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Mechanistic modelling reveals tuna physiological condition is not a driver of floating object association

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Assessing the proximate and ultimate causes of animal behaviour is crucial for understanding the impact of human activities on wild species. However, for animals that are difficult to observe in the wild, such as pelagic fish species, identifying the causes and consequences of their behaviour can be particularly challenging. Here, we show the effectiveness of mechanistic modelling, combined with correlative approaches on empirical data, to determine the causation and consequences of behaviour. A behavioural model is developed to investigate the causal relationship between the associative behaviour of tropical tunas with floating objects and their physiological condition. Comparison with empirical data on tuna condition measured in the Western Indian Ocean suggests the rejection of the hypothesis that the physiological condition of tuna is a proximate cause of their associative behaviour. This study contributes to the assessment of the impact on tuna physiology of habitat changes induced by the massive use of floating objects introduced by tuna fishers.

1. Introduction

In defining a framework for ethology, the ‘biological study of animal behavior’, Tinbergen outlined four key questions [1]. These questions are as follows: what is the physiological causation of the behaviour, designated as *causation*; how does behaviour develop in individuals, *ontogeny*; what is the fitness of a particular behaviour, *survival value*; and how did this behaviour evolve, *evolution* [2]. The former two questions are the so-called *proximate* causes of behaviour, while the latter are referred to as the *ultimate* causes [3]. Later, Hogan [4] reviewed this framework to create a new one that aligns with the field’s advancements and the various scales at which behaviour is studied, ranging from behavioural genetics to behavioural ecology. He suggests that the study of behaviour 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 behaviour. Here, we focus on the causation and consequences of behaviour which, based on the time scale considered, can be motivational, ontogenetic or phylogenetic. Differentiating causes from consequences can be challenging, leading to widespread confusion in behavioural ecology between the *function* of a behaviour—i.e. why it has been selected—and its causes [4,5]. Based on Hogan’s [4] suggestion, we use the term *phylogenetic consequence* to designate the reason why a behaviour has been selected. Beside these two categories (causation and function), animal behaviour can also imply collateral consequences, i.e. unwanted side effects of a given behaviour that appear in the short term, which still allow the behaviour to be selected. Assessing the causation or consequences of behaviour without knowledge of behaviour's function (i.e. unknown phylogenetic consequences) can be very challenging, particularly for wild species that are difficult to access.

When assessing the proximate causes and/or consequences of a behaviour, one may encounter the correlation vs causation dilemma, a classical dilemma in observational science. For example, two species of honeyeaters, *Phylidonyris novaehollandiae* and *P. nigra*, are less territorial when food is abundant, i.e. researchers observed lower rates of territorial aggression when the available food quantity increased [6]. However, despite this correlation, Armstrong [6] demonstrated experimentally that the territorial behaviour was seasonal and did not follow artificial changes in nectar abundance, showing that there was correlation but no causation. Many ecological studies rely on correlative models, and these models are not able to determine causal effects [7]. Causal effects in ecology can be determined through randomized experiments [8]. These experiments depend on several elements (e.g. controls, replication) that can be hard to implement, specifically when focusing on marine ecosystems [9]. Hence, when focusing on a specific behaviour for which the phylogenetic consequences are unknown and where experimental testing cannot be implemented, how can one assess this behaviour's proximate causation and consequences?

We assess that question by focusing on a specific behaviour displayed by pelagic fish species. Several pelagic fish species associate with floating objects (FOBs), such as logs or branches, which are natural components of their habitat. Although this behaviour has been known and used by fishers for almost two millennia, its phylogenetic consequences are still unknown [10,11]. Since the early 1980s, industrial tropical tuna purse seine fleets have been deploying their own artificial FOBs (called drifting fish aggregating devices, DFADs; [12]). In this article, we designate as FOBs all the floating objects, including both natural FOBs and DFADs. 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 ([13], with data from 2013). The large-scale deployment and use of DFADs throughout the world's tropical oceans have led to several direct ecological impacts, including pollution, damage to coastal habitats through DFAD stranding, increased bycatch and ghost fishing [14–16]. Moreover, for tropical tunas (skipjack SKJ – *Katsuwonus pelamis* –, yellowfin YFT – *Thunnus albacares* – and bigeye BET – *Thunnus obsesus* – tunas), the use of DFADs has increased the availability of tuna to the purse seine fleets by increasing the time that tuna spend associated with FOBs [17]. However, in the absence of knowledge on the causation of tuna associative behaviour, it is difficult to assess the impact of such behavioural modification apart from that directly stemming from fisheries.

Fish physiological condition, characterized by morphological, physiological and biochemical indicators, can indicate the magnitude of stored energy reserves and therefore allows the definition of an individual's health and nutritional status [18]. It can be used as a proxy to assess individuals' fitness [18,19]. Marsac *et al.* [20] and Hallier and Gaertner [21] compared a morphological indicator, the thorax girth (body width divided by fork length), of tuna caught at DFADs with those caught in free-swimming schools (FSCs). They showed that DFAD-associated tuna were in poorer condition than FSC tuna (i.e. tuna not associated with FOBs) in the Indian and Atlantic Oceans. This evidence led scientists to hypothesize that DFADs could act as an ecological trap for tropical tuna [20]. An ecological trap occurs when individuals make poor habitat choices, misled by cues that are no longer correlated with habitat quality [22,23]. This poor habitat selection leads to a reduction of individual fitness, which can lead to population-level impacts. The ecological trap hypothesis applied to DFADs and tuna relied on the *indicator-log* hypothesis. This hypothesis posits that tunas and other associated species use natural FOBs as cues to select good-quality habitats [21,24,25]. Natural FOBs would be located in productive areas because they originate from rivers and tend to accumulate in rich frontal zones. By affecting the density and distribution of FOBs, the deployment of DFADs could retain or transport individuals into ecologically unsuitable areas, leading to a reduction in their condition and their survival, which could ultimately impact tuna populations [20,26].

