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## Drifting Fish Aggregating Devices (DFADs) as ecological traps: no evidence displayed by a long-term analysis of yellowfin tuna condition

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1 **Drifting Fish Aggregating Devices (DFADs) as**  
2 **ecological traps: no evidence displayed by a**  
3 **long-term analysis of yellowfin tuna condition**

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11 **Abstract**

12 Habitat modifications are one of the major human-induced rapid  
13 environmental changes. Drifting Fish Aggregating Devices (DFADs), used by  
14 industrial purse seine tropical tuna fisheries, significantly increased the  
15 number of floating objects with which tropical tuna associate, raising  
16 concerns over the risk of modifying the behavior and altering the biology

17 of these fish (the so-called ecological trap hypothesis). Relying on a  
18 time-series of more than 25,000 length-weight samples collected in the  
19 western Indian Ocean (1987–2019), we reject the hypothesis that the body  
20 condition (Le Cren's relative condition factor  $K_n$ ) of yellowfin tuna  
21 (*Thunnus albacares*) decreased concurrently with the increased number of  
22 DFADs. This result suggest the absence of negative long-term impacts of  
23 DFADs on the biology of tuna. However, as other factors may have  
24 counteracted possible negative effects of DFADs, we recommend a long-term  
25 monitoring of habitat, biological and behavioral parameters of tunas to  
26 detect any critical change.

## 27 **Keywords**

28 Indicator log, relative condition factor, *Thunnus albacares*, Indian Ocean,  
29 industrial tuna fisheries, floating objects

## 30 **Introduction**

31 Floating objects (FOBs), such as logs or branches, are natural components  
32 of the oceanic habitat of tropical tunas, which naturally associate with  
33 them. If the reasons for this associative behavior are poorly understood,  
34 fishers have traditionally used this behavior to find and capture  
35 associated fish (Freon and Dagorn 2000). In the early 1980s, industrial  
36 tropical tuna purse-seine fleets began to commonly deploy their own FOBs,

37 called drifting Fish Aggregating Devices (DFADs, Dagorn et al. 2013b). In  
38 the Indian Ocean (IO), deployment and use of DFADs began in the 1990s and  
39 has steadily increased since then, such that from 2012 to 2018, DFADs were  
40 demonstrated to represent more than 85% of the total floating objects in  
41 the western IO (Dupaix et al. 2021).

42 Soon after their wide-scale use began, it was hypothesized that DFADs may  
43 act as “ecological traps” for tropical tunas (see Figure 1) (Marsac et  
44 al. 2000; Hallier and Gaertner 2008). An ecological trap occurs when  
45 individuals select poor-quality habitats, being misled by cues that no  
46 longer correlate to habitat quality due to anthropogenic changes (Gilroy  
47 and Sutherland 2007). This decorelation between habitat quality and  
48 habitat selection cues ultimately leads to a reduction in the fitness of  
49 individuals (Gilroy and Sutherland 2007; Swearer et al. 2021). The  
50 hypothesis of DFADs acting as ecological traps, as it was first formulated,  
51 relies on the assumption that tropical tunas and other associated species  
52 originally used floating objects to select good-quality habitats (the  
53 *indicator-log* hypothesis, see Freon and Dagorn 2000). The massive  
54 deployment of DFADs would modify the density and spatial distribution of  
55 floating objects, with potentially large numbers of artificial objects  
56 occurring in areas that are not optimal for tunas, creating the risk of an  
57 ecological trap. Hence, there is an urgent need to assess the likelihood of  
58 DFADs acting as ecological traps.

59 A proxy which can be used to assess tuna fitness is physiological  
60 condition. Tunas caught at DFADs are considered to be in poorer condition  
61 than those caught in free-swimming schools which infers a negative  
62 biological consequence from the association with DFAD (Marsac et al. 2000;  
63 Hallier and Gaertner 2008). Robert et al. (2014) also found a difference  
64 between the condition of associated and non-associated tunas, but in an  
65 area (the Mozambique Channel, Indian Ocean) that was rich in natural  
66 floating objects and thus only marginally modified by the addition of  
67 DFADs. Hence, it is possible that the association with a floating object  
68 results in a poorer condition, but that the evolutionary advantage of the  
69 associative behavior would not be related to short-term trophic benefits.  
70 Tunas could recover faster after associating because they are in a more  
71 productive area or in larger schools. This led us to consider the  
72 ecological trap hypothesis over a long period of time, to examine the  
73 condition of tuna before and after the use of DFADs.

