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1 **No evidence from long-term analysis of yellowfin tuna condition that**

2 **Drifting Fish Aggregating Devices act as ecological traps**

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, to 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
16 from 1987 to 2019 of more than 25,000 length-weight samples collected in the western
17 Indian Ocean, we reject the hypothesis that the body condition (Le Cren's relative
18 condition factor K_n) of yellowfin tuna (*Thunnus albacares*) decreased concurrently with
19 the increased number of DFADs. This result suggests the absence of negative long-term
20 impacts of DFADs on the condition 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 **1. Introduction**

26 Natural floating objects (designated as NLOGs), such as logs or branches, are a
27 component of the oceanic habitat of tropical tunas, which associate with them. Although
28 the reasons for this associative behavior are poorly understood, fishers traditionally
29 used this behavior to find and capture associated fish (Fréon & Dagorn 2000). In the
30 early 1980s, industrial tropical tuna purse-seine fleets began to commonly attach buoys
31 on NLOGs and to construct and deploy their own man-made floating objects (FOBs),
32 called drifting Fish Aggregating Devices (DFADs) (Dagorn et al. 2013b). In the Indian
33 Ocean (IO), deployment and use of DFADs began in the 1990s and has steadily increased
34 since then, such that from 2012 to 2018, DFADs were demonstrated to represent more
35 than 85% of the total floating objects in the western IO (Dupaix et al. 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 &
38 Gaertner 2008). An ecological trap occurs when individuals exhibit a higher or equal
39 preference for a poor-quality habitat (*i.e.* associated with a lower fitness) over another
40 habitat, being misled by cues that no longer correlate to habitat quality due to
41 anthropogenic changes (Robertson & Hutto 2006, Gilroy & Sutherland 2007). This
42 decorrelation between habitat quality and habitat selection cues ultimately leads to a
43 reduction in the fitness of individuals (Gilroy & Sutherland 2007, Swearer et al. 2021).
44 The hypothesis of DFADs acting as ecological traps, as it was first formulated, relies on
45 one of the hypotheses formulated to explain tuna associative behavior: the *indicator-log*
46 hypothesis (Fréon & Dagorn 2000), which posits that natural floating objects are
47 located in productive areas because they originate from rivers and tend to accumulate

48 in rich frontal areas (Hall 1992, Hallier & Gaertner 2008). Thus tropical tunas and other
49 associated species would select natural floating objects as a cue for good-quality habitat.
50 The massive deployment of DFADs would modify the density and spatial distribution of
51 floating objects, with potentially large numbers of artificial objects occurring in areas
52 that are not optimal for tunas, creating the risk of an ecological trap. Hence, there is an
53 urgent need to assess the likelihood of DFADs acting as ecological traps.

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

67 The objective of this study was to test the hypothesis that the body condition of
68 yellowfin tuna has decreased since the wide-spread use of DFADs began in the Indian
69 Ocean, in the 1990s. We used length and weight measurements to calculate Le Cren's

70 relative condition factor (K_n), and investigated the temporal evolution of the body
71 condition of yellowfin tuna (*Thunnus albacares*) from 1987 to 2019 in the Indian Ocean.

72 **2. Material and Methods**

73 *2.1. Biological data*

74 A total of 25,914 yellowfin tuna (*Thunnus albacares*) were sampled from 1987 to 2019
75 in the Indian Ocean Tuna canning factory (IOT) in Victoria, Seychelles (Guillou et al.
76 2021). All the sampled fish were caught by purse seine vessels in the western IO (details
77 of the sample sizes are provided in Tables S1 & S2 in Supplement 1). The total weight
78 (W) of the individuals and their fork length (FL) were measured. For each sampled tuna,
79 the fishing vessel and the fishing trip were recorded, but not the specific fishing set from
80 which it was caught. As a consequence, all fishing sets from a trip are a potential catch
81 location for every samples (see statistical analyses section for details on how the
82 uncertainty on location and date was managed). The type of school (either FOB-
83 associated or FSC) was not considered in the main analysis because it was unknown for
84 a large proportion of the sampled fish (around 75 %, Table S1 in Supplement 1). The
85 year (Y) and quarter (Q) of the catch of each tuna were estimated from the middle of the
86 interval covered by the fishing trip dates. The quarters were defined to be synchronous
87 with the general movement of the fleet, fishing seasons and areas (Dupaix et al. 2021):
88 Q1, December to February; Q2, March to May; Q3, June to August; and Q4, September to
89 November. The total range of FL was divided in three intervals, defining size classes
90 (SC): small (<75cm), medium (75-120cm) and large (>120cm).