Robert *et al.* [27] used bioelectrical impedance analysis (BIA) as a proxy for physiological condition to compare the condition of associated and non-associated tunas in the Mozambique Channel, Western Indian Ocean, an area rich in natural FOBs, i.e. only marginally modified by the addition of DFADs at the time. They also found that the condition of FOB-associated tuna was lower than that of FSC tuna suggesting that this lower condition was not induced only by DFADs. Hence, while tuna may be in relatively lower condition when associated with FOBs (table 1; [32]), the causation of this relationship has not yet been determined. In other words, we do not know if a lower condition is the cause of tuna associative behaviour or the consequence of this behaviour. The *meeting-point* hypothesis [10,33] suggests that tuna associate with FOBs to find conspecifics and form bigger schools, which may improve their foraging efficiency [34–36]. It is then possible that tuna associate with FOBs when they are in a low condition to form schools that would allow them to recover. Therefore, the correlation between the association of tuna with FOBs and their lower physiological condition could imply either that association with an FOB results in poorer condition or that tunas tend to associate more when in poorer condition.

The specific objective of this study is to investigate whether the low condition of tuna is a cause or a consequence of their associative behaviour with FOBs. The ideal experiment would involve monitoring the physiological condition of tuna during their association/absence times and tracking its trend. However, no device can currently provide such measures. In this paper, we consider a dataset of FOB-associated yellowfin tuna condition measured within DFAD arrays in the Western Indian Ocean, together with a mechanistic model accounting for both the associative behaviour of tuna with DFADs and their physiological condition. The model is formulated based on two different causation hypotheses to explain the lower condition of DFAD-associated tuna: either (H_1) tuna association with DFADs induces a decrease in condition (which would be in agreement with studies arguing that tuna are fasting when associated with FOBs; [20,21,29]) or (H_2) tuna with lower condition are more likely to associate with DFADs. Based on these formulations of the model, we make projections of the theoretical impact of an increase in DFAD numbers on the mean condition of associated and non-associated tuna. By comparing the predicted trends with physiological condition data collected within DFAD arrays of increasing density, we determine whether the low condition of associated tuna is the cause or the consequence of their associative behaviour with FOBs.

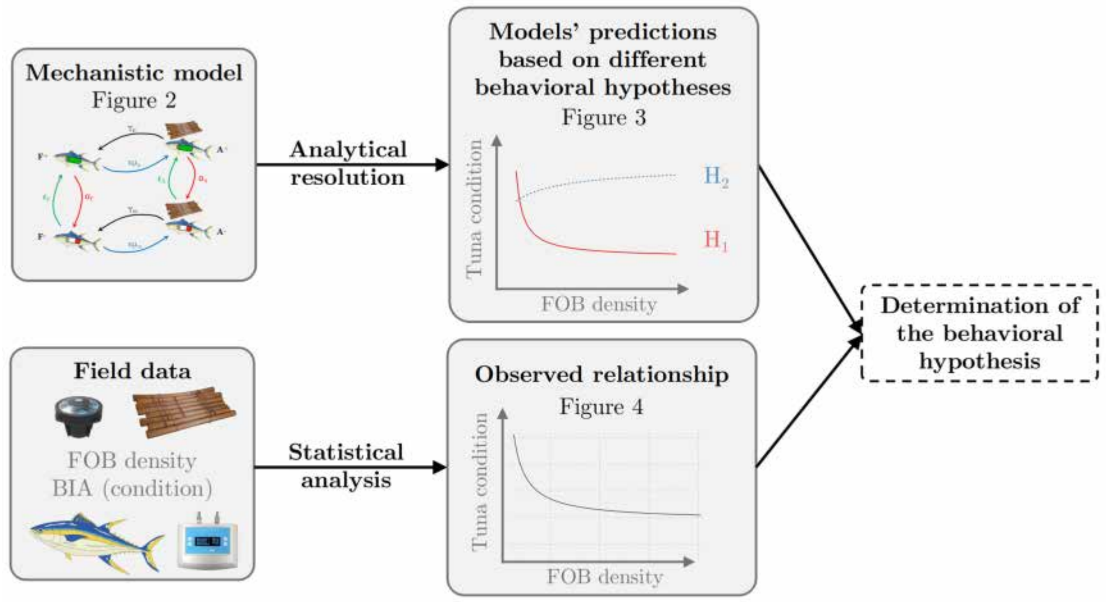

Figure 1. Schematic representation of the study methodology. FOB: floating object. BIA: bioelectrical impedance analysis. Behavioural hypotheses: H_1 tuna association with DFADs *induces* a reduction of their condition; H_2 tuna association with DFADs *is induced by* their low condition.

Table 1. Studies demonstrating that tuna are in lower physiological condition in associated schools than in free-swimming schools. AO, Atlantic Ocean; BIA, bioelectrical impedance analysis; TG, thorax girth; WCPO, Western and Central Pacific Ocean; WIO, Western Indian Ocean.

species	ocean	indicator used	study
skipjack tuna	WIO	phase angle (BIA) and TG	Robert *et al.* [27]
	WIO and AO	TG	Hallier & Gaertner [21]
	AO	body width divided by fork length	Marsac *et al.* [20]
	WCPO	relative condition factor (K_n)	Ashida *et al.* [28]
	AO	stomach fullness	Ménard *et al.* [29]
yellowfin tuna	WIO	lipid content (in gonads)	Zudaire *et al.* [30]
	WIO and AO	TG	Hallier & Gaertner [21]
	WIO	K_n	Dupaix *et al.* [31]
	AO	stomach fullness	Ménard *et al.* [29]
bigeye tuna	AO	stomach fullness	Ménard *et al.* [29]

2. Material and methods

We formulate a mechanistic model of tuna association with DFADs, accounting for their physiological condition (§2a, figure 1). The space of model parameters is then constrained to account for the two behavioural hypotheses (§2b,c), and, for each hypothesis, the relationship between average tuna condition and DFAD density is derived (§2d). Finally, the correlation between tuna condition and DFAD density is estimated from field data and compared with the model predictions to assess which behavioural hypothesis better explains the observations (§2(e)).

