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

## Drifting Fish Aggregating Devices act as ecological traps

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

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### Abstract

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

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

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## 1. Introduction

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

Soon after their wide-scale use began, it was hypothesized that DFADs may act as “ecological traps” for tropical tunas (see Figure 1) (Marsac et al. 2000, Hallier & Gaertner 2008). An ecological trap occurs when individuals exhibit a higher or equal preference for a poor-quality habitat (*i.e.* associated with a lower fitness) over another habitat, being misled by cues that no longer correlate to habitat quality due to anthropogenic changes (Robertson & Hutto 2006, Gilroy & Sutherland 2007). This decorrelation between habitat quality and habitat selection cues ultimately leads to a reduction in the fitness of individuals (Gilroy & Sutherland 2007, Swearer et al. 2021). The hypothesis of DFADs acting as ecological traps, as it was first formulated, relies on one of the hypotheses formulated to explain tuna associative behavior: the *indicator-log* hypothesis (Fréon & Dagorn 2000), which posits that natural floating objects are 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

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

## 2. Material and Methods

### 2.1. Biological data

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

## 2.2. Relative condition factor

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

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

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

## 2.3. Statistical analysis

In order to determine if  $K_n$  decreased with the concurrent increase in DFAD numbers during the study period, a Generalized Additive Model (GAM) was performed considering  $K_n(i)$  as the dependent variable, with a Gaussian link function to account for explanatory variables. Explanatory variables were chosen to assess the effect of the fishing year (Y), season (fishing quarter, Q), size of the individuals (size class, SC), and fishing location (longitude, Lon; latitude, Lat, see details below). Longitude and latitude were included in the model as a smoothed term, and other variables were considered as 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

([https://github.com/adupaix/Historical\\_YFT\\_condition](https://github.com/adupaix/Historical_YFT_condition)  
<https://doi.org/10.5281/zenodo.6123417>).

## 3. Results

### *3.1. Mean relative condition factors ( $K_n$ )*

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

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

The most parsimonious model, selected using the AIC, included year (Y), quarter (Q), size class (SC) and the smoothed term for longitude and latitude. The selected model explained 29.2% of the deviance. The residuals displayed no spatial autocorrelation and their distribution was not significantly different from a Gaussian distribution (Figure S4 in Supplement 1). The GAM performed on the transformed relative condition factor,  $T(K_n(i))$ , showed that strongest  $T(K_n(i))$  variations were significantly correlated with fishing year (Figure 2B; Figures S5 & S6 in Supplement 1). The annual GAM coefficients displayed a non-monotonous trend which was non-decreasing in time, with 1987 being the year with 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  $K_n$  (Figures 2A&B).



## 4. Discussion

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

Data used in this study were not uniformly distributed across size classes and years (Figure S7 in Supplement 1), and tunas from both fishing modes (FOB-associated and FSC) were considered, which could influence the results (Hallier & Gaertner 2008, 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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244 and the European Union.

