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Abstract

Behavioral ecology aims at characterizing animal behavior in relation to their physical and biological environment. A key aspect of this field is assessing the causation and consequences of behaviors. When manipulative experiments are technically challenging to implement, alternative approaches must be developed to investigate these aspects. In this study, we evaluate the effectiveness of mechanistic modelling, combined with correlative approaches on empirical data, to determine behavior causation and consequences. Many pelagic fish species, such as tropical tunas, display an associative behavior with floating objects. Although several studies suggest that that tunas have a lower relative condition when associated with DFADs, the causal link between the two remains undetermined. We develop a behavioral model to investigate the relationship between the associative dynamics of tropical tunas with DFADs and their physiological condition. We consider two hypotheses: H_1 that tuna physiological condition decreases when they are associated with DFADs (condition as a *consequence* of associative behavior), and H_2 that tuna tend to associate more when they are in lower condition (condition as a *causation* of associative behavior). Using bio-electrical impedance analysis data of associated yellowfin tuna at different DFAD densities in the western Indian Ocean, we then show that the lower condition observed for this species is a consequence of its associative behavior. This study demonstrates the relevance of combining mechanistic modelling with correlative approaches when studying behavior in cases where experiments are hard to implement. The use of such approaches rooted in conceptual frameworks allows a better characterization of animal behavior causes and consequences at the relevant time scales.

Keywords: behavioral ecology; causation; correlation; fitness; tropical tuna; purse-seine fisheries; indicators; floating objects; bio-electrical impedance analysis

1 Introduction

In defining a framework for ethology, the "biological study of animal behavior", Tinbergen outlined four key questions (Tinbergen 1963). Although overlapping, the fields covered by these questions need to be studied thoroughly to gain a coherent and comprehensive view of behavior. These questions are: the *causation* – what is the physiological causation of the behavior; *ontogeny* – how does behavior develop in individuals; *survival value* – what is the fitness of a particular behavior – and *evolution* – how did this behavior evolved (Westneat and Fox 2010). Later, Hogan 2015 reviewed this framework to create a new one that aligns with the field's advancements and with the various scale at which behavior is studied, ranging from behavioral genetics to behavioral ecology. Hogan suggests that the study of behavior can be interpreted through Aristotelian terminology, considering the matter (neurons, muscles, etc.), the *causation*, the structure (the perceptual, central and motor mechanisms) and the *consequences* of behavior. Focusing on causation and consequences, both can be of several types, based on the time scale considered: motivational, ontogenetic and phylogenetic (as designated in Hogan 2015). Differentiating causes from consequences can be challenging, leading to widespread confusion in behavioral ecology between the *function* of a behavior – i.e. why it has been selected, the phylogenetic consequences – and its causes (Sherry 2005; Hogan 2015). Despite this potential confusion, understanding the function of a behavior can still help to understand its causation (Sherry 2005). However, in some cases, determining the function of a behavior can be difficult and solutions might be needed to assess causation without it.

When assessing the causation of a behavior, one can face the correlation *vs* causation dilemma, a classical dilemma in experimental science. For example, two species of honeyeaters, *Phylidonyris novaehollandiae* and *P. nigra*, display less territorial behavior when the food is abundant, i.e. the number of territorial aggression is negatively correlated with available food quantity (Armstrong 1992). However, despite this correlation, Armstrong 1992 demonstrated experimentally that the territorial behavior was seasonal and did not follow artificial changes in nectar abundance, demonstrating that there was correlation but no causation. A lot of ecological studies rely on correlative models, and these models are not able to determine causal effect (Addicott et al. 2022). Causal effects in ecology can be determined through randomized experiments (Rutter 2007). These experiments rely on several elements – controls, replication – which can be hard to implement, specifically when focusing on marine ecosystems (Hilborn 2016). Hence, when focusing on a specific behavior, of which the phylogenetic consequences are unknown and where experimental testing cannot be implemented, how can one assess this behavior's motivational and ontogenetic causation and consequences?

We assess that question focusing on a specific behavior displayed by pelagic fish species. Several pelagic fish species associate with floating objects, such as logs or branches, which are natural components of their habitat (referred to as NLOGs). Although this behavior is known and used by fishers for almost two millennia, its phylogenetic consequences are still unknown (Fréon and Dagorn 2000; Oppian 200 AD). Since the early 1980s, industrial tropical tuna purse-seine fleets have been using radio and GPS buoys to follow NLOGs and have also been constructing and deploying their own man-made floating objects, left adrift (called drifting fish aggregating devices DFADs; Dagorn et al. 2013). The deployment of DFADs has increased significantly over the past few decades, with the latest global estimate suggesting between 81,000 and 121,000 deployments per year (Gershman et al. 2015, with data from 2013). The large scale deployment and use of DFADs throughout the world's tropical oceans has led to several direct ecological impacts, including pollution, damage to coastal habitats through stranding, increased bycatch, and ghost fishing (Imzilen et al. 2021; Tolotti et al. 2022; Filmalter et al. 2013). Moreover, for tropical tunas (skipjack SKJ – *Katsuwonus pelamis* –, yellowfin YFT – *Thunnus albacares* – and bigeye BET – *Thunnus obsesus* – tunas), the use of DFADs has increased purse seine fleets efficiency and tuna availability to this fishery by increasing the time tuna spend associated with floating objects (noted FOBs, Dupaix et al. 2024a). However, in the absence of knowledge on the causation of tuna associative behavior, it is difficult to assess the impact such behavioral modification can have apart from that directly stemming from fisheries.

Fish physiological condition can be used as a proxy to assess their fitness (Barton et al. 2002; Lloret et al. 2014). Marsac et al. 2000 and Hallier and Gaertner 2008 compared the thorax girth (body width divided by fork length) of tuna caught at DFADs to those caught in free-swimming schools (FSC) and showed that DFAD-associated tuna were in lower condition than FSC tuna in the Indian and Atlantic Oceans. This evidence was seen as suggesting that DFAD could have a negative impact on tuna condition. However, Robert et al. 2014 used Bioelectrical Impedance Analysis as a proxy of physiological condition to compare the condition of associated and non-associated tunas in the Mozambique Channel, Western Indian Ocean, an area rich in NLOGs, *i.e.* only marginally modified by the addition of DFADs at the time. They also found that FOB-associated tuna condition was lower that FSC tuna condition. Hence, while tuna may be in a relatively lower condition when associated with floating objects (Table 1), the causation of this relationship has not yet been determined, *i.e.* we do not know if the lower condition is the causation of tuna associative behavior or if it is a consequence of this behavior. The *meeting-point* hypothesis (Fréon and Dagorn 2000; Soria et al. 2009) suggests that tuna associate with floating objects to find conspecifics and form bigger schools, which may improve foraging efficiency (Ioannou 2017; Maury 2017; Rubenstein 1978). It is then possible that tuna associate with floating objects when they are in a low condition to form schools and increase their condition recovery afterwards. Therefore, the correlation between tuna association with floating objects and low individual condition could imply either that the association with a floating object results in a poorer condition or that tuna tend to associate more when they are in a lower condition.

The specific objective of this study is to investigate whether the low condition of tuna is the cause or the consequence of their associative behavior with floating objects. Experimental study of tuna associative behavior are challenging technically, hence we design a mechanistic model accounting for both the associative behavior of tuna with DFADs and their physiological condition. The model is used to test two different causation hypotheses to explain a lower condition of DFAD-associated tuna: either (H_1) tuna association to DFADs induces a decrease of condition (which would be in agreement with studies arguing that tuna are fasting when associated with FOBs; Hallier and Gaertner 2008; Marsac et al. 2000; Ménard et al. 2000) or (H_2) tuna with a lower condition are more prone to associating with DFADs. Based on these two hypotheses, we determine the influence of an increase of DFAD number on the mean condition of associated and non-associated tuna. Then, using physiological condition data of associated yellowfin tuna in the western Indian Ocean and DFAD density data, we determine if the low condition of associated tuna is the cause or the consequence of their associative behavior with floating objects.

Table 1. Studies demonstrating that tuna are in lower physiological condition in associated schools than in free-swimming schools. WIO, AO, WCPO: Western Indian, Atlantic and Western and Central Pacific Oceans respectively

Species	Ocean	Indicator used	Study
Skipjack tuna	WIO	Phase angle (Bioelectrical Impedance Analysis)	Robert et al. 2014
	WIO & AO	Thorax Girth (TG)	Hallier and Gaertner 2008
	AO	Body width divided by fork length	Marsac et al. 2000
	WCPO	Relative condition factor (K_n)	Ashida et al. 2017
	AO	Stomach fullness	Ménard et al. 2000
Yellowfin tuna	WIO	Lipid content (in gonads)	Zudaire et al. 2014
	WIO & AO	TG	Hallier and Gaertner 2008
	WIO	K_n	Dupaix et al. 2023 in Supplement
	AO	Stomach fullness	Ménard et al. 2000
Bigeye tuna	AO	Stomach fulness	Ménard et al. 2000

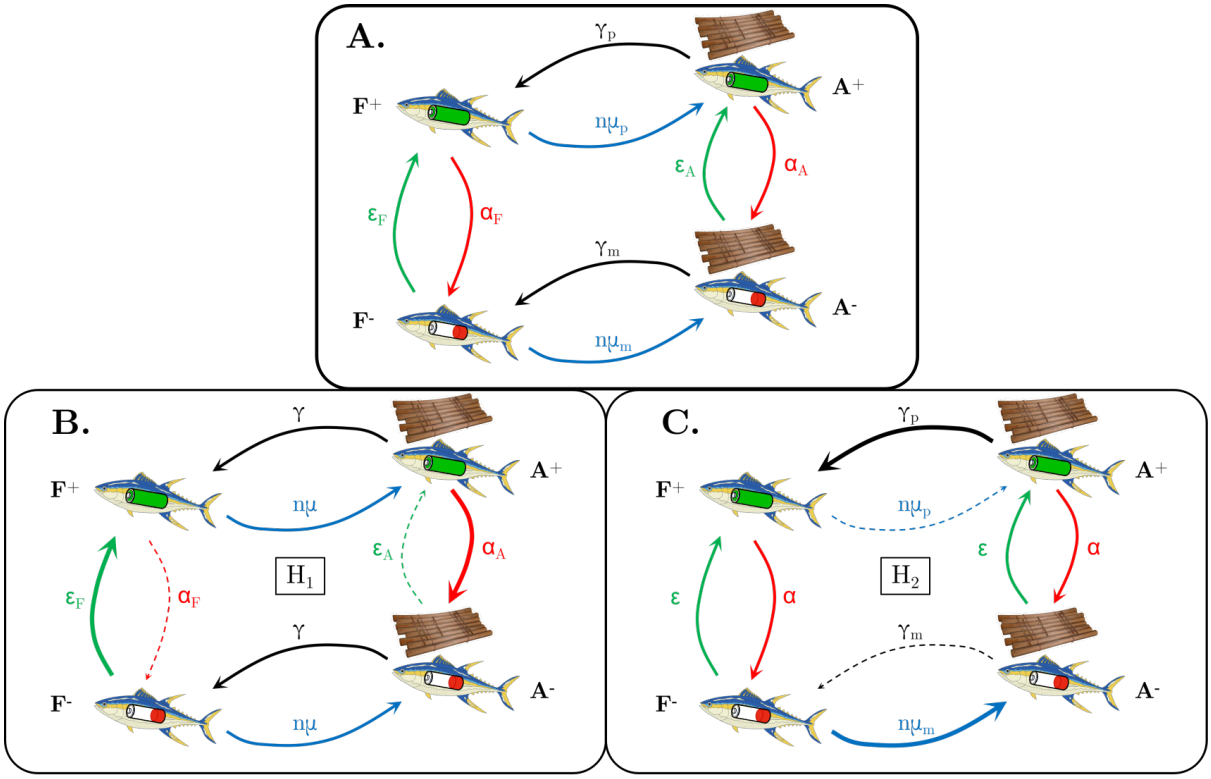

Figure 1. Schematic of the models used in the study. **(A)** General model, **(B)** H_1 model following the hypothesis that tuna association with DFADs *induces* a reduction of their condition ($\mu_p = \mu_m = \mu$; $\gamma_p = \gamma_m = \gamma$ and $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$), **(C)** H_2 model following the hypothesis that tuna associate with DFADs *is induced by* their low condition ($\alpha_F = \alpha_A = \alpha$; $\varepsilon_F = \varepsilon_A = \varepsilon$ and $\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p}$). F^+ and F^-: free-swimming state with high condition and low condition respectively. A^+ and A^-: associated state with high condition and low condition respectively.