91 *2.2. Relative condition factor*

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

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

97 where $W_{th}(i)$ is the theoretical weight of individual i calculated from length-weight
98 allometric relationship coefficients according to $FL(i)$, and $W(i)$ is the measured total
99 weight. By definition, $K_n(i)$ measures the deviation of an individual from the weight of a
100 mean individual of the same length. The mean relative condition factor calculated for a
101 group of individuals (either per year, per size class or per quarter) is denoted as K_n .

102 *2.3. Statistical analysis*

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

111 deployment of DFADs increased during that period, hence we considered the fishing
112 year as a proxy for DFAD density.

113 Because K_n is the ratio of two correlated random variables (Pearson's correlation
114 coefficient between W and W_{th} , Pearson's $\rho = 0.99$), it did not follow a normal
115 distribution and displayed overdispersion. For this reason, and because it did not
116 change the interpretation of the GAM results, we transformed the $K_n(i)$ using a Geary-
117 Hinkley transformation before performing the GAM (Geary 1930, see Supplement 3).
118 The Generalized Additive Model was performed on the transformed $K_n(i)$, noted
119 $T(K_n(i))$. Complementary analyses showed that size class and its interaction with other
120 explanatory variables and fishing mode (Figures S1 & S2 in Supplement 1 respectively)
121 did not impact the main results of the study. These results remained consistent when
122 considering only fish from FOB-associated schools (Figure S3 in Supplement 1).

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

131 All analyses were performed using R software v.4.0.3 (R Core Team 2020), and the
132 scripts used for the study are available on GitHub

133 (https://github.com/adupaix/Historical_YFT_condition
134 <https://doi.org/10.5281/zenodo.6123417>).

135 **3. Results**

136 *3.1. Mean relative condition factors (K_n)*

137 The mean relative condition factor value (K_n) was 1.01 ± 0.088 and mean annual K_n
138 values varied between 0.93 ± 0.064 (in 1987) and 1.07 ± 0.079 (in 2012). The relative
139 condition factor displayed annual variations, with low K_n values in 1987-1990 and
140 around 2005-2007, and the highest K_n values observed around 2012 (Figure 2A). The
141 mean annual K_n displayed similar variations per size class as when all the sampled fish
142 were considered together (Figure 2A). No clear trend in K_n variations were observed.

143 *3.2. Yearly variations of K_n*

144 The most parsimonious model, selected using the AIC, included year (Y), quarter (Q),
145 size class (SC) and the smoothed term for longitude and latitude. The selected model
146 explained 29.2% of the deviance. The residuals displayed no spatial autocorrelation and
147 their distribution was not significantly different from a Gaussian distribution (Figure S4
148 in Supplement 1). The GAM performed on the transformed relative condition factor,
149 $T(K_n(i))$, showed that strongest $T(K_n(i))$ variations were significantly correlated with
150 fishing year (Figure 2B; Figures S5 & S6 in Supplement 1). The annual GAM coefficients
151 displayed a non-monotonous trend which was non-decreasing in time, with 1987 being
152 the year with the lowest coefficient (-0.475 ± 0.007) while 2012 was the year with the
153 highest coefficient (0.673 ± 0.006 ; Figure 2B). The observed patterns were similar to
154 those displayed when considering only the mean annual K_n (Figures 2A&B).