(a) General model formulation

Tuna individuals are considered in two states relative to their association with DFADs: they are either associated with DFADs (denoted A) or free-swimming (denoted F, figure 2A). 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 'low' (e^-) physiological condition. The physiological condition of a fish is a continuous variable, but individuals can be categorized into three different physiological states referred to as 'phases' during fasting [37,38]. In phase I, they mainly produce energy from carbohydrates and lipids and can be considered in a 'good' physiological state. Then, in phase II, they mobilize stored lipids and can be considered in a lower physiological state (designated as 'low' for simplification throughout the article). If individuals experience starving for too long in phase II, 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 its consideration would not modify our conclusions.

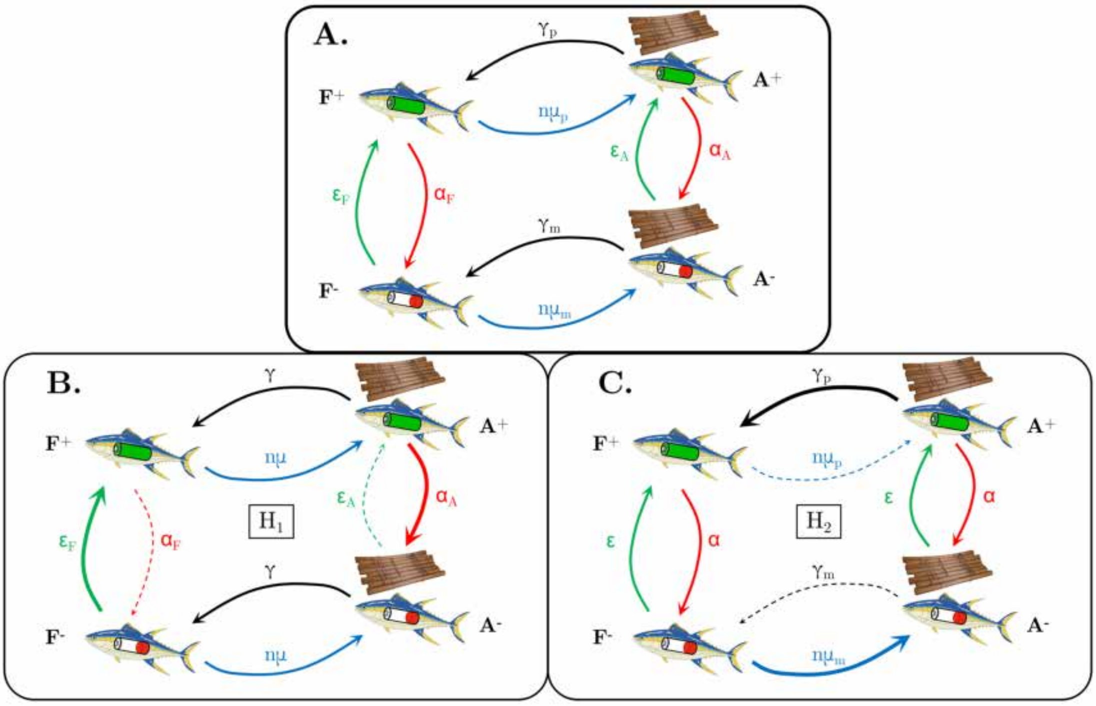

Figure 2. Schematic of the models used in the study. (A) General model, (B) H_1 model following the hypothesis that tuna association with DFADs *induces* a reduction of their condition ($\mu_p = \mu_m = \mu$; $\gamma_p = \gamma_m = \gamma$ and $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$), (C) H_2 model following the hypothesis that tuna association 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.

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

	associated (A) 'good' condition (+)	associated (A) 'low' condition (−)	free-swimming (F) 'good' condition (+)	free-swimming (F) 'low' 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	$1-(\varepsilon_F+\mu_m)$

The overall model describing the behaviour and physiology of tunas corresponds to a four-state model: A^+ (associated with good condition), A^- (associated with low condition), F^+ (free-swimming with good condition) and F^- (free-swimming with low 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 system of equations:

$$\begin{cases} \dfrac{dN_{A^+}(t)}{dt} = -(\gamma_p + \alpha_A)N_{A^+}(t) + \varepsilon_A N_{A^-}(t) + \mu_p n\, N_{F^+}(t) \\ \dfrac{dN_{A^-}(t)}{dt} = -(\gamma_m + \varepsilon_A)N_{A^-}(t) + \alpha_A N_{A^+}(t) + \mu_m n\, N_{F^-}(t) \\ \dfrac{dN_{F^+}(t)}{dt} = -(\mu_p n + \alpha_F)N_{F^+}(t) + \gamma_p N_{A^+}(t) + \varepsilon_F N_{F^-}(t) \\ \dfrac{dN_{F^-}(t)}{dt} = -(\mu_m n + \varepsilon_F)N_{F^-}(t) + \gamma_m N_{A^-}(t) + \alpha_F N_{F^+}(t) \end{cases} \tag{2.1}$$

where $\mu_p n$, $\mu_m n$, 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 time t. The model assumes that the probability of associating with DFADs is directly proportional to n ($\mu_p n$ or $\mu_m n$ depending on the physiological state, figure 2). 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 population ($\overline{e_A}$) and the mean condition of the free-swimming population ($\overline{e_F}$):

$$\overline{e_A} = \frac{N_{A^+}}{N_{A^+} + N_{A^-}} e^+ + \frac{N_{A^-}}{N_{A^+} + N_{A^-}} e^- \tag{2.2}$$

$$\overline{e_F} = \frac{N_{F^+}}{N_{F^+} + N_{F^-}} e^+ + \frac{N_{F^-}}{N_{F^+} + N_{F^-}} e^- \tag{2.3}$$