2 Material and methods

2.1 General model formulation

Tuna individuals are considered in two states relative to their association with DFADs: they are either associated with DFADs (noted A) or free-swimming (noted F, Figure 1A). In each state A or F, individuals can be in two discrete and binary physiological states: they are either in "good" (with a given physiological variable equal to e^+) or "bad" (e^-) physiological condition. The physiological condition of individuals is a continuous variable but fish individuals can be categorized into three different physiological states referred to as "phases" during fasting (Bar and Volkoff 2012; Le Maho et al. 1981). During phase I, they mainly produce energy from carbohydrates and lipids, and we can consider them in a "good" physiological state. Then, in phase II, they mobilize stored lipids, and we consider them to be in a lower physiological state (designated as "bad" for simplification in the rest of the text). If individuals experience starving for too long, they can enter a "critical" phase III, where they have depleted their lipid reserves and start degrading proteins to produce energy. As phase III is happening late in the fasting process, we did not consider it in our study, but it's consideration would not modify our conclusions.

The overall model describing the behavior and physiology of tuna corresponds to a 4-state model: A^+ (associated with good condition), A^- (associated with bad condition), F^+ (free-swimming with good condition) and F^- (free-swimming with bad condition). The temporal evolution of the number of individuals in each state (N_{A^+}, N_{A^-}, N_{F^+} and N_{F^-}) can be written using the following equations:

$$\begin{cases} \frac{dN_{A^+}(t)}{dt} &= -(\gamma_p + \alpha_A)N_{A^+}(t) + \varepsilon_A N_{A^-}(t) + \mu_p n N_{F^+}(t) \\ \frac{dN_{A^-}(t)}{dt} &= -(\gamma_m + \varepsilon_A)N_{A^-}(t) + \alpha_A N_{A^+}(t) + \mu_m n N_{F^-}(t) \\ \frac{dN_{F^+}(t)}{dt} &= -(\mu_p n + \alpha_F)N_{F^+}(t) + \gamma_p N_{A^+}(t) + \varepsilon_F N_{F^-}(t) \\ \frac{dN_{F^-}(t)}{dt} &= -(\mu_m n + \varepsilon_F)N_{F^-} + \gamma_m N_{A^-}(t) + \alpha_F N_{F^+}(t) \end{cases} \quad (1)$$

where $n\mu_p$, $n\mu_m$, γ_p, γ_m, ε_F, ε_A, α_F and α_A are probabilities to change state per unit-time ($\in [0, 1]$) and n is the number of DFADs ($\in \mathbb{N}^+$). The probabilities and n are independent of the time t. The model assumes that the probability to associate with DFADs is directly proportional to n (Figure 1). A summary of the probabilities is provided in Table 2. Also, we define N, the total tuna population; $N = N_{A^+} + N_{A^-} + N_{F^+} + N_{F^-}$.

We introduce the mean condition of the associated fraction ($\overline{e_A}$) and the mean condition of the free-swimming fraction of the population ($\overline{e_F}$):

$$\overline{e_A} = \frac{N_{A^+}}{N_{A^+} + N_{A^-}} e^+ + \frac{N_{A^-}}{N_{A^+} + N_{A^-}} e^- \quad (2)$$

$$\overline{e_F} = \frac{N_{F^+}}{N_{F^+} + N_{F^-}} e^+ + \frac{N_{F^-}}{N_{F^+} + N_{F^-}} e^- \quad (3)$$

Table 2. Transition probabilities of the models. States at time t are indicated in lines and states at time $t + 1$ are in column. For example, the probability to transition from A^+ to A^- is α_A.

	Associated (A) "Good" condition (+)	Associated (A) "Bad" condition (-)	Free-swimming (F) "Good" condition (+)	Free-swimming (F) "Bad" condition (-)
A^+	$1 - (\gamma_p + \alpha_A)$	α_A	γ_p	0
A^-	ε_A	$1 - (\gamma_m + \varepsilon_A)$	0	γ_m
F^+	μ_p	0	$1 - (\alpha_F + \mu_p)$	α_F
F^-	0	μ_m	ε_F	$1 - (\varepsilon_F + \mu_m)$

2.2 Hypothesis 1: The association to DFADs induces a bad condition

To formulate the first hypothesis (H_1: tuna are in bad condition at DFADs because their condition decreases when they are associated, Figure 1B) using Eq. 1 we consider that (i) tuna associative behavior is independent of their condition ($\mu_p = \mu_m = \mu$ and $\gamma_p = \gamma_m = \gamma$) and (ii) tuna condition increases slower or decreases faster when they are associated with DFADs than when they are in free-swimming schools – *i.e.* $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$). We obtain a model with the following equations:

$$\begin{cases} \frac{dN_{A^+}(t)}{dt} &= -(\gamma + \alpha_A)N_{A^+}(t) + \varepsilon_A N_{A^-}(t) + \mu n N_{F^+}(t) \\ \frac{dN_{A^-}(t)}{dt} &= -(\gamma + \varepsilon_A)N_{A^-}(t) + \alpha_A N_{A^+}(t) + \mu n N_{F^-}(t) \\ \frac{dN_{F^+}(t)}{dt} &= -(\mu n + \alpha_F)N_{F^+}(t) + \gamma N_{A^+}(t) + \varepsilon_F N_{F^-}(t) \\ \frac{dN_{F^-}(t)}{dt} &= -(\mu n + \varepsilon_F)N_{F^-}(t) + \gamma N_{A^-}(t) + \alpha_F N_{F^+}(t) \end{cases} \quad (4)$$

2.3 Hypothesis 2: Individuals with a bad condition tend to associate

To formulate the second hypothesis (H_2: tuna associate with DFADs because they have a low condition, Figure 1C), using Eq. 1 we consider that (i) changes in tuna condition are independent of their association ($\alpha_F = \alpha_A = \alpha$ and $\varepsilon_F = \varepsilon_A = \varepsilon$) and (ii) tuna tend to associate more with DFADs when they are in bad condition than when they are in good condition – *i.e.* $\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p}$. We obtain a model with the following equations:

$$\begin{cases} \frac{dN_{A^+}(t)}{dt} &= -(\gamma_p + \alpha)N_{A^+}(t) + \varepsilon N_{A^-}(t) + \mu_p n N_{F^+}(t) \\ \frac{dN_{A^-}(t)}{dt} &= -(\gamma_m + \varepsilon)N_{A^-}(t) + \alpha N_{A^+}(t) + \mu_m n N_{F^-}(t) \\ \frac{dN_{F^+}(t)}{dt} &= -(\mu_p n + \alpha)N_{F^+}(t) + \gamma_p N_{A^+}(t) + \varepsilon N_{F^-}(t) \\ \frac{dN_{F^-}(t)}{dt} &= -(\mu_m n + \varepsilon)N_{F^-}(t) + \gamma_m N_{A^-}(t) + \alpha N_{F^+}(t) \end{cases} \quad (5)$$

2.4 Stationary model solution

We considered the stationary model solution (i.e. when $\frac{dN_{A^+}}{dt} = \frac{dN_{A^-}}{dt} = \frac{dN_{F^+}}{dt} = \frac{dN_{F^-}}{dt} = 0$). For the two hypotheses, first, we verified that the mean condition of the associated fraction was lower than the mean condition of the free-swimming fraction of the population for any number of DFADs ($\forall\, n \in \mathbb{N}^+, \quad \overline{e_A}(n) < \overline{e_F}(n)$). Then, because the aim was to determine the impact of DFADs on the condition of tuna, we determined the trends of $\overline{e_A}(n)$ and $\overline{e_F}(n)$ for increasing number of DFADs (n).

2.5 Hypotheses testing with field data

Bio-electrical impedance analysis (BIA) and DFAD density data were used to determine which hypothesis of the model was verified for yellowfin tuna (*Thunnus albacares*) in the western Indian Ocean. BIA data was collected by observers onboard purse seine vessels from May 2021 to March 2023, along with individual fork length. A total of 232 yellowfin tuna (34 to 79 cm FL) were sampled from 13 DFAD sets. BIA is primarily based on the calculation of the phase angle (PA), derived from the measurements of resistance (R) and reactance (X_c) of tissues subject to a given voltage:

$$PA = \arctan\left(\frac{X_c}{R}\right) \quad (6)$$

Phase angle is interpreted as an indicator of membrane integrity and water distribution between the intracellular and extracellular spaces and has been used as a proxy of nutritional status of animals (Robert et al. 2014). For each DFAD set, the floating object density in the area was determined using data from the 3-BU form of the Indian Ocean Tuna Commission (IOTC 2023) and data from observers onboard purse seine vessels. The IOTC dataset contains the monthly mean of the number of *operational buoys*, i.e., the echosounder buoys whose GPS position is remotely transmitted to one or several fishing vessels, for each 1°×1° cell of the Indian Ocean. This value was divided by the sea area of each cell, to obtain a mean monthly DFAD density (ρ_{DFAD}). Total floating object (FOB) densities were calculated combining DFAD densities with data recorded by scientific observers onboard purse seine vessels (2021-2023). Observers' data include the date, time, and location of the main activities of the fishing vessel (*e.g.* fishing sets, installation or modification of FOBs, searching for FOBs). For every activity occurring on a FOB, the type of operation (*e.g.* deployment, removal, and observation of a FOB) and the type of floating object (DFAD or LOG) are recorded. Using the methodology developed in Dupaix et al. 2021 applied to these observations, we calculated a mean monthly ratio $m = \frac{n_{LOG}}{n_{DFAD}}$ (with n_{LOG} and n_{DFAD} the number of LOG, *i.e.* floating objects other than DFADs, and DFAD observations respectively) per 2° cell. This ratio was used to calculated the density of FOBs ($\rho_{FOB} = (1 + m)\,\rho_{DFAD}$).
Because the available dataset came from 13 fishing sets, fitting a model accounting for several other variables potentially impacting PA presented the risk of over-fitting the data. Hence, the correlation between the phase angle and the density of FOBs (ρ_{FOB}) was tested using a Spearman's rank correlation test, with a significance level of $p = 0.05$. To test the impact of extreme phase angle values, the correlation test was also performed removing samples with $PA > 40$ °. The calculation of Spearman's rank correlation coefficient was complemented with the fitting of a non-linear regression model, presented in Supplementary S1. The above-described statistical analysis was performed with the R statistical software (R Core Team 2021).

3 Results

All the detailed calculation of the results presented in Sections 3.1 & 3.2 are available in Supplementary S2.

3.1 Comparison of the mean condition of associated and free-swimming populations

In the general model (see Sections S2.3.1&S2.3.2), we can show that

$$\overline{e_A} = \frac{1+\varphi R(n)}{1+R(n)} e^+$$

with $\varphi = \frac{e^-}{e^+}$ and $R(n) = \frac{N_{A^-}}{N_{A^+}}$. And

$$\overline{e_F} = \frac{1+\varphi T(n)}{1+T(n)} e^+$$

with $T(n) = \frac{N_{F^-}}{N_{F^+}}$. Hence we can demonstrate that

$$\overline{e_A} < \overline{e_F} \Leftrightarrow \frac{N_{F^-}}{N_{F^+}} < \frac{N_{A^-}}{N_{A^+}}$$

From that, in the model formulated according to H_1 (the association to DFADs induces a bad physiological condition, see Section S2.3.5), we can demonstrate that

$$\frac{\alpha_F}{\varepsilon_F} < \frac{\alpha_A}{\varepsilon_A} \Leftrightarrow \overline{e_A} < \overline{e_F}$$

In the second model, formulated according to H_2 (individuals tend to associate more with DFADs when in a bad physiological condition, see Section S2.3.6), we can demonstrate that

$$N_{A^+} + N_{F^+} = \frac{N\varepsilon}{\alpha+\varepsilon}$$
$$N_{A^-} + N_{F^-} = \frac{N\alpha}{\alpha+\varepsilon}$$
$$\overline{e_A} < \overline{e_F} \Leftrightarrow \frac{N_{A^+}}{N_{A^-}} < \frac{\varepsilon}{\alpha}$$

From these equations and using Eq. 5, we can demonstrate that, when H_2 is verified,

$$\frac{\mu_p}{\gamma_p} < \frac{\mu_m}{\gamma_m} \Leftrightarrow \overline{e_A} < \overline{e_F}$$

The models formulated according to both hypotheses (H_1 and H_2) verify that $\forall n \in \mathbb{N}^+$, $\overline{e_A}(n) < \overline{e_F}(n)$. Hence, the models do verify that the mean condition of associated tuna is lower than the mean condition of free-swimming tuna.

