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

Abstract

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 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.

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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 (Fischer and 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 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, 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, Capello, et al., 2021)

and their impact on species behavior, condition and survival (Hallier and Gaertner, 2008). Detailed movement data can be more cumbersome to acquire for marine than for terrestrial species (Hussey et al., 2015). Currently, it is possible to record 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 has been used to demonstrate the impacts of habitat modifications on the behavior of tropical tuna (Pérez, Dagorn, 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 obsesus*) tunas. The main fishing gear targeting tropical tunas is purse seining, which made 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 and 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 floating objects, 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, e.g. 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 to free-swimming schools (Dagorn, Holland, Restrepo, et al., 2013). Furthermore, the massive deployment of DFADs can also have indirect impacts, affecting the behavior and natural mortality of tuna (Hallier and Gaertner, 2008; Marsac et al., 2000). Pérez, Dagorn, et al., 2020 demonstrated, on arrays of anchored fish aggregating devices (AFADs), that a decrease of 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 to a given AFAD and less time between two associations. If an increase of DFAD density also increases the percentage of time tunas spend associated, it would strongly impact their catchability and therefore their mortality.

Several acoustic tagging studies characterized the behavior of tuna around AFADs, both through active (Girard et al., 2004) and passive tagging (Pérez, Dagorn, et al., 2020; Robert, Dagorn, JL Deneubourg, 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, Holland, and Itano, 2007; Govinden, Capello, 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 of 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 yellowfin tuna in the Western Indian Ocean. In the Indian Ocean (IO), both the bigeye and yellowfin tuna stocks are currently overfished and subject to overfishing (IOTC, 2022a,b,c). 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 floating objects having increased from around 60 % (mainly on natural floating objects) 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 and Gaertner, 2008; Marsac et al., 2000). Recent studies investigated habitat modi-

fications induced by the use of DFADs by industrial purse seine fleets in the Western IO (Dagorn, Bez, et al., 107
2013; Dupaix, Capello, et al., 2021). Using data from observers onboard tuna purse seine vessels from 2006 108
to 2018, Dupaix, Capello, et al., 2021 highlighted that DFADs multiplied the densities of FOBs by at least 2 and 109
represented more than 85 % of the overall FOBs. This study aims at quantifying how such habitat changes 110
have affected the behavior of tropical tuna and its availability to the fisheries. Since 2020, detailed informa- 111
tion on the total number of DFADs equipped with echosounder buoys has been made available to scientists 112
(IOTC, 2019) at a 1°/monthly scale. This new data allows for the first time to have quantitative estimates of 113
the density of DFADs in the Indian Ocean. Furthermore, a recent study (Pérez, Dupaix, et al., 2022) developed 114
an individual-based model fitting the movement behavior of yellowfin tuna in an array of AFADs measured 115
from acoustic telemetry data. In the following, we used this newly available dataset, combined with observers' 116
data and the outputs of the individual-based model from (Pérez, Dupaix, et al., 2022), to predict the time that 117
yellowfin tuna spend between two DFAD associations in the Western IO. Using these predictions, we assess 118
the impact of the modification of the pelagic habitat – FOB density increase due to the introduction of DFADs 119
– on the percentage of their time YFT spend associated. This percentage of time spent associated has a direct 120
impact on tuna availability to fishers and can thus affect their mortality due to fishing. Furthermore, we discuss 121
how this habitat modifications can have other potential indirect impacts on tuna's fitness. 122

Material and Methods 123

In order to compare tuna behavior in modified habitats (due to the introduction of DFADs) relative to an 124
unmodified environment (where only FOBs other than DFADs, either of natural or anthropic origin, noted 125
LOGs, are present), we estimated the percentage of time tuna spend associated with floating objects (P_a) 126
in FOB arrays characterized by different FOB densities. Simulations were run to model tuna movements in 127
arrays of FOBs, using an individual-based model calibrated on passive acoustic data recorded for yellowfin 128
tuna (Pérez, Dupaix, et al., 2022). These simulations allowed estimating a theoretical relation between the 129
time spent by tuna between two consecutive FOB associations (named CAT, Continuous Absence Time) and 130
the density of FOBs. Observers data, combined with data on the density of DFADs at a 1°/monthly scale, were 131
used to estimate the total density of FOBs (DFADs and LOGs) and the density of FOBs in the environment 132
not modified by DFAD use (LOGs only). Predictions of CATs obtained in the pristine and modified habitat, 133
combined with acoustic telemetry data informing on the amount of time spent by tuna associated with FOBs 134

(named CRT, Continuous Residence Time) 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, et al., 2023), an individual-based model simulating tuna trajectories in an array of FOBs based on a Correlated Random Walk (Pérez, Dupaix, 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 towards 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 strait to a simple random walk. These parameters were fitted on passive acoustic tagging data of 70 cm long YFT in arrays of AFADs, in Pérez, Dupaix, et al. (2022) (Table 1). We considered twelve 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, Dagorn, et al. (2020), we define a Continuous Absence Time (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) CAT_{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, *i.e.* 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, Robert, et al., 2015; Pérez, Dupaix, et al., 2022). Hence, each time a CAT_{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 CAT_{return} or after 1,500 days of simulation. The obtained Continuous Absence

Time (CAT) was saved. A total of 100,000 CATs were simulated per FOB density, totaling 1,200,000 simulated CATs.