155 **4. Discussion**

156 Ecological traps in animals are likely to become more common as human-induced
157 environmental changes increase. These traps can increase extinction risk locally and
158 regionally, impacting population persistence, and present an important challenge for
159 the management of animal populations (Battin 2004, Hale et al. 2015, Swearer et al.
160 2021). The yellowfin tuna population in the Indian Ocean (IO) is currently overfished
161 and subject to overfishing (IOTC 2021). It is therefore critical to assess not only direct
162 impacts of DFADs – through fisheries – but also potential indirect impacts which could
163 also negatively impact tuna populations (Hallier & Gaertner 2008). The hypothesis that
164 DFADs could act as ecological traps was developed more than 20 years ago (Marsac et
165 al. 2000) and implies that the introduction of DFADs would have negatively impacted
166 the condition of tunas, following roughly three decades of DFAD deployment (Figure 1).
167 Under the hypothesis that DFAD number increased during the study period, we
168 expected a decrease of yellowfin tuna condition throughout the years. The relative
169 condition factor ($K_n(i)$) values obtained here did not display any clear temporal trend
170 over the study period (Figure 2), which does not support the tested hypothesis. Hence,
171 the present study suggests that under the conditions encountered by yellowfin tuna in
172 the IO during the last three decades, the addition of DFADs to the pelagic environment
173 has not led to the creation of an ecological trap for this species.

174 Data used in this study were not uniformly distributed across size classes and years
175 (Figure S7 in Supplement 1), and tunas from both fishing modes (FOB-associated and
176 FSC) were considered, which could influence the results (Hallier & Gaertner 2008,
177 Robert et al. 2014). However, no decreasing trend of condition factor was observed

178 concurrently with increasing DFAD use when performing a GAM on data of each size
179 class independently (Figure S1 in Supplement 1). Also, even though the mean K_n of FOB-
180 associated tuna was lower than that of FSC tuna, no decreasing trend of condition was
181 observed when considering the fishing mode (Figures S2 & S3 in Supplement 1).

182 For a habitat modification to lead to an ecological trap, individuals selecting the
183 modified habitat have to experience a reduction in their fitness, namely their
184 reproductive success, which includes survival and reproduction. Physiological condition
185 can be considered a good proxy of individual fitness as it can impact both individual's
186 survival and reproduction. The morphometric index used here, K_n , was the only
187 condition indicator for which a long time-series was available. Other indices can be used
188 to assess physiological condition, such as Bio-Impedance Analysis (BIA; Robert et al.
189 2014), organosomatic indices or measurements of biomarkers (Lloret et al. 2014).
190 Sardenne et al. (2016) alerted on the fact that different morphometric indices could
191 show inconsistency and are not always the best proxies of tropical tuna condition. All of
192 these stresses the need to develop experimental approaches, to measure a set of
193 condition indices on captive tuna under various feeding/fasting conditions, in order to
194 better understand the validity of these indices. DFADs could also impact the biology of
195 tuna in a variety of complex ways, impacting other biological processes leading to a
196 reduction of fitness, like growth rate (Hallier & Gaertner 2008), or reproduction
197 (Zudaire et al. 2014). This highlights the need to monitor tuna physiological condition
198 more thoroughly, by performing regular data collection of biological data.

199 Many studies demonstrated that tuna associated with DFADs tend to be in lower
200 condition than FSC tunas (Marsac et al. 2000, Hallier & Gaertner 2008, Jaquemet et al.

201 2011). However, Robert et al. (2014) observed a similar result when comparing tuna
202 associated with NLOGs and FSC tuna, and concluded that the associative behavior could
203 be the consequence and not the cause of a lower physiological condition. These studies
204 testing the ecological trap hypothesis were performed on short temporal scales of up to
205 a few months and therefore were not able to conclude on a potential long-term impact
206 of DFADs. Other long-term phenomena could also impact the physiology of tropical
207 tuna. For example, since the 1980s, climate change has already impacted tuna habitat,
208 by inducing changes in sea surface temperature or oxygen concentration
209 (Erauskin-Extramiana et al. 2019). Erauskin-Extramiana et al. (2019) projected that
210 yellowfin tuna will become more abundant under a climate change scenario. Our study
211 is the first performed on a time-series long enough to allow assessing the potential long-
212 term impact of the increase of DFAD density on tuna condition. A decreasing trend of
213 small tunas' condition was observed in the later years of the study (Figure 2A), which
214 was not correlated with the number of FOBs (Supplement 4). Hence, to investigate
215 possible long-term physiological changes due to climate change and/or any
216 environmental disturbances, continuous effort to develop routine biological sampling
217 and routinely monitor fish condition should be established to develop long time-series
218 of biological indices. This effort should be combined with the collection of data on
219 habitat modifications induced by DFADs.

