



HAL
open science

Assessing an ecological trap using longterm condition data: case study on yellowfin tuna and Drifting Fish Aggregating Devices (DFADs)

Amaël Dupaix, Laurent Dagorn, Antoine Duparc, Aurélie Guillou, Jean-Louis Deneubourg, Manuela Capello

► To cite this version:

Amaël Dupaix, Laurent Dagorn, Antoine Duparc, Aurélie Guillou, Jean-Louis Deneubourg, et al.. Assessing an ecological trap using longterm condition data: case study on yellowfin tuna and Drifting Fish Aggregating Devices (DFADs). 2022. hal-03690665v1

HAL Id: hal-03690665

<https://hal.science/hal-03690665v1>

Preprint submitted on 8 Jun 2022 (v1), last revised 4 Apr 2023 (v4)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Assessing an ecological trap using long-**
2 **term condition data: case study on**
3 **yellowfin tuna and Drifting Fish**
4 **Aggregating Devices (DFADs)**

5 **Authors**

6 Amaël Dupaix^{1*}, Laurent Dagorn¹, Antoine Duparc¹, Aurélie Guillou¹,
7 Jean-Louis Deneubourg², Manuela Capello¹

8 ¹: MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France

9 ²: Unit of Social Ecology, Université Libre de Bruxelles (ULB), Bruxelles,
10 Belgium

11 * corresponding author: e-mail: amael.dupaix@ens-lyon.fr

12 **Abstract**

13 Ecological traps occurs when animals choose low-quality habitats,
14 leading to a reduction in their reproduction and survival. In the marine
15 environment, this phenomenon has received little attention so far.
16 Habitat modifications are one of the major human-induced rapid
17 environmental change which could provoke such traps. Floating objects
18 are a component of the habitat of pelagic fish species, including tropical

19 tunas, which are known to associate with them. The deployment of
20 thousands of man-made floating objects (called drifting Fish Aggregating
21 Devices - DFADs) by industrial tuna fisheries worldwide over the past
22 three decades has raised concerns over the risk of DFADs forming
23 ecological traps. Relying on a three-decade time series of more than
24 25,000 length-weight samples collected in the western Indian Ocean
25 (from 1987 to 2019), we reject the hypothesis that the body condition of
26 yellowfin tuna *Thunnus albacares* decreased concurrently with the
27 increased number of DFADs. While body condition is not the only
28 variable that may indicate a decline in individual fitness, this result ruled
29 out one of the potential negative impacts of DFADs on tuna postulated by
30 a twenty-years-old hypothesis. We recommend that long-term monitoring
31 of biological and behavioral parameters of tunas be conducted to detect
32 any critical change.

33 **Keywords**

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

36 **Introduction**

37 Floating objects, such as logs or branches, are natural components of the
38 oceanic habitat of pelagic species. A large variety of these species,
39 including tropical tunas, naturally associate with floating objects,
40 however the reasons for this associative behavior are often poorly

41 understood [1,2]. Fishers targeting tropical tunas have traditionally used
42 this behavior to find and capture associated fish [3]. In the early 1980s,
43 reliance on this strategy by industrial tropical tuna purse-seine fleets
44 began to increase as the deployment of drifting Fish Aggregating Devices
45 (DFADs) became a common practice [4-6]. DFADs are typically man-
46 made rafts and are now each equipped with satellite-linked buoys so that
47 fishers can track them in the open ocean. In the Indian Ocean (IO),
48 deployment and use of DFADs began in the 1990s and has steadily
49 increased since then. Unfortunately, data on the exact number of DFADs
50 in use are scarce, and nearly absent for the first two decades. A fourfold
51 increase in the number of DFADs was estimated between 2007 and 2013,
52 with a total of 10,300 active DFADs recorded in September 2013 [7].
53 More recently, from 2012 to 2018, DFADs were demonstrated to
54 represent more than 85% of the total floating objects in the western IO
55 [8].

56 Soon after their wide-scale use began, it was hypothesized that DFADs
57 may act as “ecological traps” for tropical tunas (see Figure 1) [9,10]. An
58 ecological trap occurs when individuals select poor-quality habitats,
59 being misled by cues that no longer correlate to habitat quality due to
60 anthropogenic changes [11,12]. This decorrelation between habitat
61 quality and habitat selection cues ultimately leads to a reduction in the
62 fitness of individuals [11-13]. The hypothesis of DFADs acting as
63 ecological traps, as it was first formulated, relies on the assumption that
64 tropical tunas and other associated species originally used floating
65 objects to select good-quality habitats. For tropical tunas, the ecological

66 trap scenario relies on the so-called “indicator-log” hypothesis, stating
67 that their associative behavior has been selected because natural floating
68 objects (NLOGs), which originate from rivers, are located in productive
69 areas [1,2,14]. The massive deployment of DFADs would modify the
70 density and spatial distribution of floating objects, with potentially large
71 numbers of artificial objects occurring in areas that are not optimal for
72 tunas, creating the risk of an ecological trap. DFADs are now present in a
73 large portion of tuna habitat, they are highly attractive and could
74 severely reduce fitness, which leads to their potential to represent most
75 severe traps [15]. Hence, there is an urgent need to assess the likelihood
76 of DFADs acting as ecological traps.

77 By modifying the environment, and possibly the cues that tunas use to
78 find suitable areas (following the log-indicator hypothesis), DFADs could
79 (i) modify the large-scale movements of tunas and/or (ii) decrease the
80 body condition of tunas, impacting their fitness. Although acoustic
81 tagging studies [16–25] have revealed that anchored FADs affect the fine-
82 scale movement behavior of tunas (attracting and retaining tunas nearby
83 the FADs for periods spanning a few hours to several days), investigating
84 the effects of drifting FADs on large-scale movements is more
85 challenging. The fine-scale behavior of tunas results from an interplay
86 between environmental variables (abiotic factors, including the number
87 of floating objects), and biotic factors, including social interactions [26–
88 29]. Currently available field data do not allow for the determination of
89 exactly which drivers play the biggest role in tuna movements at large-
90 scales. Investigating the effects of DFADs on the large-scale movements

91 of tunas would theoretically be possible through a comparative approach
92 between movements prior to, and following, the wide spread use of
93 DFADs, assuming other environmental conditions have remained similar.
94 Unfortunately, such data does not exist.