CAT trends for different FOB densities

For each FOB density, the mean Continuous Absence Time (noted $\overline{\text{CAT}}$) 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, Dagorn, 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 follow:

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

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

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

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

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

where $R = \frac{A}{B}$, 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:

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

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.

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 organisation managing tuna fishing in the Indian Ocean), was used as a proxy for DFAD data (IOTC, 2021b). This dataset contains the monthly mean of the number of

operational buoys, i.e., the echosounder buoys whose GPS position is remotely transmitted to one or several fishing vessels, for each $1^\circ \times 1^\circ$ cell of the Indian Ocean. 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 floating object (DFAD or LOG) are recorded. Using the methodology developed in Dupaix, Capello, et al., 2021 applied to 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 DFAD observations respectively) per 5° cell which was used to calculate the density of FOBs ($\rho_{FOB} = (1 + m)\rho_{DFAD}$) and the density of LOGs ($\rho_{LOG} = m\rho_{DFAD}$). Because observers 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 Continuous Absence Time and Percentage of time associated in the IO

Using the density values calculated above and the fitted models' coefficients, 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, Robert, et al., 2015). Pérez, Dagorn, 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, Capello, 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 (ρ_{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 ρ_{FOB} and ρ_{LOG} . This comparison allows to determine the impact of the DFADs induced habitat modification on tuna availability to fishers.

Results

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 ρ 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

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 $\rho = 8.39 \times 10^{-3} \text{ km}^{-2}$, in August, which corresponds to 84 operational 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 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 $100 \text{ km} \times 100 \text{ km}$ square. Mean density over the whole area was $\bar{\rho} = 3.45 \times 10^{-4} \text{ km}^{-2}$, corresponding to 3.45 buoys per $100 \text{ km} \times 100 \text{ km}$ 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 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 towards the Eastern IO during this period (Figure 3E&L).

Predicted $\overline{\text{CAT}(\rho_{\text{DFAD}})}$ values in 5° cells are presented in Figure 4 (see Appendix S3 for predictions of $\overline{\text{CAT}_{\text{diff}}}$, $\overline{\text{CAT}_{\text{return}}}$ and R , and Appendix S4 for predictions on ρ_{FOB} and ρ_{LOG}). Minimum $\overline{\text{CAT}(\rho_{\text{DFAD}})}$ predicted value was 1.06 days in February 2020. The area with shortest predicted $\overline{\text{CAT}(\rho_{\text{DFAD}})}$ 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 $\overline{\text{CAT}(\rho_{\text{DFAD}})}$ 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 ($P_a(\rho_{\text{DFAD}})$) displayed similar spatial patterns as $\overline{\text{CAT}(\rho_{\text{DFAD}})}$ (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 Table 4. The mean density of all types of FOBs ($\overline{\rho_{\text{FOB}}} = 1.32 \times 10^{-3} \text{ km}^{-2}$) was 6.6 times higher than the mean LOG density ($\overline{\rho_{\text{LOG}}} = 2.00 \times 10^{-4} \text{ km}^{-2}$), resulting in much shorter $\overline{\text{CAT}}$ 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 a increase of the predicted proportion of time tuna spent associated (P_a), from $\overline{P_a(\rho_{\text{LOG}})} = 20 \%$ for the environment without DFADs, to $\overline{P_a(\rho_{\text{FOB}})} = 68 \%$ 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). Continuous Absence Times (CATs) and Continuous Residence Times (CRTs) are two behavioral metrics allowing to assess the impact of the modification of one habitat component – the density of floating objects – on pelagic species. Several studies measured CATs (Robert, Dagorn, JL Deneubourg, et al., 2012; Robert, Dagorn, Lopez, et al., 2013; Rodriguez-Tress et al., 2017) or CRTs (Govinden, Jauhary, et al., 2013; Robert, Dagorn, JL Deneubourg, et al., 2012; Robert, Dagorn, Lopez, et al., 2013) in arrays of anchored FADs. CRTs were also measured at drifting FADs (Govinden, Capello, 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. 261
In the Indian ocean, this data deficiency could only be overcome recently, with the provision of the number 262
of operational buoys by the IOTC secretariat. This study is, to our knowledge, the first to give estimates of 263
CATs of yellowfin tuna (YFT) in arrays of DFADs. These estimates show a strong influence of fisheries-induced 264
habitat modifications on tuna associative behavior in the Western Indian Ocean (WIO). By modifying tuna 265
habitat, purse seine fisheries increase the percentage of time tuna spend associated (P_a), which has a direct 266
influence on YFT availability to fishers, which can impact fishing mortality and tuna's fitness. 267

