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No evidence from long-term analysis of yellowfin tuna condition that drifting fish aggregating devices act 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, with which tropical tuna associate. This habitat change has 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 1987-2019 of more than 25000 length-weight samples collected in the western Indian Ocean, we reject the hypothesis that the body condition (Le Cren's relative condition factor, Kn) 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 long-term monitoring of the habitat along with 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

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

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

The objective of this study was to test the hypothesis that the body condition of yellowfin tuna has decreased since the wide-spread use of DFADs began in the Indian 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 deployment of DFADs increased during that period, hence we considered the fishing year as a proxy for DFAD density.

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

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

All analyses were performed using R software v.4.0.3 (R Core Team 2020), and the scripts used for the study are available on GitHub (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 ± 0.088 and mean annual K_n values varied between 0.93 ± 0.064 (in 1987) and 1.07 ± 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 ± 0.007) while 2012 was the year with the highest coefficient (0.673 ± 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 concurrently with increasing DFAD use when performing a GAM on data of each size class independently (Figure S1 in Supplement 1). Also, even though the mean K_n of FOB-associated tuna was lower than that of FSC tuna, no decreasing trend of condition was observed when considering the fishing mode (Figures S2 & S3 in Supplement 1).

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

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

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

Tuna associative behavior plays a key role in determining the potential indirect impacts of DFADs on tuna condition. This associative behavior could also depend on several other factors than DFAD density, such as environmental conditions or social behavior (Capello et al. 2022). It could also be impacted by their physiological condition, for example one could hypothesize that tuna would associate with a DFAD until its condition lowers a given threshold value that would cause it to leave. Several hypotheses – *e.g.* the association being a consequence of a low condition and individuals departing from FOBs beyond a given condition threshold – could explain the absence of a long-term impact of DFADs on tuna condition, which need to be further explored.

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

Declaration of Competing Interest

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

Data availability statement

Data used in this study is available in Guillou et al. (2021) and were collected through the Data Collection Framework (Reg 2017/1004 and 2021/1167) funded by both IRD and the European Union.

A preprint version of the article is available at:

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References

Battin J (2004) When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. Conserv Biol 18:1482–1491.

Capello M, Rault J, Deneubourg J-L, Dagorn L (2022) Schooling in habitats with aggregative sites: The case of tropical tuna and floating objects. J Theor Biol 547:111163.

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.

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.

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.

Fréon P, Dagorn L (2000) Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. Rev Fish Biol Fish 10:183–207.

Gilroy J, Sutherland W (2007) Beyond ecological traps: perceptual errors and undervalued resources. Trends Ecol Evol 22:351–356.

Guillou A, Bodin N, Chassot E, Duparc A, Fily T, Sabarros P, Depetris M, Amande MJ, Lucas J, Diaha C, Floch L, Barde J, Pascual Alayon PJ, Baez JC, Cauquil P, Briand K, Bach P, Lebranchu J (2021) Tunabio: biological traits of tropical tuna and bycatch species caught by purse seine fisheries in the Western Indian and Eastern Central Atlantic Oceans.

Hale R, Treml EA, Swearer SE (2015) Evaluating the metapopulation consequences of ecological traps. Proc R Soc B Biol Sci 282:20142930.

Hall M (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. In: *International Workshop on Fishing for Tunas Associated with Floating Objects*. Inter-American Tropical Tuna Commission, La Jolla, CA, February 11-13, 1992, p 7

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.

IOTC (2021) Executive Summary Yellowfin Tuna (2021). Indian Ocean Tuna Commission.

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.

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.

Lloret J, Shulman GE, Love RM (2014) Condition and health indicators of exploited marine fishes. Wiley Blackwell, Chichester, West Sussex ; Hoboken, NJ.

Marsac F, Fonteneau A, Ménard F (2000) Drifting FADs used in tuna fisheries: an ecological trap? Pêche Thonière Dispos Conc Poissons 28:537–552.

R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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.

Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

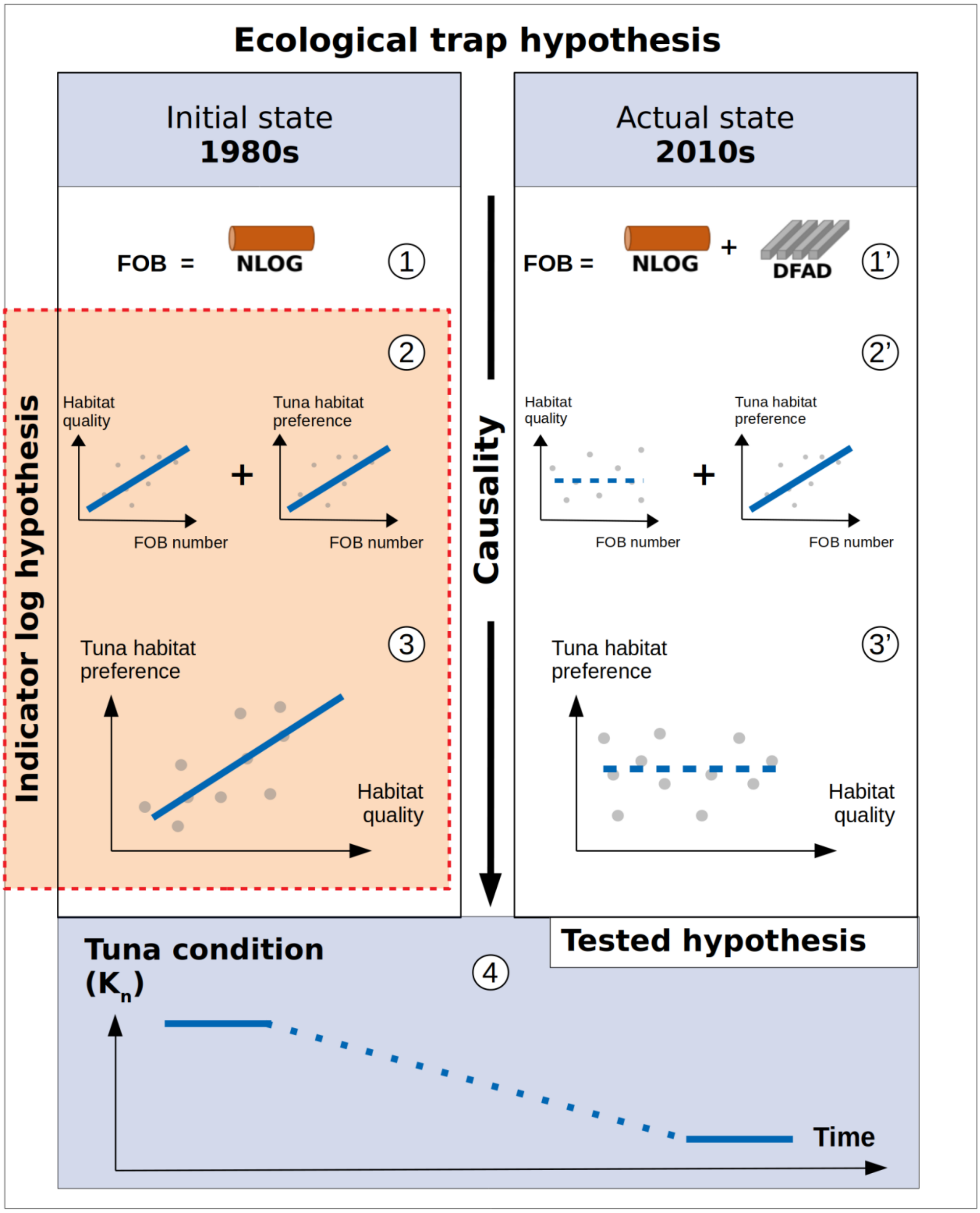
Sardenne F, Chassot E, Fouché E, Ménard F, Lucas V, Bodin N (2016) Are condition factors powerful proxies of energy content in wild tropical tunas? Ecol Indic 71:467–476.

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.

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

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.