95 Several studies have investigated the impacts of DFADs on tuna
96 condition and have suggested that tunas caught at DFADs were in poorer
97 condition than those caught in free-swimming schools and that they are
98 more likely to have an empty stomach when associated [9,10,30,31].
99 These results infer a negative biological consequence from the
100 association with DFADs. Robert et al. (2014) [32] found the same
101 difference between the condition of associated and non-associated tunas,
102 but in an area (the Mozambique Channel, Indian Ocean) that was rich in
103 natural floating objects and thus only marginally modified by the addition
104 of DFADs. This result led to two new interpretations of the body
105 condition differences. First, the lower condition of tuna associated with
106 floating objects could be the cause of their association, rather than the
107 consequence. In other words, tuna would associate with floating objects
108 when they are in a lower condition, as it could be indicative of a good
109 quality area or in order to form larger schools and improve their foraging
110 efficiency (see the meeting point hypothesis) [2,33]. Secondly, it is
111 possible that the association with a floating object results in a poorer
112 condition, but that the evolutionary advantage of the associative behavior
113 would not be related to short-term trophic benefits. The absence of a
114 direct, short-term benefit of associating with natural floating objects does
115 not dismiss the possibility that the associative behavior was selected

116 despite a short-term disadvantage. Tunas could recover faster after
117 associating because they are in a more productive area or in larger
118 schools. In general, ecological traps are often studied with a 'control-
119 impact' approach, which is not recommended [34]. This lead us to
120 consider the ecological trap hypothesis over a long period of time. In the
121 same way that tuna movements before and after the use of FADs should
122 be compared, the conditions of tuna before and after the use of these
123 devices should be examined.

124 One way to assess fish condition is by using indices closely related with
125 the health of individuals, stocks and populations. Fish health underlies
126 the degree of general well-being and constitutes a significant component
127 of physiological condition [35]. Condition indices of several types are
128 used when assessing fish health (or more specifically tropical tuna),
129 ranging from those based on morphometric information [36,37] to those
130 using biochemical data [38,39]. Biochemical indices, which are
131 considered better proxies of the individuals condition than those derived
132 from morphometrics, are much more costly and cumbersome to measure
133 [35]. For that reason, morphometric indices are often the best option
134 when working on historical data or trying to assess long-term variations
135 of physiological condition. Among them, the Le Cren's relative condition
136 factor (K_n), used in this study, was commonly used in studies on tunas
137 and other pelagic fish species [38-43].

138 The objective of this study was to test the hypothesis that the body
139 condition of yellowfin tuna has decreased since the wide-spread use of

140 DFADs began in the Indian Ocean. We used length and weight
141 measurements to calculate Le Cren's K_n , and investigated the temporal
142 evolution of the body condition of yellowfin tuna (*Thunnus albacares*)
143 from 1987 to 2019 in the Indian Ocean. Using a Generalized Additive
144 Model, we tested the variations of K_n accounting for catch location,
145 season and size class. We expected, after taking the effect of these other
146 variables into consideration, that the condition factor of yellowfin tuna
147 would decrease during the study period (Figure 1).

148 **Material and Methods**

149 **Biological data**

150 A total of 25,914 yellowfin tuna (*Thunnus albacares*) were sampled from
151 1987 to 2019 in the Indian Ocean Tuna canning factory (IOT) in Victoria,
152 Seychelles [44]. All the sampled fish were caught by purse seine vessels
153 in the western Indian Ocean (details of the sample sizes are provided in
154 Tables S1 & S2). The total weight (W) of the individuals and their fork
155 length (FL) were measured. For each sampled tuna, the fishing vessel
156 and the fishing trip were recorded, but not the specific fishing set from
157 which it was caught, which meant that the exact fishing date and location
158 were unknown (see statistical analyses section for details on how the
159 uncertainty on location and date was managed). The year (Y) and quarter
160 (Q) of the catch of each tuna were estimated from the middle of interval
161 covered by the fishing trip dates. The quarters were defined to be
162 synchronous with the general movement of the fleet, fishing seasons and

163 areas [8,45]: Q1, December to February; Q2, March to May; Q3, June to
164 August; and Q4, September to November. The fishing mode (M) - either
165 fishing on floating object-associated school (FOB) or on free school (FSC)
166 - was also defined, when available (6,615 yellowfin tuna). The total range
167 of FL was divided in three intervals, defining size classes (SC): small
168 (<75cm), medium (75-120cm) and large (>120cm).

169 **Relative condition factor**

170 We aimed to investigate changes in the condition factor of yellowfin tuna
171 throughout the study period and how variations related to a range of
172 explanatory variables. Firstly, to calculate the theoretical weight of
173 individuals (W_{th}), FL and W measures were used to estimate the
174 parameters of the length-weight allometric relationship, using the
175 theoretical power-law equation of $W_{th} = a FL^b$. Details on the fit of this
176 power-law are presented in Supplementary Material 1. Secondly, for
177 each individual fish (i), the relative condition factor [42] was calculated
178 as follows:

$$179 \quad K_n(i) = \frac{W(i)}{W_{th}(i)}$$

180 where $W_{th}(i)$ is the theoretical weight of individual (i) calculated from
181 length-weight allometric relationship coefficients according to FL(i) and
182 $W(i)$ is the measured total weight. By definition, K_n measures the
183 deviation of an individual from the weight of a mean individual of the
184 same length. For the remainder of the text, the relative condition factor

185 of one individual is denoted as $K_n(i)$, while the mean relative condition
186 factor calculated for a group of individuals is denoted as K_n .

187 **Statistical analysis**

188 In order to determine if K_n decreased with the concurrent increase in
189 DFAD numbers during the study period, a Generalized Additive Model
190 (GAM) was performed, with a Gaussian link function to account for other
191 explanatory variables. Explanatory variables were chosen to assess the
192 effect of the fishing year (Y), season (fishing quarter, Q), size of the
193 individuals (size class, SC), and fishing location (longitude, Lon; latitude,
194 Lat). Longitude and latitude were included in the model as a smoothed
195 term, and other variables were considered as factors.

196 Because K_n is the ratio of two correlated random variables (Pearson's
197 correlation coefficient between W and W_{th} , Pearson's $\rho = 0.99$), it did not
198 follow a normal distribution and displayed overdispersion [46]. For this
199 reason, and because it did not change the interpretation of the GAM
200 results (see Figure S2), we transformed the K_n using a Geary-Hinkley
201 transformation before performing the GAM [47]. The transformed $K_n(i)$,
202 noted $T(K_n(i))$ was obtained as follows:

$$203 \quad T(K_n(i)) = \frac{\overline{W}_{th} \times K_n(i) - \overline{W}}{\sqrt{\sigma_{th}^2 K_n(i)^2 - 2\rho\sigma\sigma_{th}K_n(i) + \sigma^2}}$$

204 where $K_n(i)$ is the relative condition factor of individual i ; \overline{W} is the mean
205 measured weight, and σ its standard deviation; \overline{W}_{th} is the mean
206 theoretical weight, and σ_{th} its standard deviation. Geary (1930) [47]
207 demonstrated that $T(K_n)$ is normally distributed with mean zero and

208 standard deviation unity. Generalized Additive Models were performed
209 on $T(K_n)$. As the fishing mode was only available for a limited portion of
210 the dataset it was not considered in the GAM. Moreover, a
211 complementary analysis showed that fishing mode, size class and their
212 interaction with other explanatory variables did not impact the main
213 results of the study (see Figures S3 & S4).