(b) Hypothesis 1: The association to DFADs induces a low condition

To formulate the first hypothesis (H_1: tuna are in low condition at DFADs because their condition decreases when they are associated, figure 2B) using equation (2.1), we consider that (i) tuna associative behaviour is independent of their condition ($\mu_p = \mu_m = \mu$ and $\gamma_p = \gamma_m = \gamma$) and (ii) tuna condition increases more slowly or decreases more quickly when associated with DFADs than when in FSCs — i.e. $\frac{\alpha_A}{\varepsilon_A} > \frac{\alpha_F}{\varepsilon_F}$. This leads to the following system of equations:

$$\begin{cases} \dfrac{dN_{A^+}(t)}{dt} = -(\gamma + \alpha_A)N_{A^+}(t) + \varepsilon_A N_{A^-}(t) + \mu n\, N_{F^+}(t) \\ \dfrac{dN_{A^-}(t)}{dt} = -(\gamma + \varepsilon_A)N_{A^-}(t) + \alpha_A N_{A^+}(t) + \mu n\, N_{F^-}(t) \\ \dfrac{dN_{F^+}(t)}{dt} = -(\mu n + \alpha_F)N_{F^+}(t) + \gamma N_{A^+}(t) + \varepsilon_F N_{F^-}(t) \\ \dfrac{dN_{F^-}(t)}{dt} = -(\mu n + \varepsilon_F)N_{F^-}(t) + \gamma N_{A^-}(t) + \alpha_F N_{F^+}(t) \end{cases} \tag{2.4}$$

(c) Hypothesis 2: Individuals with a low condition are more likely to associate

To formulate the second hypothesis (H_2: tuna are more likely to associate with DFADs when they have a lower condition, figure 2C), using equation (2.1) 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 in low condition than when in good condition — i.e. $\frac{\mu_m}{\gamma_m} > \frac{\mu_p}{\gamma_p}$. This leads to the following system of equations:

$$\begin{cases} \dfrac{dN_{A^+}(t)}{dt} = -(\gamma_p + \alpha)\, N_{A^+}(t) + \varepsilon\, N_{A^-}(t) + \mu_p n\, N_{F^+}(t) \\ \dfrac{dN_{A^-}(t)}{dt} = -(\gamma_m + \varepsilon)\, N_{A^-}(t) + \alpha\, N_{A^+}(t) + \mu_m n\, N_{F^-}(t) \\ \dfrac{dN_{F^+}(t)}{dt} = -(\mu_p n + \alpha)\, N_{F^+}(t) + \gamma_p\, N_{A^+}(t) + \varepsilon\, N_{F^-}(t) \\ \dfrac{dN_{F^-}(t)}{dt} = -(\mu_m n + \varepsilon)\, N_{F^-}(t) + \gamma_m\, N_{A^-}(t) + \alpha\, N_{F^+}(t) \end{cases} \tag{2.5}$$

(d) Models' solutions

For both hypotheses, we consider the models' solutions at equilibrium (i.e. when $dN_{A^+}/dt = dN_{A^-}/dt = dN_{F^+}/dt = dN_{F^-}/dt = 0$). First, we verify that the mean condition of the associated population is lower than that of the free-swimming population for any number of DFADs ($\forall\, n \in \mathbb{N}^+, \quad \overline{e_A}(n) < \overline{e_F}(n)$). Then, the aim being to determine how tuna condition evolves with increasing DFAD density, we analyse the trends of $\overline{e_A}(n)$ and $\overline{e_F}(n)$ for an increasing number of DFADs (n).

(e) Hypotheses testing with field data

(i) Data on tuna physiological condition

BIA was used to estimate tuna condition. BIA is primarily based on the calculation of the phase angle (PA), derived from measurements of resistance (R) and reactance (X_c) of tissues subjected to a given AC voltage:

$$PA = \arctan\left(\frac{X_c}{R}\right) \tag{2.6}$$

The phase angle is interpreted as an indicator of membrane integrity and water distribution between the intracellular and extracellular spaces, and is used as a proxy for the nutritional status of animals. Average PA values for tuna are typically around 30°, and an increase in PA is interpreted as an increase in tuna condition [27].

BIA data were collected by observers onboard purse seine vessels from May 2021 to March 2023 using a 50 kHz portable BIA device (Seafood Analytics Inc.), along with individual fork length (FL). A total of 232 yellowfin tuna (34 to 79 cm FL) were sampled from 13 DFAD sets, i.e. purse seine fishing operations conducted on DFAD-associated tuna (figure 4A).