74 The objective of this study was to test the hypothesis that the body  
75 condition of yellowfin tuna has decreased since the wide-spread use of  
76 DFADs began in the Indian Ocean. We used length and weight measurements to  
77 calculate Le Cren's relative condition factor ( $K_n$ ), and investigated the  
78 temporal evolution of the body condition of yellowfin tuna (*Thunnus*  
79 *albacares*) from 1987 to 2019 in the Indian Ocean. We expected, that the

80 condition factor of yellowfin tuna would decrease during the study period  
81 (Figure 1).

## 82 **Material and Methods**

### 83 **Biological data**

84 A total of 25,914 yellowfin tuna (*Thunnus albacares*) were sampled from 1987  
85 to 2019 in the Indian Ocean Tuna canning factory (IOT) in Victoria,  
86 Seychelles (Guillou et al. 2021). All the sampled fish were caught by purse  
87 seine vessels in the western IO (details of the sample sizes are provided  
88 in Table S1). The total weight (W) of the individuals and their fork length  
89 (FL) were measured. For each sampled tuna, the fishing vessel and the  
90 fishing trip were recorded, but not the specific fishing set from which it  
91 was caught, which meant that the exact fishing date and location were  
92 unknown (see statistical analyses section for details on how the  
93 uncertainty on location and date was managed). The year (Y) and quarter (Q)  
94 of the catch of each tuna were estimated from the middle of the interval  
95 covered by the fishing trip dates. The quarters were defined to be  
96 synchronous with the general movement of the fleet, fishing seasons and  
97 areas (Dupaix et al. 2021): Q1, December to February; Q2, March to May; Q3,  
98 June to August; and Q4, September to November. The total range of FL was

99 divided in three intervals, defining size classes (SC): small (<75cm),  
100 medium (75–120cm) and large (>120cm).

## 101 **Relative condition factor**

102 To calculate the theoretical weight of individuals ( $W_{th}$ ), FL and W measures  
103 were used to estimate the parameters of the length–weight allometric  
104 relationship, using the theoretical power–law equation:  $W_{th} = a FL^b$ . Details  
105 on the fit of this power–law are presented in Supplementary Material 1.  
106 Secondly, for each individual fish, the relative condition factor (Le Cren  
107 1951) was calculated as follows:

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

108 where  $W_{th}(i)$  is the theoretical weight of individual  $i$  calculated from  
109 length–weight allometric relationship coefficients according to  $FL(i)$ , and  
110  $W(i)$  is the measured total weight. By definition,  $K_n(i)$  measures the  
111 deviation of an individual from the weight of a mean individual of the same  
112 length. For the remainder of the text, the relative condition factor of one  
113 individual is denoted as  $K_n(i)$ . The mean relative condition factor, denoted  
114  $K_n$ , calculated for a group of individuals is denoted as  $K_n$ .

## 115 **Statistical analysis**

116 In order to determine if  $K_n$  decreased with the concurrent increase in DFAD  
117 numbers during the study period, a Generalized Additive Model (GAM) was

118 performed considering  $K_n(i)$  as the dependent variable, with a Gaussian link  
119 function to account for explanatory variables. Explanatory variables were  
120 chosen to assess the effect of the fishing year (Y), season (fishing  
121 quarter, Q), size of the individuals (size class, SC), and fishing location  
122 (longitude, Lon; latitude, Lat). Longitude and latitude were included in  
123 the model as a smoothed term, and other variables were considered as  
124 factors. No precise time-series of DFAD number exist in the IO over 1987-  
125 2018, but the deployment of DFADs increased during that period, hence we  
126 considered the fishing year as a proxy.