214 As specified above, the exact geographic coordinates were not available
215 for most of the sampled fish. Hence, a bootstrap process was applied: a
216 dataset was generated by sampling one set of coordinates from all the
217 fishing sets of the trip for each individual and a GAM was then
218 performed. This operation was repeated 1,000 times and for every model
219 built, we selected the most parsimonious explanatory variables based on
220 the Akaike information criterion (AIC), using a stepwise selection
221 procedure and a threshold of 2. All the iterated GAM coefficients of the
222 explanatory variables considered as factors (Y, Q and SC) were averaged
223 and their standard deviation calculated. The spatial prediction of every
224 GAM was calculated and an average spatial prediction was calculated.
225 Finally, spatial autocorrelation in the residuals of each model were
226 assessed considering Moran's I and the Gaussian distribution of the
227 residuals was assessed on a quantile-quantile plot.

228 We performed all analyses using R software v.4.0.3 [48] and packages
229 *mgcv* 1.8.33 to fit general additive models [49] and *spdep* 1.1_5 to test
230 for spatial autocorrelation [50].

231 **Results**

232 **Mean relative condition factors (K_n)**

233 The mean relative condition factor value (K_n) was 1.01 ± 0.088 and mean
234 annual K_n values varied between 0.93 ± 0.064 (in 1987) and 1.07 ± 0.079
235 (in 2012). The relative condition factor displayed annual variations, with
236 low K_n values in 1987-1990 and around 2006, and the highest K_n values
237 observed around 2012 (Figure 2). The mean annual K_n displayed similar
238 variations per size class as when all the sampled fish were considered
239 together (Figure 2). No clear trend in K_n variations were observed.

240 No clear difference was observed between the relative condition factor of
241 tuna caught in free schools (FSC) and FOB-associated schools (FOB,
242 Figure 3). The mean K_n by fishing mode displayed a similar pattern as the
243 mean annual K_n obtained when all sampled fish were considered
244 together.

245 **Yearly variations of K_n**

246 The most parsimonious model, selected using the AIC, included year (Y),
247 quarter (Q), size class (SC) and the smoothed term for longitude and
248 latitude. The selected model explained 29.2% of the deviance. The
249 residuals displayed no spatial autocorrelation and their distribution was
250 not significantly different from a Gaussian distribution (Figure S5). The
251 GAM performed on the transformed relative condition factor ($T(K_n)$)
252 showed that strongest $T(K_n)$ variations were significantly correlated with
253 fishing year (Figure 4; Figure S6 & S7). The annual GAM coefficients

254 displayed a non-monotonous trend which was non-decreasing in time,
255 with 1987 being the year with the lowest coefficient (-0.475 ± 0.007)
256 while 2012 was the year with the highest coefficient (0.673 ± 0.006 ;
257 Figure 4). The observed patterns were similar to those displayed when
258 considering only the mean annual K_n (Figures 2&4).

259 **Discussion**

260 The main hypothesis tested in this study was that the introduction of
261 DFADs would have negatively impacted the condition of tunas, following
262 roughly three decades of DFAD deployment in the ocean (Figure 1). The
263 relative condition factor (K_n) values obtained here did not display any
264 clear temporal trend over the study period (Figures 2 & 4), which goes
265 against the tested hypothesis. Hence, the present study concludes that
266 under the conditions encountered by yellowfin tuna in the Indian Ocean
267 during the last three decades, the addition of DFADs to the pelagic
268 environment has not led to the creation of an ecological trap for this
269 species.

270 However, several precautions must be considered when interpreting this
271 result. Firstly, as stated above, the study is valid only for the conditions
272 experienced by yellowfin tuna in the western Indian Ocean in the last
273 three decades. Furthermore, the habitat change induced by DFADs could
274 also impact other biological processes, such as natural mortality, growth
275 rate [9,51], or reproduction [52,53], that could not be assessed through
276 our biological index. For example, if the growth rate of tunas is

277 negatively altered by DFADs [see 9], a tuna of a given size in the 1980s
278 could be younger than a tuna of the same size in the 2010-2020s, with
279 the two individuals having a similar physiological condition.

280 Data used in this study were not uniformly distributed across size classes
281 and years (Figure S6). Such uneven size class distribution, which was
282 primarily a result of sampling effort, could influence the results.
283 However, Wang et al. (2002) [54] found no relationship between the size
284 and the condition factor of yellowfin and bigeye tunas, and Diaha et al.
285 (2015) [55] found no correlation between the condition factor and the
286 maturity stage. We also performed a GAM on data of each size class
287 independently, and the main result of the study remained unchanged: no
288 decreasing trend of physiological condition was observed concurrently
289 with increasing DFAD deployments (Figure S3). Therefore, we are
290 confident that the methodology used here did not suffer from any bias
291 induced through the uneven sampling.

292 Our study is based on the assumption that, since the late 1980s, the
293 number of DFADs increased in the western IO. While assessing a time-
294 series of the exact density of DFADs is cumbersome, this assumption is
295 undeniably true [8,45,56-58]. Data on the number of DFADs are scarce
296 but the trend, although lacking in precision, was most likely increasing,
297 reaching highest density levels very recently. In the early 1990s, less
298 than 50% of purse seine sets were performed on FOB-associated schools
299 [58]. Then, two steep increases were observed, around 1996 and again
300 around 2008, and FOB-associated sets reached 75% of all the purse-seine

301 sets in the IO in 2010 [58]. Maufroy et al. (2017) [57] demonstrated that
302 between 2007 and 2013, the French fleet in the IO multiplied the number
303 of tracking buoys used by more than 5. Combining these results with the
304 percentage of DFADs that are French, estimated in Katara et al. (2018)
305 [59], suggests that the number of DFADs used by both the French and
306 Spanish fleets (the two main fleets deploying DFADs in this ocean)
307 increased during that period, but not so drastically. Moreover, the
308 authors recognize that the percentage estimation may be relatively
309 unreliable prior to 2014. From 2014 to 2018, data on DFAD deployment
310 suggest a strong increase of DFAD use [59,60]. Hence, if the exact trend
311 is unknown, studies suggest that the number of DFADs in the Indian
312 Ocean continued to increase throughout the study period [see also 8,45].
313 The conditions leading to an ecological trap might also have only been
314 reached in recent years, without being detectable in our study. This
315 highlights the need to keep developing long-term monitoring programs,
316 collecting data on DFAD densities [61] and standardized physiological
317 indicators, to study the impact of DFADs on tuna physiology.

318 Aside from the increase of DFAD density, other long-term phenomena
319 could also impact the physiology of tropical tuna. Since the 1980s,
320 climate change has already impacted tuna habitat, by inducing changes
321 in sea surface temperature or oxygen concentration, for example [62,63].
322 These impacts may have concealed the impacts of the increase in DFAD
323 density. Climate change impacts are complex and may differ from one
324 tropical tuna species to another [62,64]. Increasing water temperatures
325 can impact fish metabolism, by increasing inefficiencies in mitochondrial

326 energy transduction, meaning that fish would need to eat more to
327 achieve a particular rate of growth or energy production (Little et al.,
328 2020). Climate change is expected to provoke a poleward relocation of
329 tropical tuna habitats [65–67], and shifts in oxygen concentration may
330 provoke vertical habitat compressions [68]. Erauskin-Extramiana et al.
331 (2019) [62] projected that yellowfin tuna will become more abundant
332 under a climate change scenario (the authors used the RCP8.5 and
333 expect the same projected changes of abundance under other scenarios
334 until 2050). Hence, climate change impact on the physiological condition
335 of yellowfin tuna is complex and may have concealed a potential negative
336 impact of increasing DFAD density.

