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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 ecological traps: no**  
2           **evidence displayed by a long-term analysis of yellowfin tuna condition**

3           **Running Page Head:** DFADs as ecological traps

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8

9           **Abstract**

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

23          **Keywords:** Indicator log, relative condition factor, *Thunnus albacares*, Indian Ocean,  
24          industrial tuna fisheries, floating objects

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## 25 **Introduction**

26 Floating objects (FOBs), such as logs or branches, are natural components of the oceanic  
27 habitat of tropical tunas, which naturally associate with them. If the reasons for this  
28 associative behavior are poorly understood, fishers have traditionally used this  
29 behavior to find and capture associated fish (Fréon and Dagorn 2000). In the early  
30 1980s, industrial tropical tuna purse-seine fleets began to commonly deploy their own  
31 FOBs, called drifting Fish Aggregating Devices (DFADs, Dagorn et al. 2013b). In the  
32 Indian Ocean (IO), deployment and use of DFADs began in the 1990s and has steadily  
33 increased since then, such that from 2012 to 2018, DFADs were demonstrated to  
34 represent more than 85% of the total floating objects in the western IO (Dupaix et al.  
35 2021).

36 Soon after their wide-scale use began, it was hypothesized that DFADs may act as  
37 “ecological traps” for tropical tunas (see Figure 1) (Marsac et al. 2000; Hallier and  
38 Gaertner 2008). An ecological trap occurs when individuals select poor-quality habitats,  
39 being misled by cues that no longer correlate to habitat quality due to anthropogenic  
40 changes (Gilroy and Sutherland 2007). This decorrelation between habitat quality and  
41 habitat selection cues ultimately leads to a reduction in the fitness of individuals (Gilroy  
42 and Sutherland 2007; Swearer et al. 2021). The hypothesis of DFADs acting as ecological  
43 traps, as it was first formulated, relies on the assumption that tropical tunas and other  
44 associated species originally used floating objects to select good-quality habitats (the  
45 *indicator-log* hypothesis, see Fréon and Dagorn 2000). The massive deployment of  
46 DFADs would modify the density and spatial distribution of floating objects, with  
47 potentially large numbers of artificial objects occurring in areas that are not optimal for

48 tunas, creating the risk of an ecological trap. Hence, there is an urgent need to assess the  
49 likelihood of DFADs acting as ecological traps.

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

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

## 68 **Material and Methods**

### 69 *Biological data*

70 A total of 25,914 yellowfin tuna (*Thunnus albacares*) were sampled from 1987 to 2019  
71 in the Indian Ocean Tuna canning factory (IOT) in Victoria, Seychelles (Guillou et al.  
72 2021). All the sampled fish were caught by purse seine vessels in the western IO (details  
73 of the sample sizes are provided in Table S1). The total weight (W) of the individuals  
74 and their fork length (FL) were measured. For each sampled tuna, the fishing vessel and  
75 the fishing trip were recorded, but not the specific fishing set from which it was caught,  
76 which meant that the exact fishing date and location were unknown (see statistical  
77 analyses section for details on how the uncertainty on location and date was managed).  
78 The year (Y) and quarter (Q) of the catch of each tuna were estimated from the middle  
79 of the interval covered by the fishing trip dates. The quarters were defined to be  
80 synchronous with the general movement of the fleet, fishing seasons and areas (Dupaix  
81 et al. 2021): Q1, December to February; Q2, March to May; Q3, June to August; and Q4,  
82 September to November. The total range of FL was divided in three intervals, defining  
83 size classes (SC): small (<75cm), medium (75-120cm) and large (>120cm).

### 84 *Relative condition factor*

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

90 
$$K_n(i) = \frac{W(i)}{W_{th}(i)}$$

91 where  $W_{th}(i)$  is the theoretical weight of individual  $i$  calculated from length-weight  
92 allometric relationship coefficients according to  $FL(i)$ , and  $W(i)$  is the measured total  
93 weight. By definition,  $K_n(i)$  measures the deviation of an individual from the weight of a  
94 mean individual of the same length. For the remainder of the text, the relative condition  
95 factor of one individual is denoted as  $K_n(i)$ . The mean relative condition factor, denoted  
96  $K_n$ , calculated for a group of individuals is denoted as  $K_n$ .

