# 1 No evidence from long-term analysis of yellowfin

2 tuna condition that Drifting Fish Aggregating

3

## Devices act as ecological traps

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#### 10 Abstract

11 Human-induced habitat modifications can severely impact the biology 12 and behavior of wild species. Drifting Fish Aggregating Devices (DFADs), used by industrial purse seine tropical tuna fisheries, significantly 13 14 increased the number of floating objects found in the open ocean, to which tropical tuna associate. This habitat change raised concerns over 15 the risk of modifying the behavior and altering the biology of tuna and 16 17 other associated species (the so-called ecological trap hypothesis). 18 Relying on a time-series from 1987 to 2019 of more than 25,000 length-19 weight samples collected in the western Indian Ocean, we reject the 20 hypothesis that the body condition (Le Cren's relative condition factor K<sub>n</sub>) 21 of yellowfin tuna (Thunnus albacares) decreased concurrently with the 22 increased number of DFADs. This result suggests the absence of negative 23 long-term impacts of DFADs on the condition of tuna. As other factors 24 may have counteracted possible negative effects of DFADs, we 25 recommend a long-term monitoring of habitat, biological and behavioral parameters of tunas to detect any critical change. 26

Keywords: Indicator log, relative condition factor, *Thunnus albacares*,
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#### 29 1. Introduction

30 Natural floating objects (designated as NLOGs), such as logs or 31 branches, are a component of the oceanic habitat of tropical tunas, which 32 associate with them. Although the reasons for this associative behavior 33 are poorly understood, fishers traditionally used this behavior to find and 34 capture associated fish (Fréon & Dagorn 2000). In the early 1980s, 35 industrial tropical tuna purse-seine fleets began to commonly attach 36 buoys on NLOGs and to construct and deploy their own man-made 37 floating objects (FOBs), called drifting Fish Aggregating Devices (DFADs) 38 (Dagorn et al. 2013b). In the Indian Ocean (IO), deployment and use of 39 DFADs began in the 1990s and has steadily increased since then, such 40 that from 2012 to 2018, DFADs were demonstrated to represent more 41 than 85% of the total floating objects in the western IO (Dupaix et al. 42 2021).

Soon after their wide-scale use began, it was hypothesized that DFADs 43 may act as "ecological traps" for tropical tunas (see Figure 1) (Marsac et 44 45 al. 2000, Hallier & Gaertner 2008). An ecological trap occurs when individuals exhibit a higher or equal preference for a poor-quality habitat 4647 (i.e. associated with a lower fitness) over another habitat, being misled 48 by cues that no longer correlate to habitat guality due to anthropogenic 49 changes (Robertson & Hutto 2006, Gilroy & Sutherland 2007). This 50 decorrelation between habitat quality and habitat selection cues 51 ultimately leads to a reduction in the fitness of individuals (Gilroy &

52 Sutherland 2007, Swearer et al. 2021). The hypothesis of DFADs acting 53 as ecological traps, as it was first formulated, relies on one of the 54 hypotheses formulated to explain tuna associative behavior: the 55 indicator-log hypothesis (Fréon & Dagorn 2000), which posits that 56 natural floating objects are located in productive areas because they 57 originate from rivers and tend to accumulate in rich frontal areas (Hall 1992, Hallier & Gaertner 2008). Thus tropical tunas and other associated 58 species would select natural floating objects as a cue for good-guality 59 habitat. The massive deployment of DFADs would modify the density and 60 61 spatial distribution of floating objects, with potentially large numbers of 62 artificial objects occurring in areas that are not optimal for tunas, 63 creating the risk of an ecological trap. Hence, there is an urgent need to 64 assess the likelihood of DFADs acting as ecological traps.