3.2 Variations of the mean condition of the two populations for an increasing number of DFADs

In the general model (Sections S2.1.1-S2.1.4), we can demonstrate that the average condition of associated tuna ($\overline{e_A}$) is a decreasing sequence of n if and only if

$$\frac{d\overline{e_A}(n)}{dn} < 0 \Leftrightarrow \alpha_A \mu_p \varepsilon_F \gamma_m - \alpha_F \mu_m \varepsilon_A \gamma_p > 0 \quad (7)$$

Applying this relationship to the models formulated according to H_1 and H_2 hypotheses (see Sections S2.1.5&S2.1.6), we can demonstrate that

$$H_1 \Rightarrow \frac{d\overline{e_A}(n)}{dn} < 0 \quad (8)$$

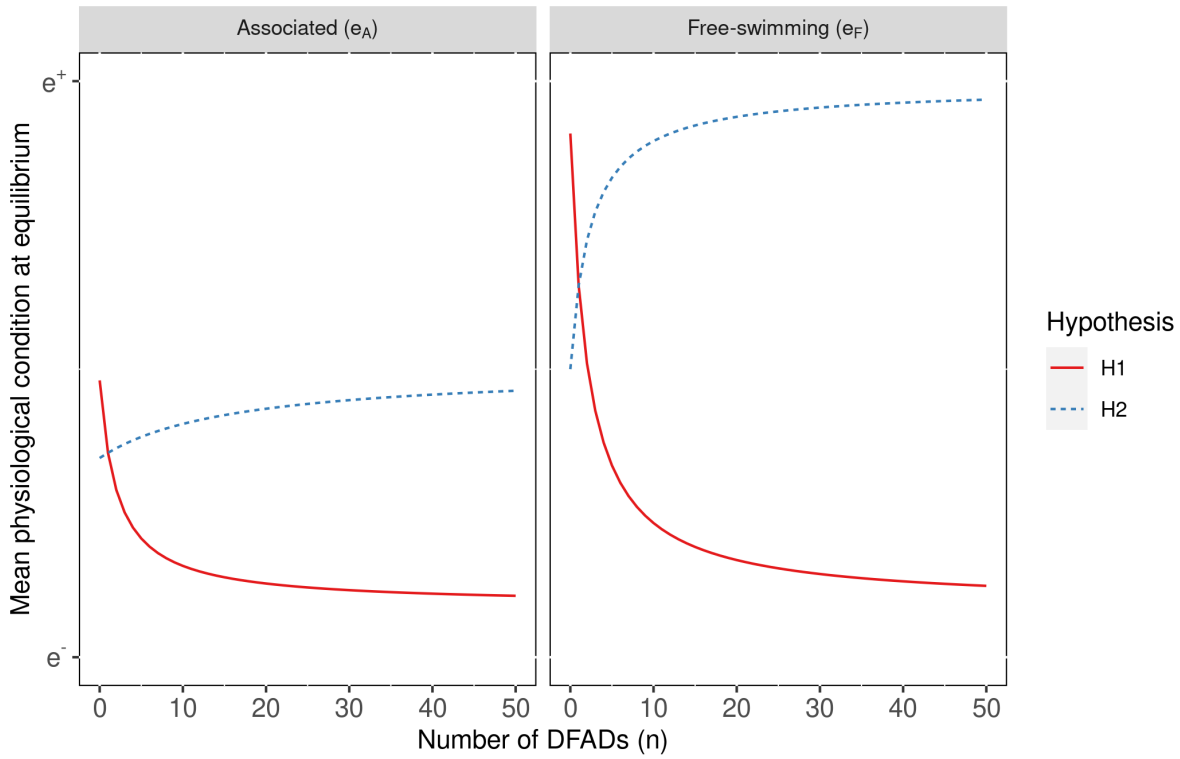

Figure 2. Variations of $\overline{e_A}$ and $\overline{e_F}$ as a function of the number of DFADs (n). Left panel: Mean physiological condition of the associated population ($\overline{e_A}$), based on the two hypotheses. Right panel: Mean physiological condition of the free-swimming population ($\overline{e_F}$), based on the two hypotheses. H_1 (red line): tuna association with DFADs *induces* a reduction of their condition. H_2 (blue dotted line): associate with DFADs *because* they are in low condition. Examples with all probabilities set to 10^{-2}, except, for H_1, $\alpha_F = \varepsilon_A = 10^{-3}$ and for H_2, $\mu_P = \gamma_M = 10^{-3}$.

and

$$H_2 \Rightarrow \frac{d\overline{e_A}(n)}{dn} > 0 \tag{9}$$

Concerning the average condition of free-swimming tuna ($\overline{e_A}$, Section S2.2), in the general model we can also demonstrate that $\overline{e_F}$ is a decreasing sequence of n under the same conditions as $\overline{e_A}$ (Eq. 7), i.e. if and only if

$$\frac{d\overline{e_F}(n)}{dn} < 0 \Leftrightarrow \alpha_A \mu_p \varepsilon_F \gamma_m - \alpha_F \mu_m \varepsilon_A \gamma_p > 0 \tag{10}$$

Hence, as for the condition of associated tuna, we have

$$H_1 \Rightarrow \frac{d\overline{e_F}(n)}{dn} < 0 \tag{11}$$

and

$$H_2 \Rightarrow \frac{d\overline{e_F}(n)}{dn} > 0 \tag{12}$$

To summarize, under the hypothesis that the association to DFADs induces a bad physiological condition (H_1), we can demonstrate that an increasing number of DFADs will reduce both the mean condition of associated tuna and that of free-swimming tuna (Eq. 8&11, Figure 2). When we hypothesize that individuals tend to associate with DFADs when in bad condition (H_2), an increasing number of DFADs will increase the average condition of associated and free-swimming tuna (Eq. 9&12, Figure 2).

3.3 Hypotheses testing with field data

Phase angle values ranged from 11.1 to 59.4 °, with a median value of 26.2 °. Within-set standard-deviation was low for most of the sets: average within-set standard deviation of 3.1 ° (Figure 3). Phase angle values did not display any clear trend as a function of FOB density (Figure 3).
However, PA displayed a significant decreasing trend for increasing ρ_{FOB} values (Spearman's $\rho = -0.24$, $p = 1.9 \times 10^{-4}$). Similar results were also observed when removing outliers (Spearman's $\rho = -0.22$, $p = 9.0 \times 10^{-4}$). These results were confirmed when performing a non-linear regression (see Supplementary S1).

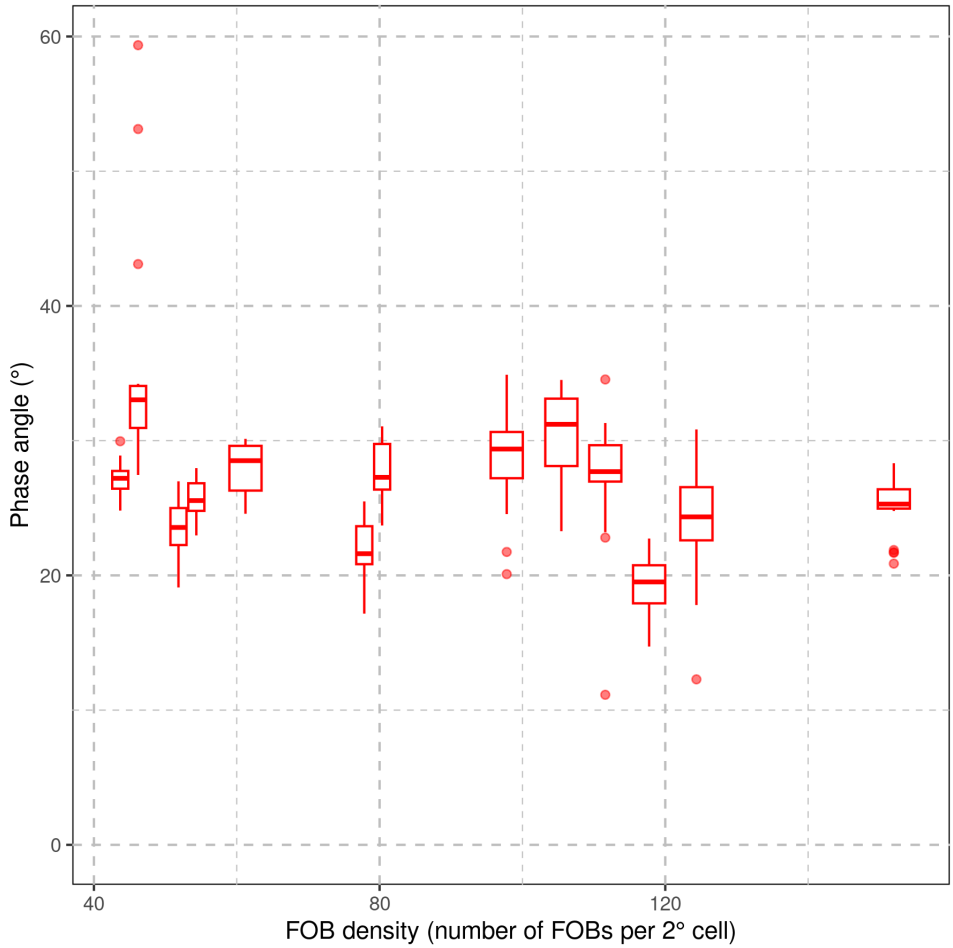

Figure 3. Phase angle (PA) of associated tuna as a function of floating object (FOBs) density. PA was measured on 232 yellowfin tuna (YFT) fished on DFAD-associated schools. Each boxplot corresponds to a given set.

4 Discussion

Tuna associative behavior has unique characteristics, making it an important case study in behavioral ecology. Despite being known for nearly two millennia, this behavior remains unexplained, with its phylogenetic consequences (or *function*) still unknown. Additionaly, because tuna are highly migratory pelagic species, designing manipulative experiments to study this behavior is technically challenging. Thus, determining the causation and consequences of this behavior – specifically if tuna lower condition is a cause or a consequence of their associative behavior – poses a challenge. This study demonstrates that, when experimental approaches are not feasible, mechanistic modelling combined with correlative approaches can determine the causation and consequences of behavior.

4.1 Lower condition of tuna when associated

In this study, we develop two mechanistic models to assess the causal link between tuna condition at DFADs and their associative behavior. The first model (based on H_1) posits that tuna condition decreases when they are associated with DFADs. The second model (based on H_2) assumes that tuna tend to associate more with DFADs when they have a lower condition. Both theoretical models provide an average lower condition for DFAD-associated tuna than tuna in free-swimming schools (FSC), in agreement with previous studies conducted considering various condition indicators (Table 1, Dupaix et al. 2024b). As FSC tuna are caught while actively feeding, caution must be taken when interpreting the conclusions drawn from indicators such as thorax girth and stomach fullness (Hallier and Gaertner 2008; Marsac et al. 2000; Ménard et al. 2000), as these indicators are probably responding to tuna feeding on a very short-term basis. In addition, Sardenne et al. 2016 compared morphometric indices such as thorax girth or relative condition factor (K_n, used in Ashida et al. 2017; Dupaix et al. 2023) with energy contents in the tissues and showed that such indices should be used carefully on tropical tunas as they do not always properly reflect individuals' condition. Other evidence by Zudaire et al. 2014, which found a difference in total lipid content in female yellowfin tuna gonads, could also be attributed to a different reproductive strategy rather than a difference in physiological condition. Therefore, most studies that show a difference in condition between FSC and FOB-associated tuna relied on indicators that require careful interpretation. Robert et al. 2014 relying on the phase angle measured by Bioelectrical Impedance Analysis, as we did in this study, also found a lower condition of FOB-associated tuna compared to FSC tuna. Because it represents an indicator of membrane integrity, BIA is considered a good indicator of physiological condition. However, to date and like other condition indicators, it has not been validated yet. To be able to rely with confidence on condition indicators, experimental validations are needed. These validations could be performed experimentally, by monitoring a set of condition indicators on captive tuna while fasting. It would allow the confirmation of the fact that tuna are in lower condition when associated, but it would also allow to determine the exact meaning of this difference of tuna's condition and the temporal scale of these indicators variations.

4.2 Causation or consequence of associative behavior

Before our study, the causation between the low condition at floating objects and the associative behavior of tuna was yet to be determined (Robert et al. 2014). We develop a mathematical framework allowing to determine if (H_1) tuna condition decreases when they are associated or if (H_2) tuna tend to associate more when they are in a lower condition. We show that, as the number of DFADs increases, the mean condition of the associated and free-swimming fractions of a tuna population will not vary identically depending on the causation hypothesis made. Dupaix et al. 2023 found no decreasing nor increasing trend of the mean condition of associated yellowfin tuna (assessed through the relative condition factor K_n, see their Figure S3) concurrently with the increasing use of DFADs from 1987 to 2019. However, in their study performed with data from 1987 to 2019, the authors could not test the relationship between the average condition and the density of FOB, as precise density data was not available. Here, thanks to a dataset made available recently by the Indian Ocean Tuna Commission, we determine the DFAD densities corresponding to the measured mean condition of associated yellowfin tuna. With this dataset we assess the causal link between tuna low condition and association to DFADs for these two species. The BIA does not show clear trends as a function of the FOB density, suggesting that, if an impact of FOB density exists, we are currently beyond the range of densities where such impact is clearly visible. Such conclusion are strengthened by a complementary analysis performed on skipjack tuna (Supplementary S3), calling for more data, especially for lower FOB densities. However, the results of the correlation test (confirmed by the non-linear model presented in Supplementary S1) suggest a significant negative effect of the FOB density for yellowfin tuna, which reject H_2 and implies that yellowfin tuna associative behavior provokes a decrease of their average condition (H_1). Hence, it shows that the low condition of yellowfin tuna at FOBs is a consequence of their associative behavior, not a cause.