337 Most results on tropical tuna condition were obtained using
338 morphometric indicators [9,30,36,37]. These indicators should however
339 be used with caution as they do not always reflect the energy compounds
340 in the tissues [35,39,69]. Hence, while these morphometric indicators
341 can be informative [41,43], and are often the only available metrics (as
342 was the case in this study), further efforts are needed to validate them
343 against proper benchmarks [35]. Such validation could be achieved
344 through the development of experimental studies to assess variations in
345 morphometric indicators, such as Le Cren's K_n , during fasting. However,
346 in our study, a morphometric indicator (K_n) was the only available
347 indicator to test our hypothesis on historical data, as no long-term time-
348 series of biochemical indicators exist for tuna.

349 Ecological traps are likely to become more common as human-induced
350 environmental changes increase, and they have important implications
351 for the management of animal populations [15,34]. The hypothesis that
352 DFADs could act as ecological traps was developed over 20 years ago
353 [10]. It suggests that, by modifying the density and spatial distribution of
354 FOBs, the massive deployment of DFADs could retain or transport
355 individuals to areas that are ecologically unsuitable for them [6,10]. By
356 demonstrating the absence of any decreasing trend in yellowfin tuna
357 condition concurrent to the observed increasing DFAD density in the
358 Indian Ocean during the past three decades, this study rejects the
359 ecological trap hypothesis as it was originally formulated. However, as
360 explained above, DFADs can impact the biology of tuna in a variety of
361 complex ways, and this impact can be intertwined with the effects of
362 other factors such as climate change. Therefore, it is necessary to
363 establish long-term monitoring programs to track (i) habitat changes, (ii)
364 temporal variations of behavioral features in tuna, such as large-scale
365 movements and schooling behavior, and (iii), temporal variations of
366 physiological parameters in tuna.

367 **Data availability statement**

368 Data used in this study is available in Guillou *et al.* (2021; [https://doi.org/](https://doi.org/10.17882/73500)
369 [10.17882/73500](https://doi.org/10.17882/73500)) [44].

370 The scripts used for the study are available on GitHub:
371 https://github.com/adupaix/Historical_YFT_condition
372 <https://doi.org/10.5281/zenodo.6123417>).

373 **Acknowledgments**

374 The authors sincerely thank IRD's Ob7—"Observatoire des Ecosystèmes
375 Pélagiques Tropicaux Exploités"—in charge of the observer data
376 collection, processing, management, and for sharing the data used in this
377 study; M. Simier for her inputs on statistical analyses; J.D. Filmalter for
378 his proofreading.

379 **References**

1. Castro JJ, Santiago JA, Santana-Ortega AT. 2002 A general theory on fish aggregation to floating objects: An alternative to the meeting point hypothesis. *Rev. Fish Biol. Fish.* **11**, 255–277.
2. Freon P, Dagorn L. 2000 Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. *Rev. Fish Biol. Fish.* **10**, 183–207. (doi:10.1023/A:1016666108540)
3. Dempster T, Taquet M. 2004 Fish aggregation device (FAD) research: gaps in current knowledge and future directions for ecological studies. *Rev. Fish Biol. Fish.* **14**, 21–42.
4. Dagorn L, Holland KN, Restrepo V, Moreno G. 2013 Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? *Fish Fish.* **14**, 391–415. (doi:10.1111/j.1467-2979.2012.00478.x)
5. Davies TK, Mees CC, Milner-Gulland EJ. 2014 Modelling the spatial behaviour of a tropical tuna purse seine fleet. *PloS One* **9**, e114037. (doi:10.1371/journal.pone.0114037)
6. Fonteneau A, Chassot E, Bodin N. 2013 Global spatio-temporal patterns in tropical tuna purse seine fisheries on drifting fish aggregating devices (DFADs): Taking a historical perspective to inform current challenges. *Aquat. Living Resour.* **26**, 37–48. (doi:https://doi.org/10.1051/alr/2013046)

7. Maufroy A, Chassot E, Joo R, Kaplan DM. 2015 Large-Scale Examination of Spatio-Temporal Patterns of Drifting Fish Aggregating Devices (dFADs) from Tropical Tuna Fisheries of the Indian and Atlantic Oceans. *PLOS ONE* **10**, e0128023. (doi:10.1371/journal.pone.0128023)
8. Dupaix A, Capello M, Lett C, Andrello M, Barrier N, Viennois G, Dagorn L. 2021 Surface habitat modification through industrial tuna fishery practices. *ICES J. Mar. Sci.* **78**, 3075–3088. (doi:10.1093/icesjms/fsab175)
9. Hallier J-P, Gaertner D. 2008 Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Mar. Ecol. Prog. Ser.* **353**, 255–264. (doi:10.3354/meps07180)
10. Marsac F, Fonteneau A, Ménard F. 2000 Drifting FADs used in tuna fisheries: an ecological trap? *Pêche Thonière Dispos. Conc. Poissons* **28**, 537–552.
11. Battin J. 2004 When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. *Conserv. Biol.* **18**, 1482–1491. (doi:https://doi.org/10.1111/j.1523-1739.2004.00417.x)
12. Gilroy J, Sutherland W. 2007 Beyond ecological traps: perceptual errors and undervalued resources. *Trends Ecol. Evol.* **22**, 351–356. (doi:10.1016/j.tree.2007.03.014)
13. Swearer SE, Morris RL, Barrett LT, Sievers M, Dempster T, Hale R. 2021 An overview of ecological traps in marine ecosystems. *Front. Ecol. Environ.* **19**, 234–242. (doi:10.1002/fee.2322)
14. Hall MA. 1992 The association of tunas with floating objects and dolphins in the Eastern Pacific Ocean. 1992. Part VII. Some hypotheses on the mechanisms governing the association of tunas with floating objects and dolphins. Inter-American Tropical Tuna Commission.
15. Hale R, Treml EA, Swearer SE. 2015 Evaluating the metapopulation consequences of ecological traps. *Proc. R. Soc. B Biol. Sci.* **282**, 20142930. (doi:10.1098/rspb.2014.2930)
16. Cayre P. 1991 Behaviour of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. *Aquat. Living Resour.* **4**, 1–12. (doi:10.1051/alr/1991000)
17. Dagorn L, Josse E, Bach P. 2000 Individual differences in horizontal movements of yellowfin tuna (*Thunnus albacares*) in nearshore areas in French Polynesia, determined using ultrasonic telemetry. *Aquat. Living Resour.* **13**, 193–202. (doi:10.1016/S0990-7440(00)01063-9)

