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ORIGINAL PAPER

Tuna, floating objects, and habitat suitability: an analysis of the indicator-log hypothesis in the Western Indian ocean

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Abstract

Tropical tunas are known to associate with floating objects, forming large aggregations around them. Taking advantage of this behavior, fishers deploy artificial floating objects (known as Fish Aggregating Devices, or FADs) worldwide to facilitate their fishing activities. The lack of understanding of why tuna associate with these devices hinders the assessment of their ecological impacts. The "indicator-log" hypothesis posits that floating objects of natural origin (NLOGs) concentrate in productive areas and that tunas associate with them to reach and remain in these areas. This study tests the validity of the indicator-log hypothesis, by testing if the presence and abundance of NLOGs are positively correlated with environmental variables that serve as proxies for habitat preference and suitability for tropical tunas. Using data (1,550 observations of NLOGs) recorded by scientific observers on-board purse seine vessels from 2014 to 2022 in the Western Indian Ocean, along with Lagrangian simulations of NLOG densities in the same area, we found no relationship between NLOG abundance and environmental variables in oceanic regions. We did find a weak correlation only in more coastal areas (Mozambique Channel). Consequently, at both spatial and temporal scales considered in this analysis (2°/month and 1°/week), NLOGs do not appear to constitute environmental cues that can be used by tuna to identify productive oceanic areas. Additional research is needed to explore other hypotheses regarding tuna associative behavior, which may also imply potential detrimental impacts of FADs on tuna populations.

Keywords Ecological trap · Associative behavior · Tuna fisheries · Habitat suitability · Habitat preference · Indicator-log hypothesis · Western indian ocean

Introduction

Tropical tunas, like many other pelagic species, are known to associate with floating objects (designated as FOBs) (Fréon and Dagorn 2000; Castro et al. 2002). According to Fréon and Dagorn (2000), an association is defined as "the spatial relationship between an animal (or group) of one species and an animal of another species or an object, based on the decision of at least one of the two individuals to maintain contact but not to feed on the other".

FOBs are of various kinds and can be of terrestrial or marine origin, plant or animal, natural or anthropogenic. The most common natural FOBs come from trees (logs and branches), macroalgae and other terrestrial or marine plants (Solana-Soares 2001; Castro et al. 2002; Williams et al. 2005; Hinojosa et al. 2011). Tunas may also associate with slow-swimming organisms, like whale sharks (*Rhincodon typus*, Smith 1828) as well as with the corpses of marine mammals such as whales (Gaertner et al. 1996; Solana-Soares 2001;

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Castro et al. 2002). In addition, marine debris originating from human pollution and fisheries (e.g. buoys, nets) may also act effectively as artificial logs (Solana-Soares 2001). All these objects, whether natural or artificial, drift on the ocean surface under the influence of wind, tides, waves, and ocean currents (Solana-Soares 2001; Hinojosa et al. 2011).

The associative behavior of pelagic fish species with floating objects has been used by fishers to facilitate their catches for thousands of years. The Roman author Oppian (cited by Dempster and Taquet 2004) first described the use of floating objects to catch dolphinfish (*Coryphaena hippurus*, Linnaeus 1758) in the Mediterranean Sea more than 1800 years ago. As FOBs increase the catchability of fish by gathering large aggregations in their nearby, fishers have constructed their own FOBs, known as Fish Aggregating Devices (designated as FADs) (Dempster and Taquet 2004). FADs are human-made floating objects deployed by fishers that can be anchored in coastal areas or left drifting in the open ocean. Anchored FADs are generally exploited by artisanal or semi-industrial fisheries in coastal countries while drifting FADs are used by industrial tropical tuna purse-seine fisheries (Taquet 2013; IOTC 2022; Dupaix et al. 2024b). Despite recent studies characterising the associative behavior of tuna with FOBs (Forget et al. 2015; Tolotti et al. 2020; Pérez et al. 2020; Dupaix et al. 2024a), the hypotheses on why tuna associate with FOBs have not changed since they were formulated (Fréon and Dagorn 2000; Castro et al. 2002; Dempster and Taquet 2004). The two main hypotheses put forward, which are not necessarily mutually exclusive, are the "meeting point" hypothesis and the "indicator-log" hypothesis (Fréon and Dagorn 2000; Castro et al. 2002). The "meeting-point" hypothesis considers that tunas use FOBs to form larger schools. It relies on the assumption that tunas can detect FOBs from further away than they can detect other schools, thus facilitating their encounter rate (Fréon and Dagorn 2000). However, to date, this hypothesis has only been validated for one small pelagic fish species (bigeye scad, *Selar crumenophthalmus*, Bloch 1793) (Soria et al. 2009). The "indicator-log" hypothesis postulates that floating objects of natural origin (designated as NLOGs) are located in productive areas and that tunas associate with them in order to reach and remain in these areas (Hall 1992; Castro et al. 2002). NLOGs would indicate productive areas because they mainly originate from river mouths or mangroves (Hall 1992) but also because they accumulate in rich frontal areas (Hallier and Gaertner 2008). The indicator-log hypothesis suggests that tunas would better locate NLOGs than preys, which has not yet been demonstrated (Fréon and Dagorn 2000).

