightly individual speed (fitted  
287 value  $v = 0.7 \text{ m}\cdot\text{s}^{-1}$  in Pérez et al., 2022). Also, as tuna orient themselves towards FADs several kilometers away (4 to  
288 17 km, Girard et al., 2004), it was suggested that they could detect FADs using acoustic stimuli (Pérez et al., 2022).  
289 Although FAD design has not been identified to influence the attractiveness of FADs (Fréon and Dagorn, 2000), there  
290 might be a difference in detectability between anchored, which are composed of a bigger structure containing a metal  
291 chain, and drifting FADs. Hence, both the type of FAD (anchored or drifting) and tuna size class could change some  
292 model parameters, such as the orientation radius ( $R_0$ , fitted value of 5 km) and swimming speed ( $v$ , fitted value of  $0.7$   
293  $\text{m}\cdot\text{s}^{-1}$ ). To account for these uncertainties, we also performed predictions using other parameters ( $v = 0.5 \text{ m}\cdot\text{s}^{-1}$  and  
294  $R_0 = 2$  km). The obtained  $\overline{CAT}$  were longer, resulting in smaller  $P_a$  values (see Supplementary Materials 5). However,  
295 it should be noted that changing the parameters do not change the observed trend: the habitat modification induced  
296 by DFAD increases YFT catchability, whatever the parameter set considered.

297 Since 2016, in the IO, more than 80 % of purse seine catch on tropical tuna was made on floating objects, reaching  
298 a maximum of almost 95 % in 2018 (see Figure 5 in IOTC, 2022e). YFT caught by industrial purse seine vessels on  
299 FOBs in the IO has steadily increased since 2008 and represented around 22 % of the total YFT catch, by all gear types,  
300 in 2021 (ISSF, 2023; IOTC, 2022e). The predicted  $P_a$  were very high in the Western IO, with a mean of 68 % (calculated  
301 on all FOBs), mainly due to DFAD introduction (mean prediction without DFADs of 20 %). As the habitat modification  
302 induced by DFADs strongly increases the percentage of their time YFT spend associated with floating objects, it  
303 increases their vulnerability to purse seine sets. In the IO, the YFT stock is currently overfished (*i.e.* the biomass is  
304 below the biomass reference point corresponding to the maximum sustainable yield) and subject to overfishing (*i.e.*  
305 the fishing mortality is above the reference point corresponding to the maximum sustainable yield; IOTC, 2021a).  
306 The Indian Ocean Tuna Commission (IOTC) imposes limits on the number of operational buoys (buoys which transmit  
307 DFAD position and other information to fishers) at 300 per vessel at any one time (IOTC, 2019). The present results  
308 show that limiting the number of floating objects and of operational buoys directly affects tuna catchability by purse  
309 seine vessels. Therefore, if the yellowfin tuna stock is to remain overfished, efforts should be made to further limit  
310 the number of floating objects in the ocean, through limits on operational buoy numbers and on DFAD deployments.

311 In addition to the increase of fishing availability to fishers, the observed increase of the percentage of time as-

sociated ( $P_a$ ) could also have indirect impacts (*i.e.* not linked with fishing mortality) on YFT and other associated species. One of the main hypothesis to explain the association of tuna with floating objects is the *meeting-point* hypothesis (Fréon and 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 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 of FOB density, inducing an increase of  $P_a$ , could result in a disruption of schooling behavior and provoke the dispersion of individuals among FOBs. Capello et al. (2022) developed a model to study school behavior in a heterogeneous 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 tuna behavior and its link with fitness. Echosounder buoys 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.

Also, 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, tend to suggest that DFADs did not act as an ecological trap in the WIO. However, DFAD impact could have been counteracted by other environmental effects or could have act on other biological processes than condition (Dupaix et al., 2023a). 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). Nevertheless, the increase of FOB density increases  $P_a$  and FOB array connectivity (increase of  $R$ , *i.e.* of the proportion of  $CAT_{diff}$ ). Added to previous evidence suggesting that an increase of FAD density induces an increase of 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's fitness – through other biological parameters than condition – still needs to be investigated further.