127 Because  $K_n$  is the ratio of two correlated random variables (Pearson's  
128 correlation coefficient between  $W$  and  $W_{th}$ , Pearson's  $\rho = 0.99$ ), it did not  
129 follow a normal distribution and displayed overdispersion. For this reason,  
130 and because it did not change the interpretation of the GAM results, we  
131 transformed the  $K_n(i)$  using a Geary-Hinkley transformation before  
132 performing the GAM (Geary 1930, see Supplementary Material 2). The  
133 Generalized Additive Model was performed on the transformed  $K_n(i)$ , noted  
134  $T(K_n(i))$ . A complementary analysis showed that size class and its  
135 interaction with other explanatory variables did not impact the main  
136 results of the study (see Figure S3).

137 As the exact geographic coordinates were not available for most of the  
138 sampled fish, a bootstrap process was applied: a dataset was generated by  
139 sampling one set of coordinates from all the fishing sets of the trip for



140 each individual and a GAM was then performed. This operation was repeated  
141 1,000 times and for every model built, we selected the most parsimonious  
142 explanatory variables based on the Akaike information criterion (AIC),  
143 using a stepwise selection procedure and a threshold of 2. The iterated GAM  
144 coefficients of the explanatory variables considered as factors (Y, Q and  
145 SC) were averaged over the bootstrap replica and their standard deviation  
146 calculated.

## 147 Results

### 148 Mean relative condition factors ( $K_n$ )

149 The mean relative condition factor value ( $K_n$ ) was  $1.01 \pm 0.088$  and mean  
150 annual  $K_n$  values varied between  $0.93 \pm 0.064$  (in 1987) and  $1.07 \pm 0.079$  (in  
151 2012). The relative condition factor displayed annual variations, with low  
152  $K_n$  values in 1987–1990 and around 2006, and the highest  $K_n$  values observed  
153 around 2012 (Figure 2A). The mean annual  $K_n$  displayed similar variations  
154 per size class as when all the sampled fish were considered together  
155 (Figure 2A). No clear trend in  $K_n$  variations were observed.

### 156 Yearly variations of $K_n$

157 The most parsimonious model, selected using the AIC, included year (Y),  
158 quarter (Q), size class (SC) and the smoothed term for longitude and  
159 latitude. The selected model explained 29.2% of the deviance. The residuals

160 displayed no spatial autocorrelation and their distribution was not  
161 significantly different from a Gaussian distribution (Figure S4). The GAM  
162 performed on the transformed relative condition factor,  $T(K_n(i))$ , showed  
163 that strongest  $T(K_n(i))$  variations were significantly correlated with  
164 fishing year (Figure 2B; Figure S5 & S6). The annual GAM coefficients  
165 displayed a non-monotonous trend which was non-decreasing in time, with  
166 1987 being the year with the lowest coefficient ( $-0.475 \pm 0.007$ ) while 2012  
167 was the year with the highest coefficient ( $0.673 \pm 0.006$ ; Figure 2B). The  
168 observed patterns were similar to those displayed when considering only the  
169 mean annual  $K_n$  (Figures 2A&B).

## 170 Discussion

171 The main hypothesis tested in this study was that the introduction of DFADs  
172 would have negatively impacted the condition of tunas, following roughly  
173 three decades of DFAD deployment in the ocean (Figure 1). Under the  
174 hypothesis that DFAD number increased during the study period, we expected  
175 a monotonous decrease of yellowfin tuna condition throughout the years. The  
176 relative condition factor ( $K_n(i)$ ) values obtained here did not display any  
177 clear temporal trend over the study period (Figure 2), which goes against  
178 the tested hypothesis. Hence, the present study concludes that under the  
179 conditions encountered by yellowfin tuna in the Indian Ocean during the

180 last three decades, the addition of DFADs to the pelagic environment has  
181 not led to the creation of an ecological trap for this species.