Numerous factors could affect the obtained \overline{CAT} and P_a predictions. Predictions were made based on 268
operational buoys densities deployed on FOBs (IOTC, 2021b), which is a proxy of the actual DFAD density in 269
the ocean. Among the instrumented FOBs, those for which the buoy was remotely deactivated (and thus could 270
not transmit its position anymore), are not present in the data. Moreover, if most Contracting Parties provided 271
their buoys' positions to the IOTC, some countries did not share their data (IOTC, 2021b), so densities could 272
be underestimated. 273

The other datasets used for the predictions are French observers data and measurement of CRTs. The 274
use of French observers data restricted the study area, highlighting the need to better share this data among 275
countries, as it is done for instrumented buoys, and to increase observers coverage. Only the mean CRT value 276
for the WIO was used in our study (measured in Govinden, Capello, et al., 2021) and we considered CRT as 277
constant. This approximation could influence the predictions, as it was demonstrated that CRTs also depend 278
on FAD density, even if to a lesser extent than CATs (Pérez, Dagorn, et al., 2020). CRT measurements on DFADs 279
also showed a variability between oceans as well as strong inter-individual variations (Govinden, Capello, et 280
al., 2021; Govinden, Jauhary, et al., 2013; Matsumoto et al., 2016; Tolotti et al., 2020). Further measurements 281
of CRTs at DFADs and some modelling approach would then be needed to take this variability into account. 282
However, Pérez, Dagorn, et al. (2020) found that, as AFAD density increases, CRT also increases, suggesting 283
that the increase in catchability observed in this study should be conserved or even intensified. 284

The model used for the predictions was fitted on passive acoustic tagging data from YFT of fork length 285
 70 ± 10 cm, tagged in an array of AFADs (Pérez, Dupaix, et al., 2022). At DFADs, two main size classes of YFT 286
are found: individuals around 50 cm and individuals around 120 cm (IOTC, 2022e, p. 52). Fitting the model 287
on bigger individuals (70 cm instead of 50 cm) should not change drastically the obtained parameters, but 288
could change slightly individual speed (fitted value $v = 0.7 \text{ m.s}^{-1}$ in Pérez, Dupaix, et al., 2022). Also, as tuna 289

orient themselves towards FADs several kilometers away (4 to 17 km, Girard et al., 2004), it was suggested that they could detect FADs using acoustic stimuli (Pérez, Dupaix, et al., 2022). Although FAD design has not been identified to influence the attractiveness of FADs (Fréon and Dagorn, 2000), there might be a difference in detectability between anchored, which are composed of a bigger structure containing a metal chain, and drifting FADs. Hence, 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 $0.7 \text{ m}\cdot\text{s}^{-1}$). To account for these uncertainties, we also performed predictions using other parameters ($v = 0.5 \text{ m}\cdot\text{s}^{-1}$ and $R_0 = 2 \text{ km}$). The obtained $\overline{\text{CAT}}$ were longer, resulting in smaller P_a values (see Appendix S5). However, it should be noted that changing the parameters do not change the observed trend: the habitat modification induced by increasing DFADs increases YFT catchability, whatever the parameter set considered.

Since 2016, in the IO, more than 80 % of purse seine catch on tropical tuna was made on floating objects, reaching a maximum of almost 95 % in 2018 (see Figure 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 floating objects, 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 Indian Ocean Tuna Commission (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 floating objects and of operational buoys directly affects tuna catchability by purse seine vessels. Therefore, if the yellowfin tuna stock is to remain overfished, efforts should be made to further limit the number of floating objects in the ocean, through limits on operational buoy numbers and on DFAD deployments.

In addition to the increase of fishing availability to fishers, the observed increase of 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 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 319
would increase protection, mate choice and information, but would also increase inter-individual competi- 320
tion and the propensity to be detected by predators (Maury, 2017). The increase of FOB density, inducing an 321
increase of P_a , could result in a disruption of schooling behavior and provoke the dispersion of individuals 322
among FOBs. Capello, Rault, et al. (2022) developed a model to study school behavior in a heterogeneous 323
habitat, using tuna and FADs as a case study. Using several social scenarios, they demonstrated that social 324
behavior has an influence on how the fraction of schools which are associated varies with FAD density. Con- 325
sidering social behavior could help further understanding tuna behavior and its link with fitness. Echosounder 326
buoys data allow to determine tuna aggregation dynamics (Baidai et al., 2020), and could be used to assess 327
the impact of DFADs on tuna association dynamics, taking their social behavior into account. 328