4.3 Mechanistic models to assess behavior causation and consequences

This study relies on the formulation of a mechanistic model, based on two different causation hypotheses, which can then be used to determine the right hypothesis through classical correlative methods. This approach is conceptually similar to the one developed in ecosystem models, which posit mechanisms and validate them using correlative approaches (Fulton et al. 2005; Dueri et al. 2014; Hilborn 2016). Craver 2006 argues that not all models are explanatory, some a merely phenomenal models which can predict the outcomes of a mechanism, but can not explain this mechanism. For example, Ptolemy's model of the solar system predicted the location of the planets but did not explain why the planets moved. In our case, previous knowledge predicted that associated tuna were in lower condition than free-swimming ones, but the causation of this relationship was unknown. This study highlights the importance of combining mechanistic modeling with empirical data to disentangle complex ecological interactions and determine the causation and consequences of specific behaviors. Furthermore, the findings underscore the potential of using mechanistic models as valuable tools in ecological research, particularly when experimental manipulations are impractical or impossible.

Craver 2006 also states that models lie somewhere between *sketches* and *complete descriptions* and that the proper degree of abstraction has to be found depending on the model's intended use. Here, some simplifications were done, which could influence the obtained results: we considered a direct proportion between the number of DFADs and the probability to associate. Capello et al. 2022, using a model with several social scenarios, demonstrated that social behavior influences the way the fraction of schools which are associated varies with DFAD density. This model could be calibrated using data from echo-sounder buoys associated with DFADs, which can be used to determine the presence or absence of associated tuna aggregations under DFADs (Baidai et al. 2020). Then, adding a physiological state variable would allow to determine the impact of an increasing DFAD density on tuna condition, accounting for both their associative and social behavior. Although the relationship between the number of FADs and tuna association changes quantitatively under different social scenarios, it remains qualitatively consistent (Capello et al. 2022): an increase of the number of FADs always resulted in an increase of the proportion of tuna schools associated, strengthening our findings.

4.4 Motivational, ontogenetic and phylogenetic causes and consequences of behavior

It has been argued that determining a behavior's *function* can inform on its causation and consequences (Sherry 2005). The reverse is also possible. This study determines an ontogenetic consequence of yellowfin tuna associative behavior. However, this result highlights the lack of knowledge on the phylogenetic consequence of this behavior. If associating with floating objects has a direct negative consequence on tropical tuna, there has to be an important phylogenetic consequence being able to compensate for that decrease in condition. Two main hypotheses are formulated as phylogenetic consequences of tropical tuna associative behavior of tropical tunas with floating objects: the *meeting-point* (explicited in Introduction) and the *indicator-log* hypotheses (Hall 1992; Fréon and Dagorn 2000; Castro et al. 2002). The *indicator-log* hypothesis posits that tunas and other associated species use natural floating objects as cues to select good-quality habitat (Hall 1992; Hallier and Gaertner 2008). NLOGs would be located in productive areas because they originate from rivers and tend to accumulate in rich frontal zones.

In a context of global change, determining this phylogenetic consequence is central as it can strongly influence the response to antropogenic human modification (Dupaix et al. 2024b). This could be done using a similar approach as the one developed here and in Capello et al. 2022. The importance of determining phylogenetic consequences of behavior for species conservation are twofold. First, it will influence the impact of human activities on species populations – e.g. if the *meeting-point* hypothesis is verified, i.e. tuna associate to form larger schools, increasing the number of DFADs can disturb schooling behavior, impacting their fitness.

Then, it can allow to predict the potential changes of these consequences induced by human activities. Again, if we consider the *meeting-point* hypothesis in a context of an increase of DFAD density increase, we should observe a reduction of the fitness associated with associative behavior. This reduction could result in a change in that behavior, induced by human activities.

4.5 Conclusion

The model presented in this study, coupled with field data, allows to advance our understanding of tuna associative behavior and of the processes underlying the association with floating objects. Based on this framework one can now determine the causal link between tuna condition and their associative behavior to DFADs. It also demonstrates the relevance of coupling mechanistic modelling with correlative approaches when studying behavior in cases where experiments are hard to implement. The use of such approaches rooted in conceptual frameworks such as the one developed by Hogan 2015 will allow a better characterization of animal behavior causes and consequences at the relevant time scales.

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6 Conflict of interest disclosure

The authors declare that they have no conflicts of interest in relation to the content of the article.

7 Data, script, code, and supplementary information availability

All the scripts used for this study are available on GitHub (https://github.com/adupaix/Test_causality_with_BIA; DOI:10.5281/zenodo.10711575). Observers data (both BIA and fishing data) are available upon request to the IRD's Ob7 (https://ob7-ird.science/les-donnees/, accessed 2024-07-05). Indian Ocean Tuna Commission (IOTC) instrumented buoys data can be downloaded from the IOTC website (https://iotc.org/documents/instrumented-buoy-data-january-2020-june-2023, accessed 2024-04-04). Chlorophyll-a concentrations used in Supplementary can be downloaded from Copernicus Marine Service (https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_104/services, accessed 2024-04-04; Dataset id: cmems_obs-oc_glo_bgc-plankton_my_l4-gapfree-multi-4km_P1D).

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S1 Supplementary – Non-linear regressions

S1.1 Material and Methods

From the relationship obtained in Eq. S6, we know that the relationship between PA and ρ_{FOB} is not linear. We can express $\overline{e_A}$ as follow:

$$\overline{e_A} = \frac{1 + \varphi R(n)}{1 + R(n)} e^+$$

We introduce $a, b, c, d \in (\mathbb{R}^{+*})^4$ such that

$$R(n) = \frac{an + b}{cn + d}$$

Hence

$$\begin{aligned}
\overline{e_A} &= \frac{1 + \varphi \frac{an+b}{cn+d}}{1 + \frac{an+b}{cn+d}} e^+ \\
&= \frac{cn + d + \varphi(an + b)}{cn + d + an + b} e^+ \\
&= \frac{n(c + \varphi a) + d + \varphi b}{n(a + c) + d + b} e^+ \\
&= \frac{n + \frac{d+\varphi b}{c+\varphi a}}{n\frac{a+c}{d+\varphi b} + \frac{d+b}{c+\varphi a}} e^+
\end{aligned}$$

So, PA can be expressed as a function of ρ_{FOB} with the following relationship:

$$PA = \frac{\rho_{FOB} + \beta}{\delta \rho_{FOB} + \zeta} \tag{S1}$$

with β,δ,$\zeta \in (\mathbb{R}^{+*})^3$.

Based on Eq. S1, we fitted a non-linear model (noted NLM), using the Levenberg-Marquardt algorithm, with the function *nls.lm* of the R package *minpack.lm* (Elzhov et al. 2023). To account for seasonal variations, for variations due to the richness of the area and for variations due to the size of the individual, the quarter (Q), the chlorophyll-a concentration ($Chla$), and individual fork length (FL) were included as explanatory variables. Chlorophyll-a concentration (in mg.m^{-3}) at the fishing set locations were obtained from Copernicus marine service, giving access to daily concentrations at a spatial resolution of 4 km$\times$4 km. The model can be written as:

$$PA(i) = \frac{\rho_{FOB}(i) + \beta}{\delta \rho_{FOB}(i) + \zeta} + \eta\, Chla(i) + \theta\, FL(i) + \iota\, Q(i) + \epsilon(i)$$

where $PA(i)$ is the phase angle of individual i, $\rho_{FOB}(i)$ the FOB density at the fishing set, $FL(i)$ the fork length of the individual, $Chla(i)$ the cholorphyll-a concentration and $Q(i)$ the quarter. β, δ, ζ, η, θ and ι are the parameters to estimate and $\epsilon(i)$ is the residual error term. The Aikake Information Criterion was calculated and the goodness-of-fit of the model was assessed calculating its R^2. To test the robustness of the model a Leave-One-Out Cross Validation was performed (LOOCV): non-linear models were built removing each data points one by one and the obtained coefficients and model statistics were assessed.

S1.2 Results

The results of the NLMs assessing the relationship between the phase angle of associated YFT and the density of FOBs and other explanatory variables are presented in Table S3. YFT displayed a decreasing condition factor with increasing fork length (θ = -0.27; p-value: 1.5×10^{-10}) and a lower condition factor in the first quarter of the year (PA in Q2 and Q4 significantly greater than Q1 for YFT).
The coefficient δ was significantly different from 0 ($\delta = 0.03$, p-value < 2×10^{-16}) and ζ was found to be equal to 0. Therefore, we performed another non-linear model, removing ζ, noted YFT_2 in Table S3. In that second model, which had a smaller than the first model, both β and δ were found to be significant, suggesting the following relationship between PA and ρ_{FOB}:

$$PA(\text{YFT}) = \frac{1}{\delta} + \frac{\beta}{\rho_{FOB}}$$

As the results from the Spearman's correlation test presented in the main manuscript, these results reject H_2 hypothesis for YFT, suggesting that YFT follow the H_1 hypothesis (the association to DFADs induces a bad condition).

Table S3. Non-linear models performed on the condition (phase angle - PA) of yellowfin tuna associated with DFADs. YFT: yellowfin tuna;; β,δ and ζ: coefficients used to fit the density of FOBs; FL: fork length (cm); Chla: chlorophyll-a concentration ($mg.m^{-3}$); Q: quarter; AIC: Aikake Information Criterion. LOOCV: Leave-One-Out Cross Validation, the last column presents the minimum and maximum estimate obtained performing the LOOCV.

Non-linear model	Coefficient	Estimate	Significance (p-value)	LOOCV	
				min	max
YFT_1	β	9.65	0.87	9.1	10.6
	δ	0.03	$< 2 \times 10^{-16}$	0.030	0.033
	ζ	0.00	1.00	0	0
	Chla	5.8	0.40	4.8	8.2
	FL	-0.27	1.5×10^{-10}	-0.28	-0.24
	Q2	6.5	$< 2 \times 10^{-16}$	6.2	6.9
	Q3	1.1	0.40	0.9	1.3
	Q4	7.2	2.67×10^{-11}	6.7	7.5
	R^2: 0.51			0.49	0.53
	AIC: 1276			1217	1272
YFT_2	β	10.2	1.18×10^{-7}	9.1	10.5
	δ	0.03	$< 2 \times 10^{-16}$	0.031	0.033
	Chla	6.3	0.29	4.9	8.7
	FL	-0.26	2.9×10^{-10}	-0.27	-0.23
	Q2	6.6	$< 2 \times 10^{-16}$	6.2	6.9
	Q3	1.1	0.32	0.9	1.3
	Q4	7.0	2.08×10^{-11}	6.7	7.4
	R^2: 0.51			0.49	0.53
	AIC: 1274			1215	1270

Despite the presence of outliers, the NLMs obtained through the Leave-One-Out Cross Validation (LOOCV) confirmed the robustness of the relationship (or absence of relationship) between PA and ρ_{FOB} and between PA and other variables for both species (Table S3). The values of the coefficients showed little variation and no modification of their significance was observed.

S2 Supplementary - Equilibrium model solution

All the solutions are determined when the system is at equilibrium, *i.e* when

$$\frac{dN_{A^+}}{dt} = \frac{dN_{A^-}}{dt} = \frac{dN_{F^+}}{dt} = \frac{dN_{F^-}}{dt} = 0$$

S2.1 Variations of the average condition of the associated fraction of the population

S2.1.1 N_{A^-} / N_{A^+} ratio

From Eq. 1 we have

$$N_{F^+} = \frac{\gamma_p + \alpha_A}{n\mu_p} N_{A^+} - \frac{\varepsilon_A}{n\mu_p} N_{A^-} \tag{S2}$$

$$N_{F^-} = \frac{\gamma_m + \varepsilon_A}{n\mu_m} N_{A^-} - \frac{\alpha_A}{n\mu_m} N_{A^+} \tag{S3}$$

and

$$N_{A^+} = \frac{n\mu_p + \alpha_F}{\gamma_p} N_{F^+} - \frac{\varepsilon_F}{\gamma_p} N_{F^-} \tag{S4}$$

Hence, we have

$$\begin{aligned}
& N_{A^+} = \frac{n\mu_p + \alpha_F}{\gamma_p}\left[\frac{\gamma_p + \alpha_A}{n\mu_p} N_{A^+} - \frac{\varepsilon_A}{n\mu_p} N_{A^-}\right] - \frac{\varepsilon_F}{\gamma_p}\left[\frac{\gamma_m + \varepsilon_A}{n\mu_m} N_{A^-} - \frac{\alpha_A}{n\mu_m} N_{A^+}\right] \\
\Leftrightarrow \quad & N_{A^+} = \frac{n\mu_p + \alpha_F}{\gamma_p}\frac{\gamma_p + \alpha_A}{n\mu_p} N_{A^+} - \frac{n\mu_p + \alpha_F}{\gamma_p}\frac{\varepsilon_A}{n\mu_p} N_{A^-} - \frac{\varepsilon_F}{\gamma_p}\frac{\gamma_m + \varepsilon_A}{n\mu_m} N_{A^-} + \frac{\varepsilon_F}{\gamma_p}\frac{\alpha_A}{n\mu_m} N_{A^+} \\
\Leftrightarrow \quad & N_{A^+}\left[1 - \frac{n\mu_p + \alpha_F}{\gamma_p}\frac{\gamma_p + \alpha_A}{n\mu_p} - \frac{\varepsilon_F}{\gamma_p}\frac{\alpha_A}{n\mu_m}\right] = -\left[\frac{n\mu_p + \alpha_F}{\gamma_p}\frac{\varepsilon_A}{n\mu_p} + \frac{\varepsilon_F}{\gamma_p}\frac{\gamma_m + \varepsilon_A}{n\mu_m}\right] N_{A^-}
\end{aligned}$$