(ii) DFAD density data

For each DFAD set, the FOB density in the area was determined using data from the 3BU form from the Indian Ocean Tuna Commission (IOTC, https://data.iotc.org/reference/latest/forms/) [39] and from observers onboard purse seine vessels. The IOTC dataset, derived from the 3-BU form, contains the monthly mean for each 1° × 1° cell of the Indian Ocean of the number of *operational buoys*, i.e. echosounder buoys whose GPS positions are remotely transmitted to one or several fishing vessels. This value was divided by the sea area of each cell to obtain a mean monthly echosounder buoy density, used as a proxy for DFAD density (ρ_{DFAD}). Although DFADs represent the majority of FOBs encountered in the Western Indian Ocean, FOBs of natural origin or originating from pollution are also encountered [40]. To account for these other FOBs, total FOB densities were calculated by 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 an FOB, the type of operation (e.g. deployment, removal and observation of an FOB) and the type of FOB (DFAD or others) are recorded. Using the methodology developed in the study by Dupaix *et al*. [40] and applied to these observations, we calculated a mean monthly ratio $m = n_{\mathrm{OTH}}/n_{\mathrm{DFAD}}$ (where n_{OTH} is the number of observations of FOBs other than DFADs, and n_{DFAD} is the number of observations of DFADs). For the ratio to be reliable and the observers' coverage to be sufficient, the ratio was calculated per 2° cell and considered constant over the entire cell. It was then used to calculate the density of FOBs per 1° cell ($\rho_{\mathrm{FOB}} = (1 + m)\,\rho_{\mathrm{DFAD}}$).

(iii) Statistical analysis

Because the available dataset come from 13 fishing sets, fitting a model accounting for several other variables potentially impacting *PA* presented the risk of overfitting the data. Hence, the correlation between the phase angle and the density of FOBs (ρ_{FOB}) was first 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 after removing samples with $PA > 40$ °.

The calculation of Spearman's rank correlation coefficient was complemented with the fit of nonlinear regression models (NLMs). Using the mechanistic model, we hypothesize that the relationship between *PA* and ρ_{FOB} is not linear and can be expressed as follows (electronic supplementary material, S1):

$$PA = \frac{\rho_{FOB} + \beta}{\delta\rho_{FOB} + \zeta} \tag{2.7}$$

with $\beta,\delta,\zeta \in (\mathbb{R}^{+*})^3$. Based on equation (2.7), we fitted an NLM, using the Levenberg–Marquardt algorithm, with the function *nls.lm* from the R package *minpack.lm* [41].

Individual condition can also be influenced by a number of different phenomena unrelated to DFAD density. Hence, to account for seasonal variations, variations due to the richness of the area and variations owing to the size of the individual, the quarter (*Q*; *Q*1: January to March; *Q*2: April to June; *Q*3: July to September; *Q*4: October to December), the chlorophyll-a concentration (*Chla*) and individual fork length (*FL*) were also included as explanatory variables. Chlorophyll-a concentration (in mg m^{-3}) at the fishing set locations was obtained from the E.U. Copernicus Marine Service Information (DOI: 10.48670/moi-00281), which gives access to daily concentrations at a spatial resolution of 4 km × 4 km. The model can be written as:

$$PA(i) = \frac{\rho_{FOB}(i) + \beta}{\delta\rho_{FOB}(i) + \zeta} + \eta\ Chla(i) + \theta\ FL(i) + \iota\ Q(i) + \epsilon(i) \tag{2.8}$$

where $PA(i)$ is the phase angle of individual i, $\rho_{FOB}(i)$ is the FOB density at the fishing set, $Chla(i)$ is the chlorophyll-a concentration at the fishing set, $FL(i)$ is the fork length of the individual and $Q(i)$ is the quarter. β, δ, ζ, η, θ and ι are the parameters to estimate, and $\epsilon(i)$ is the residual error term. The best model was selected using a backward selection procedure based on the Akaike Information Criterion (AIC) with a threshold of 2, and the goodness-of-fit of the final model was assessed by calculating its R^2. To test the robustness of the model, a leave-one-out cross-validation was performed (LOOCV): nonlinear models were built by removing each data point one by one, and the obtained coefficients and model statistics were assessed. The above-described statistical analysis was performed using the R statistical software [42].

3. Results

(a) Comparison of the mean condition of associated and free-swimming populations

First, we tested whether the model solutions are consistently demonstrating that the average condition of DFAD-associated tuna (eA) is lower than the condition of tuna in FSC. In the general model (see electronic supplementary material, sections S2.3.1 and S2.3.2), we can express $\overline{e_A}$ and $\overline{e_F}$ according to the following equations:

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

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

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

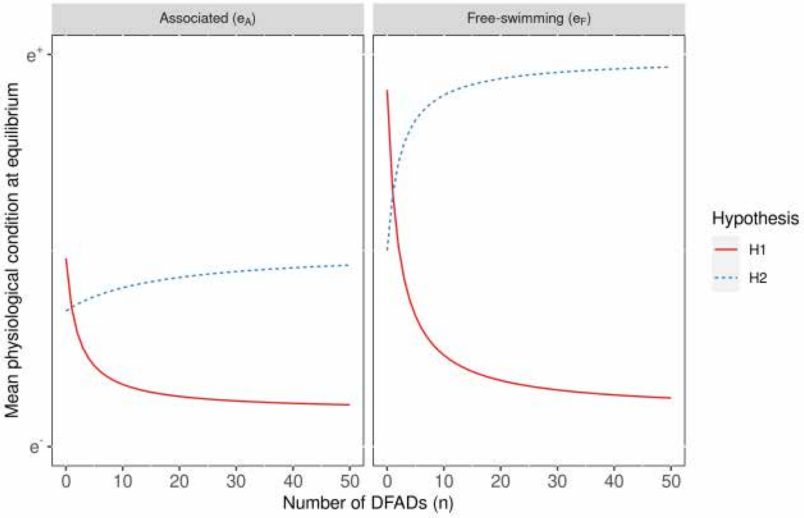

Figure 3. Variations of $\overline{e_A}$ and $\overline{e_F}$ as a function of the number of DFADs (n). Left panel: Mean physiological condition of the associated population ($\overline{e_A}$), based on the two hypotheses. Right panel: Mean physiological condition of the free-swimming population ($\overline{e_F}$), based on the two hypotheses. H_1 (red line): tuna association with DFADs *induces* a reduction of their condition. H_2 (blue dotted line): tuna 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, $\mu_P = \gamma_M = 10^{-3}$.