Also, Marsac et al., 2000 suggested that DFADs could act as ecological traps on tropical tuna. This hypothesis 329
was based on another behavioral hypothesis, the *indicator-log*, which suggests that tuna associate with FOBs 330
to select rich areas. Natural FOBs would be located mainly in rich areas because they originate from rivers 331
and accumulate in rich frontal zones (Castro et al., 2002). By modifying the distribution of FOBs, DFADs could 332
attract or retain individual tuna in areas that are detrimental to them and ultimately impact their fitness. 333
Recent evidence, using a condition indicator as a proxy for tuna's fitness, tend to suggest that DFADs did not act 334
as an ecological trap in the WIO. However, DFAD impact could have been counteracted by other environmental 335
effects or could have act on other biological processes than condition (Dupaix, Dagorn, Duparc, et al., 2023). 336
Tuna associative behavior can also be influenced by climate change, which modifies prey abundance and 337
physical characteristics of the environment (Arrizabalaga et al., 2015; Druon et al., 2017). Our study shows 338
that the increase of FOB density impacts P_a and FOB array connectivity (increase of R , *i.e.* of the proportion 339
of CAT_{diff}). Added to previous evidence suggesting that an increase of FAD density induces an increase of tuna 340
residence times around FADs (Pérez, Dagorn, et al., 2020), it suggests that DFAD use could retain tuna in some 341
areas. Whether these areas can be considered poor for tropical tuna and the impact this retention can have 342
on tuna's fitness – through other biological parameters than condition – still needs to be investigated further. 343

Conclusion and perspectives 344

Human activities impact species habitat, potentially impacting their fitness (IPBES, 2019). Several studies 345
assessed the direct impact of habitat modifications on species fitness, or on fitness proxies (IPBES, 2018; Mulu, 346

2016). These impacts on fitness can also be behaviorally mediated, *e.g.* through ecological traps (Dwernychuk and Boag, 1972; Gilroy and Sutherland, 2007; Marsac et al., 2000; Swearer et al., 2021). 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 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 could also be used as a predictive tool for assessing the potential benefits of management measures, *e.g.* DFAD number reductions, on the behavior and fishing mortality of tropical tuna.

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Conflict of Interests statement

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.

Authorship statement

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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.

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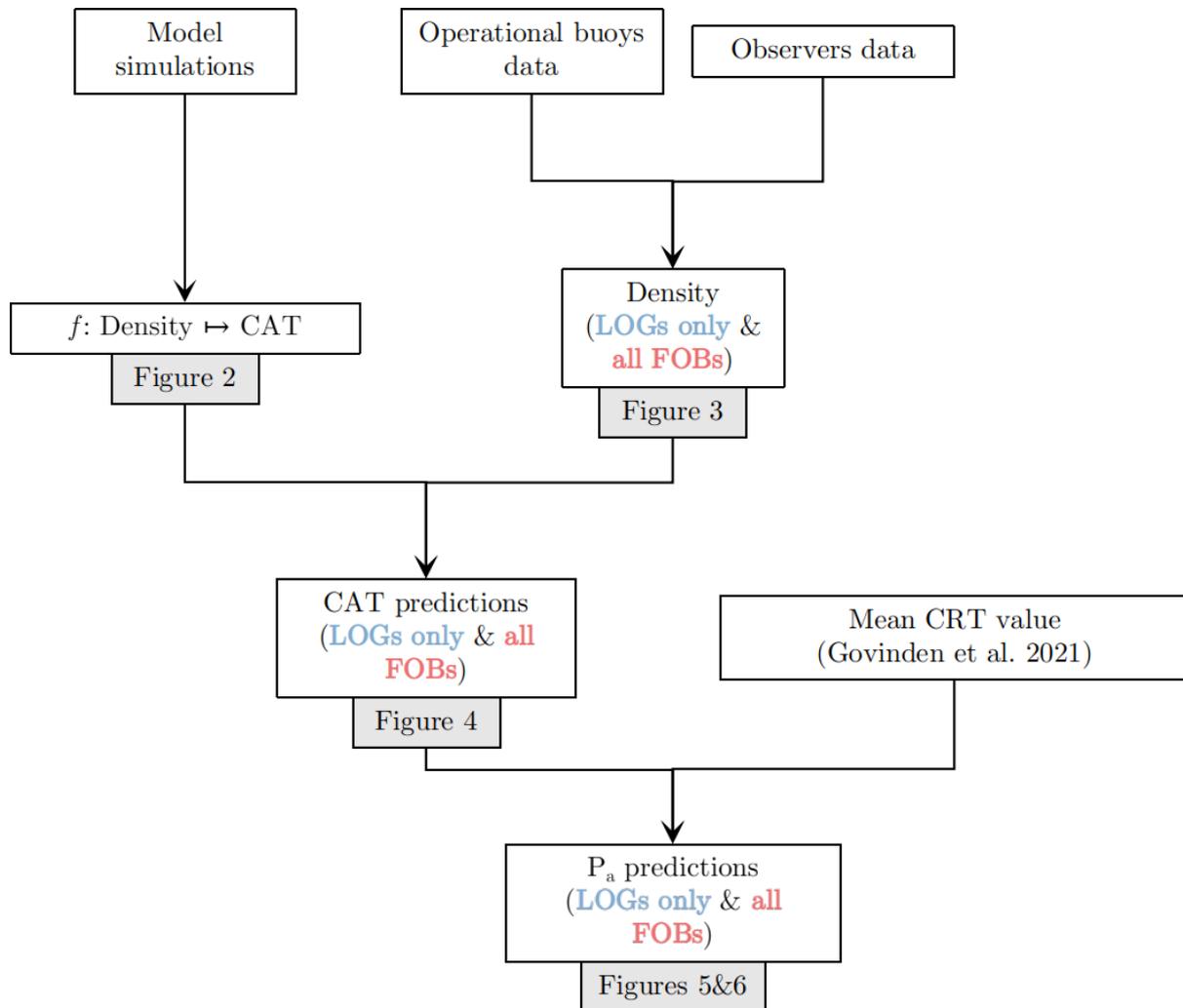