182 However, several precautions must be considered when interpreting this  
183 result. Sampling was not uniformly distributed across size classes and  
184 years, which could have influenced the results (Table S1 & Figure S7).  
185 However, Wang et al. (2002) found no relationship between the size and the  
186 condition factor of yellowfin and bigeye tunas. Also, when performing a GAM  
187 on data of each size class independently, no decreasing trend of  
188 physiological condition was observed (Figure S3). Therefore, we are  
189 confident that the methodology used here did not suffer from any bias  
190 induced through the uneven sampling.

191 Also, morphometric indices, such as  $K_n$  used here, should be used with  
192 caution as they do not always reflect the energy compounds in the tissues  
193 (Lloret et al. 2014). Hence, further efforts are needed to validate them  
194 against proper benchmarks (Lloret et al. 2014), which could be achieved  
195 through the development of experimental studies. However, these  
196 morphometric indices can be informative (Hallier and Gaertner 2008), and  
197 are often the only available metrics as it was the case in this study (no  
198 long-term time-series of biochemical indices exist for tuna).

199 Furthermore, the habitat change induced by DFADs could also impact other  
200 biological processes, such as natural mortality, growth rate (Hallier and  
201 Gaertner 2008), or reproduction (Zudaire et al. 2014), that could not be

202 assessed through our biological index. For example, if the growth rate of  
203 tunas is negatively altered by DFADs (see Hallier and Gaertner 2008), a  
204 tuna of a given size in the 1980s could be younger than a tuna of the same  
205 size in the 2010–2020s, with the two individuals having a similar  
206 physiological condition.

207 Our study is based on the assumption that, since the late 1980s, the number  
208 of DFADs increased in the western IO. While assessing a time-series of the  
209 exact density of DFADs is cumbersome, studies suggest that the number of  
210 DFADs in the Indian Ocean continued to increase throughout the study period  
211 (Dupaix et al. 2021). The conditions leading to an ecological trap might  
212 also have only been reached in recent years, without being detectable in  
213 our study. This highlights the need to keep developing long-term monitoring  
214 programs, collecting data on DFAD densities and standardized physiological  
215 indices, to study the impact of DFADs on tuna physiology.

216 As stated above, the study is valid only for the conditions experienced by  
217 yellowfin tuna in the western IO in the last three decades. Aside from the  
218 increase of DFAD density, other long-term phenomena could also impact the  
219 physiology of tropical tuna. Since the 1980s, climate change has already  
220 impacted tuna habitat, by inducing changes in sea surface temperature or  
221 oxygen concentration, for example (Erauskin - Extramiana et al. 2019).  
222 Erauskin - Extramiana et al. (2019) projected that yellowfin tuna will  
223 become more abundant under a climate change scenario (the authors used the

224 RCP8.5 and expect the same projected changes of abundance under other  
225 scenarios until 2050). Hence, a potential negative impact of increasing  
226 DFAD density may have been concealed by other phenomena like climate  
227 change.

228 Ecological traps are likely to become more common as human-induced  
229 environmental changes increase, and they have important implications for  
230 the management of animal populations (Swearer et al. 2021). The hypothesis  
231 that DFADs could act as ecological traps was developed over 20 years ago  
232 (Marsac et al. 2000). It suggests that, by modifying the density and  
233 spatial distribution of FOBs, the massive deployment of DFADs could retain  
234 or transport individuals to areas that are ecologically unsuitable for them  
235 (Marsac et al. 2000). By demonstrating the absence of any decreasing trend  
236 in yellowfin tuna condition concurrent to the observed increasing DFAD  
237 density in the Indian Ocean during the past three decades, this study  
238 rejects the ecological trap hypothesis as it was originally formulated.  
239 However, DFADs can impact the biology of tuna in a variety of complex ways,  
240 and this impact can be intertwined with the effects of other factors such  
241 as climate change. Therefore, it is necessary to establish long-term  
242 monitoring programs to track (i) habitat changes, (ii) temporal variations  
243 of behavioral features in tuna, such as large-scale movements and schooling  
244 behavior, and (iii), temporal variations of physiological parameters in  
245 tuna.