We define Q such that

$$\begin{aligned}
Q &= 1 - \frac{n\mu_p + \alpha_F}{\gamma_p}\frac{\gamma_p + \alpha_A}{n\mu_p} - \frac{\varepsilon_F}{\gamma_p}\frac{\alpha_A}{n\mu_m} \\
&= \frac{\gamma_p n\mu_p n\mu_m - n\mu_m(n\mu_p + \alpha_F)(\gamma_p + \alpha_A) - n\mu_p\varepsilon_F\alpha_A}{\gamma_p n\mu_p n\mu_m}
\end{aligned}$$

and

$$\begin{aligned}
S &= -\left[\frac{n\mu_p + \alpha_F}{\gamma_p}\frac{\varepsilon_A}{n\mu_p} + \frac{\varepsilon_F}{\gamma_p}\frac{\gamma_m + \varepsilon_A}{n\mu_m}\right] \\
&= -\frac{n\mu_m(n\mu_p + \alpha_F)\varepsilon_A + n\mu_p\varepsilon_F(\gamma_m + \varepsilon_A)}{\gamma_p n\mu_p n\mu_m}
\end{aligned}$$

Hence

$$\begin{aligned}
N_{A^-} = \frac{Q}{S} N_{A^+} &= -\frac{\gamma_p n\mu_p n\mu_m - n\mu_m(n\mu_p + \alpha_F)(\gamma_p + \alpha_A) - n\mu_p\varepsilon_F\alpha_A}{n\mu_m(n\mu_p + \alpha_F)\varepsilon_A + n\mu_p\varepsilon_F(\gamma_m + \varepsilon_A)} N_{A^+} \\
&= \frac{n\mu_p n\mu_m\alpha_A + n\mu_m\gamma_p\alpha_F + n\mu_m\alpha_F\alpha_A + n\mu_p\varepsilon_F\alpha_A}{n\mu_p n\mu_m\varepsilon_A + n\mu_m\alpha_F\varepsilon_A + n\mu_p\varepsilon_F\gamma_m + n\mu_p\varepsilon_F\varepsilon_A} N_{A^+}
\end{aligned}$$

Hence

$$N_{A^-} = \frac{n\mu_p\mu_m\alpha_A + \mu_m\gamma_p\alpha_F + \mu_m\alpha_F\alpha_A + \mu_p\varepsilon_F\alpha_A}{n\mu_p\mu_m\varepsilon_A + \mu_m\alpha_F\varepsilon_A + \mu_p\varepsilon_F\gamma_m + \mu_p\varepsilon_F\varepsilon_A} N_{A^+}$$

We define

$$R = \frac{N_{A^-}}{N_{A^+}} = \frac{n\mu_p\mu_m\alpha_A + \mu_m\gamma_p\alpha_F + \mu_m\alpha_F\alpha_A + \mu_p\varepsilon_F\alpha_A}{n\mu_p\mu_m\varepsilon_A + \mu_m\alpha_F\varepsilon_A + \mu_p\varepsilon_F\gamma_m + \mu_p\varepsilon_F\varepsilon_A} \tag{S5}$$

$$\overline{e_A}(n) = \frac{e^+N_{A^+} + e^-N_{A^-}}{N_{A^+} + N_{A^-}} = \frac{e^+ + e^-\frac{N_{A^-}}{N_{A^+}}}{1 + \frac{N_{A^-}}{N_{A^+}}} = \frac{1 + \varphi R(n)}{1 + R(n)} e^+ \tag{S6}$$

with $\varphi = \frac{e^-}{e^+}$.

S2.1.2 Derivative of R

$$\frac{dR(n)}{dn} = \Bigg[(\mu_p\mu_m\alpha_A)(n\mu_p\mu_m\varepsilon_A + \mu_m\alpha_F\varepsilon_A + \mu_p\varepsilon_F\gamma_m + \mu_p\varepsilon_F\varepsilon_A) - (n\mu_p\mu_m\alpha_A + \mu_m\gamma_p\alpha_F + \mu_m\alpha_F\alpha_A + \mu_p\varepsilon_F\alpha_A)(\mu_p\mu_m\varepsilon_A)\Bigg]\Bigg[n\mu_p\mu_m\varepsilon_A + \mu_m\alpha_F\varepsilon_A + \mu_p\varepsilon_F\gamma_m + \mu_p\varepsilon_F\varepsilon_A\Bigg]^{-2}$$

$$\begin{aligned}
&\frac{dR(n)}{dn} > 0 \\
\Leftrightarrow\ &(\mu_p\mu_m\alpha_A)(n\mu_p\mu_m\varepsilon_A + \mu_m\alpha_F\varepsilon_A + \mu_p\varepsilon_F\gamma_m + \mu_p\varepsilon_F\varepsilon_A) - \\
&\quad (n\mu_p\mu_m\alpha_A + \mu_m\gamma_p\alpha_F + \mu_m\alpha_F\alpha_A + \mu_p\varepsilon_F\alpha_A)(\mu_p\mu_m\varepsilon_A) > 0 \\
\Leftrightarrow\ &\alpha_A\mu_m\alpha_F\varepsilon_A + \alpha_A\mu_p\varepsilon_F\gamma_m + \alpha_A\mu_p\varepsilon_F\varepsilon_A - \varepsilon_A\mu_m\gamma_p\alpha_F - \varepsilon_A\mu_m\alpha_F\alpha_A - \varepsilon_A\mu_p\varepsilon_F\alpha_A > 0 \\
\Leftrightarrow\ &\alpha_A\mu_p\varepsilon_F\gamma_m - \alpha_F\mu_m\varepsilon_A\gamma_p > 0
\end{aligned}$$

S2.1.3 Derivative of $\overline{e_A}$

$$\begin{aligned}
\frac{d\overline{e_A}(n)}{dn} = \frac{d\left(e^+\frac{1+\varphi R}{1+R}\right)}{dn} &= \frac{\varphi\frac{dR(n)}{dn}\big(1 + R(n)\big) - \big(1 + \varphi R(n)\big)\frac{dR(n)}{dn}}{\big(1 + R(n)\big)^2} e^+ \\
&= \frac{e^+(\varphi - 1)}{\big(1 + R(n)\big)^2}\frac{dR(n)}{dn}
\end{aligned}$$

S2.1.4 General model conclusion

$\overline{e_A}$ is a decreasing sequence of n if and only if

$$\frac{d\overline{e_A}(n)}{dn} < 0 \Leftrightarrow \frac{dR(n)}{dn} > 0 \Leftrightarrow \alpha_A\mu_p\varepsilon_F\gamma_m - \alpha_F\mu_m\varepsilon_A\gamma_p > 0 \tag{S7}$$

S2.1.5 H_1 hypothesis: FAD association induces tuna bad condition

We make the following hypotheses: $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$; $\mu_p = \mu_m = \mu$ and $\gamma_p = \gamma_m = \gamma$
Then

$$
\begin{aligned}
&\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F} \\
\Leftrightarrow\ & \alpha_A\varepsilon_F - \alpha_F\varepsilon_A > 0 \\
\Leftrightarrow\ & \alpha_A\mu_p\varepsilon_F\gamma_m - \alpha_F\mu_m\varepsilon_A\gamma_p > 0 \\
\Leftrightarrow\ & \frac{d\overline{e_A}(n)}{dn} < 0
\end{aligned}
$$

So, under hypothesis H_1, $\overline{e_A}$ is a decreasing sequence of n.

S2.1.6 H_2 hypothesis: the bad condition induces the associative behavior

We make the following hypotheses: $\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p}$; $\alpha_A = \alpha_F = \alpha$ and $\varepsilon_A = \varepsilon_F = \varepsilon$
Then

$$
\begin{aligned}
&\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p} \\
\Leftrightarrow\ & \mu_p\gamma_m - \mu_m\gamma_p < 0 \\
\Leftrightarrow\ & \alpha_A\mu_p\varepsilon_F\gamma_m - \alpha_F\mu_m\varepsilon_A\gamma_p < 0 \\
\Leftrightarrow\ & \frac{d\overline{e_A}(n)}{dn} > 0
\end{aligned}
$$

So, under hypothesis H_2, $\overline{e_A}$ is an increasing sequence of n.

S2.2 Variations of the average condition of the free-swimming fraction of the population

S2.2.1 N_{F^-} / N_{F^+} ratio

At equilibrium, from Eq. 1, we have

$$
N_{F^+} = \frac{\gamma_p + \alpha_A}{n\mu_p} N_{A^+} - \frac{\varepsilon_A}{n\mu_p} N_{A^-}
$$

$$
N_{A^+} = \frac{n\mu_p + \alpha_F}{\gamma_p} N_{F^+} - \frac{\varepsilon_F}{\gamma_p} N_{F^-}
$$

and

$$
N_{A^-} = \frac{n\mu_m + \varepsilon_F}{\gamma_m} N_{F^-} - \frac{\alpha_F}{\gamma_m} N_{F^+}
$$

Hence

$$
\begin{aligned}
& N_{F^+} = \frac{\gamma_p + \alpha_A}{n\mu_p}\left[\frac{n\mu_p + \alpha_F}{\gamma_p} N_{F^+} - \frac{\varepsilon_F}{\gamma_p} N_{F^-}\right] - \frac{\varepsilon_A}{n\mu_p}\left[\frac{n\mu_m + \varepsilon_F}{\gamma_m} N_{F^-} - \frac{\alpha_F}{\gamma_m} N_{F^+}\right] \\
\Leftrightarrow\ & N_{F^+} = \frac{\gamma_p + \alpha_A}{n\mu_p}\frac{n\mu_p + \alpha_F}{\gamma_p} N_{F^+} - \frac{\gamma_p + \alpha_A}{n\mu_p}\frac{\varepsilon_F}{\gamma_p} N_{F^-} - \frac{\varepsilon_A}{n\mu_p}\frac{n\mu_m + \varepsilon_F}{\gamma_m} N_{F^-} + \frac{\varepsilon_A}{n\mu_p}\frac{\alpha_F}{\gamma_m} N_{F^+} \\
\Leftrightarrow\ & N_{F^+}\left[1 - \frac{\gamma_p + \alpha_A}{n\mu_p}\frac{n\mu_p + \alpha_F}{\gamma_p} - \frac{\varepsilon_A}{n\mu_p}\frac{\alpha_F}{\gamma_m}\right] = -\left[\frac{\gamma_p + \alpha_A}{n\mu_p}\frac{\varepsilon_F}{\gamma_p} + \frac{\varepsilon_A}{n\mu_p}\frac{n\mu_m + \varepsilon_F}{\gamma_m}\right] N_{F^-} \\
\Leftrightarrow\ & N_{F^+}\big(n\mu_p\gamma_p\gamma_m - \gamma_p\varepsilon_A\alpha_F - \gamma_m\gamma_p n\mu_p - \alpha_F\alpha_A\gamma_m - \alpha_F\gamma_p\gamma_m - \alpha_A n\mu_p\gamma_m\big) = \\
& \quad - \big(\varepsilon_F\gamma_p\gamma_m + \alpha_A\varepsilon_F\gamma_m + \varepsilon_A\gamma_p n\mu_m + \varepsilon_F\varepsilon_A\gamma_p\big) N_{F^-} \\
\Leftrightarrow\ & N_{F^-} = \frac{\gamma_p\varepsilon_A\alpha_F + \alpha_F\alpha_A\gamma_m + \alpha_F\gamma_p\gamma_m + \alpha_A n\mu_p\gamma_m}{\varepsilon_F\gamma_p\gamma_m + \alpha_A\varepsilon_F\gamma_m + \varepsilon_A\gamma_p n\mu_m + \varepsilon_F\varepsilon_A\gamma_p} N_{F^+}
\end{aligned}
$$

We define

$$T = \frac{N_{F^-}}{N_{F^+}} = \frac{n\alpha_A\mu_p\gamma_m + \gamma_p\varepsilon_A\alpha_F + \alpha_F\alpha_A\gamma_m + \alpha_F\gamma_p\gamma_m}{n\varepsilon_A\gamma_p\mu_m + \varepsilon_F\gamma_p\gamma_m + \alpha_A\varepsilon_F\gamma_m + \varepsilon_F\varepsilon_A\gamma_p} \tag{S8}$$