### 97 *Statistical analysis*

98 In order to determine if  $K_n$  decreased with the concurrent increase in DFAD numbers  
99 during the study period, a Generalized Additive Model (GAM) was performed  
100 considering  $K_n(i)$  as the dependent variable, with a Gaussian link function to account for  
101 explanatory variables. Explanatory variables were chosen to assess the effect of the  
102 fishing year (Y), season (fishing quarter, Q), size of the individuals (size class, SC), and  
103 fishing location (longitude, Lon; latitude, Lat). Longitude and latitude were included in  
104 the model as a smoothed term, and other variables were considered as factors. No  
105 precise time-series of DFAD number exist in the IO over 1987-2018, but the deployment  
106 of DFADs increased during that period, hence we considered the fishing year as a proxy.

107 Because  $K_n$  is the ratio of two correlated random variables (Pearson's correlation  
108 coefficient between  $W$  and  $W_{th}$ , Pearson's  $\rho = 0.99$ ), it did not follow a normal  
109 distribution and displayed overdispersion. For this reason, and because it did not  
110 change the interpretation of the GAM results, we transformed the  $K_n(i)$  using a Geary-  
111 Hinkley transformation before performing the GAM (Geary 1930, see Supplementary

112 Material 2). The Generalized Additive Model was performed on the transformed  $K_n(i)$ ,  
113 noted  $T(K_n(i))$ . A complementary analysis showed that size class and its interaction with  
114 other explanatory variables did not impact the main results of the study (see Figure S3).  
115 As the exact geographic coordinates were not available for most of the sampled fish, a  
116 bootstrap process was applied: a dataset was generated by sampling one set of  
117 coordinates from all the fishing sets of the trip for each individual and a GAM was then  
118 performed. This operation was repeated 1,000 times and for every model built, we  
119 selected the most parsimonious explanatory variables based on the Akaike information  
120 criterion (AIC), using a stepwise selection procedure and a threshold of 2. The iterated  
121 GAM coefficients of the explanatory variables considered as factors (Y, Q and SC) were  
122 averaged over the bootstrap replica and their standard deviation calculated.

## 123 **Results**

### 124 *Mean relative condition factors ( $K_n$ )*

125 The mean relative condition factor value ( $K_n$ ) was  $1.01 \pm 0.088$  and mean annual  $K_n$   
126 values varied between  $0.93 \pm 0.064$  (in 1987) and  $1.07 \pm 0.079$  (in 2012). The relative  
127 condition factor displayed annual variations, with low  $K_n$  values in 1987-1990 and  
128 around 2006, and the highest  $K_n$  values observed around 2012 (Figure 2A). The mean  
129 annual  $K_n$  displayed similar variations per size class as when all the sampled fish were  
130 considered together (Figure 2A). No clear trend in  $K_n$  variations were observed.

### 131 *Yearly variations of $K_n$*

132 The most parsimonious model, selected using the AIC, included year (Y), quarter (Q),  
133 size class (SC) and the smoothed term for longitude and latitude. The selected model  
134 explained 29.2% of the deviance. The residuals displayed no spatial autocorrelation and  
135 their distribution was not significantly different from a Gaussian distribution (Figure  
136 S4). The GAM performed on the transformed relative condition factor,  $T(K_n(i))$ , showed  
137 that strongest  $T(K_n(i))$  variations were significantly correlated with fishing year (Figure  
138 2B; Figure S5 & S6). The annual GAM coefficients displayed a non-monotonous trend  
139 which was non-decreasing in time, with 1987 being the year with the lowest coefficient  
140  $(-0.475 \pm 0.007)$  while 2012 was the year with the highest coefficient  $(0.673 \pm 0.006$ ;  
141 Figure 2B). The observed patterns were similar to those displayed when considering  
142 only the mean annual  $K_n$  (Figures 2A&B).

### 143 **Discussion**

144 Ecological traps are likely to become more common as human-induced environmental  
145 changes increase, and they have important implications for the management of animal  
146 populations (Swearer et al. 2021). The yellowfin tuna stock in the Indian Ocean (IO) is  
147 currently overfished and subject to overfishing (IOTC 2021). It is therefore critical to  
148 assess not only direct impacts of DFADs – through fisheries – but also potential indirect  
149 impacts, like DFADs acting as ecological traps. The hypothesis that DFADs could act as  
150 ecological traps was developed more than 20 years ago (Marsac et al. 2000) and implies  
151 that the introduction of DFADs would have negatively impacted the condition of tunas,  
152 following roughly three decades of DFAD deployment (Figure 1). Under the hypothesis

153 that DFAD number increased during the study period, we expected a decrease of  
154 yellowfin tuna condition throughout the years. The relative condition factor ( $K_n(i)$ )  
155 values obtained here did not display any clear temporal trend over the study period  
156 (Figure 2), which goes against the tested hypothesis. Hence, the present study concludes  
157 that under the conditions encountered by yellowfin tuna in the IO during the last three  
158 decades, the addition of DFADs to the pelagic environment has not led to the creation of  
159 an ecological trap for this species.