Between 2018 and 2022, drifting FADs (DFADs) accounted for 38% of the tropical tuna catches conducted by purse seine vessels worldwide (ISSF 2025). This massive exploitation of DFADs in recent years has led to an increase in the number of their deployments in all tropical oceans. In the Indian Ocean, DFADs accounted for over 85% of the overall FOBs between 2012 and 2018 while NLOGs accounted for less than 10% (Dupaix et al. 2021). The spatial distribution of floating objects is thus modified by this massive introduction of DFADs (Dagorn et al. 2013; Dupaix et al. 2021). Such a change in surface pelagic habitat could alter the behavior and biology of tunas.

Based on the indicator-log hypothesis, if NLOGs are used by tuna to identify productive areas, the introduction of FADs could mislead them if they are deployed or drift into areas of low productivity and if tunas do not differentiate between natural and human-made objects (Hallier and Gaertner 2008; Dupaix et al. 2024b). As a consequence, FADs could trap tunas by altering their natural movements and bringing them to or retaining them in areas they would usually avoid or leave, thus affecting their fitness, growth and survival (Marsac et al. 2000; Hallier and Gaertner 2008; Dupaix et al. 2024b). Therefore, assessing the validity of the indicator-log hypothesis would be a first step in assessing such potential impacts. To our knowledge, the validity of this hypothesis, formulated more than thirty years ago, has never been tested.

Taking advantage of a large database of observations of NLOGs recorded by observers on-board purse-seine vessels in the Western Indian Ocean and of Lagrangian simulations of NLOG densities, the aim of this work was to test the validity of the indicator-log hypothesis, i.e., to identify if NLOGs can represent environmental cues that can be used by tuna to identify suitable habitats. To this purpose, we examine the link between the presence and abundance of NLOGs and environmental variables that serve as proxies for habitat preference and suitability for tropical tuna.

Materials and methods

Study area

The study was conducted in the Western Indian Ocean (35°E to 85°W, 25°N to 25°S), the main fishing ground of tropical tuna industrial purse-seiners. The study area was divided into two sub-regions, displaying very different oceanographic characteristics: the Mozambique Channel (designated as MOZ) and the oceanic area located at latitudes above 10°S in the Western Indian Ocean (designated as WIO, Fig. 1). The latter contains the Somali region, which is the fifth largest upwelling region in the global ocean and one of the most productive regions in the world (Lakshmi et al. 2020) while the northern Mozambique Channel presents high mesoscale