18. Dagorn L, Holland KN, Itano DG. 2007 Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). *Mar. Biol.* **151**, 595–606.
19. Govinden R, Jauhary R, Filmalter J, Forget F, Soria M, Adam S, Dagorn L. 2013 Movement behaviour of skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tuna at anchored fish aggregating devices (FADs) in the Maldives, investigated by acoustic telemetry. *Aquat. Living Resour.* **26**, 69–77. (doi:10.1051/alr/2012022)
20. Holland KN, Brill RW, Chang RKC. 1990 Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish. Bull.* **88**, 493–507.
21. Mitsunaga Y, Endo C, Anraku K, Selorio CM, Babaran RP. 2012 Association of early juvenile yellowfin tuna *Thunnus albacares* with a network of payaos in the Philippines. *Fish. Sci.* **78**, 15–22. (doi:10.1007/s12562-011-0431-y)
22. Ohta I, Kakuma S. 2005 Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. *Mar. Biol.* **146**, 581–594.
23. Robert M, Dagorn L, Deneubourg JL, Itano D, Holland K. 2012 Size-dependent behavior of tuna in an array of fish aggregating devices (FADs). *Mar. Biol.* **159**, 907–914.
24. Robert M, Dagorn L, Filmalter JD, Deneubourg J-L, Itano D, Holland K. 2013 Intra-individual behavioral variability displayed by tuna at fish aggregating devices (FADs). *Mar. Ecol. Prog. Ser.* **484**, 239–247.
25. Rodriguez-Tress P, Capello M, Forget F, Soria M, Beeharry SP, Dussooa N, Dagorn L. 2017 Associative behavior of yellowfin *Thunnus albacares*, skipjack *Katsuwonus pelamis*, and bigeye tuna *T. obesus* at anchored fish aggregating devices (FADs) off the coast of Mauritius. *Mar. Ecol. Prog. Ser.* **570**, 213–222.
26. Capello M, Soria M, Cotel P, Deneubourg J-L, Dagorn L. 2011 Quantifying the Interplay between Environmental and Social Effects on Aggregated-Fish Dynamics. *PLoS ONE* **6**, e28109. (doi:10.1371/journal.pone.0028109)
27. Doray M, Petitgas P, Nelson L, Mahévas S, Josse E, Reynal L. 2009 The influence of the environment on the variability of monthly tuna biomass around a moored, fish-aggregating device. *ICES J. Mar. Sci.* **66**, 1410–1416.
28. Druon JN, Chassot E, Floch L, Maufroy A. 2015 Preferred habitat of tropical tuna species in the Eastern Atlantic and Western Indian

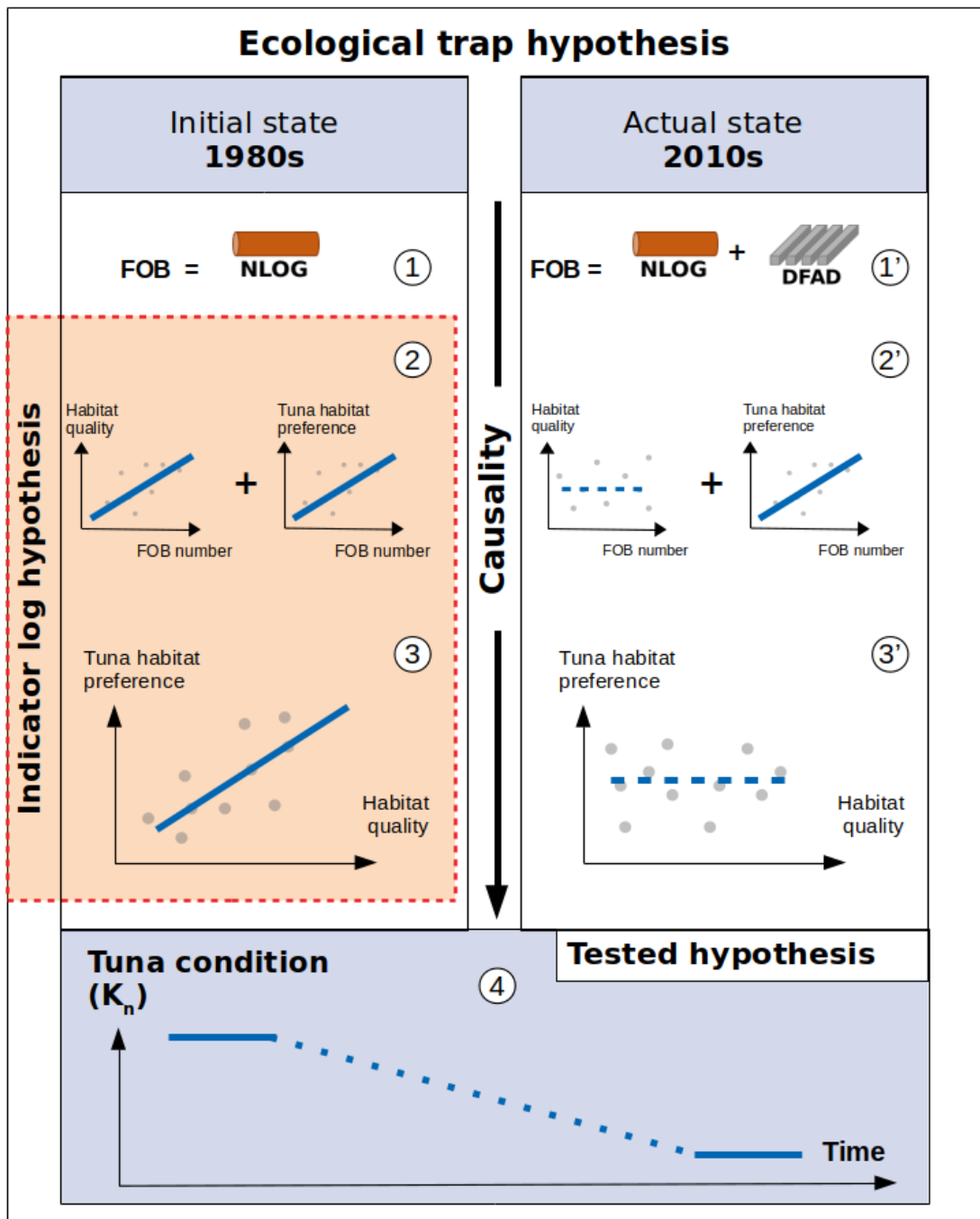
Oceans: a comparative analysis between FAD-associated and free-swimming schools. *IOTC-WPTT-17* **31**.

