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

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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. With around 5 million tons fished yearly, tuna species represent more than 7 % of global marine fish capture, of which two third are captured by purse seine vessels. Because several pelagic fish species, such as tuna, associate with floating objects, fishers have started deploying their own floating objects – Drifting Fish Aggregating Devices (DFADs) – in the early 1990s to increase tuna catchability. Since then, the massive deployment of DFADs has modified tuna habitat, by increasing the density of floating objects, with potential consequences on tuna associative behavior. This use of DFADs by purse seine fisheries is a major concern and it offers an important case study to assess the impact of habitat modifications on species behavior and mortality. In this study we use an individual-based model, based on a correlated random walk calibrated on passive acoustic tagging data, to determine a general relationship between DFAD density and the time tuna spend between two associations

with a DFAD. Using this general relationship and fisheries data in the Indian Ocean, we predict that the increase of floating object density, due to DFAD use, strongly increases the percentage of time tuna spend associated, which directly impacts tuna 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 deployments.

KEYWORDS

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

61 poleward (Alongi, 2015). Pollution is also a driver of marine habitat modification, through acidification, oil spills or
62 plastics, which can lead to changes in population dynamics (IPBES, 2022, 4.2.1.6.5). Marine habitat modifications
63 also impact benthic community composition and sensitivity (Neumann et al., 2016), and could affect fish recruitment
64 (Macura et al., 2019).

65 In pelagic environments, fewer studies have assessed habitat modifications (Dupaix et al., 2021) and their impact
66 on species behavior, condition and survival (Hallier and Gaertner, 2008). Detailed movement data can be more cum-
67 bersome to acquire for marine than for terrestrial species, due to the limitations of satellite communication in the
68 ocean. It is possible to record horizontal and vertical movements of pelagic species, but the deployment of such track-
69 ing devices is costly and operationally challenging (Ogburn et al., 2017). For example, using active acoustic tagging,
70 one can have a good estimation of an individual trajectory but needs to follow the individual by boat. Pop-up satellite
71 archival tags are also increasingly used and allow to record the movement and depth of marine animals without having
72 to follow them. However, these tags, based on Global Location Sensors (GLS) only allow to track movement at a large
73 geographical scale. Finally, presence-absence data can be obtained through passive acoustic telemetry, by deploying
74 networks of acoustic receivers allowing the detection of tagged individuals when they are in the vicinity (Pérez et al.,
75 2020).

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

84 Since then, the deployment and use of drifting FADs (DFADs) has increased, and the last global estimate is be-
85 tween 81,000 and 121,000 DFAD deployed in 2013 (Gershman et al., 2015). In the beginning of the 2010s, fishers
86 started equipping DFADs with echosounder buoys, transmitting the position of the DFAD and an estimation of the
87 tuna biomass under it (and designated as operational buoys when transmitting), further increasing their efficiency
88 (Wain et al., 2021). In 2017-2021, around 56 % of global purse seine catch was performed on FOBs, representing
89 around 1.8 million tons per year (ISSF, 2023), and this proportion can be much higher in some regions, e.g. with more
90 than 85 % of purse seine catch around FOBs in the Indian Ocean (IOTC, 2022). The use of DFADs and their equipment
91 with echosounder buoys directly impact tuna populations, by increasing fishing efficiency (Wain et al., 2021) and the
92 proportion of juvenile tuna (Guillotreau et al., 2011). It also has an impact on pelagic species habitat, which can be
93 quantified by comparing DFAD densities with that of LOGs (floating objects other than FADs). For example, using data
94 from observers onboard tuna purse seine vessels, Dupaix et al. (2021) highlighted the habitat modifications provoked
95 by the drastic increase of DFAD use in the Western Indian Ocean (WIO) from 2006 to 2018. DFADs multiplied the
96 densities of FOBs by at least 2 and represented more than 85 % of the overall FOBs.

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

104 therefore their mortality.

105 Several acoustic tagging studies characterized the behavior of tuna around AFADs, both through active (Girard
106 et al., 2004) and passive tagging (Pérez et al., 2020; Robert et al., 2012). These studies allowed to determine both
107 residence times and duration between two associations. On DFADs, residence times were measured and showed
108 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
109 for yellowfin, skipjack and bigeye tuna respectively (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al.,
110 2016). However, times between two DFAD associations are not known because neighbor DFADs are difficult to
111 locate and exhaustively instrument with acoustic receivers. Without these measures, the percentage of time tuna
112 spend associated with DFADs cannot be assessed, nor can the consequences of an increase of DFAD density on
113 tuna.

114 This study focuses on the impact of pelagic habitat modifications, driven by fisheries, on a pelagic species, the
115 YFT. We use an individual-based model, based on a Correlated Random Walk (Pérez et al., 2022), and fisheries data to
116 predict the time tuna spend between two associations to DFADs in the Western IO in 2020. Using these predictions,
117 we assess the impact of the modification of the pelagic habitat – DFAD density increase – on the percentage of their
118 time YFT spend associated. This percentage of time spent associated has a direct impact on tuna availability to fishers
119 and can have other potential indirect impacts on tuna’s fitness.