245 A preprint version of the article is available at:

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

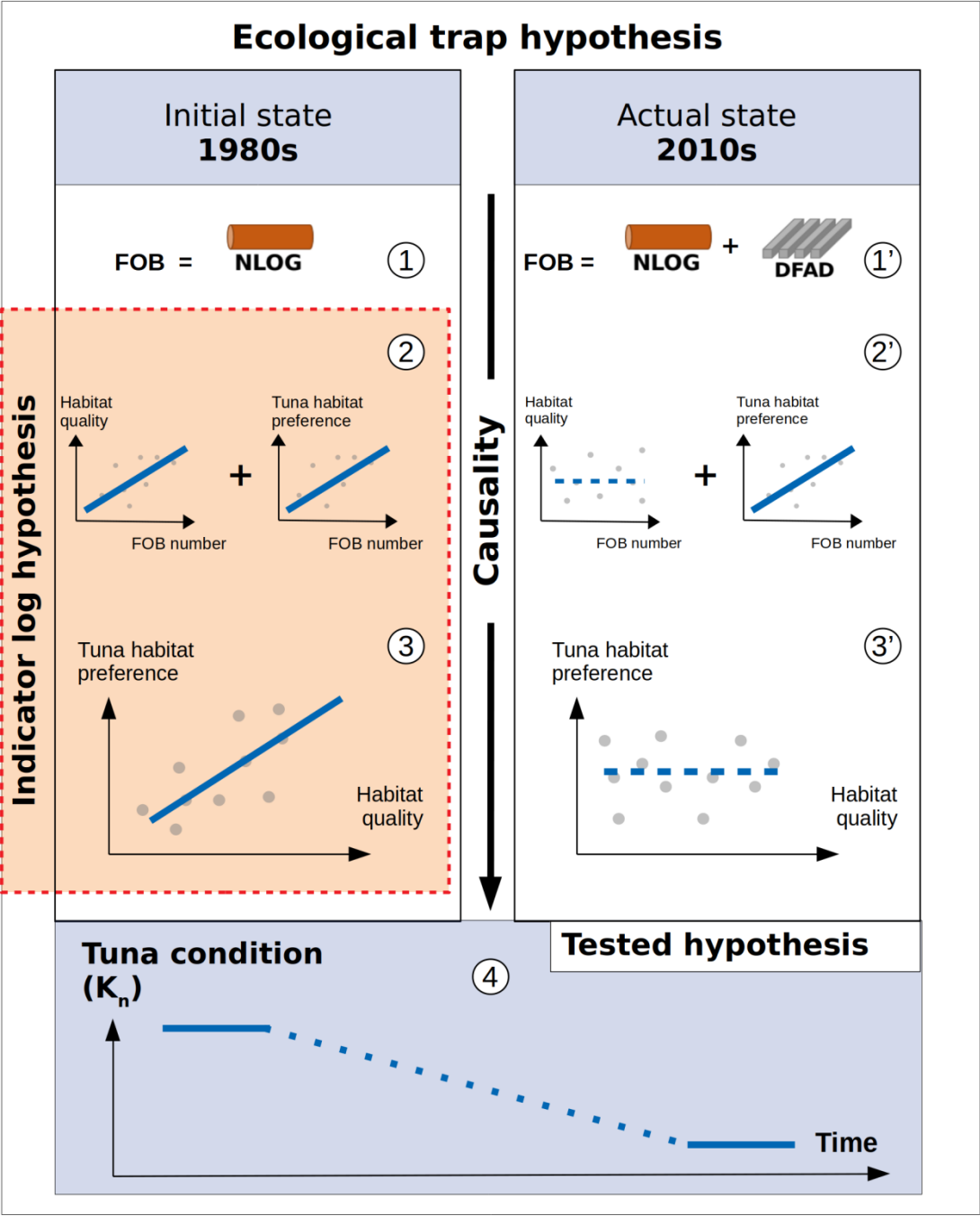
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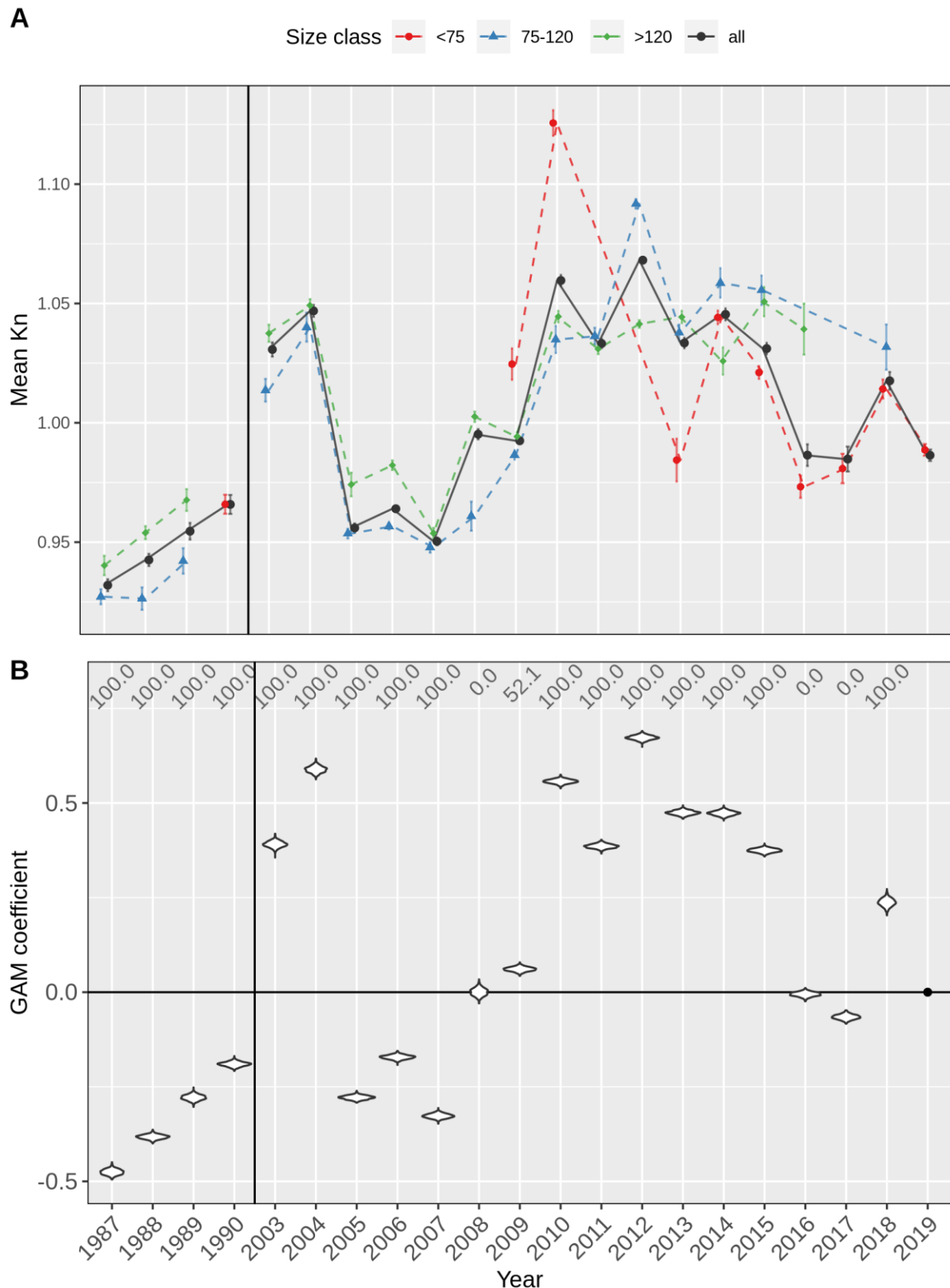


260 **Figure 1: Schematic representation of the ecological trap hypothesis applied to**  
261 **Fish Aggregating Devices and tropical tuna.** FOB: Floating object of any kind; DFAD:  
262 Fish Aggregating Device; NLOG: Natural floating object. Under this hypothesis, before  
263 DFAD introduction, when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

14

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.





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.