Then

$$\overline{e_F}(n) = \frac{e^+N_{F^+} + e^-N_{F^-}}{N_{F^+} + N_{F^-}} = \frac{e^+ + e^-\frac{N_{F^-}}{N_{F^+}}}{1 + \frac{N_{F^-}}{N_{F^+}}} = \frac{1 + \varphi T(n)}{1 + T(n)}e^+$$

S2.2.2 Derivative of T

$$\frac{dT(n)}{dn} = \Big[\alpha_A\mu_p\gamma_m\big(n\varepsilon_A\gamma_p\mu_m + \varepsilon_F\gamma_p\gamma_m + \alpha_A\varepsilon_F\gamma_m + \varepsilon_F\varepsilon_A\gamma_p\big) - \big(n\alpha_A\mu_p\gamma_m + \gamma_p\varepsilon_A\alpha_F + \alpha_F\alpha_A\gamma_m + \alpha_F\gamma_p\gamma_m\big)\varepsilon_A\gamma_p\mu_m\Big]\Big[n\varepsilon_A\gamma_p\mu_m + \varepsilon_F\gamma_p\gamma_m + \alpha_A\varepsilon_F\gamma_m + \varepsilon_F\varepsilon_A\gamma_p\Big]^{-2}$$

$$\begin{aligned}
&\frac{dT(n)}{dn} > 0 \\
\Leftrightarrow\ &\alpha_A\mu_p\gamma_m\big(n\varepsilon_A\gamma_p\mu_m + \varepsilon_F\gamma_p\gamma_m + \alpha_A\varepsilon_F\gamma_m + \varepsilon_F\varepsilon_A\gamma_p\big) - \\
&\quad\big(n\alpha_A\mu_p\gamma_m + \gamma_p\varepsilon_A\alpha_F + \alpha_F\alpha_A\gamma_m + \alpha_F\gamma_p\gamma_m\big)\varepsilon_A\gamma_p\mu_m > 0 \\
\Leftrightarrow\ &\alpha_A\mu_p\gamma_m\varepsilon_F\gamma_p\gamma_m + \alpha_A\mu_p\gamma_m\alpha_A\varepsilon_F\gamma_m + \alpha_A\mu_p\gamma_m\varepsilon_F\varepsilon_A\gamma_p - \\
&\quad\varepsilon_A\gamma_p\mu_m\gamma_p\varepsilon_A\alpha_F - \varepsilon_A\gamma_p\mu_m\alpha_F\alpha_A\gamma_m - \varepsilon_A\gamma_p\mu_m\alpha_F\gamma_p\gamma_m > 0 \\
\Leftrightarrow\ &\mu_p\gamma_m\varepsilon_F\gamma_p\gamma_m + \mu_p\gamma_m\alpha_A\varepsilon_F\gamma_m + \mu_p\gamma_m\varepsilon_F\varepsilon_A\gamma_p - \frac{\varepsilon_A}{\alpha_A}\gamma_p\mu_m\gamma_p\varepsilon_A\alpha_F - \frac{\varepsilon_A}{\alpha_A}\gamma_p\mu_m\alpha_A\alpha_F\gamma_m - \frac{\varepsilon_A}{\alpha_A}\gamma_p\mu_m\alpha_F\gamma_p\gamma_m > 0 \\
\Leftrightarrow\ &\frac{\varepsilon_F}{\alpha_F}\mu_p\gamma_m\gamma_p\gamma_m + \frac{\varepsilon_F}{\alpha_F}\mu_p\gamma_m\alpha_A\gamma_m + \frac{\varepsilon_F}{\alpha_F}\mu_p\gamma_m\varepsilon_A\gamma_p - \frac{\varepsilon_A}{\alpha_A}\gamma_p\mu_m\gamma_p\varepsilon_A - \frac{\varepsilon_A}{\alpha_A}\gamma_p\mu_m\alpha_A\gamma_m - \frac{\varepsilon_A}{\alpha_A}\gamma_p\mu_m\gamma_p\gamma_m > 0 \\
\Leftrightarrow\ &\frac{\varepsilon_F}{\alpha_F}\gamma_m\gamma_p\gamma_m + \frac{\varepsilon_F}{\alpha_F}\gamma_m\alpha_A\gamma_m + \frac{\varepsilon_F}{\alpha_F}\gamma_m\varepsilon_A\gamma_p - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\mu_m\gamma_p\varepsilon_A - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\mu_m\alpha_A\gamma_m - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\mu_m\gamma_p\gamma_m > 0 \\
\Leftrightarrow\ &\frac{\varepsilon_F\gamma_m}{\alpha_F\mu_m}\gamma_p\gamma_m + \frac{\varepsilon_F\gamma_m}{\alpha_F\mu_m}\alpha_A\gamma_m + \frac{\varepsilon_F\gamma_m}{\alpha_F\mu_m}\varepsilon_A\gamma_p - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\gamma_p\varepsilon_A - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\alpha_A\gamma_m - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\gamma_p\gamma_m > 0 \\
\Leftrightarrow\ &\frac{\varepsilon_F\gamma_m}{\alpha_F\mu_m}\big(\gamma_p\gamma_m + \alpha_A\gamma_m + \varepsilon_A\gamma_p\big) - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p}\big(\gamma_p\varepsilon_A + \alpha_A\gamma_m + \gamma_p\gamma_m\big) > 0 \\
\Leftrightarrow\ &\frac{\varepsilon_F\gamma_m}{\alpha_F\mu_m} - \frac{\varepsilon_A\gamma_p}{\alpha_A\mu_p} > 0 \\
\Leftrightarrow\ &\varepsilon_F\gamma_m\alpha_A\mu_p - \varepsilon_A\gamma_p\alpha_F\mu_m > 0
\end{aligned}$$

S2.2.3 Derivative of $\overline{e_F}$

$$\begin{aligned}
\frac{d\overline{e_F}(n)}{dn} = \frac{d\Big(e^+\frac{1+\varphi T}{1+T}\Big)}{dn} &= \frac{\varphi\frac{dT(n)}{dn}\big(1 + T(n)\big) - \big(1 + \varphi T(n)\big)\frac{dT(n)}{dn}}{\big(1 + T(n)\big)^2}e^+ \\
&= \frac{e^+(\varphi - 1)}{\big(1 + T(n)\big)^2}\frac{dT(n)}{dn}
\end{aligned}$$

S2.2.4 General model conclusion

$\overline{e_F}$ is a decreasing sequence of n if and only if

$$\frac{d\overline{e_F}(n)}{dn} < 0 \Leftrightarrow \frac{dT(n)}{dn} > 0 \Leftrightarrow \varepsilon_F\gamma_m\alpha_A\mu_p - \varepsilon_A\gamma_p\alpha_F\mu_m > 0 \tag{S9}$$

S2.2.5 H_1 hypothesis: FAD association induces tuna bad condition

We make the following hypotheses: $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$; $\mu_p = \mu_m = \mu$ and $\gamma_p = \gamma_m = \gamma$
Then

$$\begin{aligned}
&\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F} \\
\Leftrightarrow\ &\alpha_A\varepsilon_F - \alpha_F\varepsilon_A > 0 \\
\Leftrightarrow\ &\alpha_A\mu_p\varepsilon_F\gamma_m - \alpha_F\mu_m\varepsilon_A\gamma_p > 0 \\
\Leftrightarrow\ &\frac{d\overline{e_F}(n)}{dn} < 0
\end{aligned}$$

So, under hypothesis H_1, $\overline{e_F}$ is a decreasing sequence of n.

S2.2.6 H_2 hypothesis: the bad condition induces the associative behavior

We make the following hypotheses: $\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p}$; $\alpha_A = \alpha_F = \alpha$ and $\varepsilon_A = \varepsilon_F = \varepsilon$
Then

$$\begin{aligned}
&\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p} \\
\Leftrightarrow\ &\mu_p\gamma_m - \mu_m\gamma_p < 0 \\
\Leftrightarrow\ &\alpha_A\mu_p\varepsilon_F\gamma_m - \alpha_F\mu_m\varepsilon_A\gamma_p < 0 \\
\Leftrightarrow\ &\frac{d\overline{e_F}(n)}{dn} > 0
\end{aligned}$$

So, under hypothesis H_2, $\overline{e_F}$ is an increasing sequence of n.

S2.3 Comparison of the average condition of the two fractions of the population

We want to verify that, under both hypotheses (H_1 and H_2), the average condition of the free-swimming fraction of the population is greater than that of the associated fraction of the population – i.e. we want to verify that $\forall n \in \mathbb{N}^{+*}$, $\overline{e_F}(n) > \overline{e_A}(n)$.

S2.3.1 Expression of $T(n)$ as a function of $R(n)$

From Eq. S5&S8: $R(n) = \frac{N_{A^-}}{N_{A^+}}$ et $T(n) = \frac{N_{F^-}}{N_{F^+}}$

$$\begin{aligned}
T(n) = \frac{N_{F^-}}{N_{F^+}} &= \left[\frac{\gamma_m + \varepsilon_A}{\mu_m}N_{A^-} - \frac{\alpha_A}{\mu_m}N_{A^+}\right]\left[\frac{\gamma_p + \alpha_A}{\mu_p}N_{A^-} - \frac{\varepsilon_A}{\mu_p}N_{A^+}\right]^{-1} \\
&= \left[\frac{\gamma_m + \varepsilon_A}{\mu_m}\frac{N_{A^-}}{N_{A^+}} - \frac{\alpha_A}{\mu_m}\right]\left[\frac{\gamma_p + \alpha_A}{\mu_p} - \frac{\varepsilon_A}{\mu_p}\frac{N_{A^-}}{N_{A^+}}\right]^{-1} \\
&= \frac{\mu_p}{\mu_m}\frac{(\gamma_m + \varepsilon_A)R(n) - \alpha_A}{\gamma_p + \alpha_A - \varepsilon_A R(n)}
\end{aligned}$$

S2.3.2 General model - sign of $\overline{e_F}(n) - \overline{e_A}(n)$

$$
\begin{aligned}
\overline{e_F}(n) - \overline{e_A}(n) &= e^+ \left[\frac{1+\varphi T(n)}{1+T(n)} - \frac{1+\varphi R(n)}{1+R(n)} \right] \\
&= e^+ \left[\frac{\big(1+\varphi T(n)\big)\big(1+R(n)\big) - \big(1+\varphi R(n)\big)\big(1+T(n)\big)}{\big(1+T(n)\big)\big(1+R(n)\big)} \right] \\
&= \frac{1+R(n)+\varphi T(n)+\varphi T(n)R(n)-1-\varphi R(n)-T(n)-\varphi T(n)R(n)}{\big(1+T(n)\big)\big(1+R(n)\big)} e^+ \\
&= \frac{\varphi T(n) - \varphi R(n) + R(n) + T(n)}{\big(1+T(n)\big)\big(1+R(n)\big)} e^+ \\
&= \frac{\big(\varphi - 1\big)\big(T(n) - R(n)\big)}{\big(1+T(n)\big)\big(1+R(n)\big)} e^+
\end{aligned}
$$

And $\varphi - 1 < 0$, $T(n) > 0$ and $R(n) > 0$. So

$$
\begin{aligned}
\overline{e_F}(n) - \overline{e_A}(n) > 0 &\Leftrightarrow T(n) - R(n) < 0 \\
&\Leftrightarrow \frac{\mu_p}{\mu_m} \frac{(\gamma_m + \varepsilon_A)R(n) - \alpha_A}{\gamma_p + \alpha_A - \varepsilon_A R(n)} - R(n) < 0 \\
&\Leftrightarrow \frac{\mu_p[(\gamma_m + \varepsilon_A)R(n) - \alpha_A] - \mu_m R(n)[\gamma_p + \alpha_A - \varepsilon_A R(n)]}{[\gamma_p + \alpha_A - \varepsilon_A R(n)]\mu_m} < 0 \\
&\Leftrightarrow \frac{\mu_p(\gamma_m + \varepsilon_A)R(n) - \alpha_A\mu_p - (\gamma_p + \alpha_A)R(n)\mu_m + \mu_m\varepsilon_A R(n)^2}{\gamma_p + \alpha_A - \varepsilon_A R(n)} < 0 \\
&\Leftrightarrow \frac{\mu_m\varepsilon_A R(n)^2 + \big[\mu_p(\gamma_m + \varepsilon_A) - \mu_m(\gamma_p + \alpha_A)\big]R(n) - \alpha_A\mu_p}{\gamma_p + \alpha_A - \varepsilon_A R(n)} < 0
\end{aligned}
$$

We define:

$$
\begin{aligned}
a &= \mu_m\varepsilon_A \\
b &= \mu_p(\gamma_m + \varepsilon_A) - \mu_m(\gamma_p + \alpha_A) \\
c &= -\alpha_A\mu_p
\end{aligned}
$$