120 2 | MATERIAL AND METHODS

121 2.1 | Simulations

122 Simulations were performed using the FAT albaCoRaW model v1.4 (Dupaix et al., 2022), an individual-based model
123 simulating tuna trajectories in an array of fish aggregating devices (FADs) based on a Correlated Random Walk (Pérez
124 et al., 2022). This model is build upon three behavioral rules: (i) tuna display a random search behavior between two
125 associations to FADs, (ii) at a certain distance from FADs (the orientation radius R_0) tuna show oriented movements
126 towards FADs and (iii) the tuna association dynamics follow a diel rythm. The random search between two associations
127 is based on three parameters: the time-step Δt , determining the time interval between two positions, the speed
128 v , determining the length of each displacement at each time step, and the sinuosity coefficient c , determining the
129 sinuosity of the path, from strait to a simple random walk. These parameters were fitted on passive acoustic tagging
130 data of 70 cm long YFT in arrays of AFADs, in Pérez et al. (2022) (Table 1). We considered twelve different FAD
131 densities (noted ρ), ranging from 1.00×10^{-4} to 4.44×10^{-3} FAD.km⁻². These densities correspond to a distance
132 to the nearest neighbor in a regular square lattice ranging from 100 to 15 km respectively (Table 1). For each of
133 these densities, 100 different random arrays were generated, with FAD longitude and latitude being randomly picked.
134 A thousand individual tunas were released from a random FAD in each of these arrays. As in Pérez et al. (2020),
135 we define a Continuous Absence Time (CAT) as the time spent between two associations to a FAD. A tuna was
136 considered associated when it was located at less than 500 m from a FAD, which corresponds to the distance at
137 which a tagged tuna can be detected by an acoustic receiver. CATs were separated into two categories: (i) CAT_{diff}
138 when the movement occurred between two different FADs and (ii) CAT_{return} when the tuna returned to its departure
139 FAD after more than 24 h. Studies processing experimental acoustic tagging data of tropical tuna relied on a Maximum
140 Blanking Period of 24 h, i.e. below a temporal separation of 24 h between two subsequent acoustic detections at the
141 same FAD, the fish is considered to be still associated (Capello et al., 2015; Pérez et al., 2022). Hence, each time a
142 CAT_{return} of less than 24 h was recorded, this movement was discarded and the simulation time was reset to the
143 beginning. The simulation was stopped when the individual either performed a CAT_{diff} , a CAT_{return} or after 1,500

144 days of simulation. The obtained Continuous Absence Time (CAT) was saved. A total of 100,000 CATs were simulated
 145 per FAD density, totaling 1,200,000 simulated CATs.

146 2.2 | CAT trends for different FAD densities

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

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

151 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).
 152 Hence, \overline{CAT}_{return} (in days) was related to ρ as follow:

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

153 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
 154 Materials 1 for more details):

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

155 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 ρ
 156 was fitted based on the following equation:

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

157 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
 158 *stats* v3.6.3.

159 2.3 | FOB density calculation

160 Predictions of the $\overline{CAT}(\rho)$ in 2020 in the Indian Ocean (IO) were performed on three different densities: DFAD, FOB
 161 and LOG (floating objects other than DFADs, either of natural origin or originating from pollution) densities. Buoy
 162 density data, provided by the Indian Ocean Tuna Commission (IOTC), was used as a proxy for DFAD data (IOTC,
 163 2021b). This dataset contains the monthly mean of the number of operational buoys for each $1^\circ \times 1^\circ$ cell of the Indian
 164 Ocean. This value was divided by the sea area of each cell, to obtain a mean monthly DFAD density (ρ_{DFAD}). Densities
 165 were then averaged over 5° cells to predict CATs (for more elements on the spatial and temporal resolution choice

166 see Supplementary Materials 2).

167 FOB and LOG densities were calculated using DFAD densities and data recorded by scientific observers on board
 168 French purse seine vessels (2014-2019). Observer data include the date, time, and location of the main activities
 169 of the fishing vessel (e.g. fishing sets, installation or modification of FOBs, searching for FOBs). For every activity
 170 occurring on a FOB, the type of operation (e.g. deployment, removal, and observation of a FOB) and the type of
 171 floating object (DFAD or LOG) are recorded. Using the methodology developed in Dupaix et al. (2021) applied to
 172 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
 173 DFAD observations respectively) per 5° cell which was used to calculate the density of FOBs ($\rho_{FOB} = (1+m)\rho_{DFAD}$)
 174 and the density of LOGs ($\rho_{LOG} = m\rho_{DFAD}$). Because observers data are only available in areas where purse seine
 175 vessels are actively fishing, the calculation of the m ratio restricted the study area to the purse seine fishing zones.

176 2.4 | Prediction of mean Continuous Absence Time and Percentage of time associated in 177 the IO

178 Using the density values calculated above and the coefficients of the models fitted in section 2.3, monthly \overline{CAT} values
 179 were predicted for each 5° cells in 2020.

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

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

181 with \overline{CRT} the mean Continuous Residence Time, defined as continuous bouts of time spent at the same FAD
 182 without any day-scale absence (>24 h, Capello et al., 2015). Pérez et al. (2020) showed that \overline{CRT} depends on AFAD
 183 density but to a lesser extent than \overline{CAT} . Hence, \overline{CRT} was considered constant and estimated to be 6.64 days, as
 184 measured on YFT at DFADs in the Western Indian Ocean by Govinden et al. (2021). Using this value and the predicted
 185 $\overline{CAT}(\rho)$, we predicted the monthly values of $P_a(\rho)$ in each 5° cells in 2020, for each floating objects categories (DFAD,
 186 FOB, LOG). Because the calculation of the m ratio reduced greatly the study area, we first predicted \overline{CAT} and P_a values
 187 based on the density of DFADs (ρ_{DFAD}). However, to determine the impact of DFADs on the predicted associative
 188 behavior, we compared the predicted values of \overline{CAT} and P_a obtained with ρ_{FOB} and ρ_{LOG} . This comparison allows
 189 to determine the impact of the DFADs induced habitat modification on tuna availability to fishers.