220 Tuna associative behavior plays a key role in determining the potential indirect impacts
221 of DFADs on tuna condition. This associative behavior could also depend on several
222 other factors than DFAD density, such as environmental conditions or social behavior
223 (Capello et al. 2022). It could also be impacted by their physiological condition, for

224 example one could hypothesize that tuna would associate with a DFAD until its
225 condition lowers a given threshold value that would cause it to leave. Several
226 hypotheses – *e.g.* the association being a consequence of a low condition and individuals
227 departing from FOBs beyond a given condition threshold – could explain the absence of
228 a long-term impact of DFADs on tuna condition, which need to be further explored.

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

238 **Declaration of Competing Interest**

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

241 **Data availability statement**

242 Data used in this study is available in Guillou et al. (2021) and were collected through
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245 A preprint version of the article is available at:

246 <https://hal.archives-ouvertes.fr/hal-03690665>

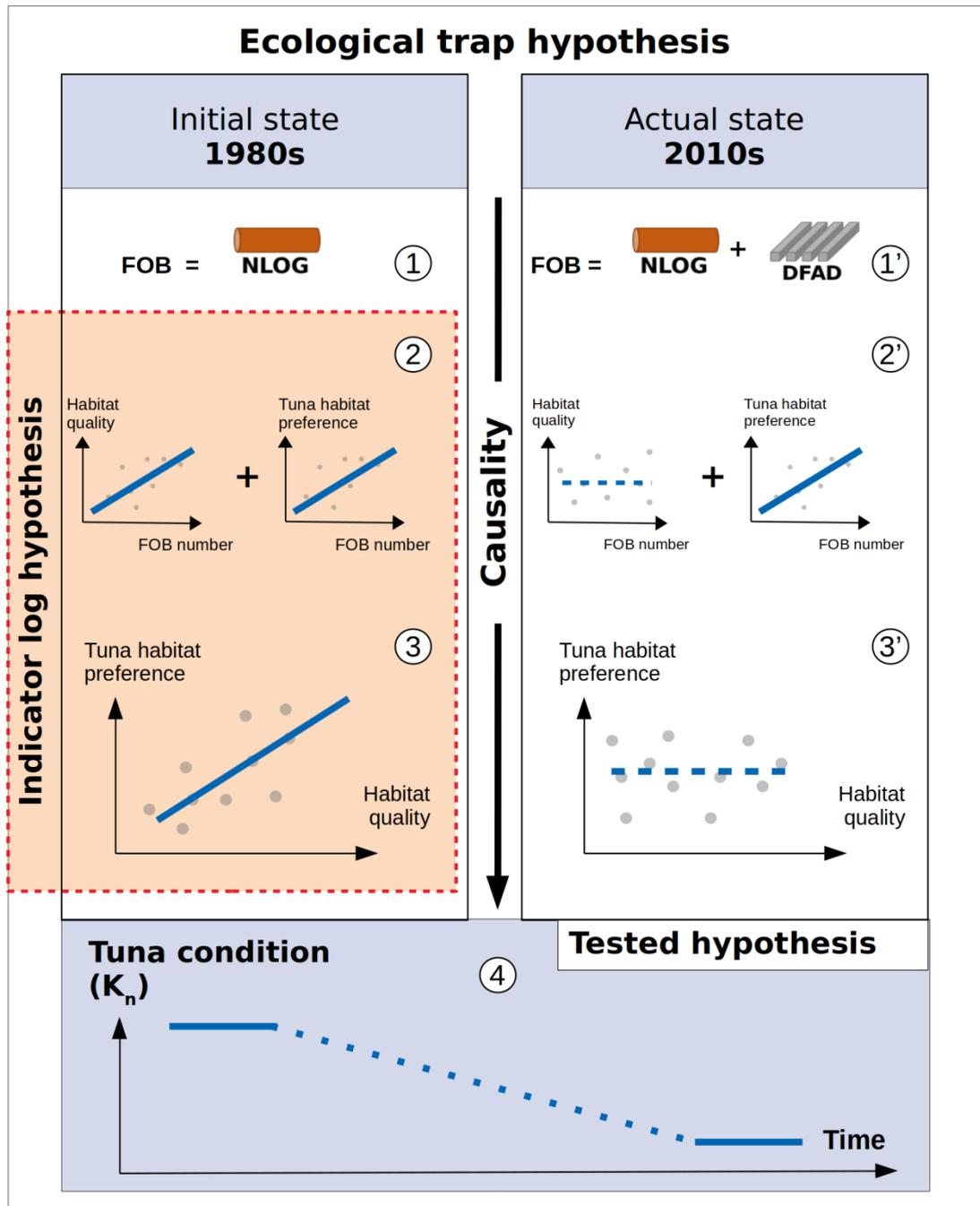
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258 **References**