## 246 **Declaration of Competing Interest**

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

## 250 **Data availability statement**

251 Data used in this study is available in Guillou et al. (2021).

252 All analyses were performed using R software v.4.0.3, and the scripts used  
253 for the study are available on GitHub:

254 [https://github.com/adupaix/Historical\\_YFT\\_condition](https://github.com/adupaix/Historical_YFT_condition)

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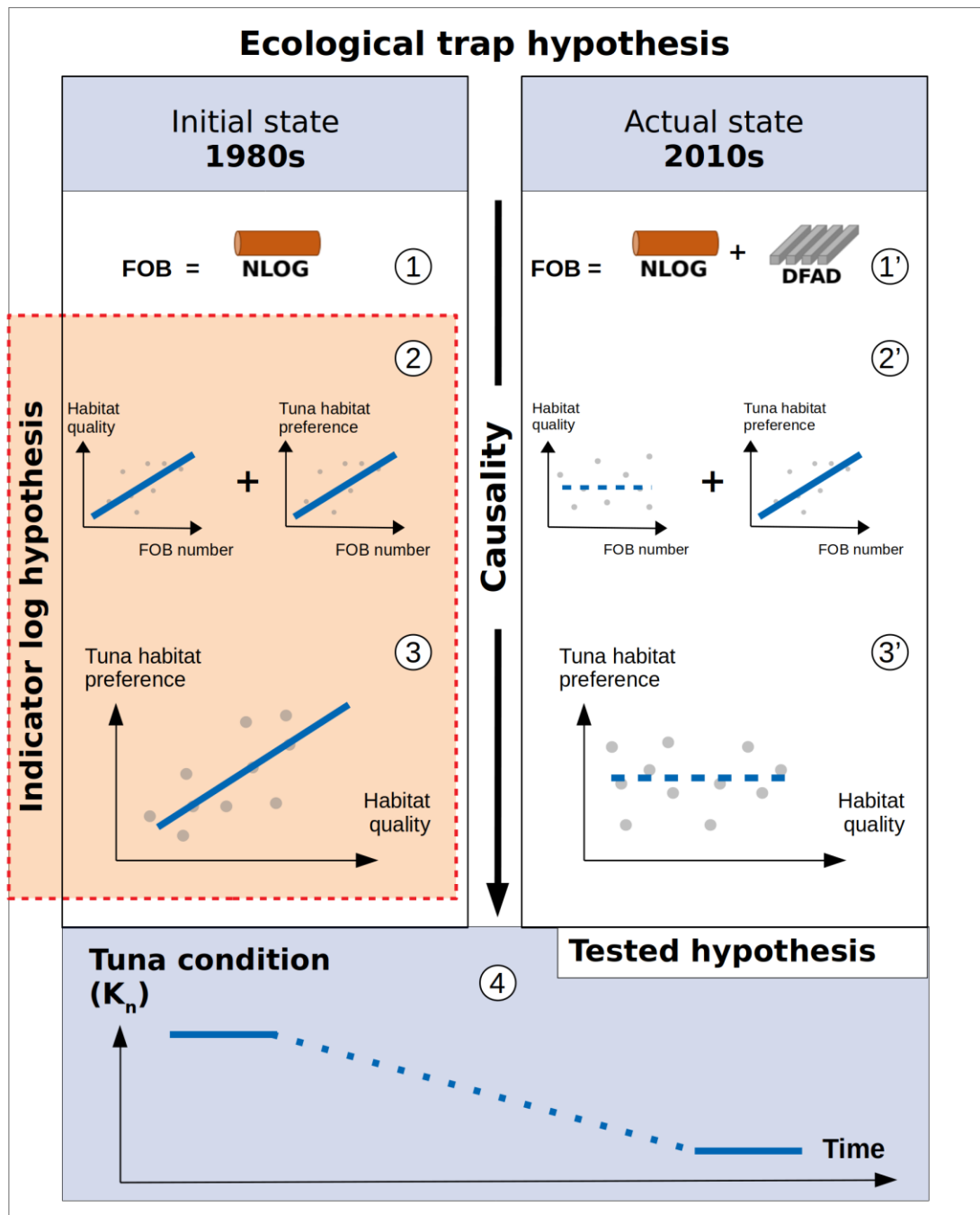