190 3 | RESULTS

191 3.1 | Simulated Continuous Absence Time trends

192 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
 193 1.88 to 10.85 days respectively. Shorter values were obtained for higher densities (Figure 1 & Table 2). R was always
 194 above 1, meaning that the majority of CATs were performed between two different FADs (\overline{CAT}_{diff}). It varied from
 195 2.82, for the lowest density ($\rho = 1.00 \times 10^{-4} \text{ km}^{-2}$), with \overline{CAT}_{return} representing 26.18 % of the number of \overline{CAT} ,
 196 to 87.11 for the highest density ($\rho = 4.44 \times 10^{-3} \text{ km}^{-2}$), with \overline{CAT}_{return} representing 1.13 % of the total number of
 197 simulated \overline{CAT} . Hence, when ρ decreases, tuna tend to return to the departure FAD more often. Consequently, \overline{CAT}
 198 values were shorter than \overline{CAT}_{diff} for lower densities, due to the higher proportion of \overline{CAT}_{return} , but were almost
 199 exclusively driven by \overline{CAT}_{diff} for high densities (Figure 1 & Table 2). Obtained parameters of the models fitting

200 $\overline{CAT}_{diff}(\rho)$, $\overline{CAT}_{return}(\rho)$ and $R(\rho)$ are presented in Table 3

201 3.2 | Operational buoy densities

202 Buoy densities obtained from the IOTC data, considered as DFAD densities (ρ_{DFAD}) are presented in Figure 2. The
 203 maximum observed density in a 1° cell was $\rho = 8.39 \times 10^{-3} \text{ km}^{-2}$, in August, which corresponds to 84 operational
 204 buoys in a $100 \text{ km} \times 100 \text{ km}$ square and a mean distance to the nearest neighbor (in a regular square lattice) of 10.9
 205 km. After averaging the densities on a 5° grid, highest observed density was $\rho = 2.8 \times 10^{-3} \text{ km}^{-2}$, corresponding
 206 to 28 operational buoys in a $100 \text{ km} \times 100 \text{ km}$ square. Mean density over the whole area was $\bar{\rho} = 3.45 \times 10^{-4}$
 207 km^{-2} , corresponding to 3.45 buoys per $100 \text{ km} \times 100 \text{ km}$ square. Areas with highest buoys densities were different
 208 according to the month, moving from the West to the East of the Seychelles from January to April. Highest buoys
 209 densities could then be observed in the Arabian Sea, from May to July. In September and forward, highest densities
 210 were observed around the Seychelles and East of the Somalian EEZ. The obtained maps showed a high number of
 211 buoys around the Maldives in May and December, suggesting a high number of buoys drifting towards the Eastern
 212 IO (Figure 2E&L).

213 3.3 | Predictions of Continuous Absence Time and Percentage of time associated

214 Predicted $\overline{CAT}(\rho_{DFAD})$ values in 5° cells are presented in Figure 3 (see Supplementary Materials 3 for predictions
 215 of $\overline{CAT}_{diff}(\rho_{DFAD})$, $\overline{CAT}_{return}(\rho_{DFAD})$ and $R(\rho_{DFAD})$, and Supplementary Materials 4 for predictions on ρ_{FOB}
 216 and ρ_{LOG}). Minimum $\overline{CAT}(\rho_{DFAD})$ predicted value was 1.06 days in February 2020. The area with shortest pre-
 217 dicted $\overline{CAT}(\rho_{DFAD})$ was spatially conserved through time: low values were observed from the North of the Mozam-
 218 bique Channel to the Arabian Sea, and from the African coast to 65°E . However, for each month, a peak of short
 219 $\overline{CAT}(\rho_{DFAD})$ was observed and moved from the South of the area to the North, from January to June (Figure 3A-
 220 F), and back to the South of the area from June to December (Figure 3F-L). The percentage of time spent by tuna
 221 associated with a DFAD ($P_a(\rho_{DFAD})$) displayed similar spatial patterns as $\overline{CAT}(\rho_{DFAD})$ (Figure 4).

222 3.4 | Impact of DFAD on tuna availability

223 The comparison of the predictions obtained with FOB and LOG densities is presented in Figure 5 and Table 4. The
 224 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
 225 ($\overline{\rho_{LOG}} = 2.00 \times 10^{-4} \text{ km}^{-2}$), resulting in much shorter \overline{CAT} with mean values, averaged over cells and months, of
 226 5 and 46 days predicted from FOB and LOG densities respectively. The strong density increase induced by DFADs
 227 also resulted in a increase of the predicted proportion of time tuna spent associated (P_a), with $\overline{P_a}(\rho_{FOB}) = 68 \%$ and
 228 $\overline{P_a}(\rho_{LOG}) = 20 \%$.