## 5 | 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 (Mullu, 2016; 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; Marsac et al., 2000). 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 also increase their availability to fishers and hence their catchability and fishing mortality. Yellowfin tuna and Drifting Fish Aggregating Devices 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 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.

## 351 Authors' Contribution

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

## 354 Declaration of Competing Interest

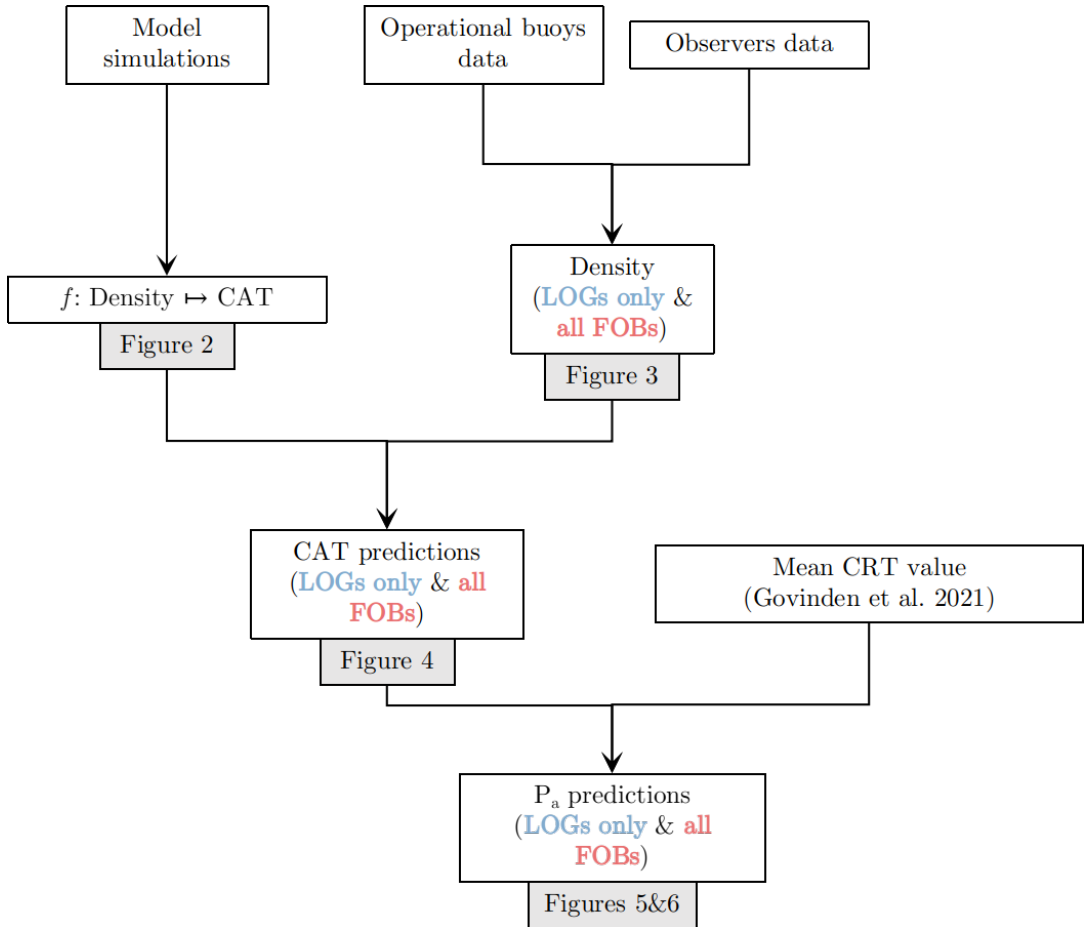
355 The authors declare that they have no known competing financial interests or personal relationships that could have  
356 appeared to influence the work reported in this paper.