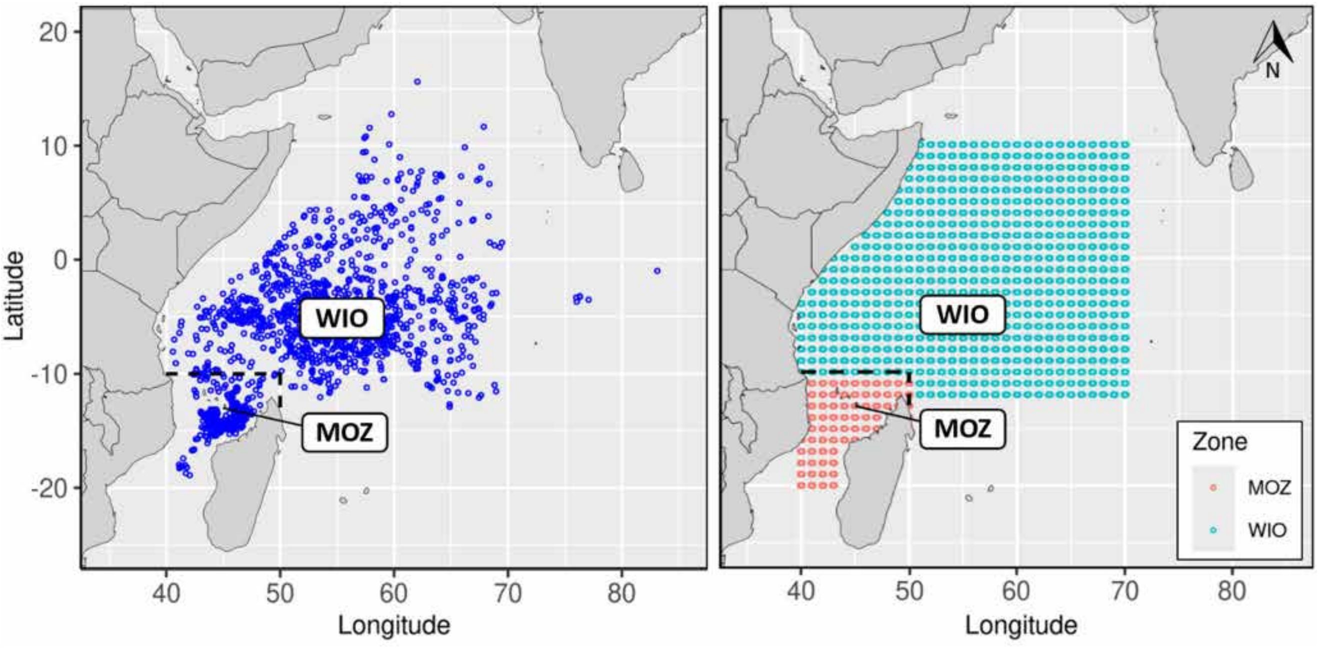

Fig. 1 Study area. Map on the left: spatial distribution of sampling records (blue circles) indicating NLOG observations ($N = 1{,}550$). Map on the right: spatial representation of the 1° cells considered in the Lagrangian simulations in each area. The dashed line indicates the geographic border between the Mozambique Channel (MOZ) and the Western Indian Ocean surveyed area (WIO)

activity leading to surface water enrichment and important NLOG densities (Chassot et al. 2019).

Environmental variables

The environmental variables considered are Sea Surface Temperature (SST, in °C), Sea Surface Currents Intensity (SSCI, in m.s^{-2}; calculated as $\sqrt{u^2 + v^2}$ where u and v represent the geostrophic eastward and northward sea surface velocity, respectively), Sea Level Anomalies (SLA, in m), Finite Size Lyapunov Exponent (FSLE, in days^{-1}), epipelagic MicroNekton biomass density (MN, in g.m^{-2}) and Chlorophyll-a concentration (Chla, in mg.m^{-3}). These variables, whether abiotic or biotic, were selected because they are known to be relevant to the characterisation of habitat preference and suitability for tropical tunas. Indeed, SST has been shown to affect the spatial distribution of tunas by modifying their movements (Brill 1994). SSCI is considered a key variable as it influences tuna habitat preferences (Druon et al. 2017) and primary productivity in upwelling regions (Vinayachandran et al. 2021). SLA allows identifying gyres and eddies, as well as frontal systems around these gyres, which are also thought to have the capacity to accumulate plankton and tuna prey species (Arrizabalaga et al. 2015; Zainuddin et al. 2017). FSLE is a measurement of near-track divergence rate, an indicator for oceanic convergence and divergence zones (Hariri 2022). Top marine predators can follow FSLE ridges to locate food patches (Tew Kai et al. 2009). In terms of biotic variables, micronekton (including gelatinous taxa, crustaceans, small fish, and cephalopods) (Kloser et al. 2009) constitutes the primary prey of most pelagic predators, such as tunas (Roger 1994; Young et al. 2010). Hence, pelagic predators are directly influenced by micronekton abundance, which in turn depend on lower trophic levels (phytoplankton and zooplankton) (Young et al. 2015). As major component of primary production that supports zooplankton production and higher trophic levels (Druon et al. 2017), Chla concentration is also a key variable for identifying productive areas that are relevant for tunas. All environmental data were retrieved from the EU's Copernicus maritime service (https://resources.marine.copernicus.eu/products) with the exception of the FSLE that was processed by SSALTO/DUACS and distributed by AVISO+ (https://www.aviso.altimetry.fr) (Table 1).