229 4 | DISCUSSION

230 Human induced habitat modifications can impact species behavior and ultimately their fitness (Swearer et al., 2021).
 231 Continuous Absence Times (CATs) and Continuous Residence Times (CRTs) are two behavioral metrics allowing to
 232 assess the impact of the modification of one habitat component – the density of floating objects – on pelagic species.
 233 Several studies measured CATs (Robert et al., 2012, 2013; Rodriguez-Tress et al., 2017) or CRTs (Robert et al., 2013,

234 2012; Govinden et al., 2013) in arrays of anchored FADs. CRTs were also measured at drifting FADs (Matsumoto
235 et al., 2016; Tolotti et al., 2020; Govinden et al., 2021). However, experimentally measuring CATs in an array of FADs
236 requires the equipment of the whole array with acoustic receivers. When these FADs are drifting, finding, equipping
237 and recovering them is difficult and has never been achieved. This study is, to our knowledge, the first to give estimates
238 of CATs of yellowfin tuna (YFT) in arrays of DFADs. These estimates show a strong influence of fisheries induced
239 habitat modifications on tuna associative behavior in the Western Indian Ocean (WIO). By modifying tuna habitat,
240 purse seine fisheries increase the percentage of time tuna spend associated (P_a), which has a direct influence on YFT
241 availability to fishers, which can impact fishing mortality and tuna's fitness.

242 Numerous factors could affect the obtained \overline{CAT} and P_a predictions. Predictions were made based on operational
243 buoys densities deployed on FOBs (IOTC, 2021b), which is a proxy of the actual DFAD density in the ocean. Among
244 equipped FOBs, those for which the buoy was turned-off are not present in the data. Moreover, if most Contracting
245 Parties provided their buoys' positions to the IOTC, some countries did not share their data (IOTC, 2021b), so densities
246 could be underestimated.

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

257 The model used for the predictions was fitted on passive acoustic tagging data from YFT of fork length 70 ± 10 cm,
258 tagged in an array of AFADs (Pérez et al., 2022). At DFADs, two main size classes of YFT are found: individuals around
259 50 cm and individuals around 120 cm (IOTC, 2022, p. 52). Fitting the model on bigger individuals (70 cm instead of
260 50 cm) should not change drastically the obtained parameters, but could change slightly individual speed (fitted value
261 $v = 0.7 \text{ m.s}^{-1}$ in Pérez et al., 2022). Also, as tuna orient themselves towards FADs several kilometers away (4 to
262 17 km, Girard et al., 2004), it was suggested that they could detect FADs using acoustic stimuli (Pérez et al., 2022).
263 Although FAD design has not been identified to influence the attractiveness of FADs (Fréon and Dagorn, 2000), there
264 might be a difference in detectability between anchored, which are composed of a bigger structure containing a metal
265 chain, and drifting FADs. Hence, both the type of FAD (anchored or drifting) and tuna size class could change some
266 model parameters, such as the orientation radius (R_0 , fitted value of 5 km) and swimming speed (v , fitted value of 0.7
267 m.s^{-1}). To account for these uncertainties, we also performed predictions using other parameters ($v = 0.5 \text{ m.s}^{-1}$ and
268 $R_0 = 2$ km). The obtained \overline{CAT} were longer, resulting in smaller P_a values (see Supplementary Materials 5). However,
269 it should be noted that changing the parameters do not change the observed trend: the habitat modification induced
270 by DFAD increases YFT catchability, whatever the parameter set considered.

271 Since 2016, in the IO, more than 80 % of purse seine catch on tropical tuna was made on floating objects, reaching
272 a maximum of almost 95 % in 2018 (see Figure 5 in IOTC, 2022). YFT caught by industrial purse seine vessels on FOBs
273 in the IO has steadily increased since 2008 and represented around 22 % of the total YFT catch, by all gear types, in
274 2021 (ISSF, 2023; IOTC, 2022). The predicted P_a were very high in the Western IO, with a mean of 68 % (calculated
275 on all FOBs), mainly due to DFAD introduction (mean prediction without DFADs of 20 %). As the habitat modification
276 induced by DFADs strongly increases the percentage of their time YFT spend associated with floating objects, it

277 increases their vulnerability to purse seine sets. In the IO, the YFT stock is currently overfished (*i.e.* the biomass is
278 below the biomass reference point corresponding to the maximum sustainable yield) and subject to overfishing (*i.e.*
279 the fishing mortality is above the reference point corresponding to the maximum sustainable yield; IOTC, 2021a).
280 The Indian Ocean Tuna Commission (IOTC) imposes limits on the number of operational buoys (buoys which transmit
281 DFAD position and other information to fishers) at 250 per vessel at any one time (IOTC, 2023). The present results
282 show that limiting the number of floating objects and of operational buoys directly affects tuna catchability by purse
283 seine vessels. Therefore, if the yellowfin tuna stock is to remain overfished, efforts should be made to further limit
284 the number of floating objects in the ocean, through limits on operational buoy numbers and on DFAD deployments.

285 In addition to the increase of fishing availability to fishers, the observed increase of the percentage of time as-
286 sociated (P_a) could also have indirect impacts (*i.e.* not linked with fishing mortality) on YFT and other associated
287 species. One of the main hypothesis to explain the association of tuna with floating objects is the *meeting-point* hy-
288 pothesis (Fréon and Dagorn, 2000). Under this hypothesis, tuna would use FOBs as meeting-points to form larger
289 schools. Fish schools can be viewed as an evolutionary trade-off: increasing school size would increase protection,
290 mate choice and information, but would also increase inter-individual competition and the propensity to be detected
291 by predators (Maury, 2017). The increase of FOB density, inducing an increase of P_a , could result in a disruption of
292 schooling behavior and provoke the dispersion of individuals among FOBs. Capello et al. (2022) developed a model
293 to study school behavior in a heterogeneous habitat, using tuna and FADs as a case study. Using several social sce-
294 narios, they demonstrated that social behavior has an influence on how the fraction of schools which are associated
295 varies with FAD density. Considering social behavior could help further understanding tuna behavior and its link with
296 fitness. Echosounder buoys data allow to determine tuna aggregation dynamics (Baidai et al., 2020), and could be
297 used to assess the impact of DFADs on tuna association dynamics, taking their social behavior into account.