## 357 Acknowledgements

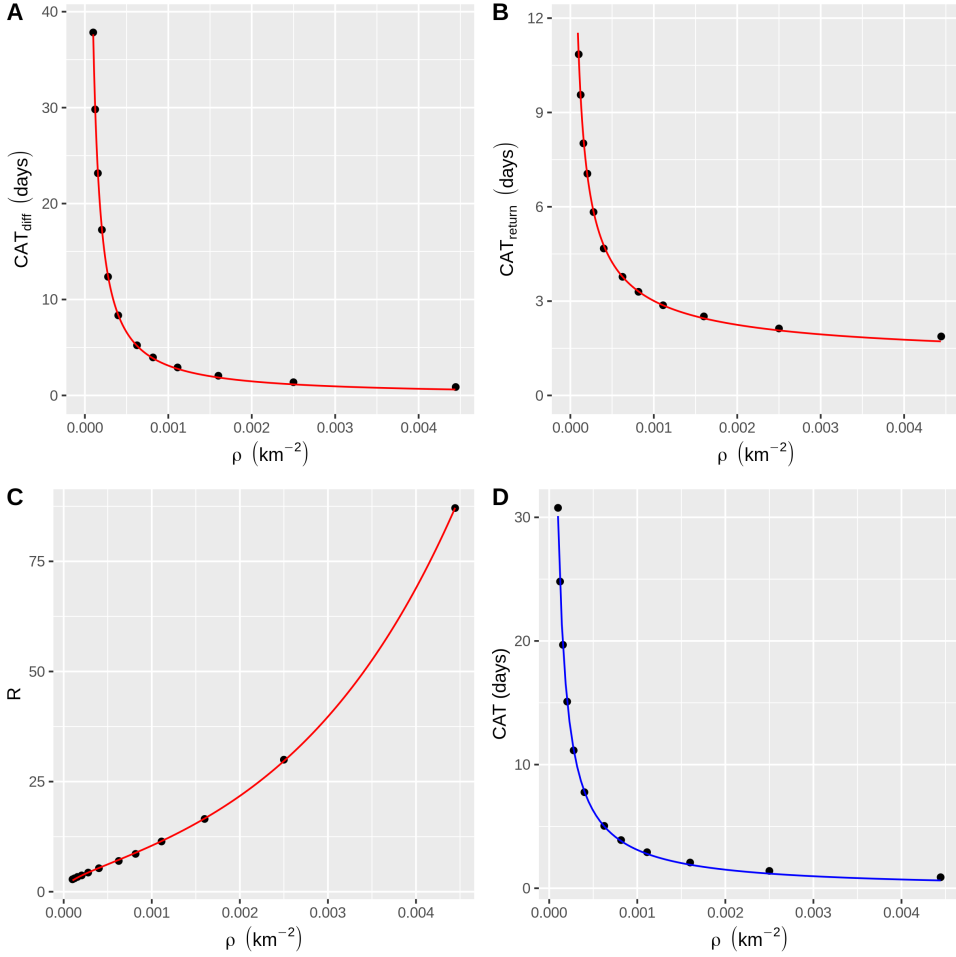
358 The authors would like to thank Q.Schull for his insights on the redaction of the paper. We acknowledge the Pôle  
359 de Calcul et des Données Marines (PCDM) for providing DATARMOR storage, data access, computational resources,  
360 visualization, web-services, consultation, support services (URL: <https://pcdm.ifremer.fr/>). This work was sup-  
361 ported by the MANFAD project (France Filière Pêche), URL: <https://manfad-project.com/en>. We thank ISSF for  
362 its involvement in the overall project.

363 We also thank the Indian Ocean Tuna Commission Secretariat for providing the data used in this study. Observer  
364 data have been collected through the "Data Collection Framework" (Reg 2017/1004 and 2016/1251) funded by both  
365 IRD and the European Union since 2005, and the OCUP program ("Observateur Commun Unique et Permanent"), an  
366 industry-funded program coordinated by ORTHONGEL since 2014. The authors sincerely thank IRD's Ob7 ("Observa-  
367 toire des Ecosystèmes Pélagiques Tropicaux Exploités") in charge of observer data collection, processing, management,  
368 and for sharing the data used in this study.