S2.3.3 General model - Case n°1: $\gamma_p + \alpha_A - \varepsilon_A R(n) > 0$

Then, because $R(n) > 0$ and $\mu_m\varepsilon_A > 0$ and $b^2 - 4ac > 0$,

$$
\begin{aligned}
\overline{e_F}(n) - \overline{e_A}(n) > 0 &\Leftrightarrow T(n) - R(n) < 0 \\
&\Leftrightarrow \mu_m\varepsilon_A R(n)^2 + \big[\mu_p(\gamma_m + \varepsilon_A) - \mu_m(\gamma_p + \alpha_A)\big]R(n) - \alpha_A\mu_m < 0 \\
&\Leftrightarrow R(n) < -\frac{b}{2a} + \frac{\sqrt{b^2 - 4ac}}{2a}
\end{aligned}
$$

S2.3.4 General model - Case n°2: $\gamma_p + \alpha_A - \varepsilon_A R(n) < 0$

Then

$$\begin{aligned}\overline{e_F}(n) - \overline{e_A}(n) > 0 &\Leftrightarrow T(n) - R(n) < 0 \\ &\Leftrightarrow \mu_m \varepsilon_A R(n)^2 + \left[\mu_p(\gamma_m + \varepsilon_A) - \mu_m(\gamma_p + \alpha_A)\right] R(n) - \alpha_A \mu_m > 0 \\ &\Leftrightarrow R(n) > -\frac{b}{2a} + \frac{\sqrt{b^2 - 4ac}}{2a}\end{aligned}$$

S2.3.5 H_1 hypothesis: FAD association induces tuna bad condition

We make the following hypotheses: $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$; $\mu_p = \mu_m = \mu$ and $\gamma_p = \gamma_m = \gamma$
Then

$$\begin{aligned}R(n) &= \frac{n\mu_p\mu_m\alpha_A + \mu_m\gamma_p\alpha_F + \mu_m\alpha_F\alpha_A + \mu_p\varepsilon_F\alpha_A}{n\mu_p\mu_m\varepsilon_A + \mu_m\alpha_F\varepsilon_A + \mu_p\varepsilon_F\gamma_m + \mu_p\varepsilon_F\varepsilon_A} \\ &= \frac{n\mu^2\alpha_A + \mu\gamma\alpha_F + \mu\alpha_F\alpha_A + \mu\varepsilon_F\alpha_A}{n\mu^2\varepsilon_A + \mu\alpha_F\varepsilon_A + \mu\varepsilon_F\gamma + \mu\varepsilon_F\varepsilon_A} \\ &= \frac{n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A}{n\mu\varepsilon_A + \alpha_F\varepsilon_A + \varepsilon_F\gamma + \varepsilon_F\varepsilon_A}\end{aligned}$$

$$\begin{aligned}a &= \mu\varepsilon_A \\ b &= \mu(\gamma + \varepsilon_A) - \mu(\gamma + \alpha_A) = \mu(\varepsilon_A - \alpha_A) \\ c &= -\mu\alpha_A\end{aligned}$$

We are in case n°1 because:

$$\begin{aligned}&\gamma + \alpha_A - \varepsilon_A R(n) > 0 \\ \Leftrightarrow\ &\big(\gamma + \alpha_A\big)\big(n\mu\varepsilon_A + \alpha_F\varepsilon_A + \varepsilon_F\gamma + \varepsilon_F\varepsilon_A\big) - \varepsilon_A\big(n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A\big) > 0 \\ \Leftrightarrow\ &n\mu\varepsilon_A\gamma + \alpha_F\varepsilon_A\gamma + \varepsilon_F\gamma^2 + \varepsilon_F\varepsilon_A\gamma + n\mu\varepsilon_A\alpha_A + \alpha_F\varepsilon_A\alpha_A + \varepsilon_F\gamma\alpha_A + \varepsilon_F\varepsilon_A\alpha_A - \\ &\quad \varepsilon_A\big(n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A\big) > 0 \\ \Leftrightarrow\ &\varepsilon_A\big(n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A\big) + \alpha_A\varepsilon_F\gamma + \varepsilon_F\gamma^2 + \gamma\varepsilon_A\varepsilon_F - \\ &\quad \varepsilon_A\big(n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A\big) > 0 \\ \Leftrightarrow\ &\alpha_A\varepsilon_F\gamma + \varepsilon_F\gamma^2 + \gamma\varepsilon_A\varepsilon_F > 0 \quad \text{which is always true}\end{aligned}$$

Hence

$$
\begin{aligned}
\overline{e_F}(n) - \overline{e_A}(n) > 0 &\Leftrightarrow R(n) < -\frac{b}{2a} + \frac{\sqrt{b^2-4ac}}{2a} \\
&\Leftrightarrow R(n) < -\frac{\varepsilon_A - \alpha_A}{2\varepsilon_A} + \frac{\sqrt{\mu^2(\varepsilon_A-\alpha_A)^2 + 4\mu^2\varepsilon_A\alpha_A}}{2\mu\varepsilon_A} \\
&\Leftrightarrow R(n) < -\frac{\varepsilon_A - \alpha_A}{2\varepsilon_A} + \frac{\sqrt{(\varepsilon_A+\alpha_A)^2}}{2\varepsilon_A} \\
&\Leftrightarrow R(n) < \frac{1}{2\varepsilon_A}\big[-\varepsilon_A + \alpha_A + \varepsilon_A + \alpha_A\big] \\
&\Leftrightarrow R(n) < \frac{\alpha_A}{\varepsilon_A} \\
&\Leftrightarrow \frac{n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A}{n\mu\varepsilon_A + \alpha_F\varepsilon_A + \varepsilon_F\gamma + \varepsilon_F\varepsilon_A} < \frac{\alpha_A}{\varepsilon_A} \\
&\Leftrightarrow \varepsilon_A\Big[n\mu\alpha_A + \gamma\alpha_F + \alpha_F\alpha_A + \varepsilon_F\alpha_A\Big] - \alpha_A\Big[n\mu\varepsilon_A + \alpha_F\varepsilon_A + \varepsilon_F\gamma + \varepsilon_F\varepsilon_A\Big] < 0 \\
&\Leftrightarrow \alpha_F\varepsilon_A - \alpha_A\varepsilon_F < 0 \\
&\Leftrightarrow \alpha_F\varepsilon_A < \alpha_A\varepsilon_F \\
&\Leftrightarrow \frac{\alpha_F}{\varepsilon_F} < \frac{\alpha_A}{\varepsilon_A}
\end{aligned}
$$

So, under hypothesis H_1, we do verify that $\forall n \in \mathbb{N}^{+*},\ \overline{e_F}(n) > \overline{e_A}(n)$

S2.3.6 H_2 hypothesis: the bad condition induces the associative behavior

We make the following hypotheses: $\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p}$; $\alpha_A = \alpha_F = \alpha$ and $\varepsilon_A = \varepsilon_F = \varepsilon$
Going back to Eq. 5:

$$
\begin{cases}
\frac{dN_{A^+}}{dt} &= -(\gamma_p + \alpha)N_{A^+} + \varepsilon N_{A^-} + n\mu_p N_{F^+} \\
\frac{dN_{A^-}}{dt} &= -(\gamma_m + \varepsilon)N_{A^-} + \alpha N_{A^+} + \mu_m n N_{F^-} \\
\frac{dN_{F^+}}{dt} &= -(n\mu_p + \alpha)N_{F^+} + \gamma_p N_{A^+} + \varepsilon N_{F^-} \\
\frac{dN_{F^-}}{dt} &= -(n\mu_m + \varepsilon)N_{F^-} + \gamma_m N_{A^-} + \alpha N_{F^+}
\end{cases}
$$

At equilibrium, we have

$$
\begin{aligned}
-\alpha N_{A^+} + \varepsilon N_{A^-} - \alpha N_{F^+} + \varepsilon N_{F^-} = 0 &\Leftrightarrow \varepsilon(N_{A^-} + N_{F^-}) = \alpha(N_{A^+} + N_{F^+}) \\
&\Leftrightarrow N_{A^-} + N_{F^-} = \frac{\alpha}{\varepsilon}(N_{A^+} + N_{F^+})
\end{aligned}
$$

Let us consider N, the total tuna population. Then:

$$
\begin{aligned}
N_{A^+} + N_{A^-} + N_{F^+} + N_{F^-} = N &\Leftrightarrow N_{A^-} + N_{F^-} = N - (N_{A^+} + N_{F^+}) \\
&\Leftrightarrow \frac{\alpha}{\varepsilon}(N_{A^+} + N_{F^+}) = N - (N_{A^+} + N_{F^+}) \\
&\Leftrightarrow N_{A^+} + N_{F^+} = \frac{\varepsilon}{\alpha}N - \frac{\varepsilon}{\alpha}(N_{A^+} + N_{F^+}) \\
&\Leftrightarrow (N_{A^+} + N_{F^+})(1 + \frac{\varepsilon}{\alpha}) = \frac{\varepsilon}{\alpha}N \\
&\Leftrightarrow N_{A^+} + N_{F^+} = \frac{N\varepsilon}{\alpha + \varepsilon}
\end{aligned}
$$

Hence

$$N_{A^+} + N_{F^+} = \frac{N\varepsilon}{\alpha + \varepsilon} \tag{S10}$$

Also, we can demonstrate that

$$N_{A^-} + N_{F^-} = \frac{N\alpha}{\alpha + \varepsilon} \tag{S11}$$

Moreover

$$\begin{aligned}
\overline{e_F}(n) > \overline{e_A}(n) &\Leftrightarrow \frac{N_{F^+} + \varphi N_{F^-}}{N_{F^+} + N_{F^-}} > \frac{N_{A^+} + \varphi N_{A^-}}{N_{A^+} + N_{A^-}} \quad \text{with } \varphi = \frac{e^-}{e^+} \\
&\Leftrightarrow N_{F^+}N_{A^+} + \varphi N_{A^+}N_{F^-} + N_{A^-}N_{F^+} + \varphi N_{A^-}N_{F^-} > \\
&\qquad N_{F^+}N_{A^+} + \varphi N_{F^+}N_{A^-} + N_{F^-}N_{A^+} + \varphi N_{F^-}N_{A^-} \\
&\Leftrightarrow \varphi N_{A^+}N_{F^-} + N_{A^-}N_{F^+} > \varphi N_{F^+}N_{A^-} + N_{F^-}N_{A^+}
\end{aligned}$$

From Eq. S10&S11

$$\begin{aligned}
& \overline{e_F}(n) > \overline{e_A}(n) \\
\Leftrightarrow \quad & \varphi N_{A^+}\Big(\frac{N\alpha}{\alpha+\varepsilon} - N_{A^-}\Big) + N_{A^-}\Big(\frac{N\varepsilon}{\alpha+\varepsilon} - N_{A^+}\Big) > \varphi N_{A^-}\Big(\frac{N\varepsilon}{\alpha+\varepsilon} - N_{A^+}\Big) + N_{A^+}\Big(\frac{N\alpha}{\alpha+\varepsilon} - N_{A^-}\Big) \\
\Leftrightarrow \quad & \varphi N_{A^+}\frac{N\alpha}{\alpha+\varepsilon} + N_{A^-}\frac{N\varepsilon}{\alpha+\varepsilon} > \varphi N_{A^-}\frac{N\varepsilon}{\alpha+\varepsilon} + N_{A^+}\frac{N\alpha}{\alpha+\varepsilon} \\
\Leftrightarrow \quad & N_{A^+}\frac{N\alpha}{\alpha+\varepsilon}(\varphi - 1) > N_{A^-}\frac{N\varepsilon}{\alpha+\varepsilon}(\varphi - 1) \\
\Leftrightarrow \quad & \frac{N_{A^+}}{N_{A^-}} < \frac{\alpha+\varepsilon}{N\alpha}\frac{N\varepsilon}{\alpha+\varepsilon} \quad (\text{as } \varphi < 1)
\end{aligned}$$

Hence

$$\overline{e_F}(n) > \overline{e_A}(n) \Leftrightarrow \frac{N_{A^+}}{N_{A^-}} < \frac{\varepsilon}{\alpha} \tag{S12}$$

From Eq. 5,S10&S11

$$\begin{aligned}
& \begin{cases} -(\gamma_p + \alpha)N_{A^+} + \varepsilon N_{A^-} + n\mu_p\big(\frac{N\varepsilon}{\varepsilon+\alpha} - N_{A^+}\big) = 0 \\ -(\gamma_m + \varepsilon)N_{A^-} + \alpha N_{A^+} + n\mu_m\big(\frac{N\alpha}{\varepsilon+\alpha} - N_{A^-}\big) = 0 \end{cases} \\
\Leftrightarrow & \begin{cases} -(\gamma_p + \alpha + n\mu_p)N_{A^+} + \varepsilon N_{A^-} + n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha} = 0 \\ -(\gamma_m + \varepsilon + n\mu_m)N_{A^-} + \alpha N_{A^+} + n\mu_m\frac{N\alpha}{\varepsilon+\alpha} = 0 \end{cases}
\end{aligned}$$