298 Also, Marsac et al. (2000) suggested that DFADs could act as ecological traps on tropical tuna. This hypothesis was
299 based on another behavioral hypothesis, the *indicator-log*, which suggests that tuna associate with FOBs to select rich
300 areas. Natural FOBs would be located mainly in rich areas because they originate from rivers and accumulate in rich
301 frontal zones (Castro et al., 2002). By modifying the distribution of FOBs, DFADs could attract or retain individual tuna
302 in areas that are detrimental to them and ultimately impact their fitness. Recent evidence, using a condition indicator
303 as a proxy for tuna's fitness, tend to suggest that DFADs did not act as an ecological trap in the WIO. However,
304 DFAD impact could have been counteracted by other environmental effects or could have act on other biological
305 processes than condition (Dupaix et al., 2023). Tuna associative behavior can also be influenced by climate change,
306 which modifies prey abundance and physical characteristics of the environment (Arrizabalaga et al., 2015; Druon et al.,
307 2017). Nevertheless, the increase of FOB density increases P_a and FOB array connectivity (increase of R , *i.e.* of the
308 proportion of CAT_{diff}). Added to previous evidence suggesting that an increase of FAD density induces an increase
309 of tuna residence times around FADs (Pérez et al., 2020), it suggests that DFAD use could retain tuna in some areas.
310 Whether these areas can be considered poor for tropical tuna and the impact this retention can have on tuna's fitness
311 – through other biological parameters than condition – still needs to be investigated further.

312 5 | CONCLUSION AND PERSPECTIVES

313 Human activities impact species habitat, potentially impacting their fitness (IPBES, 2019). Several studies assessed
314 the direct impact of habitat modifications on species fitness, or on fitness proxies (Mullu, 2016; IPBES, 2018). These
315 impacts on fitness can also be behaviorally mediated, *e.g.* through ecological traps (Swearer et al., 2021; Gilroy and
316 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.

Authors' Contribution

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

Data Availability Statement

Simulations were performed with the model FAT albaCoRaW v1.4. (doi: 10.5281/zenodo.5834056). All the scripts used in the study can be found on GitHub (https://github.com/adupaix/Quantif_impact_FAD). IOTC instrumented buoy data can be downloaded from the following URL: <https://iotc.org/WGFAD/02/Data/04-BU>. French observers data are available upon request to the IRD's Ob7 (URL: <https://www.ob7.ird.fr/en/pages/datacall.html>).

Declaration of Competing Interest

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

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352 **Figures**

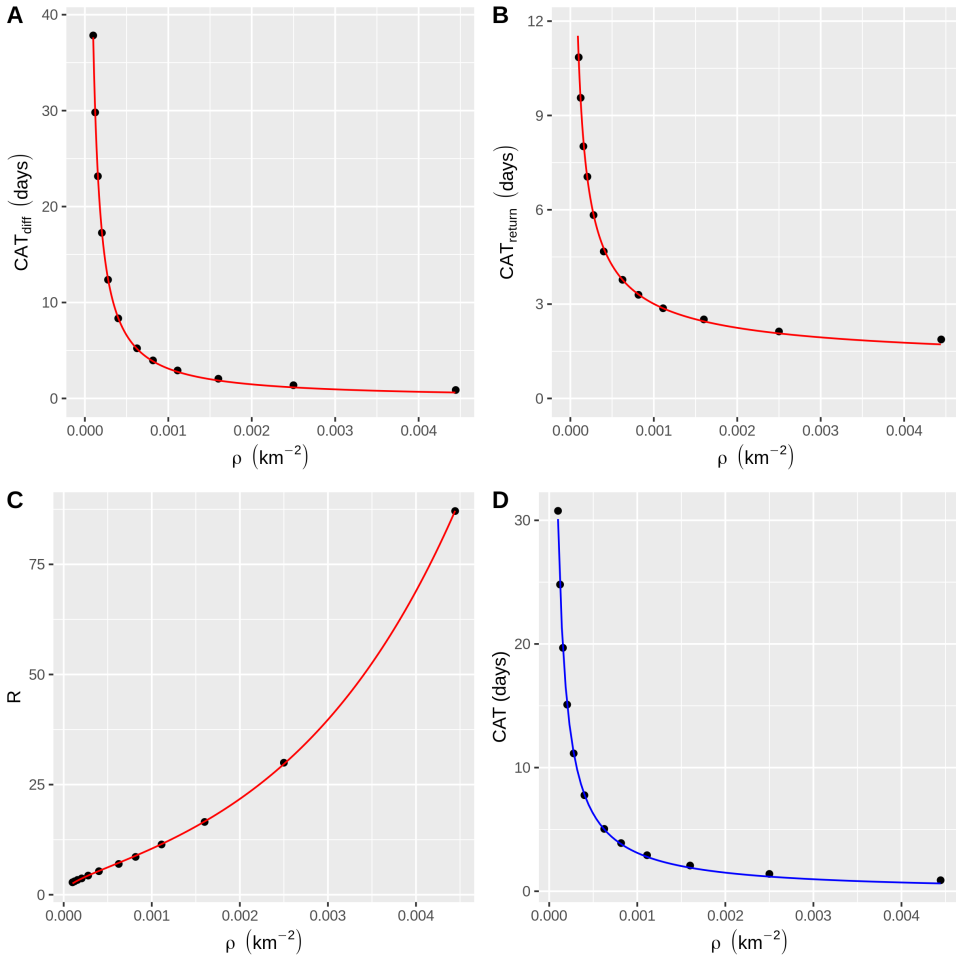


FIGURE 1 Continuous Absence Times (CATs) trends as a function of FAD density, obtained from the simulations. (A) \overline{CAT}_{diff} fitted according to Equation 1. (B) \overline{CAT}_{return} fitted according to Equation 2. (C) Ratio between the number of CAT_{diff} and the number of CAT_{return} (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). ρ : FAD density.