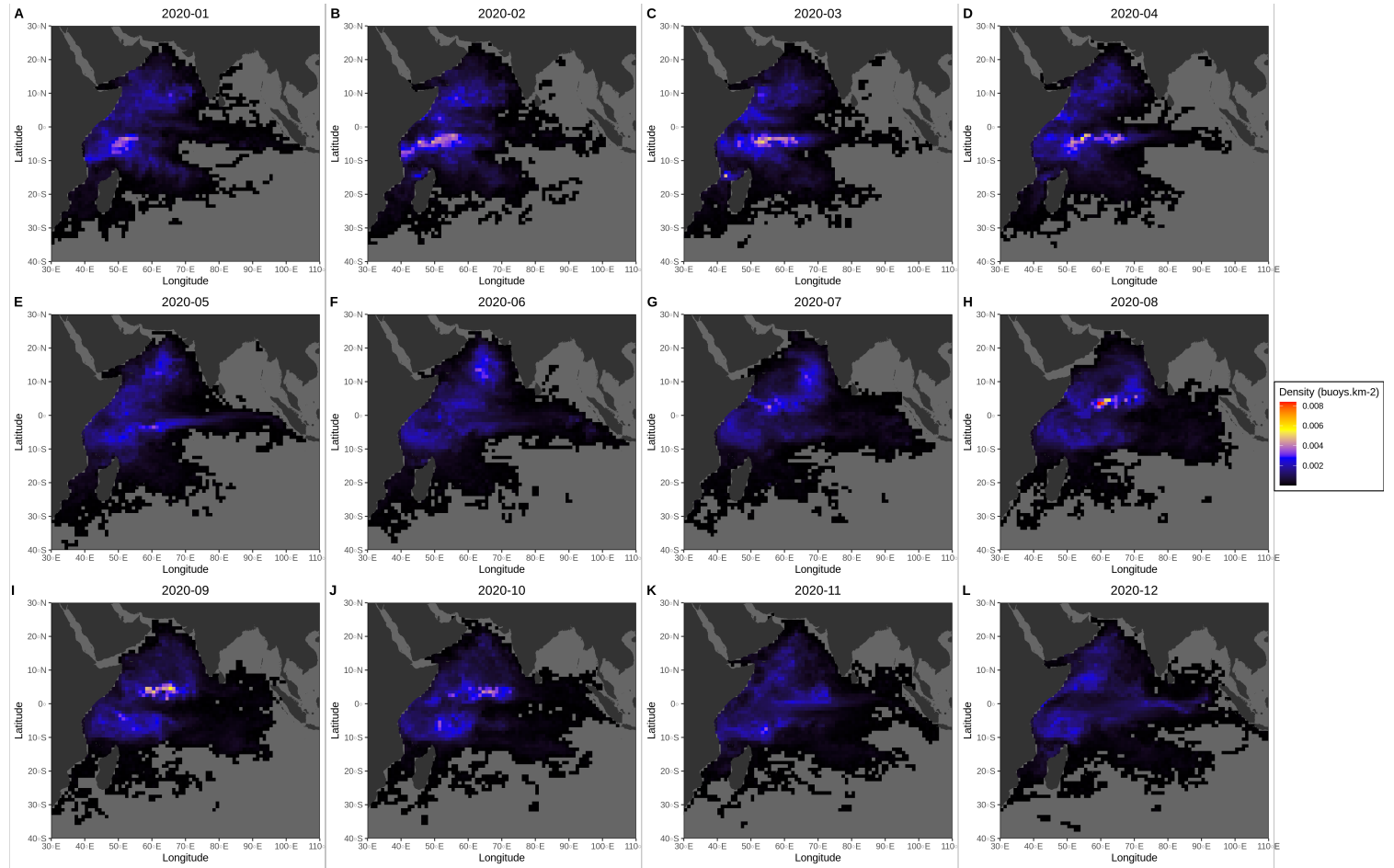
369 For the purpose of Open Access, a CC-BY public copyright licence has been applied by the authors to the present  
370 document and will be applied to all subsequent versions up to the Author Accepted Manuscript arising from this  
371 submission.