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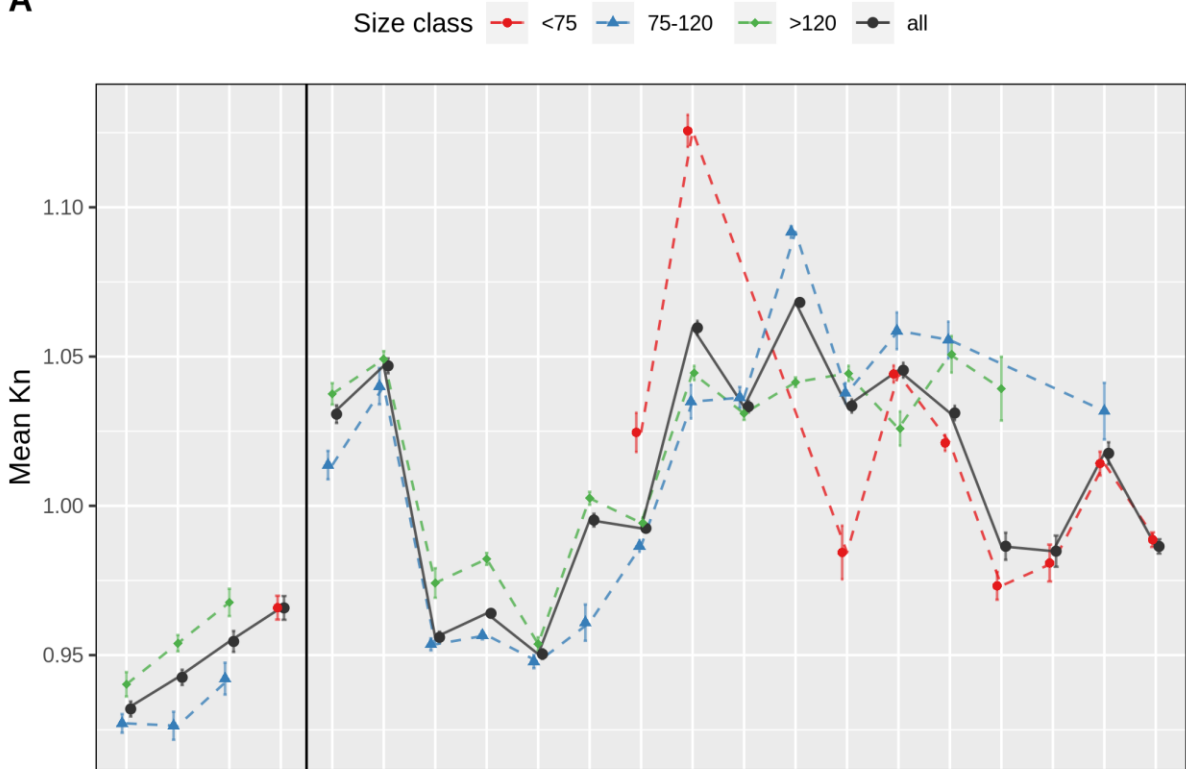
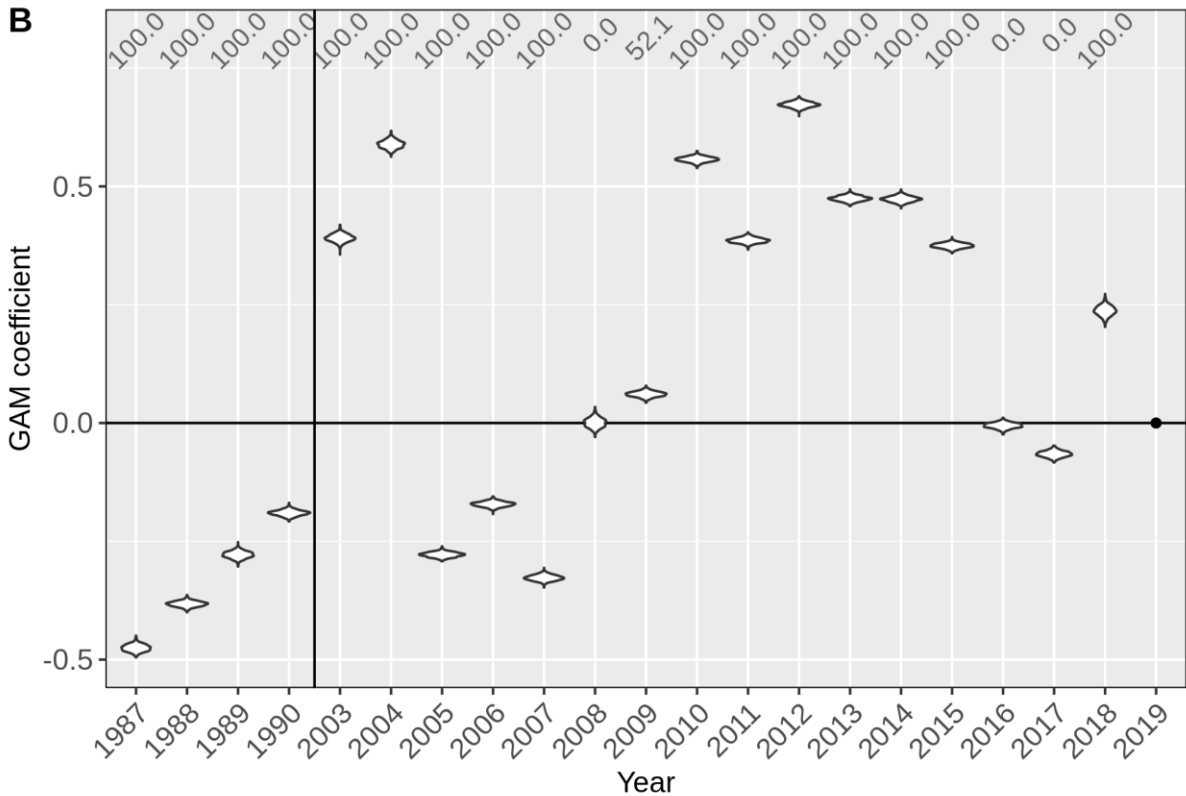
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266 Figure 1: Schematic representation of the ecological trap hypothesis  
 267 applied to Fish Aggregating Devices and tropical tuna. FOB: Floating  
 268 object of any kind; DFAD: Fish Aggregating Device; NLOG: Natural floating  
 269 object. Under this hypothesis, before DFAD introduction, when only NLOGs