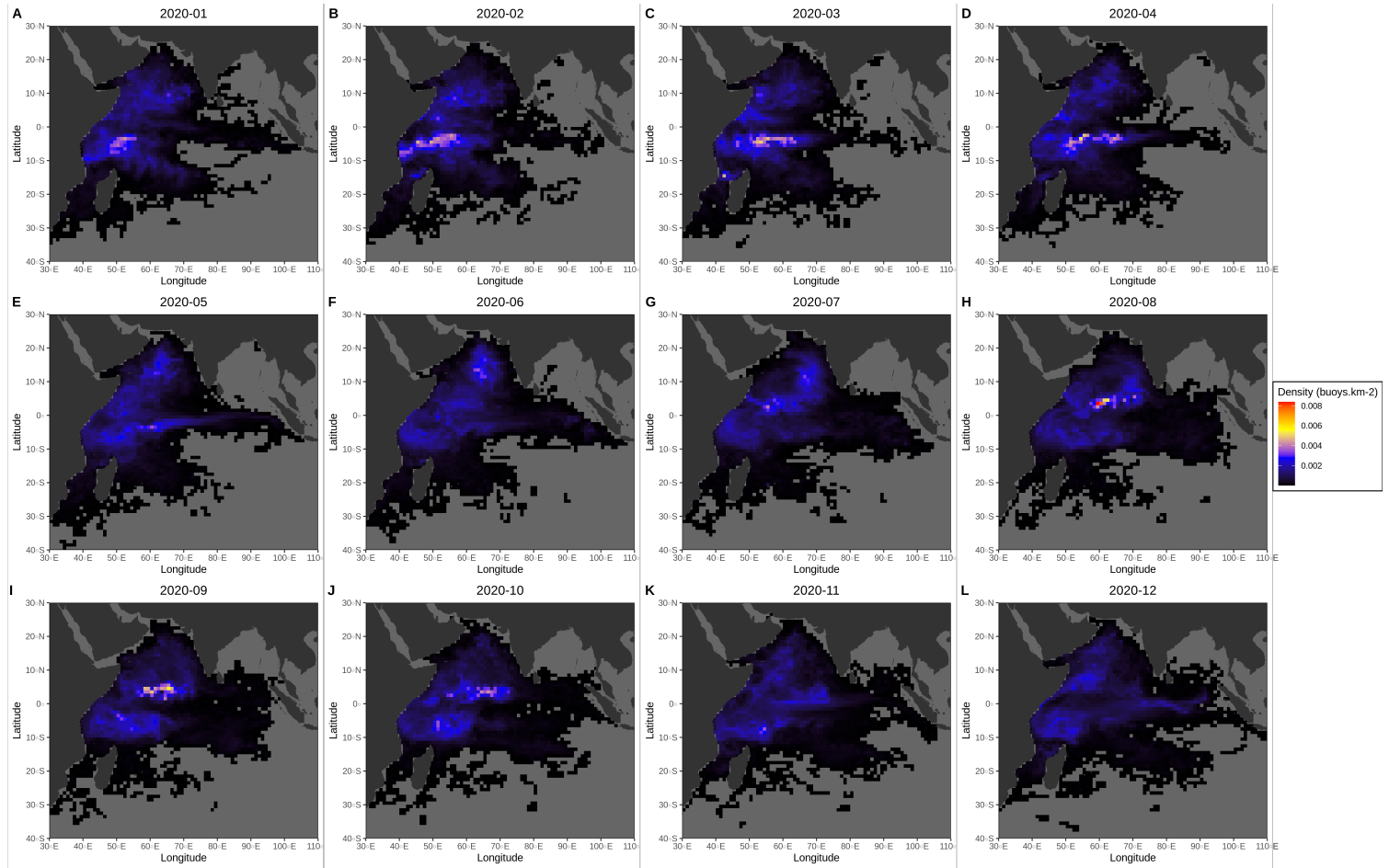


FIGURE 2 Mean monthly buoy densities per 1° cells in the western Indian Ocean calculated from IOTC (2021b), expressed in buoys.km^{-2} . Buoy densities are considered as DFAD densities, see details in section 2.3