65 A proxy to assess tuna fitness is physiological condition. Tunas caught at DFADs may be considered to be in poorer condition than those caught in 66 67 free-swimming schools (FSC) which infers a negative biological 68 consequence from the association with DFAD (Marsac et al. 2000, Hallier 69 & Gaertner 2008). Robert et al. (2014) also found a difference between 70 the condition of associated and non-associated tunas, but in an area (the 71 Mozambique Channel, Western Indian Ocean) that was rich in natural 72 floating objects and thus only marginally modified by the addition of 73 DFADs. Hence, it is possible that the association with a floating object 74 results in a poorer condition, but that the evolutionary advantage of the 75 associative behavior would not be related to short-term trophic benefits.

Tunas could recover faster after associating because they are in a more productive area or in larger schools (Fréon & Dagorn 2000). This led us to consider the ecological trap hypothesis over a long period of time, to examine the condition of tuna before and after the use of DFADs.

The objective of this study was to test the hypothesis that the body condition of yellowfin tuna has decreased since the wide-spread use of DFADs began in the Indian Ocean, in the 1990s. We used length and weight measurements to calculate Le Cren's relative condition factor (K<sub>n</sub>), and investigated the temporal evolution of the body condition of yellowfin tuna (*Thunnus albacares*) from 1987 to 2019 in the Indian Ocean.

### 87 2. Material and Methods

#### 88 2.1. Biological data

A total of 25,914 yellowfin tuna (Thunnus albacares) were sampled from 89 90 1987 to 2019 in the Indian Ocean Tuna canning factory (IOT) in Victoria, 91 Seychelles (Guillou et al. 2021). All the sampled fish were caught by 92 purse seine vessels in the western IO (details of the sample sizes are 93 provided in Tables S1 & S2 in Supplement 1). The total weight (W) of the 94 individuals and their fork length (FL) were measured. For each sampled 95 tuna, the fishing vessel and the fishing trip were recorded, but not the 96 specific fishing set from which it was caught. As a consequence, all 97 fishing sets from a trip are a potential catch location for every samples

98 (see statistical analyses section for details on how the uncertainty on location and date was managed). The type of school (either FOB-99 100 associated or FSC) was not considered in the main analysis because it 101 was unknown for a large proportion of the sampled fish (around 75 %, 102 Table S1 in Supplement 1). The year (Y) and guarter (Q) of the catch of 103 each tuna were estimated from the middle of the interval covered by the 104 fishing trip dates. The guarters were defined to be synchronous with the general movement of the fleet, fishing seasons and areas (Dupaix et al. 105 106 2021): Q1, December to February; Q2, March to May; Q3, June to 107 August; and Q4, September to November. The total range of FL was 108 divided in three intervals, defining size classes (SC): small (<75cm), 109 medium (75-120 cm) and large (>120 cm).

#### 110 2.2. Relative condition factor

111 To calculate the theoretical weight of individuals ( $W_{th}$ ), FL and W 112 measures for the whole period were used to estimate the parameters of 113 the length-weight allometric relationship, using the theoretical power-114 law equation:  $W_{th} = a FL^b$ . Details on the fit of this power-law are 115 presented in Supplement 2. Secondly, for each individual fish, the 116 relative condition factor (Le Cren 1951) was calculated as follows:

$$117 \quad K_n(i) = \frac{W(i)}{W_{th}(i)}$$

118 where  $W_{th}(i)$  is the theoretical weight of individual *i* calculated from 119 length-weight allometric relationship coefficients according to FL(i), and 120 W(i) is the measured total weight. By definition,  $K_n(i)$  measures the 121 deviation of an individual from the weight of a mean individual of the 122 same length. The mean relative condition factor calculated for a group of 123 individuals (either per year, per size class or per quarter) is denoted as 124 K<sub>n</sub>.

125 2.3. Statistical analysis

In order to determine if  $K_n$  decreased with the concurrent increase in 126 127 DFAD numbers during the study period, a Generalized Additive Model 128 (GAM) was performed considering  $K_n(i)$  as the dependent variable, with a 129 Gaussian link function to account for explanatory variables. Explanatory 130 variables were chosen to assess the effect of the fishing year (Y), season 131 (fishing quarter, Q), size of the individuals (size class, SC), and fishing 132 location (longitude, Lon; latitude, Lat, see details below). Longitude and 133 latitude were included in the model as a smoothed term, and other 134 variables were considered as factors. No precise time-series of DFAD 135 number exist in the IO over 1987-2018, but the deployment of DFADs 136 increased during that period, hence we considered the fishing year as a 137 proxy for DFAD density.