29. Pérez G. 2021 Effets du nombre d'objets flottants sur le comportement des thons tropicaux. PhD, Université de Montpellier.
30. Jaquemet S, Potier M, Ménard F. 2011 Do drifting and anchored Fish Aggregating Devices (FADs) similarly influence tuna feeding habits? A case study from the western Indian Ocean. *Fish. Res.* **107**, 283–290. (doi:10.1016/j.fishres.2010.11.011)
31. Ménard F, Fonteneau A, Gaertner D, Nordstrom V, Stéquert B, Marchal E. 2000 Exploitation of small tunas by a purse-seine fishery with fish aggregating devices and their feeding ecology in an eastern tropical Atlantic ecosystem. *ICES J. Mar. Sci.* **57**, 525–530. (doi:https://doi.org/10.1006/jmsc.2000.0717)
32. Robert M, Dagorn L, Bodin N, Pernet F, Arsenault-Pernet E-J, Deneubourg J-L. 2014 Comparison of condition factors of skipjack tuna (*Katsuwonus pelamis*) associated or not with floating objects in an area known to be naturally enriched with logs. *Can. J. Fish. Aquat. Sci.* (doi:10.1139/cjfas-2013-0389)
33. Dagorn L, Fréon P. 1999 Tropical tuna associated with floating objects: a simulation study of the meeting point hypothesis. *Can. J. Fish. Aquat. Sci.* **56**, 984–993.
34. Hale R, Swearer SE. 2016 Ecological traps: current evidence and future directions. *Proc. R. Soc. B Biol. Sci.* **283**, 20152647. (doi:10.1098/rspb.2015.2647)
35. Lloret J, Shulman GE, Love RM. 2014 *Condition and health indicators of exploited marine fishes*. Chichester, West Sussex ; Hoboken, NJ: Wiley Blackwell.
36. Ashida H, Tanabe T, Suzuki N. 2017 Difference on reproductive trait of skipjack tuna *Katsuwonus pelamis* female between schools (free vs FAD school) in the tropical western and central Pacific Ocean. *Environ. Biol. Fishes* **100**, 935–945.
37. Zudaire I, Murua H, Grande M, Bodin N. 2013 Reproductive potential of Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean. *Fish. Bull.* **111**, 252–264. (doi:10.7755/FB.111.3.4)
38. Brosset P *et al.* 2015 Measurement and analysis of small pelagic fish condition: A suitable method for rapid evaluation in the field. *J. Exp. Mar. Biol. Ecol.* **462**, 90–97. (doi:10.1016/j.jembe.2014.10.016)
39. Sardenne F, Chassot E, Fouché E, Ménard F, Lucas V, Bodin N. 2016 Are condition factors powerful proxies of energy content in wild

- tropical tunas? *Ecol. Indic.* **71**, 467–476.
(doi:10.1016/j.ecolind.2016.06.031)
40. Feuilleley G, Fromentin J-M, Stemmann L, Demarcq H, Estournel C, Saraux C. 2020 Concomitant changes in the environment and small pelagic fish community of the Gulf of Lions. *Prog. Oceanogr.* **186**, 102375. (doi:10.1016/j.pocean.2020.102375)
41. Goldstein J, Heppell S, Cooper A, Brault S, Lutcavage M. 2007 Reproductive status and body condition of Atlantic bluefin tuna in the Gulf of Maine, 2000–2002. *Mar. Biol.* **151**, 2063–2075.
(doi:10.1007/s00227-007-0638-8)
42. Le Cren ED. 1951 The Length-Weight Relationship and Seasonal Cycle in Gonad Weight and Condition in the Perch (*Perca fluviatilis*). *J. Anim. Ecol.* **20**, 201. (doi:10.2307/1540)
43. Ohshimo S, Sato T, Okochi Y, Ishihara Y, Tawa A, Kawazu M, Hiraoka Y, Ashida H, Suzuki N. 2018 Long-term change in reproductive condition and evaluation of maternal effects in Pacific bluefin tuna, *Thunnus orientalis*, in the Sea of Japan. *Fish. Res.* **204**, 390–401.
(doi:10.1016/j.fishres.2018.03.017)
44. Guillou A *et al.* 2021 Tunabio: biological traits of tropical tuna and bycatch species caught by purse seine fisheries in the Western Indian and Eastern Central Atlantic Oceans. (doi:10.17882/73500)
45. Dagorn L, Bez N, Fauvel T, Walker E. 2013 How much do fish aggregating devices (FADs) modify the floating object environment in the ocean? *Fish. Oceanogr.* **22**, 147–153. (doi:10.1111/fog.12014)
46. Bolger T, Connolly PL. 1989 The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* **34**, 171–182.
(doi:https://doi.org/10.1111/j.1095-8649.1989.tb03300.x)
47. Geary RC. 1930 The Frequency Distribution of the Quotient of Two Normal Variates. *J. R. Stat. Soc.* **93**, 442. (doi:10.2307/2342070)
48. R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
49. Wood SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. B* **73**, 3–36.
50. Bivand RS, Pebesma E, Gómez-Rubio V. 2013 *Applied Spatial Data Analysis with R*. New York, NY: Springer New York. (doi:10.1007/978-1-4614-7618-4)

