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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 ± 0.088 and mean annual K_n
126 values varied between 0.93 ± 0.064 (in 1987) and 1.07 ± 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 ± 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

219 <https://doi.org/10.5281/zenodo.6123417>

220 A preprint version of the article is available at:

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

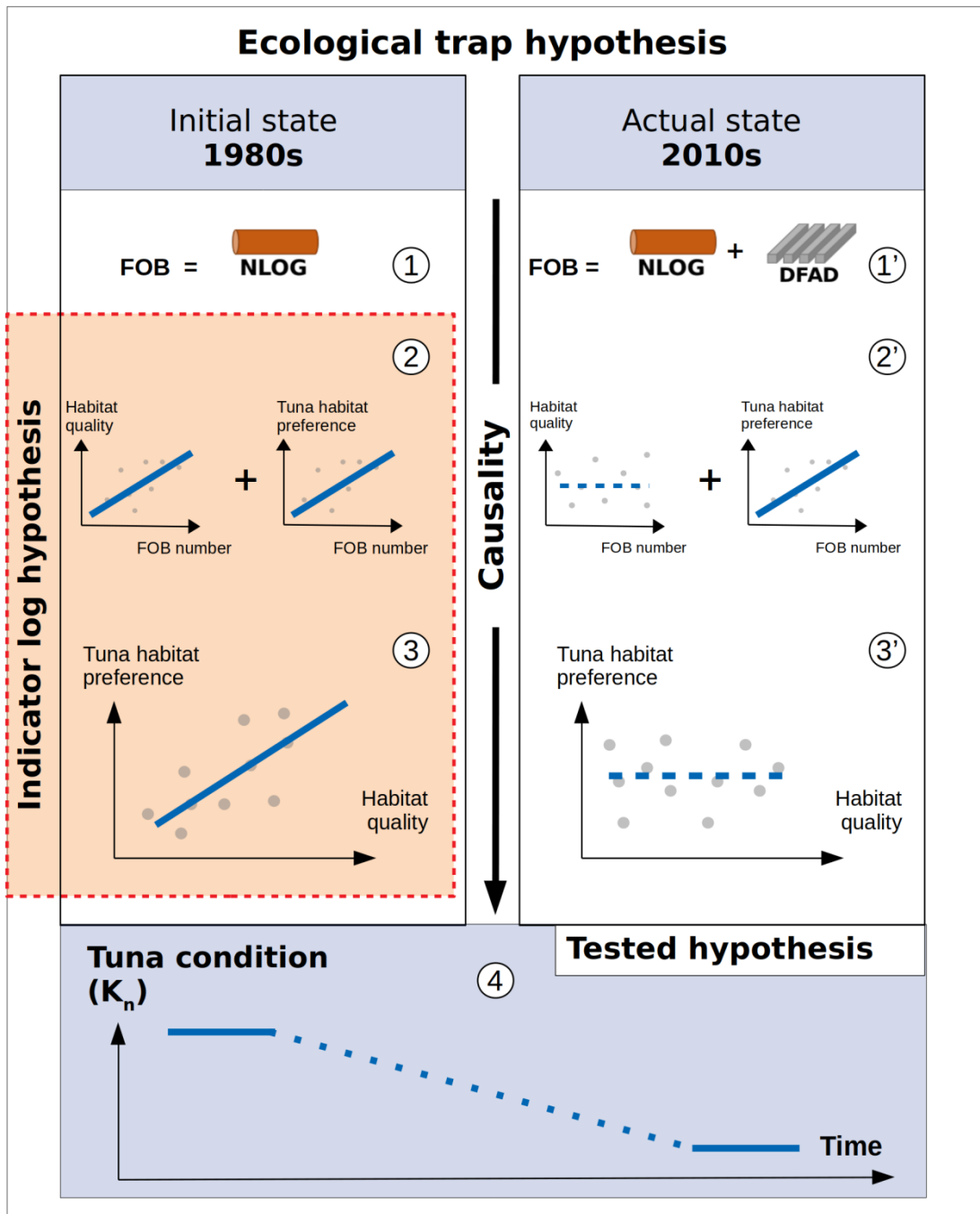
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227 **References**