Because  $K_n$  is the ratio of two correlated random variables (Pearson's correlation coefficient between W and W<sub>th</sub>, Pearson's  $\rho = 0.99$ ), it did not follow a normal distribution and displayed overdispersion. For this reason, and because it did not change the interpretation of the GAM results, we transformed the  $K_n(i)$  using a Geary-Hinkley transformation

143 before performing the GAM (Geary 1930, see Supplement 3). The 144 Generalized Additive Model was performed on the transformed  $K_n(i)$ , 145 noted T( $K_n(i)$ ). Complementary analyses showed that size class and its 146 interaction with other explanatory variables and fishing mode (Figures 147 S1 & S2 in Supplement 1 respectively) did not impact the main results of 148 the study. These results remained consistent when considering only fish 149 from FOB-associated schools (Figure S3 in Supplement 1).

As the exact geographic coordinates were not available for most of the 150 151 sampled fish, a bootstrap process was applied: a dataset was generated 152 by sampling one set of coordinates from all the fishing sets of the trip for 153 each individual and a GAM was then performed. This operation was 154 repeated 1,000 times and for every model built, we selected the most 155 parsimonious explanatory variables based on the Akaike information 156 criterion (AIC), using a stepwise selection procedure and a threshold of 2. The iterated GAM coefficients of the explanatory variables considered 157 158 as factors (Y, Q and SC) were averaged over the bootstrap replica and 159 their standard deviation was calculated.

160 All analyses were performed using R software v.4.0.3 (R Core Team161 2020), and the scripts used for the study are available on GitHub (https://

- 162 github.com/adupaix/Historical\_YFT\_condition
- 163 https://doi.org/10.5281/zenodo.6123417).

#### 164 **3. Results**

### 165 **3.1. Mean relative condition factors (K**<sub>n</sub>**)**

166 The mean relative condition factor value ( $K_n$ ) was 1.01 ± 0.088 and mean 167 annual  $K_n$  values varied between 0.93 ± 0.064 (in 1987) and 1.07 ± 0.079 168 (in 2012). The relative condition factor displayed annual variations, with 169 low  $K_n$  values in 1987-1990 and around 2005-2007, and the highest  $K_n$ 170 values observed around 2012 (Figure 2A). The mean annual K<sub>n</sub> displayed 171 similar variations per size class as when all the sampled fish were 172 considered together (Figure 2A). No clear trend in K<sub>n</sub> variations were 173 observed.

### 174 **3.2.** Yearly variations of $K_n$

175 The most parsimonious model, selected using the AIC, included year (Y), 176 quarter (Q), size class (SC) and the smoothed term for longitude and latitude. The selected model explained 29.2% of the deviance. The 177 178 residuals displayed no spatial autocorrelation and their distribution was 179 not significantly different from a Gaussian distribution (Figure S4 in 180 Supplement 1). The GAM performed on the transformed relative 181 condition factor,  $T(K_n(i))$ , showed that strongest  $T(K_n(i))$  variations were 182 significantly correlated with fishing year (Figure 2B; Figures S5 & S6 in 183 Supplement 1). The annual GAM coefficients displayed a non-monotonous 184 trend which was non-decreasing in time, with 1987 being the year with 185 the lowest coefficient ( $-0.475 \pm 0.007$ ) while 2012 was the year with the highest coefficient (0.673  $\pm$  0.006; Figure 2B). The observed patterns were similar to those displayed when considering only the mean annual K<sub>n</sub> (Figures 2A&B).