with $T(n) = \frac{N_{F-}}{N_{F+}}$. Substituting the above definitions of $\overline{e_A}$ and $\overline{e_F}$ into the inequality $\overline{e_A} < \overline{e_F}$ leads to:

$$\overline{e_A} < \overline{e_F} \Leftrightarrow \frac{N_{F-}}{N_{F+}} < \frac{N_{A-}}{N_{A+}}. \tag{3.1}$$

Considering the model at equilibrium, formulated according to H_1 (the association with DFADs induces a low physiological condition, i.e. by definition, $\mu_p = \mu_m = \mu$ and $\gamma_p = \gamma_m = \gamma$ and $\frac{\alpha_F}{\varepsilon_F} < \frac{\alpha_A}{\varepsilon_A}$), we can express equation (3.1) as:

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

(see electronic supplementary material, section S2.3.5). Considering the second model at equilibrium, formulated according to H_2 (individuals tend to associate more with DFADs when in lower physiological condition, i.e. by definition, $\alpha_F = \alpha_A = \alpha$ and $\varepsilon_F = \varepsilon_A = \varepsilon$ and $\frac{\mu_p}{p} < \frac{\mu_m}{\gamma_m}$), we can express equation (3.1) as (see electronic supplementary material, section S2.3.6):

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

(see electronic supplementary material, section S2.3.6). The models formulated according to both hypotheses (H_1 and H_2) verify that the mean condition of associated tuna is lower than the mean condition of free-swimming tuna ($\forall n \in \mathbb{N}^+, \overline{e_A}(n) < \overline{e_F}(n)$).

(b) Trends of the mean condition of the two populations for an increasing number of DFADs

(i) Associated population

In the general model (electronic supplementary material, sections S2.1.1–S2.1.4), we can demonstrate that the average condition of associated tuna ($\overline{e_A}$) is a decreasing function of the number of DFADs $n\left(d\overline{e_A}(n)/dn < 0\right)$ if and only if

$$\alpha_A \mu_p \varepsilon_F \gamma_m - \alpha_F \mu_m \varepsilon_A \gamma_p > 0 \tag{3.2}$$

Applying this relationship to the models formulated according to the H_1 and H_2 hypotheses (see electronic supplementary material, sections S2.1.5 and S2.1.6), we can demonstrate that at equilibrium, for hypothesis H_1, the condition of associated tuna *decreases* with the number of DFADs, namely:

$$H_1 \Rightarrow \frac{d\overline{e_A}(n)}{dn} < 0 \tag{3.3}$$

and, at equilibrium, for hypothesis H_2, the condition of associated tuna *increases* with the number of DFADs, namely:

$$H_2 \Rightarrow \frac{d\overline{e_A}(n)}{dn} > 0 \tag{3.4}$$

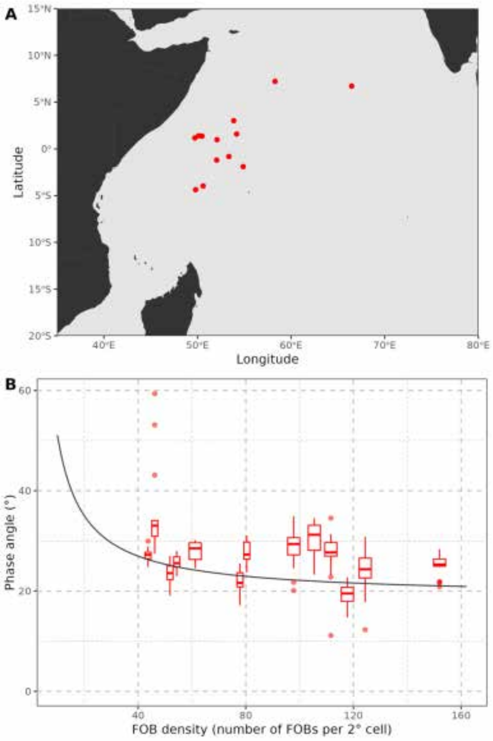

Figure 4. Hypothesis testing with field data. (A) Sampling locations. Phase angle (*PA*) was measured on 232 yellowfin tuna (YFT) fished on 13 different DFAD-associated schools. (B) *PA* of associated tuna and nonlinear regression marginal effect as a function of floating object (FOB) density. Each boxplot corresponds to a given sampling location. *PA* predictions are obtained with the nonlinear regression presented in table 3. To build the predictions, other continuous explanatory variables were set to their median observed value and the quarter was set to Q1.

(ii) Free-swimming population

Concerning the average condition of free-swimming tuna ($\overline{e_A}$, electronic supplementary material, section S2.2), in the general model, we can also demonstrate that $\overline{e_F}$ is a decreasing function of the number of DFADs under the same conditions as $\overline{e_A}$ equation (3.2), i.e. if and only if

$$\frac{d\overline{e_F}(n)}{dn} < 0 \Leftrightarrow \alpha_A \mu_p \varepsilon_F \gamma_m - \alpha_F \mu_m \varepsilon_A \gamma_p > 0 \tag{3.5}$$

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

$$H_1 \Rightarrow \frac{d\overline{e_F}(n)}{dn} < 0 \tag{3.6}$$

and

$$H_2 \Rightarrow \frac{d\overline{e_F}(n)}{dn} > 0 \tag{3.7}$$

To summarize, under the hypothesis that association with DFADs induces a lower 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 (equations (3.3) and (3.6), figure 3). When we hypothesize that individuals tend to associate with DFADs when in low condition (H_2), an increasing number of DFADs will increase the average condition of associated and free-swimming tuna (equations (3.4) and (3.7), figure 3).