Figure 1. Schematic representation of the methodology used in the study, which allowed the calculation of P_a both for the densities of all floating objects (all FOBs, habitat modified by DFADs) and for floating objects other than DFADs (LOGs only, habitat not modified). Figure number illustrating different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

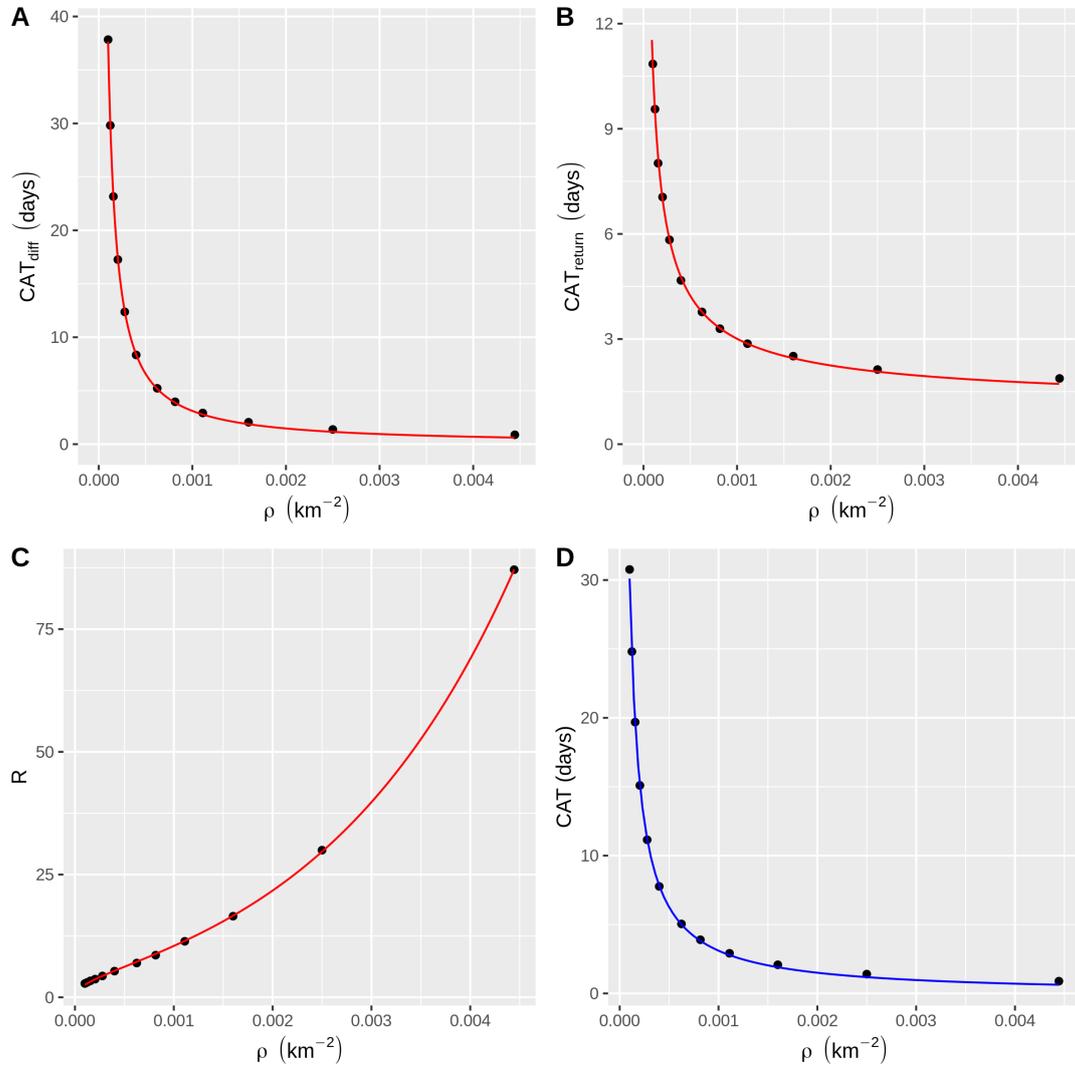


Figure 2. Continuous Absence Times (CATs) trends as a function of FOB density, obtained from the simulations. (A) \overline{CAT}_{diff} fitted according to Equation 1. (B) \overline{CAT}_{return} fitted according to Equation 2. (C) Ratio between the number of CAT_{diff} and the number of CAT_{return}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