## 189 **4. Discussion**

190 Ecological traps in animals are likely to become more common as human-191 induced environmental changes increase. These traps can increase 192 extinction risk locally and regionally, impacting population persistence, and present an important challenge for the management of animal 193 194 populations (Battin 2004, Hale et al. 2015, Swearer et al. 2021). The 195 vellowfin tuna population in the Indian Ocean (IO) is currently overfished 196 and subject to overfishing (IOTC 2021). It is therefore critical to assess 197 not only direct impacts of DFADs - through fisheries - but also potential 198 indirect impacts which could also negatively impact tuna populations 199 (Hallier & Gaertner 2008). The hypothesis that DFADs could act as 200 ecological traps was developed more than 20 years ago (Marsac et al. 201 2000) and implies that the introduction of DFADs would have negatively impacted the condition of tunas, following roughly three decades of 202 203 DFAD deployment (Figure 1). Under the hypothesis that DFAD number 204 increased during the study period, we expected a decrease of yellowfin 205 tuna condition throughout the years. The relative condition factor  $(K_n(i))$ values obtained here did not display any clear temporal trend over the 206 207 study period (Figure 2), which does not support the tested hypothesis.

Hence, the present study suggests that under the conditions encountered by yellowfin tuna in the IO during the last three decades, the addition of DFADs to the pelagic environment has not led to the creation of an ecological trap for this species.

212 Data used in this study were not uniformly distributed across size classes and years (Figure S7 in Supplement 1), and tunas from both fishing 213 modes (FOB-associated and FSC) were considered, which could influence 214 the results (Hallier & Gaertner 2008, Robert et al. 2014). However, no 215216 decreasing trend of condition factor was observed concurrently with 217 increasing DFAD use when performing a GAM on data of each size class 218 independently (Figure S1 in Supplement 1). Also, even though the mean 219  $K_n$  of FOB-associated tuna was lower than that of FSC tuna, no 220 decreasing trend of condition was observed when considering the fishing 221 mode (Figures S2 & S3 in Supplement 1).

222 For a habitat modification to lead to an ecological trap, individuals selecting the modified habitat have to experience a reduction in their 223 fitness, namely their reproductive success, which includes survival and 224225 reproduction. Physiological condition can be considered a good proxy of 226 individual fitness as it can impact both individual's survival and 227 reproduction. The morphometric index used here,  $K_n$ , was the only 228 condition indicator for which a long time-series was available. Other 229 indices can be used to assess physiological condition, such as Bio-230 Impedance Analysis (BIA; Robert et al. 2014), organosomatic indices or

231 measurements of biomarkers (Lloret et al. 2014). Sardenne et al. (2016) 232 alerted on the fact that different morphometric indices could show 233 inconsistency and are not always the best proxies of tropical tuna 234 condition. All of these stresses the need to develop experimental 235 approaches, to measure a set of condition indices on captive tuna under 236 various feeding/fasting conditions, in order to better understand the 237 validity of these indices. DFADs could also impact the biology of tuna in a 238 variety of complex ways, impacting other biological processes leading to 239 a reduction of fitness, like growth rate (Hallier & Gaertner 2008), or 240 reproduction (Zudaire et al. 2014). This highlights the need to monitor 241 tuna physiological condition more thoroughly, by performing regular data 242 collection of biological data.

243 Many studies demonstrated that tuna associated with DFADs tend to be 244in lower condition than FSC tunas (Marsac et al. 2000, Hallier & Gaertner 2008, Jaguemet et al. 2011). However, Robert et al. (2014) 245246 observed a similar result when comparing tuna associated with NLOGs 247 and FSC tuna, and concluded that the associative behavior could be the 248consequence and not the cause of a lower physiological condition. These 249 studies testing the ecological trap hypothesis were performed on short 250 temporal scales of up to a few months and therefore were not able to 251 conclude on a potential long-term impact of DFADs. Other long-term 252 phenomena could also impact the physiology of tropical tuna. For 253 example, since the 1980s, climate change has already impacted tuna 254habitat, by inducing changes in sea surface temperature or oxygen