372 **Figures**

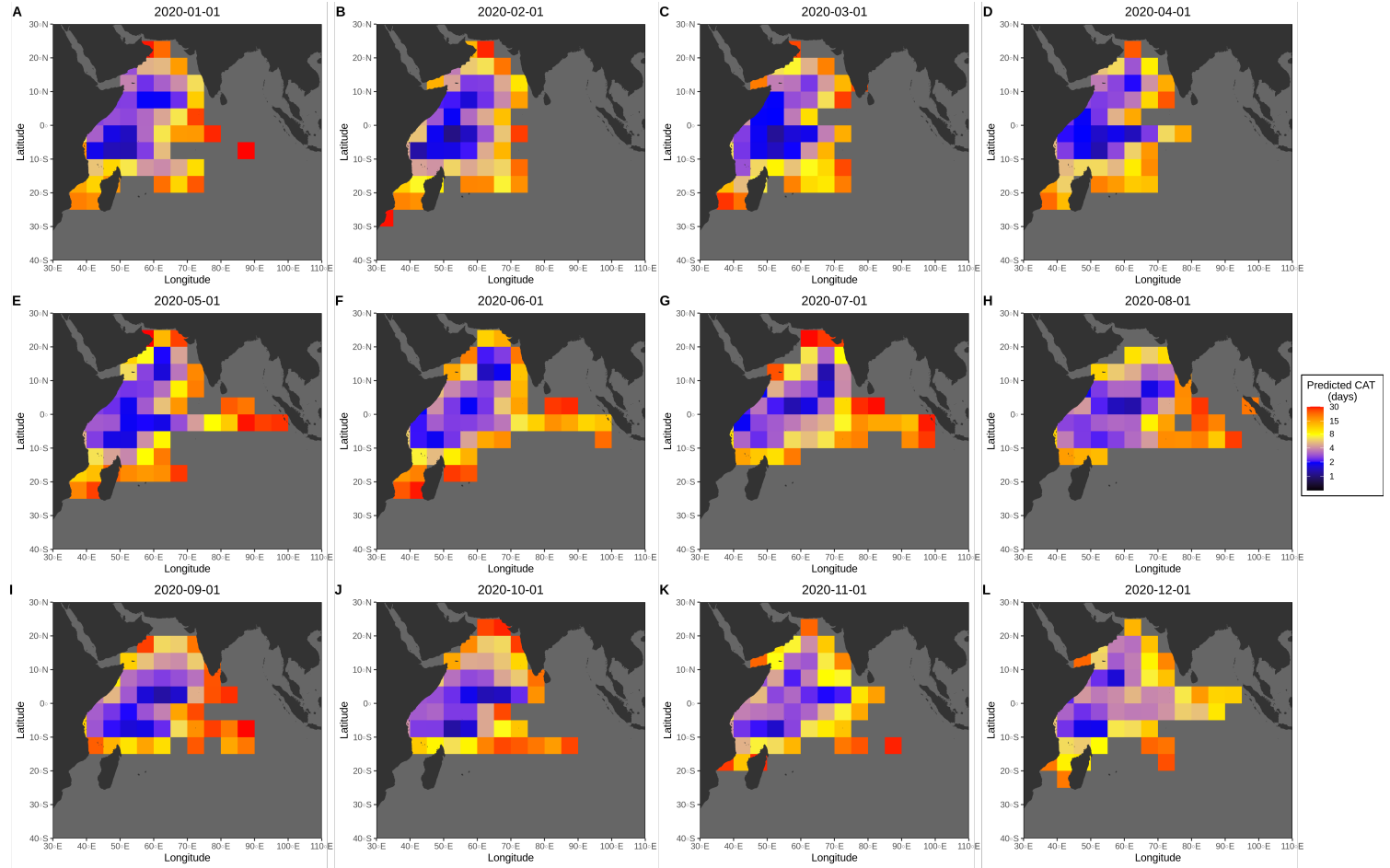
**FIGURE 1** Schematic representation of the methodology used in the study, which allowed the calculation of  $P_a$  both for the densities of all floating objects (all FOBs, habitat modified by DFADs) and for floating objects other than DFADs (LOGs only, habitat not modified). Figure number illustrating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