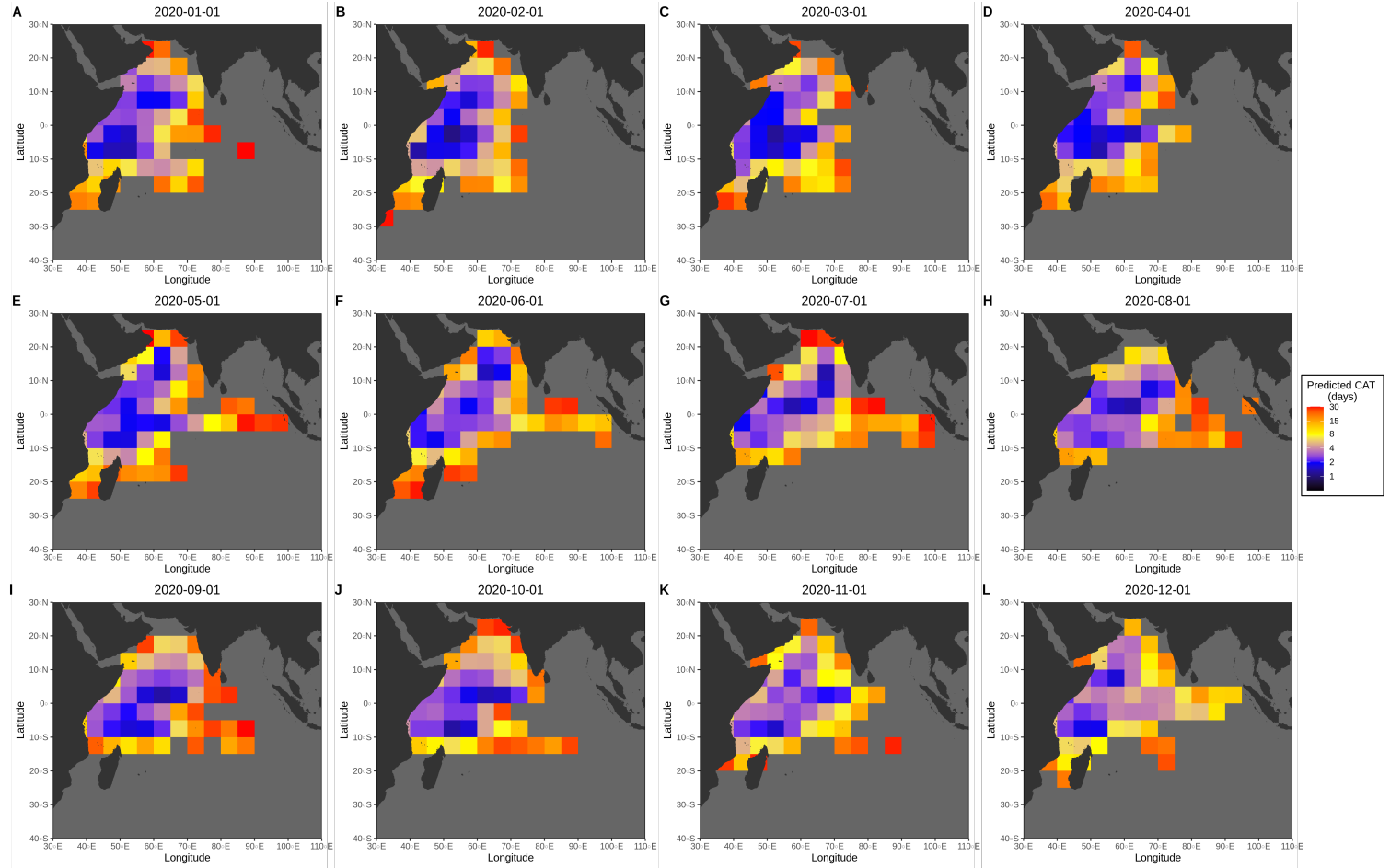


FIGURE 3 Mean monthly Continuous Absence Times of individual yellowfin tunas predicted using DFAD density ($\overline{CAT}(\rho_{DFAD})$), in days) per 5° cells in the western Indian Ocean in 2020. The color scale is log transformed. $\overline{CAT}(\rho_{DFAD})$ longer than 30 days were not represented.