Applying Cramer's rule, we have

$$N_{A^+} = \frac{\begin{vmatrix} -n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha} & \varepsilon \\ -n\mu_m\frac{N\alpha}{\varepsilon+\alpha} & -(\gamma_m + \varepsilon + n\mu_m) \end{vmatrix}}{\begin{vmatrix} -(\gamma_p + \alpha + n\mu_p) & \varepsilon \\ \alpha & -(\gamma_m + \varepsilon + n\mu_m) \end{vmatrix}}$$

and

$$N_{A^-} = \frac{\begin{vmatrix} -(\gamma_p + \alpha + n\mu_p) & -n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha} \\ \alpha & -n\mu_m\frac{N\alpha}{\varepsilon+\alpha} \end{vmatrix}}{\begin{vmatrix} -(\gamma_p + \alpha + n\mu_p) & \varepsilon \\ \alpha & -(\gamma_m + \varepsilon + n\mu_m) \end{vmatrix}}$$

So

$$\begin{aligned}
\frac{N_{A^+}}{N_{A^-}} &= \frac{\begin{vmatrix} -n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha} & \varepsilon \\ -n\mu_m\frac{N\alpha}{\varepsilon+\alpha} & -(\gamma_m+\varepsilon+n\mu_m) \end{vmatrix}}{\begin{vmatrix} -(\gamma_p+\alpha+n\mu_p) & -n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha} \\ \alpha & -n\mu_m\frac{N\alpha}{\varepsilon+\alpha} \end{vmatrix}} \\
&= \frac{n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha}(\gamma_m+\varepsilon+n\mu_m) + n\varepsilon\mu_m\frac{N\alpha}{\varepsilon+\alpha}}{n\mu_m\frac{N\alpha}{\varepsilon+\alpha}(\gamma_p+\alpha+n\mu_p) + \alpha n\mu_p\frac{N\varepsilon}{\varepsilon+\alpha}} \\
&= \frac{\varepsilon\mu_p(\gamma_m+\varepsilon+n\mu_m) + \alpha\varepsilon\mu_m}{\alpha\mu_m(\gamma_p+\alpha+n\mu_p) + \alpha\varepsilon\mu_p}
\end{aligned}$$

Hence, from Equation S12

$$\begin{aligned}
\overline{e_F}(n) > \overline{e_A}(n) &\Leftrightarrow \frac{N_{A^+}}{N_{A^-}} < \frac{\varepsilon}{\alpha} \\
&\Leftrightarrow \frac{\varepsilon\mu_p(\gamma_m+\varepsilon+n\mu_m) + \alpha\varepsilon\mu_m}{\alpha\mu_m(\gamma_p+\alpha+n\mu_p) + \alpha\varepsilon\mu_p} < \frac{\varepsilon}{\alpha} \\
&\Leftrightarrow \frac{\mu_p(\gamma_m+\varepsilon+n\mu_m) + \alpha\mu_m}{\mu_m(\gamma_p+\alpha+n\mu_p) + \varepsilon\mu_p} < 1 \\
&\Leftrightarrow \mu_p\gamma_m + \varepsilon\mu_p + n\mu_p\mu_m + \alpha\mu_m < \mu_m\gamma_p + \alpha\mu_m + n\mu_p\mu_m + \varepsilon\mu_p \\
&\Leftrightarrow \mu_p\gamma_m < \mu_m\gamma_p \\
&\Leftrightarrow \frac{\mu_p}{\gamma_p} < \frac{\mu_m}{\gamma_m}
\end{aligned}$$

So, under hypothesis H_2, we do verify that $\forall n \in \mathbb{N}^{+*},\ \overline{e_F}(n) > \overline{e_A}(n)$

S3 Supplementary – Statistical analysis on skipjack tuna (SKJ)

We applied the methodology presented in the main manuscript to skipjack tuna in the WIO. A total of 323 skipjack (41 to 68 cm FL) were sampled, from 16 DFAD sets.

Phase angle values ranged from 6.5 to 48.9 °, with a median value of 24.6 °. Within-set standard-deviation was low for most of the sets: average within-set standard deviation of 2.9 ° (Figure S4). Phase angle values did not display any clear trend as a function of FOB density (Figure S4). However, SKJ displayed a significant decreasing trend of PA for increasing ρ_{FOB} values (Spearman's $\rho = -0.23$, $p = 3.5 \times 10^{-5}$).

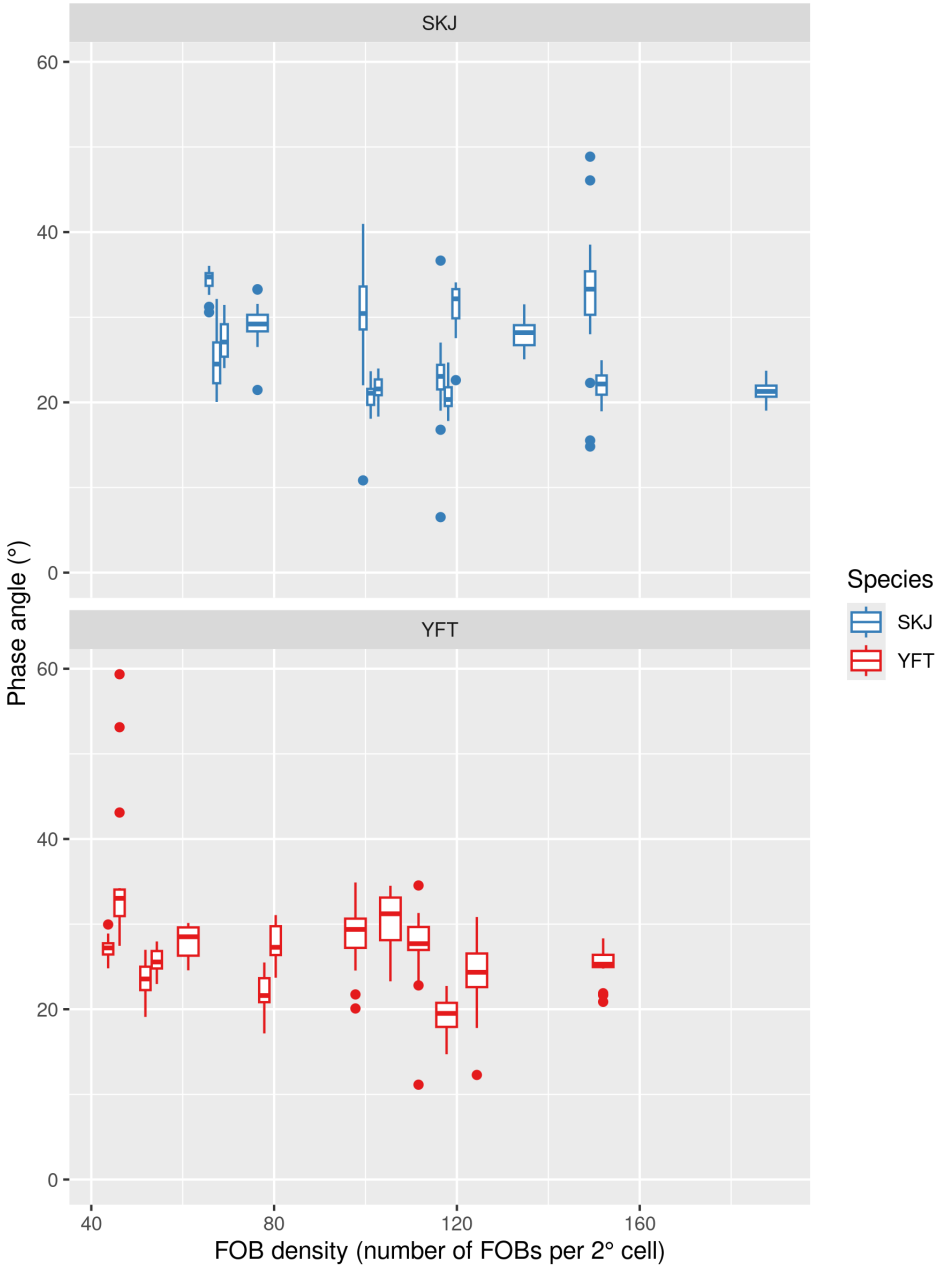

Figure S4. Phase angle (PA) of associated tuna as a function of floating object (FOBs) density. PA was measured on 323 skipjack (SKJ, upper panel) and 232 yellowfin tuna (YFT, lower panel) fished on DFAD-associated schools. Each boxplot corresponds to a given set. Note the higher range of FOB densities at which skipjack PA was measured.

The results of the non-linear model assessing the relationship between the phase angle of associated SKJ

and the density of FOBs and other explanatory variables are presented in Table S4 (Methods detailed in Supplementary S1). SKJ displayed a decreasing condition factor with increasing fork length ($\theta = -0.12$; p-value: 2.4×10^{-3}) and a lower condition factor in the first quarter of the year (PA in Q2, Q3 and Q4 significantly greater than Q1 for SKJ). SKJ condition decreased with increasing concentration of chlorophyll-a ($\eta = -12.1$; p-value: 8.5×10^{-10}). No coefficient related to ρ_{NFOB} were found significant. Hence, the available BIA data does not allow to conclude with certainty for SKJ, as the non-linear regressions do not confirm the results obtained with Spearman's correlation test.

Table S4. Non-linear models performed on the condition (phase angle - PA) of skipjack tuna associated with DFADs. SKJ: skipjack tuna; β,δ and ζ: coefficients used to fit the density of FOBs; FL: fork length (cm); Chla: chlorophyll-a concentration ($mg.m^{-3}$); Q: quarter; AIC: Aikake Information Criterion. LOOCV: Leave-One-Out Cross Validation, the last column presents the minimum and maximum estimate obtained performing the LOOCV.

Non-linear model	Coefficient	Estimate	Significance (p-value)	LOOCV	
				min	max
SKJ	β	159	0.97	0.3	655
	δ	0.03	5.6×10^{-2}	0.030	0.034
	ζ	5.5	0.97	0.00	21.7
	Chla	-12.1	8.5×10^{-10}	-12.5	-11.8
	FL	-0.12	2.4×10^{-3}	-0.13	-0.10
	Q2	9.0	$< 2 \times 10^{-16}$	8.6	9.4
	Q3	8.0	$< 2 \times 10^{-16}$	7.9	8.1
	Q4	4.4	1.1×10^{-10}	4.2	4.7
	R^2: 0.52			0.52	0.54
	AIC: 1797			1769	1792

Despite the presence of outliers, the NLMs obtained through the Leave-One-Out Cross Validation (LOOCV) confirmed the robustness of the relationship (or absence of relationship) between PA and ρ_{FOB} and between PA and other variables for both species (Table S4). The values of the coefficients showed little variation and no modification of their significance was observed.

S4 Supplementary – $\overline{e_A}$ and $\overline{e_F}$ as a function of n for different parameter values

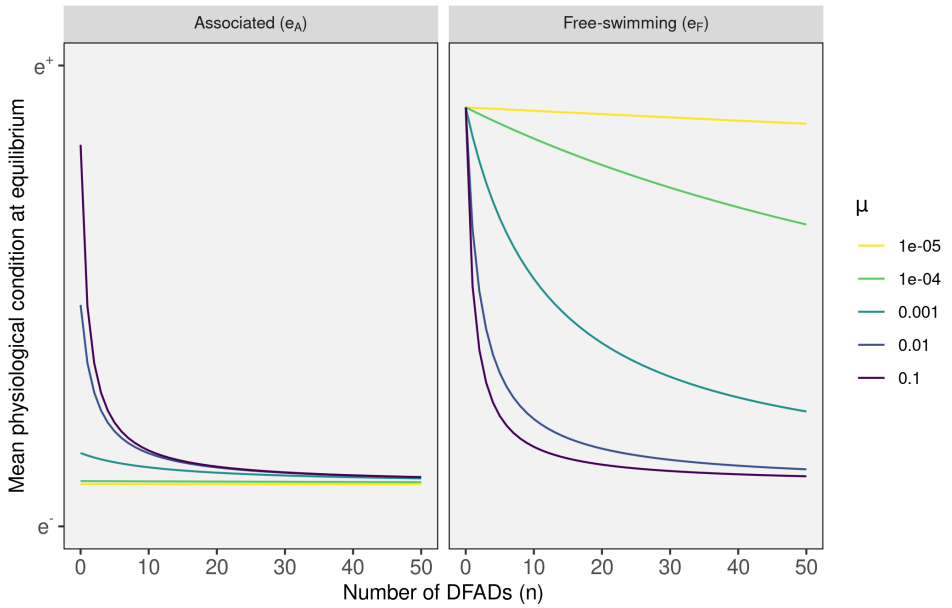

Figure S5. Variations of $\overline{e_A}$ and $\overline{e_F}$ as a function of the number of DFADs (n). H_1 model following the hypothesis that tuna condition tend to decrease when they are associated with DFADs. All the results are obtained with $\alpha_A = \varepsilon_F = 10^{-2}$ and $\alpha_F = \varepsilon_A = 10^{-3}$. The color scale represent the results considering different values of $\mu_M = \mu_P = \gamma_M = \gamma_P$ (noted μ on the color scale).