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

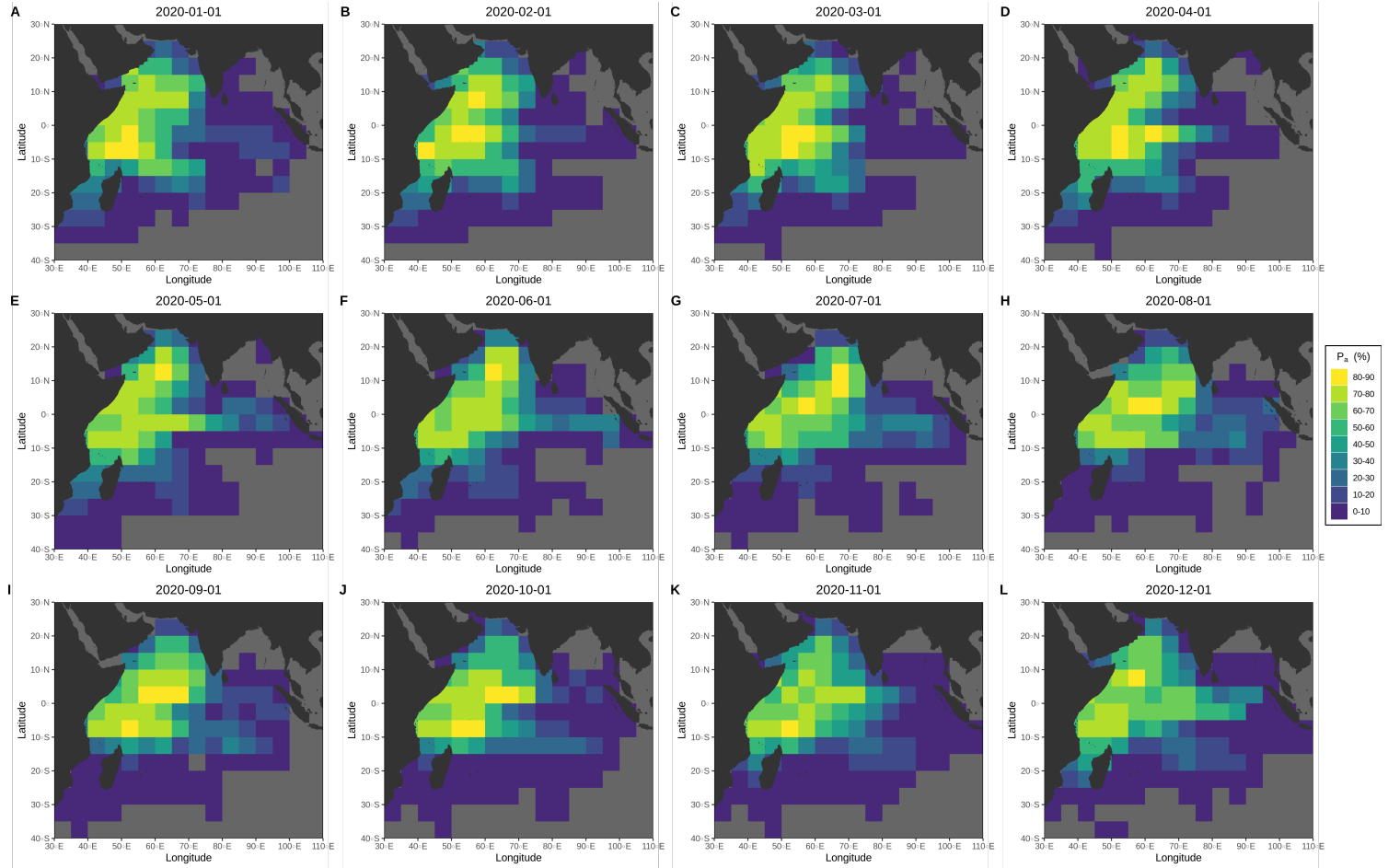


**FIGURE 3** Mean monthly buoy densities per  $1^\circ$  cells in the western Indian Ocean calculated from IOTC (2021b), expressed in  $\text{buoys.km}^{-2}$ . Buoy densities are considered as DFAD densities, see details in section 2.3