All the detailed calculations of the results presented in §§3.1 and 3.2 are available in electronic supplementary material, S2.

(c) Hypothesis testing with field data on yellowfin tuna associated with DFADs

Phase angle values ranged from 11.1 to 59.4°, with a median value of 26.2°. The within-set standard deviation (i.e. standard deviation of individuals captured in the same fishing operation) was low for most of the sets: average within-set standard deviation of 3.1° (figure 4B). A significant decreasing trend in *PA* was observed for increasing ρ_{FOB} values (Spearman's $\rho = -0.24$, $p < 0.001$). This decreasing trend was also observed when removing outliers (Spearman's $\rho = -0.22$, $p < 0.001$).

The results of the NLM assessing the relationship between the phase angle of associated YFT and the density of FOBs along with other explanatory variables are presented in table 3. Based on the AIC selection procedure, ζ was discarded (electronic supplementary material, table S5). Both β and δ were found to be significantly different from 0, suggesting the following relationship between *PA* and ρ_{FOB}:

$$PA_{\mathrm{YFT}} = \frac{1}{\delta}\left(1 + \frac{\beta}{\rho_{FOB}}\right)$$

Table 3. Nonlinear model performed on the condition (phase angle, *PA*) of yellowfin tuna associated with DFADs. β and δ: coefficients used to fit the density of FOBs; *FL*: fork length (cm); *Chla*: chlorophyll-a concentration (mg m^{-3}); Q: quarter. LOOCV: leave-one-out cross-validation. The last two columns present the minimum and maximum estimates obtained performing the LOOCV. The best model was selected based on an Akaike Information Criterion (AIC) backward selection procedure with a threshold of 2.

			LOOCV	
coefficient	**estimate**	**significance (*p*-value)**	**min**	**max**
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

with $\beta = 10.2$ ($p < 0.001$) and $\delta = 0.03$ ($p < 0.001$). YFT also displayed a decreasing condition factor with increasing fork length ($\theta = -0.27$; $p < 0.001$) and a lower condition factor in the first and third quarters of the year (*PA* in Q2 and Q4 significantly greater than Q1 for YFT).

According to the results of the Spearman's correlation test, the decreasing trend obtained with the NLM (figure 4B) suggests the rejection of the H_2 hypothesis, while the observed trends are consistent with the H_1 hypothesis (the association to DFADs induces a low condition).

The NLMs obtained through the LOOCV confirmed the robustness of the decreasing relationship between *PA* and ρ_{FOB} (table 3). The values of the coefficients showed little variation, and no modification of their significance was observed.

4. Discussion

(a) Causation or consequence of associative behaviour

In this study, we rely on the formulation of a mechanistic model, parametrized considering two different causation hypotheses, to determine the causal link between tuna condition at DFADs and their associative behaviour using classical correlative methods. For both hypotheses, the equilibrium solutions of the model provide an average lower condition for DFAD-associated tuna than tuna in FSCs, in agreement with previous studies using various condition indicators (table 1, [32]). Our previous study [27] highlighted that understanding the causation between the low condition at FOBs and the associative behaviour of tuna is key to testing the ecoogical trap hypothesis. Here, 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.* [31] found neither a decreasing nor increasing trend in the mean condition of associated yellowfin tuna (assessed using the relative condition factor K_n; see their electronic supplementary material, figure S3) concurrently with the increasing use of DFADs from 1987 to 2019. However, in their study, the authors could not test the relationship between the average condition and the density of FOBs, because precise density data were not available. Here, thanks to a dataset made available recently by the Indian Ocean Tuna Commission, we determine DFAD densities corresponding to the location of condition measurements for associated yellowfin tuna.

The BIA does not show any clear visual trend as a function of FOB density, suggesting that, if an impact of FOB density exists, we may currently be beyond the range of densities where such an impact is easily observed (figure 4B). We also performed a similar study to the one presented here, on skipjack tuna condition (electronic supplementary material, S3). Skipjack tuna were sampled at higher DFAD densities than yellowfin tuna, and no decreasing trend in condition was observed, either visually or when performing the statistical analysis. Hence, this complementary analysis on skipjack tuna also calls for more data, especially for lower FOB densities. However, the results from the correlation test and the nonlinear model suggest a significant negative effect of FOB density on yellowfin tuna, rejecting H_2 and implying that yellowfin tuna's associative behaviour would provoke a decrease in their average condition (H_1). Hence, it suggests that the low condition of yellowfin tuna at FOBs is a consequence of their associative behaviour, rather than a cause.

(b) Lower condition of tuna when associated

The main hypothesis underlying our mechanistic model is a lower condition of associated tuna compared with FSC tuna, which is supported by numerous studies (table 1). However, 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 [20,21,29]. These indicators likely reflect tuna feeding on a very short-term basis. In addition, Sardenne *et al*. [43] compared morphometric indices such as thorax girth and relative condition factor (K_n, used in [28,31]) with energy content in the tissues and showed that such indices should be used carefully for tropical tunas, as they do not always properly reflect individuals' condition. Other evidence by Zudaire *et al*. [30], who found a difference in total lipid content in female yellowfin tuna gonads, could also be attributed to different reproductive strategies rather than differences 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*. [27] relied on the phase angle measured by BIA, as we did in this study, to find a lower condition in FOB-associated tuna compared with FSC tuna. Because it represents an indicator of membrane integrity, BIA is considered a good indicator of physiological condition and is probably the most reliable of those used in table 1. However, to date, and like other condition indicators, it has not been validated. To be able to rely confidently on any condition indicators, validations are needed. These validations could be performed experimentally, by monitoring a set of condition indicators in captive tuna subjected to fasting.