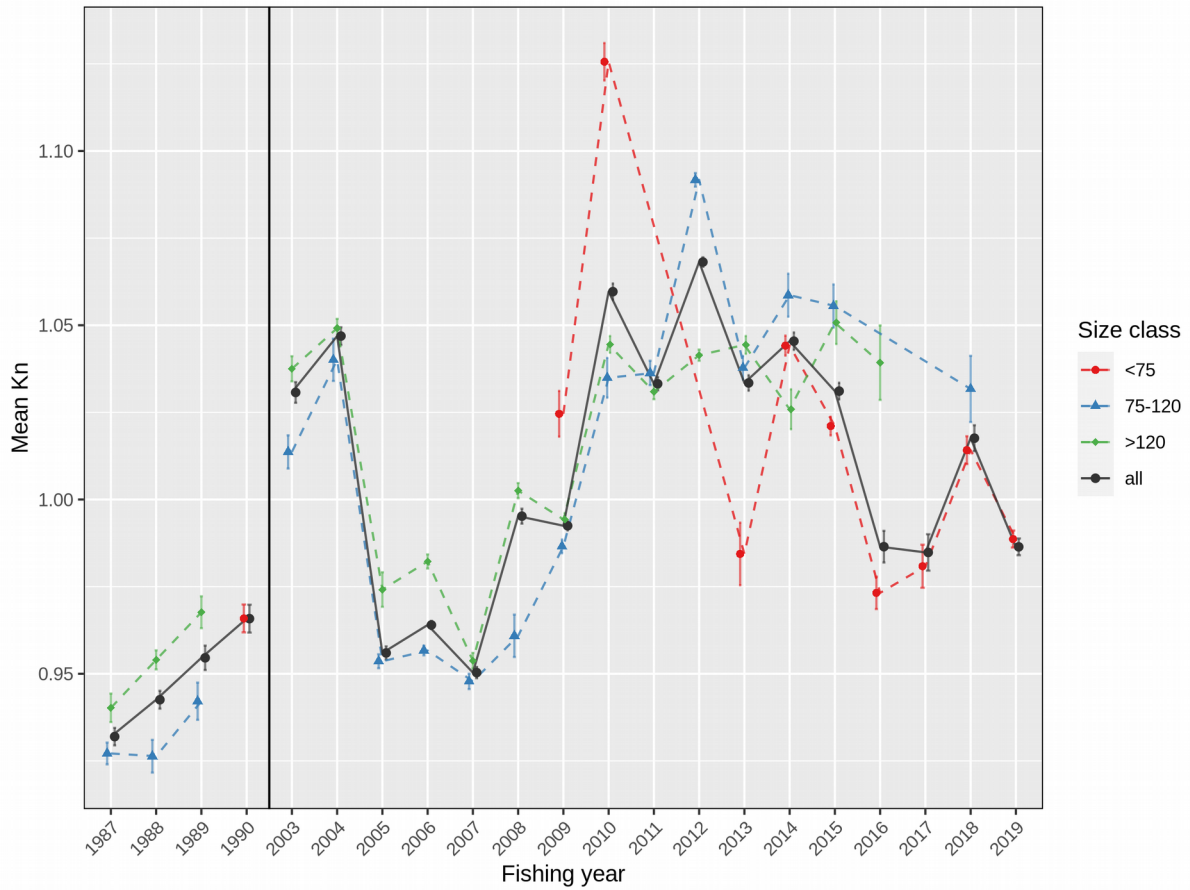
51. Rodriguez-Dominguez A, Connell SD, Leung JYS, Nagelkerken I. 2019 Adaptive responses of fishes to climate change: Feedback between physiology and behaviour. *Sci. Total Environ.* **692**, 1242-1249. (doi:10.1016/j.scitotenv.2019.07.226)
52. Zudaire I, Murua H, Grande M, Pernet F, Bodin N. 2014 Accumulation and mobilization of lipids in relation to reproduction of yellowfin tuna (*Thunnus albacares*) in the Western Indian Ocean. *Fish. Res.* **160**, 50-59.
53. Zudaire I, Murua H, Grande M, Goñi N, Potier M, Ménard F, Chassot E, Bodin N. 2015 Variations in the diet and stable isotope ratios during the ovarian development of female yellowfin tuna (*Thunnus albacares*) in the Western Indian Ocean. *Mar. Biol.* **162**, 2363-2377. (doi:10.1007/s00227-015-2763-0)
54. Wang S-B, Chang F-C, Wang S-H. 2002 Some Biological Parameters of Bigeye and Yellowfin Tunas Distributed in Surrounding Waters of Taiwan. p. 13.
55. Diaha N *et al.* 2015 Present and future of reproductive biology studies of yellowfin tuna (*Thunnus albacares*) in the eastern Atlantic Ocean. *Collect. Vol. Sci. Pap. ICCAT* **71**, 489-509.
56. Gershman D, Nickson A, O'Toole M. 2015 Estimating the Use of FADs Around the World.
57. Maufroy A, Kaplan DM, Bez N, De Molina AD, Murua H, Floch L, Chassot E. 2017 Massive increase in the use of drifting Fish Aggregating Devices (dFADs) by tropical tuna purse seine fisheries in the Atlantic and Indian oceans. *ICES J. Mar. Sci.* **74**, 215-225. (doi:10.1093/icesjms/fsw175)
58. Scott GP, Lopez J. 2014 The Use of Fads in Tuna Fisheries.
59. Katara I *et al.* 2018 Standardisation of yellowfin tuna CPUE for the EU purse seine fleet operating in the Indian Ocean. *IOTC-2018-WPTT20-36* , 23.
60. Floch L, Depetris M, Dewals P, Duparc A. 2019 Statistics of the French Purse Seine Fishing Fleet Targeting Tropical Tunas in the Indian Ocean (1981-2018). *Rep. 21st Sess. IOTC Work. Party Trop. Tunas* , 1-27.
61. IOTC. 2021 Instrumented buoy data (Jan 2020 - May 2021).
62. Erauskin-Extramiana M, Arrizabalaga H, Hobday AJ, Cabré A, Ibaibarriaga L, Arregui I, Murua H, Chust G. 2019 Large-scale distribution of tuna species in a warming ocean. *Glob. Change Biol.* **25**, 2043-2060. (doi:10.1111/gcb.14630)

63. Marsac F. 2017 The Seychelles Tuna Fishery and Climate Change. In *Climate Change Impacts on Fisheries and Aquaculture* (eds BF Phillips, M Pérez-Ramírez), pp. 523–568. Chichester, UK: John Wiley & Sons, Ltd. (doi:10.1002/9781119154051.ch16)
64. Arrizabalaga H *et al.* 2015 Global habitat preferences of commercially valuable tuna. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **113**, 102–112. (doi:10.1016/j.dsr2.2014.07.001)
65. Dueri S, Bopp L, Maury O. 2014 Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. *Glob. Change Biol.* **20**, 742–753. (doi:https://doi.org/10.1111/gcb.12460)
66. Lehodey P, Senina I, Calmettes B, Hampton J, Nicol S. 2013 Modelling the impact of climate change on Pacific skipjack tuna population and fisheries. *Clim. Change* **119**, 95–109. (doi:10.1007/s10584-012-0595-1)
67. Nataniel A, Pennino MG, Lopez J, Soto M. 2021 Modelling the impacts of climate change on skipjack tuna (*Katsuwonus pelamis*) in the Mozambique Channel. *Fish. Oceanogr.* **n/a**. (doi:10.1111/fog.12568)
68. Mislán K a. S, Deutsch CA, Brill RW, Dunne JP, Sarmiento JL. 2017 Projections of climate-driven changes in tuna vertical habitat based on species-specific differences in blood oxygen affinity. *Glob. Change Biol.* **23**, 4019–4028. (doi:10.1111/gcb.13799)
69. Goñi N, Arrizabalaga H. 2010 Seasonal and interannual variability of fat content of juvenile albacore (*Thunnus alalunga*) and bluefin (*Thunnus thynnus*) tunas during their feeding migration to the Bay of Biscay. *Prog. Oceanogr.* **86**, 115–123. (doi:10.1016/j.pocean.2010.04.016)