Each environmental variable was averaged either by month and 2° cell, or by week and 1° cell to match the spatio-temporal resolution of the NLOG abundance indices calculated from observer's or simulated data, respectively (see paragraph 2.3). For all analyses (correlation tests and comparison of medians tests), non-parametric tests were chosen because of the non-normal distribution of the variables (Shapiro tests, p.value < 0.05, with the R function "shapiro.test").

To avoid redundancy of information, correlations between the environmental variables (both monthly and weekly averaged) were investigated and Kendall tests were performed (see. Fig. A2 in the Supplementary Material). To account for the number of tests performed, a Bonferroni

Table 1 Characteristics of the environmental variables used in the study

Acronym	Environmental variable	Type	Processing Level	Original Spatial resolution	Original Temporal resolution	Source
SST	Sea Surface Temperature in °C (Abiotic)	Observation (satellite + in situ)	L4	0.25° * 0.25°	Monthly/ Weekly mean	https://resources.marine.copernicus.eu/product-detail/MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012/INFORMATION
SSCI	Sea Surface Current Intensity in $m.s^{-2}$ (Abiotic)	Observation (satellite)	L4	0.25° * 0.25°	Monthly/ Weekly mean	https://resources.marine.copernicus.eu/product-detail/MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012/DATA-ACCESS
SLA	Sea Level Anomaly in m (Abiotic)	Observation (satellite)	L4	0.25° * 0.25°/0.125° * 0.125°	Monthly/ Weekly mean	https://resources.marine.copernicus.eu/product-detail/SEALEVEL_GLO_PHY_L4_MY_008_047/INFORMATION
FSLE	Finite Size Lyapunov Exponent in $days^{-1}$ (Abiotic)	Observation (satellite)	L4	0.04° * 0.04°	Daily mean	https://doi.org/10.24400/527896/a01-2022.002
MN	Mass content of Micronekton in $g.m^{-2}$ (Biotic)	Numerical model	L4	0.083° * 0.083°	Daily	https://resources.marine.copernicus.eu/product-detail/GLOBAL_MULTIYEAR_BGC_001_033/INFORMATION
Chla	Chlorophyll a concentration in $mg.m^{-3}$ (Biotic)	Observation (satellite)	L4	4 km * 4 km	Monthly mean (comparison with observers' data)	https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_108/services
Chla	Chlorophyll a concentration in $mg.m^{-3}$ (Biotic)	Numerical model	L4	0.25° * 0.25°	Daily (comparison with Lagrangian simulations)	https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_BGC_001_029/download

(SST: Sea Surface Temperature; SSCI: Sea Surface Current Intensity; SLA: Sea Level Anomaly; FSLE: Finite Size Lyapunov Exponent; MN: mass content of Micronekton; and Chla: chlorophyll a concentration)

correction was applied. A test was considered significant when $p.value < 0.05/n = 3.33\ 10^{-3}$, where n is the number of tests performed (i.e. one between each variable, $n = 15$). A strong correlation was observed between Chla and SST (Monthly: $\tau = -0.611$, $p.value < 2.2\ 10^{-16}$; Weekly: $\tau = -0.368$, $p\text{-}value < 2.2\ 10^{-16}$) for both monthly and weekly averaged variables. Hence, to avoid redundancy of information, to improve the quality of models and because Chla is a direct indicator of an area's productivity, SST was removed from the statistical analyses developed below.