259 # Figures



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

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

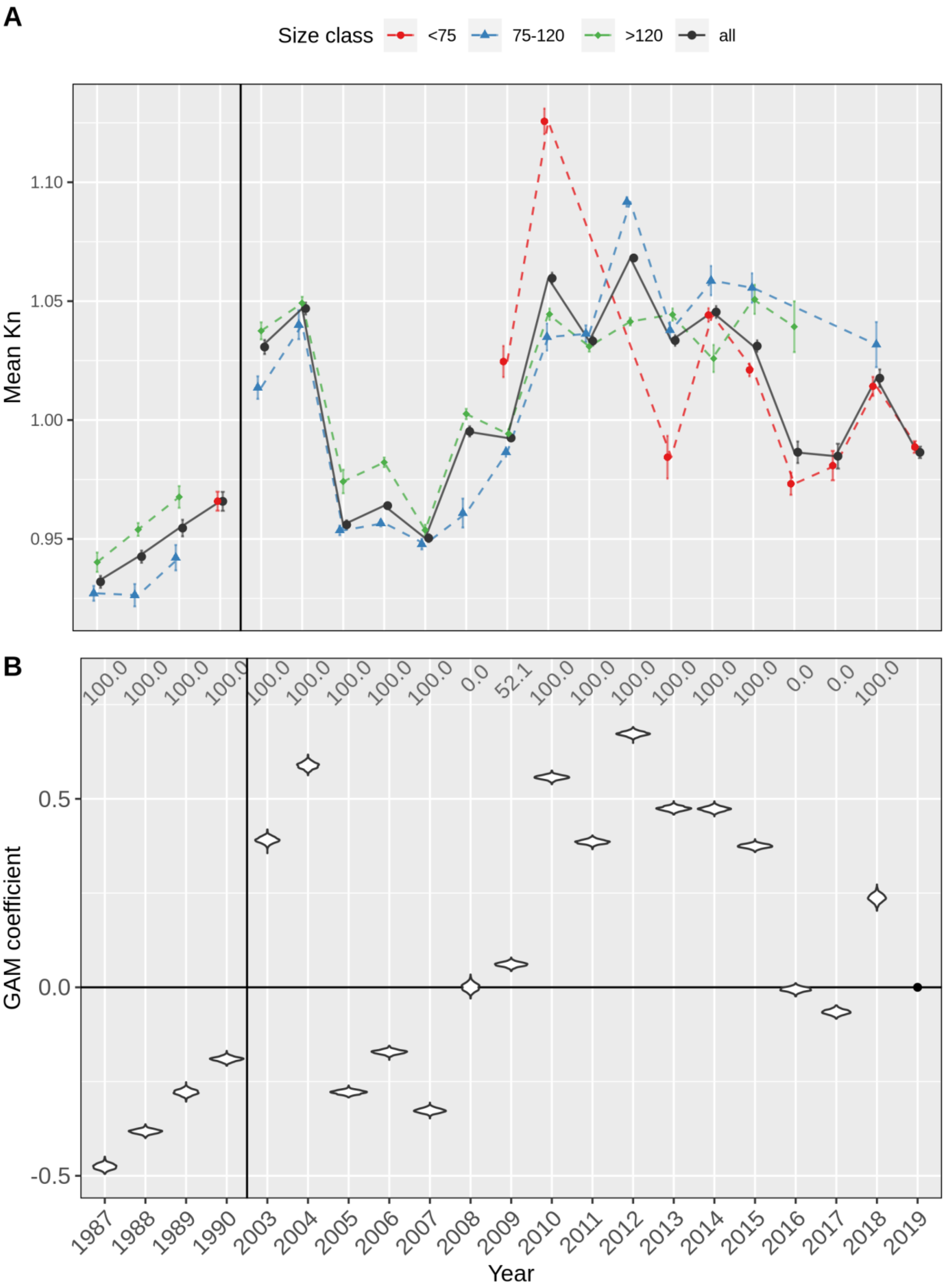


Figure 2: No observed trend in yellowfin tuna condition: (A) Mean relative condition factor per year. The K_n is represented for all individuals (all, black circles),

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