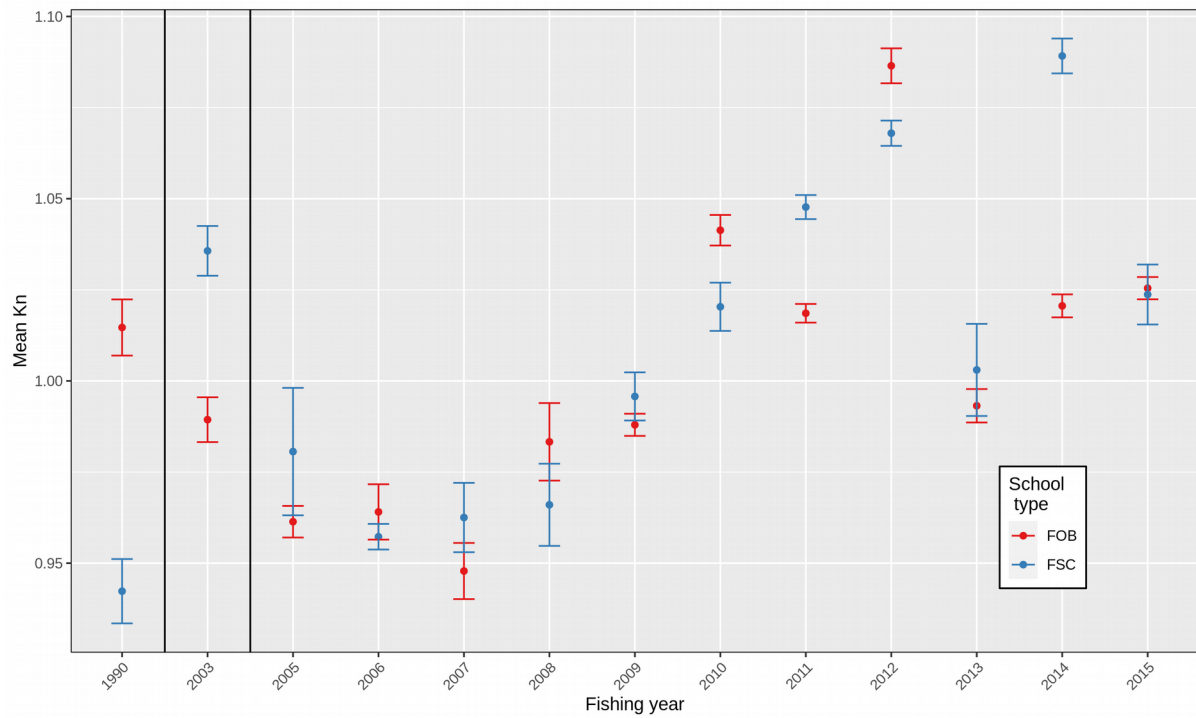


381 **Figure 1: Schematic representation of the ecological trap**
 382 **hypothesis applied to Fish Aggregating Devices and tropical tuna.**
 383 **FOB: Floating object of any kind; DFAD: Fish Aggregating Device; NLOG:**

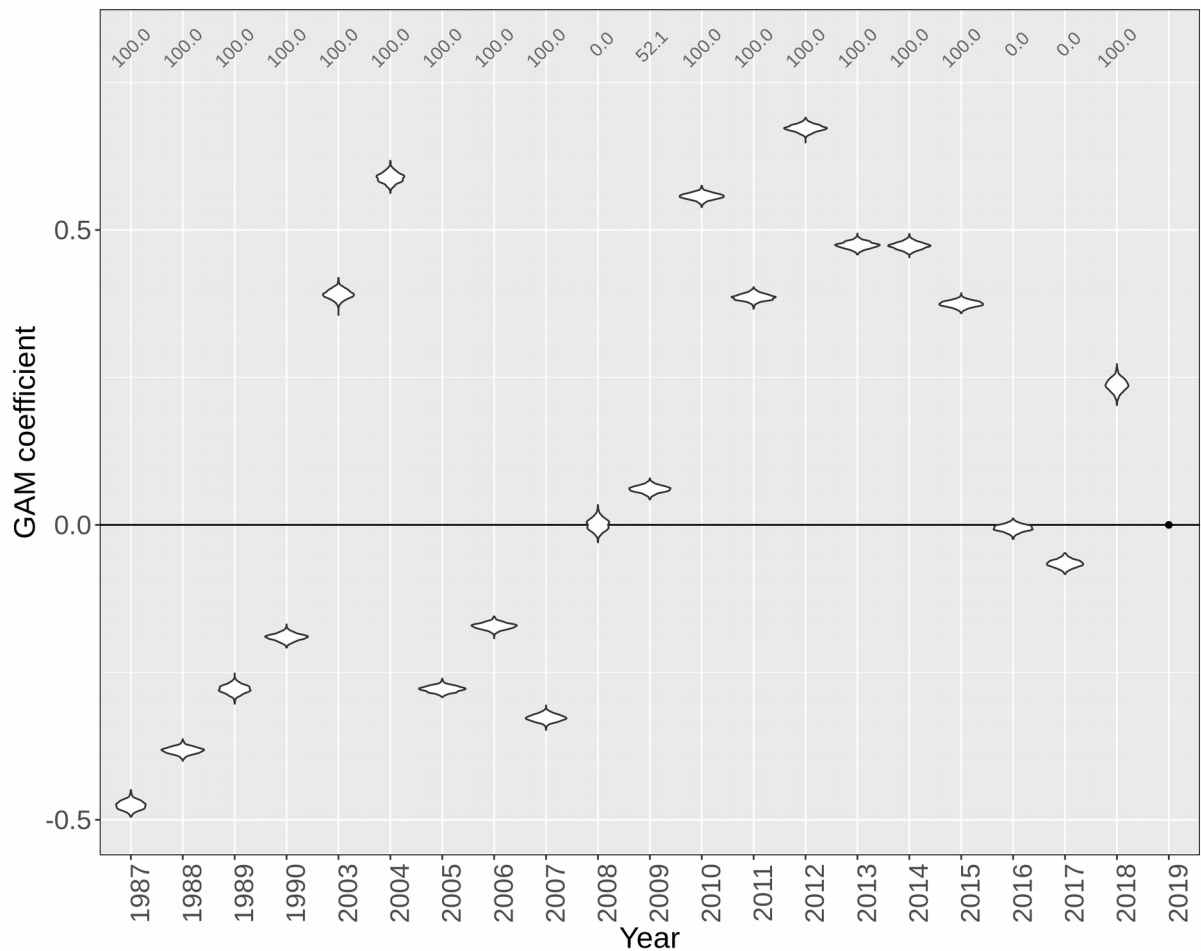
384 Natural floating object. Under this hypothesis, before DFAD introduction,
385 when only NLOGs were present (1), floating objects were distributed in
386 productive areas (2), hence tunas, which associate with floating objects,
387 preferred high quality habitats (3). Since DFAD introduction (1'), the
388 distribution of floating objects has been modified and is no longer
389 correlated with habitat quality (2'). Hence, tunas, which still associate
390 with floating objects, do not select high quality habitat anymore (3'). As a
391 consequence of this habitat modification, the physiological condition of
392 tunas would have decreased since the 1980s (4). Preference is defined
393 here as "the likelihood of a resource being chosen if offered as an option
394 with other available options" (Johnson 1980; Robertson and Hutto 2006).



395 **Figure 2: Mean relative condition factor per year.** The K_n is
 396 represented for all individuals (all, black circles), for small individuals
 397 (<75, red circles), medium-size individuals (75-120, blue triangles) and
 398 large individuals (>120, green diamonds). Values are represented only
 399 when more than 50 individuals of the given class were measured. Error
 400 bars represent the standard error of the mean.



401 **Figure 3: Mean relative condition factor per school type and per**
 402 **year.** (A): Mean K_n values per school type: FOB-associated schools (FOB)
 403 in red and free schools (FSC) in blue. Error bars represent the standard
 404 error; (B) Difference between the K_n of FOB and the K_n of FSC. A positive
 405 value means that FOB-associated tunas are in better physiological than
 406 FSC tunas.



407 **Figure 4: Coefficients of the fishing year in the Generalized**
 408 **Additive Model.** Each coefficient represents the mean deviation of $T(K_n)$
 409 from the values for a year of reference (2019, represented by a black
 410 dot). The shape of the points represents the distribution of the values
 411 obtained with the bootstrap process. Numbers in grey in the upper part
 412 of the panels represent the percentage of the models generated in the
 413 bootstrap for which a given category was significantly different from the
 414 category of reference.