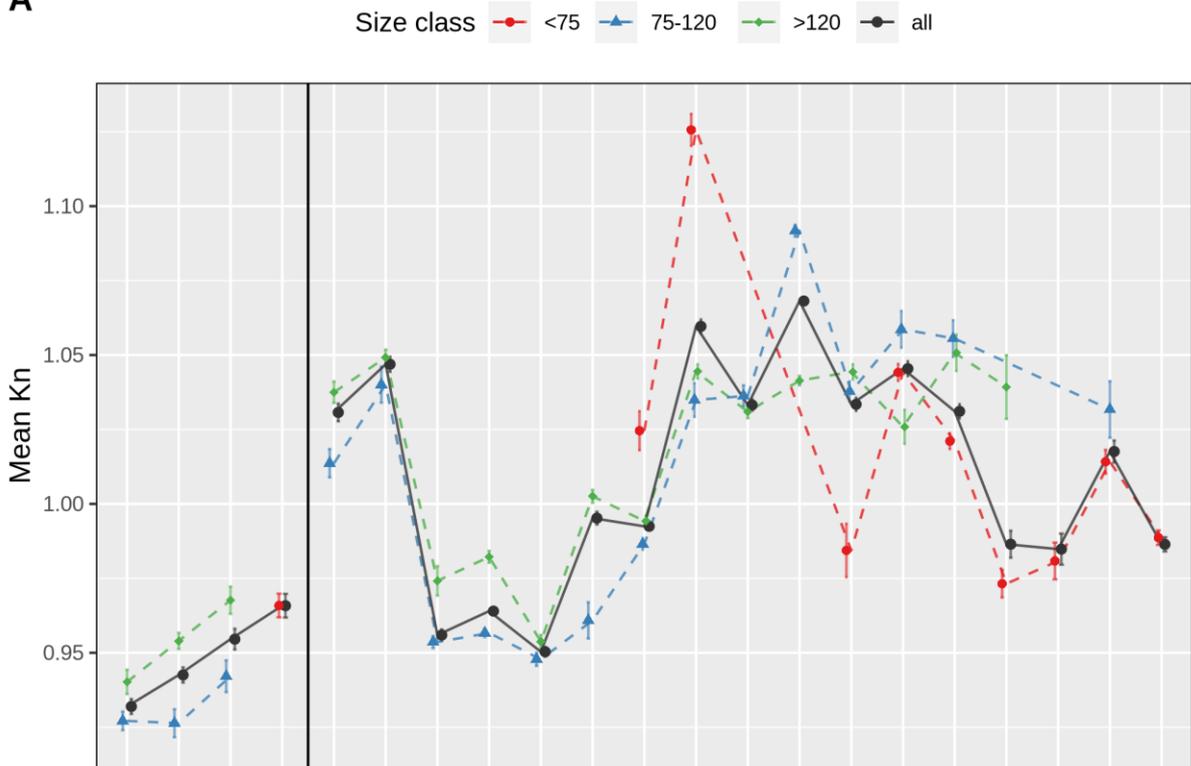
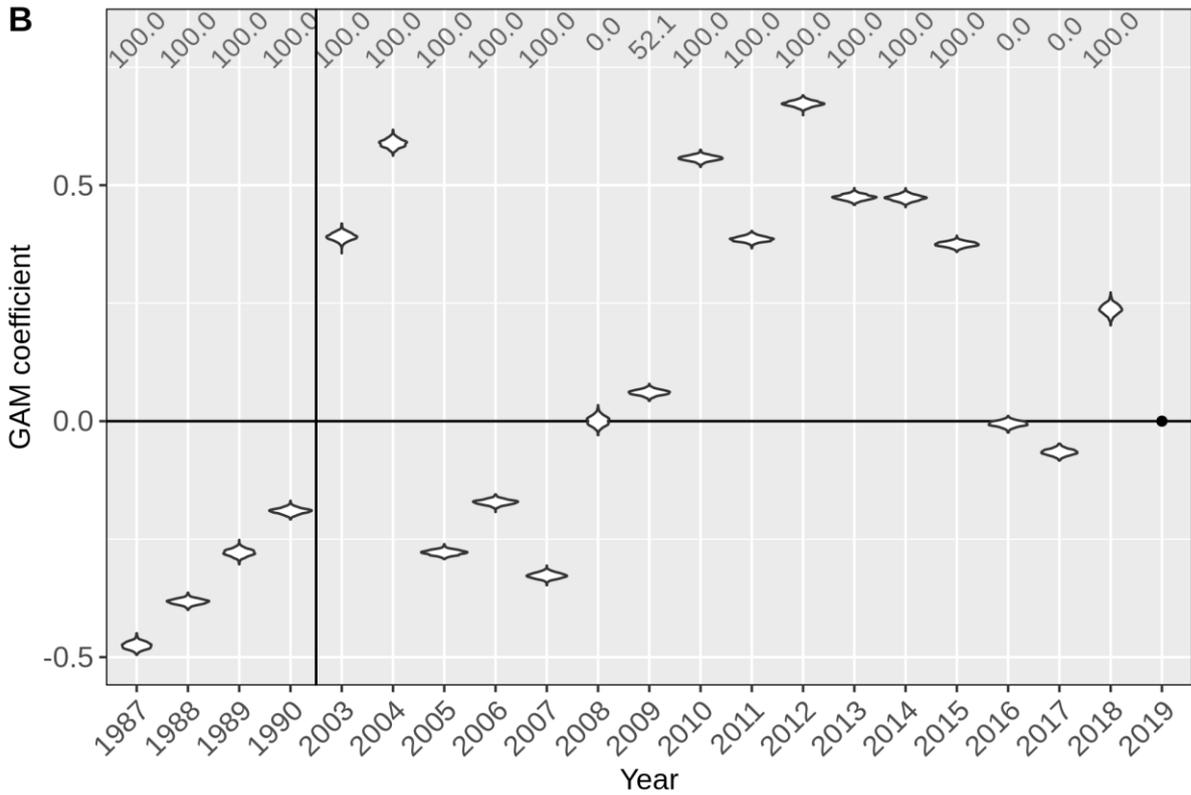
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260 **Figure 1: Schematic representation of the ecological trap hypothesis applied to**
 261 **Fish Aggregating Devices and tropical tuna.** FOB: Floating object of any kind; DFAD:
 262 Fish Aggregating Device; NLOG: Natural floating object. Under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

264 distributed in productive areas (2), hence tunas, which associate with floating objects,
265 preferred high quality habitats (3). Since DFAD introduction (1'), the distribution of
266 floating objects has been modified and is no longer correlated with habitat quality (2').
267 Hence, tunas, which still associate with floating objects, do not select high quality
268 habitat anymore (3'). As a consequence of this habitat modification, the physiological
269 condition of tunas would have decreased since the 1990s (4). Preference is defined here
270 as the likelihood of a resource being chosen if offered as an option with other available
271 options.

A**B**

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

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