NLOG datasets

The validity of the indicator-log hypothesis was tested considering two distinct NLOG datasets at two different spatio-temporal resolutions:

i. Observations of NLOGs recorded by observers on-board purse seiners were used to build an NLOG index of abundance at a scale of 2°/month.
ii. Lagrangian simulations were used to reconstruct NLOG densities at a scale of 1°/week.

The choice of the first scale (2°/month) was constrained by the availability of observers' data and aimed at ensuring a sufficient number of observations per grid cell to provide consistent NLOG abundance indices. Lagrangian simulations were conducted to overcome these data limitations and allowed working at higher resolutions. The scale of 1°/week guaranteed a good accuracy of the predicted NLOG densities (Dupaix et al. 2024c). At both scales, a significant negative correlation was observed between micronekton and FSLE (Figure A2), i.e., habitat richness and mesoscale features were correlated with each other. Although the original formulation of the indicator-log hypothesis (Hall 1992) does not specify any spatio-temporal scale, it assumes that NLOGs are used by tuna as environmental cues to identify *rich oceanic water masses located in frontal areas*. Therefore, given the observed correlation between habitat richness and mesoscale environmental features, the chosen spatio-temporal resolutions (2°/month and 1°/week) prove to be appropriate for testing this hypothesis.

Observations of NLOGs recorded by observers on-board purse Seiners

Observers' Dataset.

Data were collected over a 9-year period (2014–2022) by scientific observers on-board French purse seine vessels operating in the Western Indian Ocean. Observers collect the date, time and location of the main activities carried out on the fishing vessels (i.e. fishing sets, visiting, deploying, modifying and searching for FOBs). Whenever a FOB is observed, its constitutive elements, allowing to deduct its type (e.g., human-made, natural origin, debris), and geographical coordinates are recorded by the observers. In the following analysis, only FOBs of natural origin (NLOGs) are considered, which excludes Fish Aggregating Devices (FADs) and other artificial floating objects. A total of 1,550 observations of NLOGs are available for the study period (Fig. 1-A1), including 1,218 observations in the WIO area and 332 observations in the MOZ area (Fig. 1).

NLOG abundance index from observers' data.

A NLOG abundance index ($A_{i,\,m}$) was calculated considering a spatio-temporal resolution of 2°/month, by dividing the monthly number of observed NLOGs by the observation effort recorded in each 2° cell, following Eq. (1):

$$A_{i,m} = \frac{\sum_{d=1}^{D_m} N_{i,d}}{\sum_{d=1}^{D_m} O_{i,d}} \tag{1}$$

where $A_{i,\,m}$ represents the NLOG abundance index for cell i and month m, $N_{i,\,d}$ indicates the number of NLOGs observed in cell i on day d, $O_{i,\,d}$ represents the number of vessels with an on-board observer present in cell i on day d and D_m indicates the total number of days for month m. A vessel was considered present in cell i on day d if it has performed at least one activity in the cell on that day. The denominator of Eq. (1) represents the "observation effort". In the following, an observation effort threshold $T=6$ was considered. Cells with a low observation effort (i.e., $T \leq 6$) were excluded. A sensitivity analysis was conducted to test the impact of the observation effort threshold by comparing results with those obtained for a larger threshold ($T=10$).

Modelled densities of NLOGs through lagrangian simulations

A weekly NLOG abundance index ($\rho_{\mathrm{i,\,w}}$) at a 1° resolution was obtained using Lagrangian simulations, which consist in releasing particles (NLOGs) off the coast of the Indian Ocean on a weekly basis and simulating their drift (Dupaix et al. 2024c). In this study, NLOG densities were obtained using the outputs from the so-called "RCp scenario", which accounts for NLOG originating from the forest cover associated with rivers, the river discharge and the precipitations at the river month. This scenario better fits NLOG abundances and seasonal patterns obtained from observers data in the Western Indian Ocean (Fig. 3 in Dupaix et al. 2024c). For each week w and 1° cell i, the NLOG abundance index $\rho_{\mathrm{i,\,w}}$ was constructed considering simulated NLOG densities, normalized to the highest NLOG density recorded in the simulation period (2000–2019) over the whole Indian Ocean, resulting in $\rho_{\mathrm{i,\,w}}$ being bounded between 0 and 1.