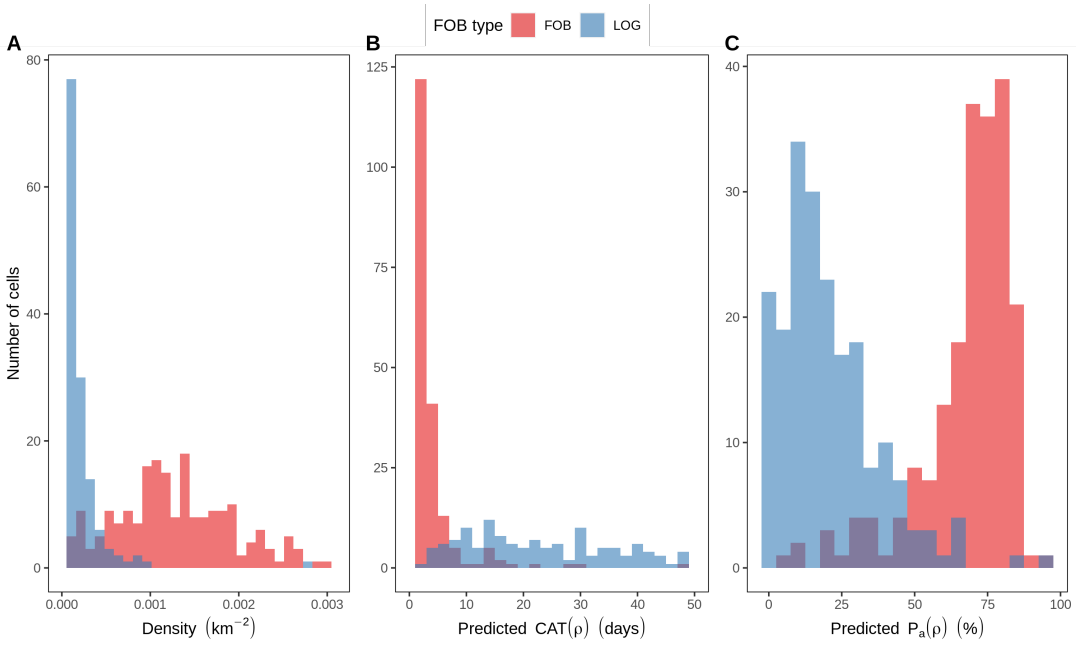


**FIGURE 4** Mean monthly Continuous Absence Times of individual yellowfin tunas predicted using DFAD density ( $\overline{CAT}(\rho_{DFAD})$ ), in days) per 5° cells in the western Indian Ocean in 2020. The color scale is log transformed.  $\overline{CAT}(\rho_{DFAD})$  longer than 30 days were not represented.





**FIGURE 5** Mean monthly percentage of time spent associated by individual yellowfin tunas predicted using DFAD density ( $P_a(p_{DFAD})$ ) per  $5^\circ$  cells in the Western Indian Ocean in 2020.



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

## 373 Tables

**TABLE 1** Parameters used in the simulations, performed using Dupaix et al. (2023b) and based on the calibration in Pérez et al. (2022).  $\Delta t$ : time-step;  $v$ : speed;  $R_0$ : orientation radius;  $c$ : sinuosity coefficient;  $D$ : mean inter-**FOB** distance.

$\Delta t$	$v$	$R_0$	$c$	$D$
100 s	0.7 m.s <sup>-1</sup>	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 **FOB** density.  $D$ : mean inter-**FOB** distance in a regular square lattice (in km);  $\rho$ : **FOB** density (in km<sup>-2</sup>);  $\overline{CAT}$ : 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 Continuous Absence Time when the individual returned to the departure **FOB** (in days);  $R$ : ratio between the number of  $\overline{CAT}_{diff}$  and the number of  $\overline{CAT}_{return}$ .

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

**TABLE 3** Summary of the fitted parameter values.

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

**TABLE 4** Summary of monthly  $CAT$  and  $P_a$  values per  $5^\circ$  cell in the Indian Ocean in 2020, predicted using FOB and LOG densities ( $\rho_{FOB}$  and  $\rho_{LOG}$ ).

FOB type	$\rho$ ( $\text{km}^{-2}$ )		$CAT$ (days)		$P_a$ (%)	
	mean	SE	mean	SE	mean	SE
FOB	$1.32 \times 10^{-3}$	$4.52 \times 10^{-6}$	4.97	$6.30 \times 10^{-2}$	68.3	$8.00 \times 10^{-2}$
LOG	$2.00 \times 10^{-4}$	$3.38 \times 10^{-6}$	46.3	$3.43 \times 10^{-1}$	20.5	$8.30 \times 10^{-2}$

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