255 concentration (Erauskin-Extramiana et al. 2019). Erauskin-Extramiana et 256 al. (2019) projected that yellowfin tuna will become more abundant 257 under a climate change scenario. Our study is the first performed on a 258 time-series long enough to allow assessing the potential long-term impact 259 of the increase of DFAD density on tuna condition. A decreasing trend of small tunas' condition was observed in the later years of the study 260 (Figure 2A), which was not correlated with the number of FOBs 261262 (Supplement 4). Hence, to investigate possible long-term physiological 263 changes due to climate change and/or any environmental disturbances, 264 continuous effort to develop routine biological sampling and routinely 265 monitor fish condition should be established to develop long time-series 266 of biological indices. This effort should be combined with the collection of 267 data on habitat modifications induced by DFADs.

268 Tuna associative behavior plays a key role in determining the potential indirect impacts of DFADs on tuna condition. This associative behavior 269 270 could also depend on several other factors than DFAD density, such as 271 environmental conditions or social behavior (Capello et al. 2022). It could 272 also be impacted by their physiological condition, for example one could 273 hypothesize that tuna would associate with a DFAD until its condition 274lowers a given threshold value that would cause it to leave. Several 275 hypotheses – *e.g.* the association being a consequence of a low condition 276and individuals departing from FOBs beyond a given condition threshold 277 - could explain the absence of a long-term impact of DFADs on tuna 278condition, which need to be further explored.

279 By demonstrating the absence of any decreasing trend in yellowfin tuna condition during the past three decades in the Indian Ocean, 280 281 concurrently to the observed increasing DFAD density, this study rejects 282 the ecological trap hypothesis as it was originally formulated more than 283 20 years ago. To continue assessing the indirect impacts of DFADs on 284 tuna condition, experimental studies are needed, to determine the relevant temporal scales and indices to monitor these impacts. Finally, it 285 is necessary to establish long-term monitoring programs to track (i) 286 287 habitat changes (e.g. DFAD density), (ii) variations of tuna behavioral 288 features (e.g. association dynamics) and (iii), temporal variations of 289 biological indicators of fitness.

### 290 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.

## 294 Data availability statement

Data used in this study is available in Guillou et al. (2021) and were
collected through the Data Collection Framework (Reg 2017/1004 and
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298 A preprint version of the article is available at:

299 https://hal.archives-ouvertes.fr/hal-03690665

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## 314 Figures



315 Figure 1: Schematic representation of the ecological trap
316 hypothesis applied to Fish Aggregating Devices and tropical tuna.

317 FOB: Floating object of any kind; DFAD: Fish Aggregating Device; NLOG: 318 Natural floating object. Under this hypothesis, before DFAD introduction, when only NLOGs were present (1), floating objects were distributed in 319 productive areas (2), hence tunas, which associate with floating objects, 320 321 preferred high quality habitats (3). Since DFAD introduction (1'), the 322 distribution of floating objects has been modified and is no longer 323 correlated with habitat quality (2'). Hence, tunas, which still associate 324 with floating objects, do not select high guality habitat anymore (3'). As a 325 consequence of this habitat modification, the physiological condition of 326 tunas would have decreased since the 1990s (4). Preference is defined 327 here as the likelihood of a resource being chosen if offered as an option 328 with other available options.



Α

330 Figure 2: No observed trend in yellowfin tuna condition: (A) Mean relative condition factor per year. The K<sub>n</sub> is represented for all 331 332 individuals (all, black circles), for small individuals (<75, red circles), 333 medium-size individuals (75-120, blue triangles) and large individuals 334 (>120, green diamonds). Values are represented only when more than 50 335 individuals of the given class were measured. Error bars represent the standard error of the mean. (B) Coefficients of the fishing year in the 336 Generalized Additive Model. Each coefficient represents the mean 337 deviation of  $T(K_n)$  from the values for a year of reference (2019, 338 339 represented by a black dot). The shape of the points represents the 340 distribution of the values obtained with the bootstrap process. Numbers 341 in grey in the upper part of the panels represent the percentage of the models generated in the bootstrap for which a given category was 342 343 significantly different from the category of reference.