160 For a habitat modification to lead to an ecological trap, individuals selecting the  
161 modified habitat have to experience a reduction in their fitness, namely their  
162 reproductive success, which includes survival and reproduction. Physiological condition  
163 can be considered a good proxy of individual fitness as it can impact both individual's  
164 survival and reproduction. The morphometric index used here,  $K_n$ , was the only  
165 condition indicator for which a long time-series was available. Other indices can be used  
166 to assess physiological condition, such as Bio-Impedance Analysis (BIA; Robert et al.  
167 2014), organosomatic indices or measurements of biomarkers (Lloret et al. 2014).  
168 Sardenne et al. (2016) alerted on the fact that different morphometric indices could  
169 show inconsistency and are not always the best proxies of tropical tuna condition. It  
170 stresses the need to develop experimental approaches, to measure a set of condition  
171 indices on captive tuna during fasting, in order to better understand the validity of these  
172 indices. DFADs could also impact the biology of tuna in a variety of complex ways,  
173 impacting other biological processes leading to a reduction of fitness, like growth rate  
174 (Hallier and Gaertner 2008), or reproduction (Zudaire et al. 2014). This highlights the

175 need to monitor tuna physiological condition more thoroughly, by performing regular  
176 data collection of biological data.

177 Many studies demonstrated that tuna associated with DFADs tend to be in lower  
178 condition than tuna fished in free-schools (FSC; Marsac et al. 2000; Hallier and Gaertner  
179 2008; Jaquemet et al. 2011). However, Robert et al. (2014) observed a similar result  
180 when comparing tuna associated with natural FOBs and FSC tuna, and concluded that  
181 the associative behavior could be the consequence and not the cause of a lower  
182 physiological condition. These studies testing the ecological trap hypothesis were  
183 performed on short temporal scales of up to a few months and therefore were not able  
184 to conclude on a potential long-term impact of DFADs. Other long-term phenomena  
185 could also impact the physiology of tropical tuna. For example, since the 1980s, climate  
186 change has already impacted tuna habitat, by inducing changes in sea surface  
187 temperature or oxygen concentration (Erauskin-Extramiana et al. 2019).  
188 Erauskin-Extramiana et al. (2019) projected that yellowfin tuna will become more  
189 abundant under a climate change scenario. Our study is the first to be performed on a  
190 time series allowing to assess the potential long-term impact of the increase of DFAD  
191 density on tuna condition. Effort should be made to keep on relying on such long time-  
192 series of indices, which need to be monitored.

193 Tuna associative behavior plays a key role in determining the potential indirect impacts  
194 of DFADs on tuna condition. It could depend on several other factors than DFAD density,  
195 such as environmental conditions or social behavior (Capello et al. 2022). It could also  
196 be impacted by their physiological condition, for example one could imagine that tuna  
197 would associate with a DFAD until its condition lowers under a given threshold value

198 that would cause it to leave. Several hypotheses – *e.g.* the association being a  
199 consequence of a low condition (see previous paragraph) and individuals departing  
200 from FOBs under a given condition threshold – could explain the absence of a long-term  
201 impact of DFADs on tuna condition, and need to be further explored.