Testing the indicator-log hypothesis

Presence and absence of NLOGs recorded from observers data

According to the indicator-log hypothesis, the presence of NLOGs indicates productive areas. However, the opposite is not necessarily true: the absence of NLOGs can occur both in areas of high and low productivity. Therefore, different distributions of environmental variables are expected between areas with and areas without NLOGs. In order to test this hypothesis, the distributions of each environmental variable corresponding to the presence of NLOGs (i.e. for monthly/2° cells with a non-null NLOG abundance index $A_{i,\,m} > 0$, see Eq. (1)) were compared to those found in the absence of NLOG observations ($A_{i,\,m} = 0$) using non-parametric tests (Wilcoxon tests, with the R function "wilcox.test"). To account for the number of tests performed, a Bonferroni correction was applied and a test was considered significant when p.value $< 0.05/n = 0.005$, (i.e. one test per zone for each of the five environmental variables, $n=10$).

Relationship between NLOG abundance index and environmental variables

The indicator-log hypothesis implies that the abundance of NLOGs should be correlated with environmental characteristics of oceanic areas. To test this hypothesis, in each sub-region, correlations between NLOG abundance and environmental variables were performed for each dataset and scale using non-parametric tests (Kendall tests, with the R function "cor.test"). Again, to account for the number of tests performed, a Bonferroni correction was applied and a test was considered significant when p.value < 0.01 ($n=5$).

Finally, for both datasets, NLOG abundance was modelled through a Generalized Additive Model (GAM):

$$log(Y_{i,t}) \sim s(Chla_{i,t}) + s(SLA_{i,t}) + s(SSCI_{i,t}) + s(FSLE_{i,t}) + s(MN_{i,t}) \tag{2}$$

where $Y_{i,\,t}$ represents the NLOG abundance index obtained from observers data ($Y_{i,\,t} = A_{i,\,t}$, with $t=m$ for the monthly scale, see Eq. (1)) and from Lagrangian simulations ($Y_{i,\,t} = \rho_{\mathrm{i,\,t}}$, with $t=w$ for the weekly timescale) and s(x) represents the GAM smoothers for each independent variable x.

Since too few observer's data were available in the Mozambique Channel area to perform a GAM, a linear model was run for this area, see Eq. (3).

Table 2 Number of monthly/2° cells (N cell) considered in the study

	N cell		
	$A_{i,m} = 0$	$A_{i,m} > 0$	Total
WIO	546	291	837
MOZ	4	30	34
Total	550	321	871

Only cells with an observation effort (number of vessels per month) larger than the threshold were considered (i.e. $\sum_{d=1}^{D_m} O_{i,d} \geq T$, with $T = 6$). The first column ($A_{i,m} = 0$) denotes cells without NLOG observation. The second column indicates cells with at least one NLOG observation ($A_{i,m} > 0$). Rows denote the zones

$$LM_{MOZobs} : log(A_{i,m}) \sim Chla_{i,m} + SLA_{i,m} + SSCI_{i,m} + FSLE_{i,m} + Mn_{i,m} \quad (3)$$

For all models, the dependent variable was log-transformed to achieve normality and homoscedasticity of the residuals. Explanatory variables were scaled to enable the comparison of their marginal effect on the NLOG abundance index. GAMs were performed using the R function "gam" from the package "mgcv", considering 3 nodes for models based on observer's data and 6 nodes for models based on simulated data (*k* parameter in smooth function). Best models were selected based on lowest Akaike Information Criterion (AIC). All statistical analyses were performed using R v3.6.2 (R Core Team 2021).

Results

A total of 871 monthly/2° cells had an observation effort above the threshold (i.e., $\sum_{d=1}^{D_m} O_{i,d} \geq T$ in the denominator of Eq. (1), with $T = 6$), of which 321 cells contained at least one NLOG observation (total number of NLOG observations = 901). Of these, 291 cells were located in the WIO area (with 614 NLOG observations) and 30 cells were located in the MOZ area (with 287 NLOG observations) (Fig. 1; Table 2).