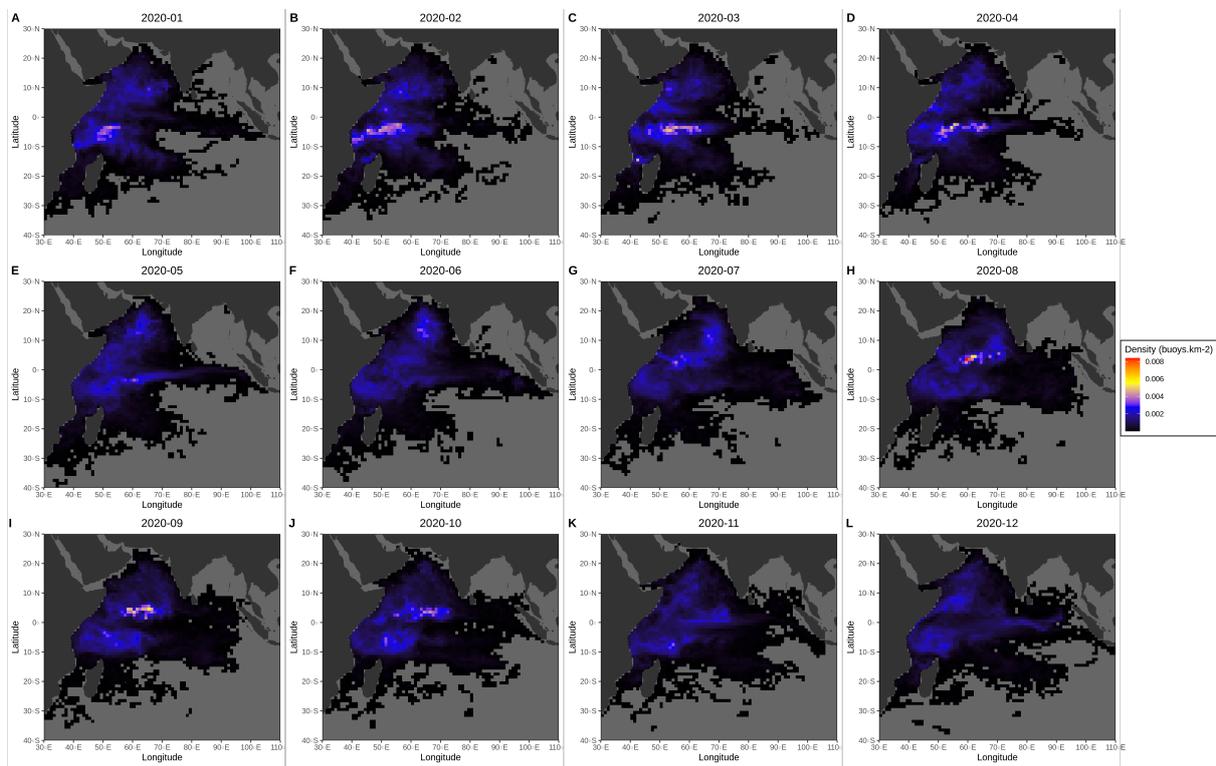


Figure 3. Mean monthly buoy densities per 1° cells in the western Indian Ocean calculated from IOTC, [2021b](#), expressed in buoys.km^{-2} . Buoy densities are considered as DFAD densities.