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

## 211 **Declaration of Competing Interest**

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

## 214 **Data availability statement**

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

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

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

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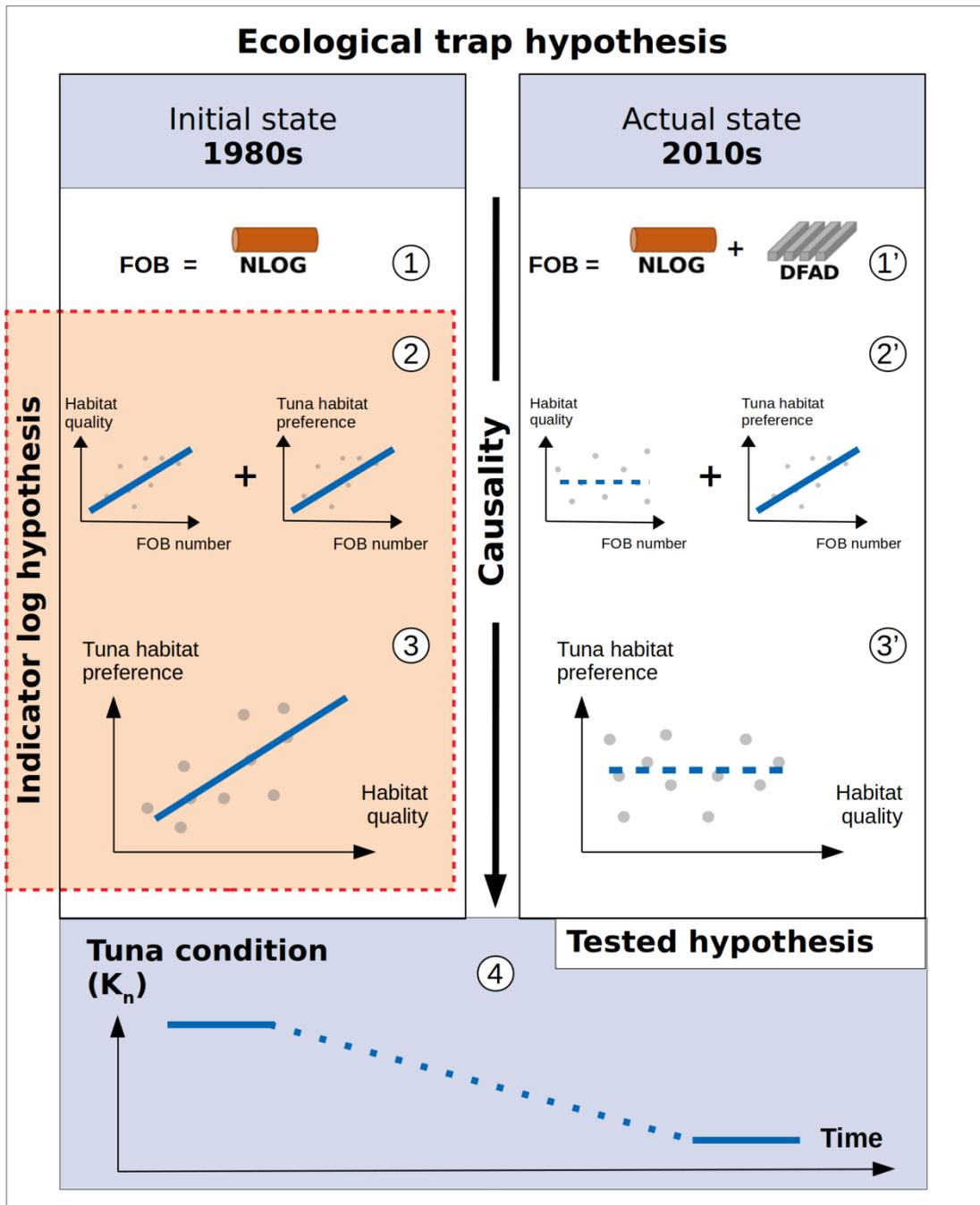
## 222 **Acknowledgments**