270 were present (1), floating objects were distributed in productive areas  
271 (2), hence tunas, which associate with floating objects, preferred high  
272 quality habitats (3). Since DFAD introduction (1'), the distribution of  
273 floating objects has been modified and is no longer correlated with habitat  
274 quality (2'). Hence, tunas, which still associate with floating objects, do  
275 not select high quality habitat anymore (3'). As a consequence of this  
276 habitat modification, the physiological condition of tunas would have  
277 decreased since the 1980s (4). Preference is defined here as the likelihood  
278 of a resource being chosen if offered as an option with other available  
279 options.

**A****B**

280 Figure 2: No observed trend in yellowfin tuna condition: (A) Mean relative  
 281 condition factor per year. The  $K_n$  is represented for all individuals (all,  
 282 black circles), for small individuals (<75, red circles), medium-size

283 individuals (75–120, blue triangles) and large individuals (>120, green  
284 diamonds). Values are represented only when more than 50 individuals of the  
285 given class were measured. Error bars represent the standard error of the  
286 mean. (B) Coefficients of the fishing year in the Generalized Additive  
287 Model. Each coefficient represents the mean deviation of  $T(K_n)$  from the  
288 values for a year of reference (2019, represented by a black dot). The  
289 shape of the points represents the distribution of the values obtained with  
290 the bootstrap process. Numbers in grey in the upper part of the panels  
291 represent the percentage of the models generated in the bootstrap for which  
292 a given category was significantly different from the category of  
293 reference.