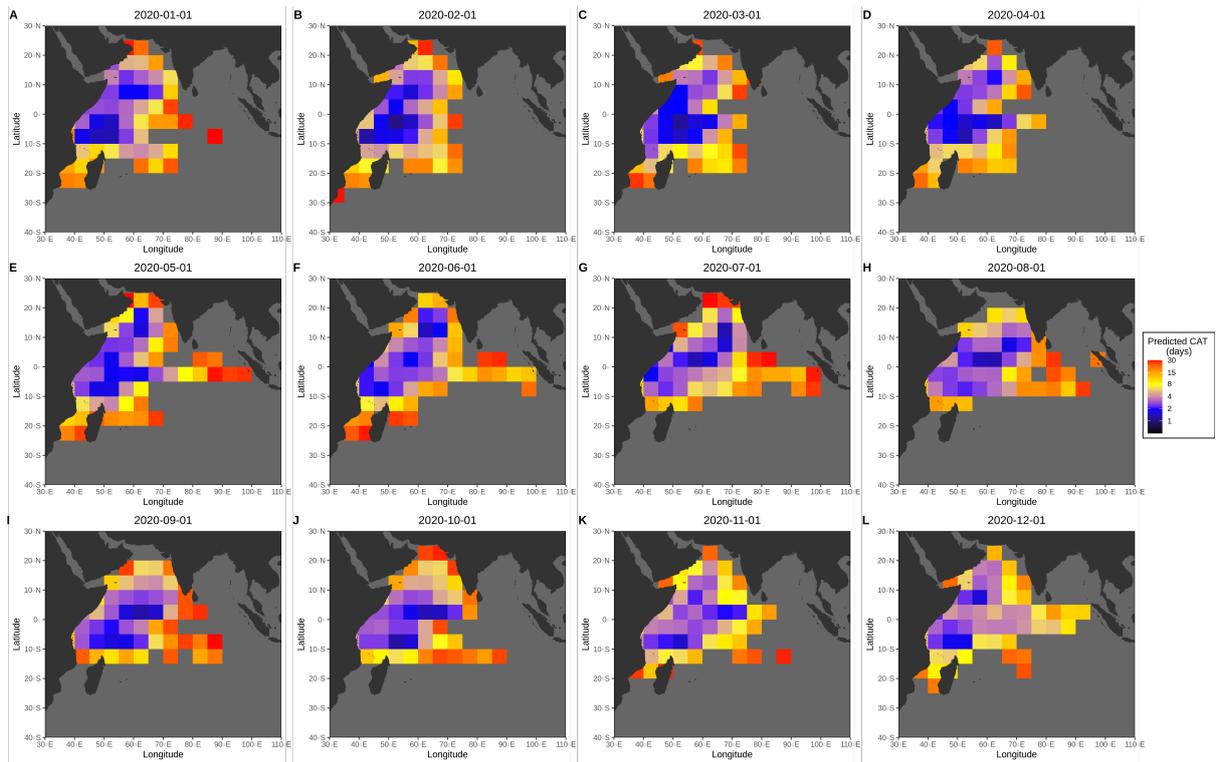


Figure 4. Mean monthly Continuous Absence Times of individual yellowfin tunas predicted using DFAD density ($\overline{\text{CAT}}(\rho_{\text{DFAD}})$, in days) per 5° cells in the western Indian Ocean in 2020. The color scale is log transformed. $\overline{\text{CAT}}(\rho_{\text{DFAD}})$ longer than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

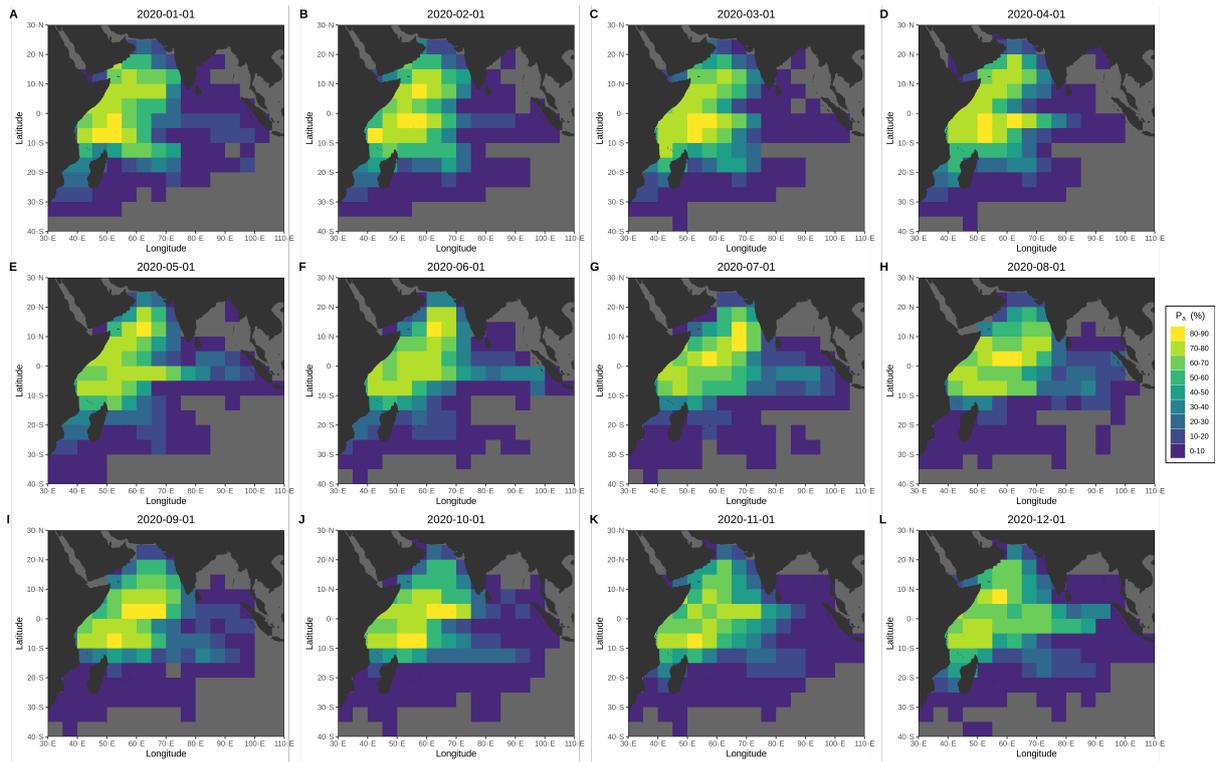


Figure 5. Mean monthly percentage of time spent associated by individual yellowfin tunas predicted using DFAD density ($P_a(\rho_{DFAD})$) per 5° cells in the Western Indian Ocean in 2020.