Being supported by a significant amount of evidence, the hypothesis that associated tuna are in lower condition than FSC tuna is consensual among researchers working on the subject [32], but experimental validation would allow its confirmation. It would also allow us to determine the exact meaning of the observed difference in tuna condition and the temporal scale at which these indicators display significant changes.

(c) Mechanistic models to assess behaviour causation and consequences

The approach developed in this study is conceptually similar to the one developed in ecosystem models, which posit mechanisms and validate them using correlative approaches [9,44,45]. Craver [46] argues that not all models are explanatory; some are merely phenomenal models that can predict a mechanism's outcome but cannot explain how this is achieved. 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 modelling with empirical data to account for complex ecological and behavioural processes and to determine the causation and consequences of specific behaviours. Furthermore, the findings underscore the potential of using mechanistic models as valuable tools in ecological research, particularly when experimental manipulations are impractical or impossible.

Our study also illustrates that correlative tests of mechanistic models can be difficult and sometimes inconclusive (electronic supplementary material, S3). This difficulty is well recognized when comparing Species Distribution Models (SDMs) built on *in situ* observations with SDMs built on mechanistic model outputs [47]. For skipjack tuna, presented in electronic supplementary material, S3, the difficulty in determining statistically which model prediction is observed in the field most probably stems from the range of observed DFAD densities (figure 4B) and from the impact of other environmental factors on tuna condition. This highlights the need for careful design of the *in situ* sampling. In our case, as DFAD density cannot be known prior to sampling and must be calculated afterwards, this bias could be addressed by further increasing the sampling effort.

Craver [46] 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 made that could influence the obtained results: e.g. the probability to associate ($n \times \mu$) was considered to be directly proportional to the number of DFADs in the area (n). Capello *et al*. [48], using a model with several social scenarios, demonstrated that social behaviour influences the way in which the fraction of schools that are associated with DFAD density varies. Their model could be calibrated using data from echosounder buoys associated with DFADs, which can be used to determine the presence or absence of associated tuna aggregations under DFADs [49]. Then, adding a physiological state variable would allow us to determine the impact of an increasing DFAD density on tuna condition, accounting for both their associative and social behaviour. Although the relationship between the number of DFADs and tuna associations changes quantitatively under different social scenarios, it remains qualitatively consistent [48]: an increase in the number of DFADs always results in an increase in the proportion of tuna schools associated, strengthening our findings.

(d) Motivational, ontogenetic and phylogenetic causes and consequences of behaviour

It has been argued that determining a behaviour's *function* can inform on its causation and consequences [5]. The reverse is also possible. Our study suggests that an ontogenetic consequence of yellowfin tuna associative behaviour is a decrease in their condition. However, this result highlights our lack of knowledge on the phylogenetic consequence of this behaviour, and the reason why it was selected. If associating with FOBs has a direct negative consequence for tropical tuna, there must be an important phylogenetic consequence that can compensate for that decrease in condition. Two main hypotheses, developed in §1, are formulated as phylogenetic consequences of tropical tuna associative behaviour with FOBs: the *meeting-point* and the *indicator-log* hypotheses [10,24,25].

In a context of global change, determining this phylogenetic consequence is central, as it can strongly influence the response to human-induced modification [32]. The *meeting-point* hypothesis could be investigated using electronic tagging data, similar to the work of Soria *et al*. [33] on small pelagic fish. Furthermore, mechanistic models that account for both schooling and associative behaviour, such as those by Capello *et al*. [48], coupled with echosounder data, could also provide insights into this hypothesis. On the other hand, testing the *indicator-log* hypothesis could be done by examining habitat-suitability indices in relation to the presence of FOBs. The importance of determining phylogenetic consequences of behaviour for species conservation is twofold. First, these consequences can determine 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 affect schooling behaviour, potentially impacting school size and ultimately tuna fitness. Then, it can allow for the prediction of potential changes in these consequences induced by human activities. Again, if we consider the *meeting-point* hypothesis in the context of increasing DFAD density, we should observe a reduction in the fitness associated with associative behaviour. This reduction could result in a behavioural change induced by human activities.

5. Conclusion

The approach developed in this study allows us to advance our understanding of tuna associative behaviour and the processes underlying the association with FOBs. It also demonstrates the relevance of coupling mechanistic modelling with correlative approaches when studying the causes and consequences of behaviour in cases where experiments are hard to implement. Based on this framework, we find that the lower condition of yellowfin tuna at FOBs is probably a consequence of their association. This finding further warns us about the potential impacts of DFADs on tuna condition, which could lead to a greater impact on tuna survival than that provoked by fishing alone.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All the scripts and data used for this study are available on GitHub (https://github.com/adupaix/Test_causality_with_BIA; [50]). 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). Chlorophyll-a concentrations used in the electronic supplementary material 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).

Supplementary material is available online [51].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.D.: conceptualization, data curation, formal analysis, methodology, software, writing—original draft, writing—review and editing; J.-L.D.: conceptualization, formal analysis, methodology, supervision, writing—review and editing; F.F.: data curation, writing—review and editing; M.T.T.: data curation, formal analysis, writing—review and editing; L.D.: conceptualization, supervision, writing—review and editing; M.C.: conceptualization, formal analysis, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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