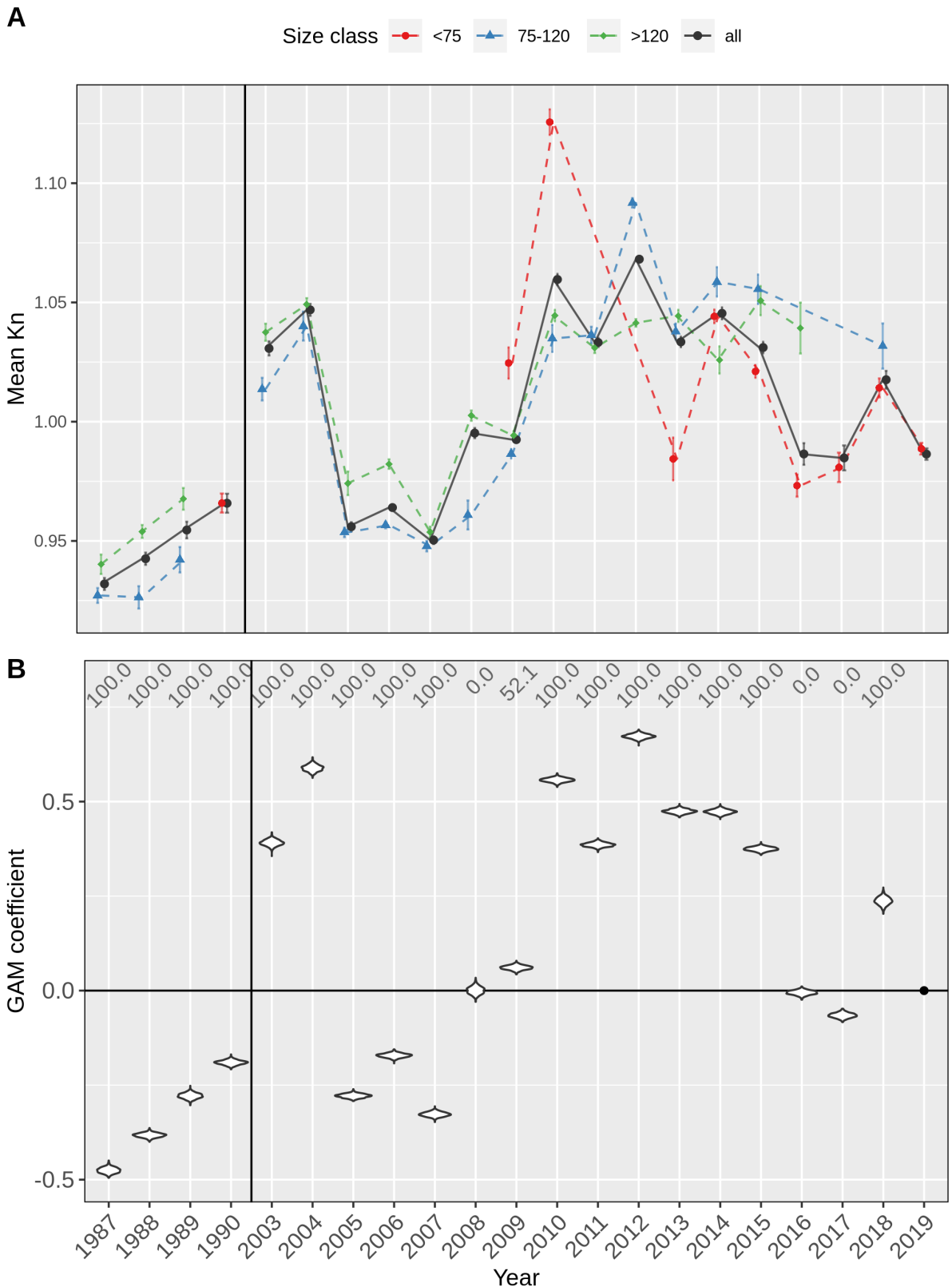
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229 **Figure 1: Schematic representation of the ecological trap hypothesis applied to**
 230 **Fish Aggregating Devices and tropical tuna.** FOB: Floating object of any kind; DFAD:
 231 Fish Aggregating Device; NLOG: Natural floating object. Under 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.