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## 227 **References**

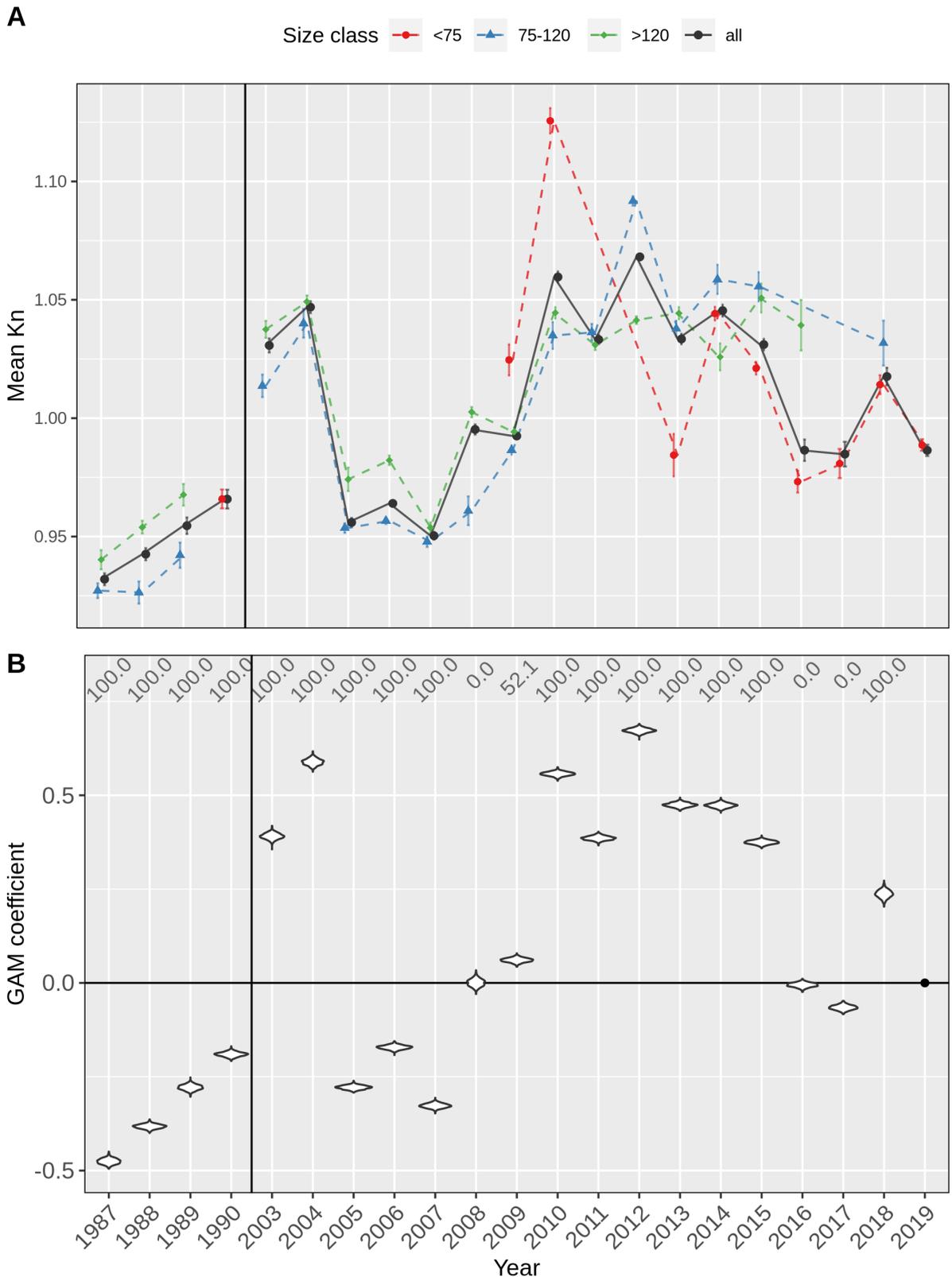
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229 **Figure 1: Schematic representation of the ecological trap hypothesis applied to**  
 230 **Fish Aggregating Devices and tropical tuna.** FOB: Floating object of any kind; DFAD:  
 231 Fish Aggregating Device; NLOG: Natural floating object. Under this hypothesis, before  
 232 DFAD introduction, when only NLOGs were present (1), floating objects were

233 distributed in productive areas (2), hence tunas, which associate with floating objects,  
234 preferred high quality habitats (3). Since DFAD introduction (1'), the distribution of  
235 floating objects has been modified and is no longer correlated with habitat quality (2').  
236 Hence, tunas, which still associate with floating objects, do not select high quality  
237 habitat anymore (3'). As a consequence of this habitat modification, the physiological  
238 condition of tunas would have decreased since the 1980s (4). Preference is defined here  
239 as the likelihood of a resource being chosen if offered as an option with other available  
240 options.



241 **Figure 2: No observed trend in yellowfin tuna condition: (A) Mean relative**  
 242 **condition factor per year. The  $K_n$  is represented for all individuals (all, black circles),**

243 for small individuals (<75, red circles), medium-size individuals (75-120, blue triangles)  
244 and large individuals (>120, green diamonds). Values are represented only when more  
245 than 50 individuals of the given class were measured. Error bars represent the standard  
246 error of the mean. (B) Coefficients of the fishing year in the Generalized Additive Model.  
247 Each coefficient represents the mean deviation of  $T(K_n)$  from the values for a year of  
248 reference (2019, represented by a black dot). The shape of the points represents the  
249 distribution of the values obtained with the bootstrap process. Numbers in grey in the  
250 upper part of the panels represent the percentage of the models generated in the  
251 bootstrap for which a given category was significantly different from the category of  
252 reference.