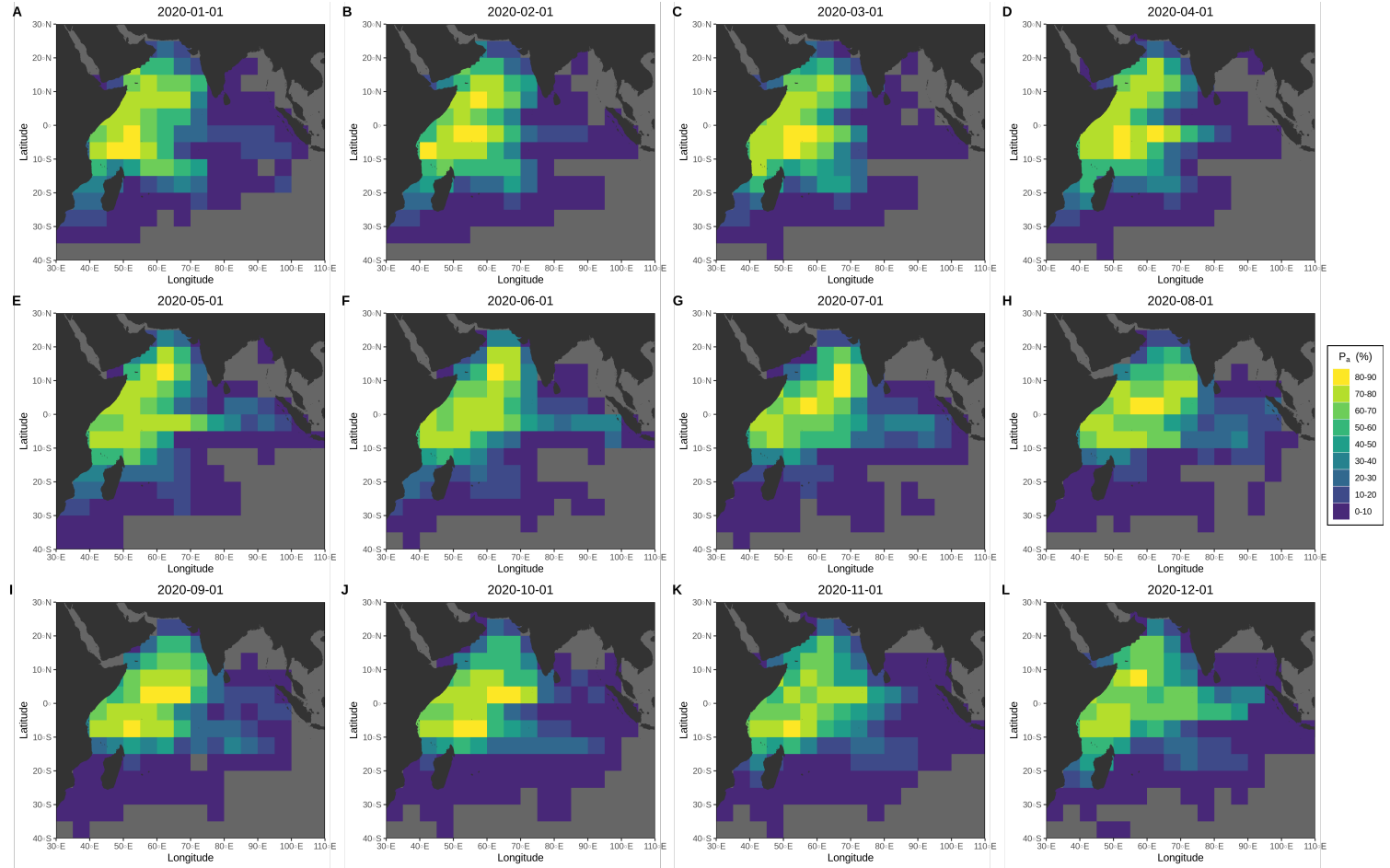


FIGURE 4 Mean monthly percentage of time spent associated by individual yellowfin tunas predicted using DFAD density ($P_a(p_{DFAD})$) per 5° cells in the Western Indian Ocean in 2020.

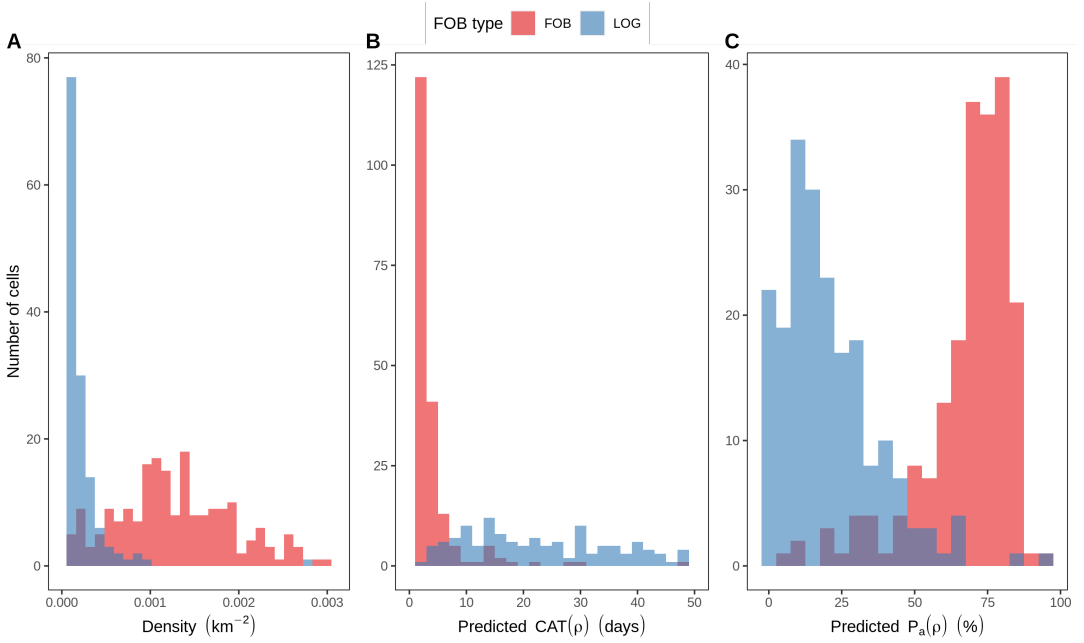


FIGURE 5 Comparison between predictions performed on the density of all FOBs (ρ_{FOB} , in red) and LOGs only (ρ_{LOG} , in blue) density. Monthly mean density of floating object (A), predicted mean monthly Continuous Absence Time ($\overline{CAT}(\rho)$) (B) and percentage of time spent associated ($P_a(\rho)$)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

353 **Tables**

TABLE 1 Parameters used in the simulations, performed using Dupaix et al. (2022) and based on the calibration in Pérez et al. (2022). Δt : time-step; v : speed; R_0 : orientation radius; c : sinuosity coefficient; D : mean inter-FAD distance.

Δt	v	R_0	c	D
100 s	0.7 m.s ⁻¹	5 km	0.99	15, 20, 25, 30, 35, 40, 50, 60, 70, 80, 90, 100 km

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

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

TABLE 3 Summary of the fitted parameter values.

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

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

FOB type	ρ (km^{-2})		CAT (days)		P_a (%)	
	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}

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