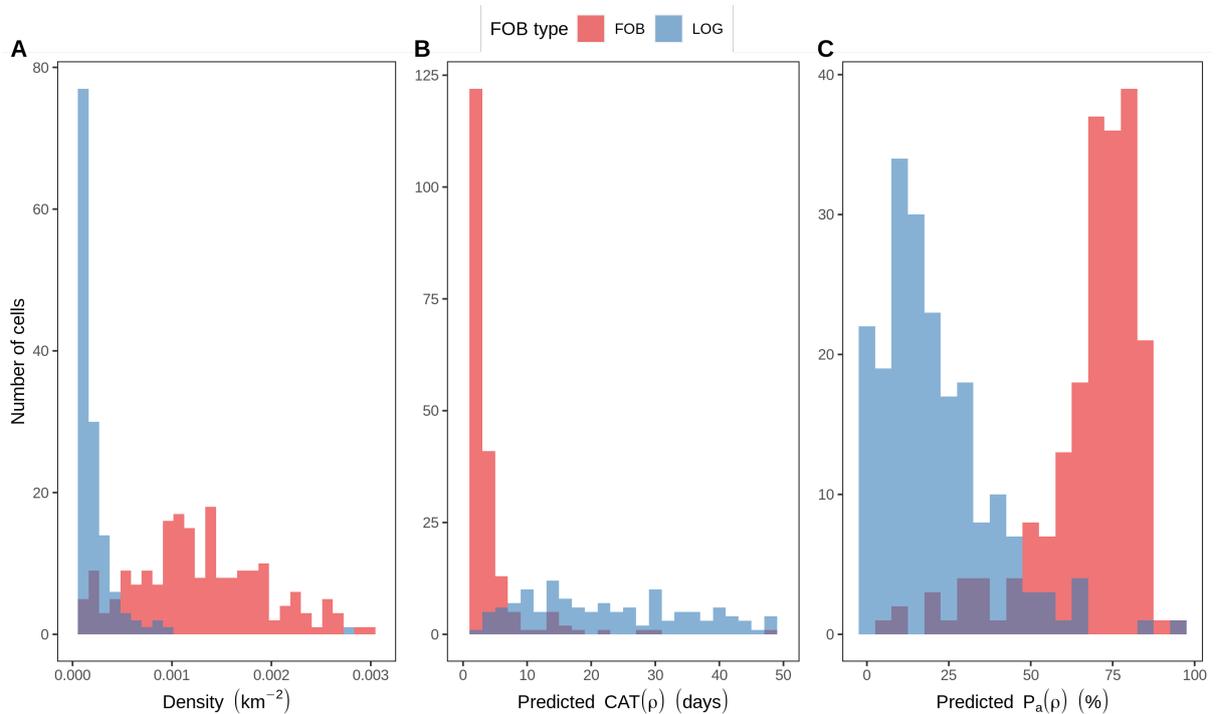


Figure 6. Comparison between predictions performed on the density of all FOBs (ρ_{FOB} , in red) and LOGs only (ρ_{LOG} , in blue) density. Monthly mean density of floating object (A), predicted mean monthly Continuous Absence Time ($\overline{CAT}(\rho)$) (B) and percentage of time spent associated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

Tables

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Table 1. Parameters used in the simulations, performed using Dupaix, Pérez, et al., 2023 and based on the calibration in Pérez, Dupaix, et al., 2022. Δt : time-step; v : speed; R_0 : orientation radius; c : sinuosity coefficient; D : mean inter-FOB 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 FOB density. D : mean inter-FOB distance in a regular square lattice (in km); ρ : FOB density (in km^{-2}); $\overline{\text{CAT}}$: mean Continuous Absence Time (in days); $\overline{\text{CAT}}_{\text{diff}}$: mean Continuous Absence Time when the movement occurred between two different FOBs (in days); $\overline{\text{CAT}}_{\text{return}}$: mean Continuous Absence Time when the individual returned to the departure FOB (in days); R : ratio between the number of CAT_{diff} and the number of $\text{CAT}_{\text{return}}$.

D	ρ	$\overline{\text{CAT}}$	$\overline{\text{CAT}}_{\text{diff}}$	$\overline{\text{CAT}}_{\text{return}}$	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
$\overline{\text{CAT}}_{\text{diff}}$	$a_d \times \rho^{-b_d}$	$a_d = 1.8 \times 10^{-3}$	1.10×10^{-4}
		$b_d = 1.08$	1.40×10^{-2}
$\overline{\text{CAT}}_{\text{return}}$	$1 + a_r \times \rho^{-b_r}$	$a_r = 1.7 \times 10^{-2}$	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}