The frequency distributions of environmental variables and their medians were similar between cells with and without NLOG observations, for both areas (Wilcoxon test, p.value > 0.01, Fig. 2). The sensitivity analysis conducted considering a higher observation effort threshold ($T = 10$) showed similar results (Table A1).

Fig. 2 Distribution of the environmental variables SSCI (a & b), SLA (c & d), FSLE (e & f), MN (g & h) and Chla (i & j) in the absence (blue) and the presence (yellow) of NLOG observations from observers' data. The histograms in the left column represent the MOZ area whereas histograms in the right column represent the WIO area. P-values (*P*) of the Wilcoxon tests are indicated on each panel

The NLOG abundance indices ($A_{i,\,m}$ and $\rho_{i,\,w}$) were higher in the MOZ ($A_{i,\,m}$: mean ± SD = 0.67 ± 0.53; $\rho_{i,\,w}$: mean ± SD = 2.0 10^{-3} ± 3.3 10^{-3}) than in the WIO ($A_{i,\,m}$: mean ± SD = 0.18 ± 0.14; $\rho_{i,\,w}$: mean ± SD = 5.2 10^{-4} ± 1.8 10^{-3}) (Wilcoxon tests, p.value = 9.3 10^{-11} and p-value < 2.2 10^{-16} for $A_{i,\,m}$ and $\rho_{i,\,w}$ respectively). $A_{i,\,m}$ was significantly correlated with SLA in the WIO (Kendall test, p.value = 0.007), with a low Kendall τ (τ = −0.102), and did not display any other significant correlations with the environmental variables in either zones (Fig. A3, Table A2). The same results were obtained for a higher observation effort threshold $T = 10$ (Table A3). Due to the very large sample size, significant correlations were found between $\rho_{i,\,w}$ and all environmental variables. However, none of the Kendall τ values showed a strong correlation and only three variables showed moderate correlations in MOZ (Kendall tests, SSCI τ = −0.163, FSLE τ = −0.265 and MN τ = 0.228, p.value < 0.05) and two variables in the WIO (Kendall tests, FSLE τ = −0.133 and MN τ = 0.169, p.value < 0.05).

The explanatory variables retained for modelling the NLOG abundance index obtained through the observers' data on the basis of AIC model selection are Chla and SLA for the WIO (GAM_{WIO_obs}) and only SLA for the MOZ area (LM_{MOZ_obs}), while all variables were retained in GAMs performed with simulated NLOG abundance data (GAM_{WIO_sim}, GAM_{WIO_sim}, Table 3). In the GAM_{WIO_obs} both Chla and SLA were significant while all variables were significant in the other GAMs (Fig. 3; Table 3). The adjusted R^2 values were very low for models based on observer's data (0.08 for the GAM_{WIO_obs} and 0.06 for the LM_{MOZ_obs}, Table 3), indicating that these models poorly explained NLOG abundances (Fig. A4). However, GAMs performed on simulated data allowed to increase the adjusted R^2 (0.104 for the GAM_{WIO_sim} and 0.279 for the GAM_{MOZ_sim}; Table 3, Fig. A4). The GAM_{MOZ_sim}, which better explained the NLOG abundance compared to the GAM_{WIO_sim} model run in the WIO area, demonstrated that variations in Chla, SLA, MN, SSCI and FSLE in the Mozambique Channel could partially explain NLOG distributions. Namely, NLOG abundance was predicted to be globally higher in areas characterized by higher values of Chla and MN (see Fig. 3 (a2) and (c2), respectively), while it showed decreasing trends for increasing SLA and SSCI (see Fig. 3 (b2) and (e2), respectively). Finally, NLOG abundance showed a minimum for intermediate values of FLSE (see Fig. 3 (d2)). Similarly, in the WIO area, increasing trends of NLOG abundance were also observed for increasing Chla and MN (Fig. 3 (a3) and (c3)), but a minimum could be observed at low Chla values and maximums occurred at high values for both variables, where fewer data was available. The contribution of FSLE also showed a minimum (Fig. 3 (d3)). On the other hand, NLOG abundance appeared to be positively correlated with SLA and SSCI in the WIO (Fig. 3 (b3) and (e3)), in contrast with what could be observed in the MOZ area. Finally, when models were run on the NLOG abundance derived from

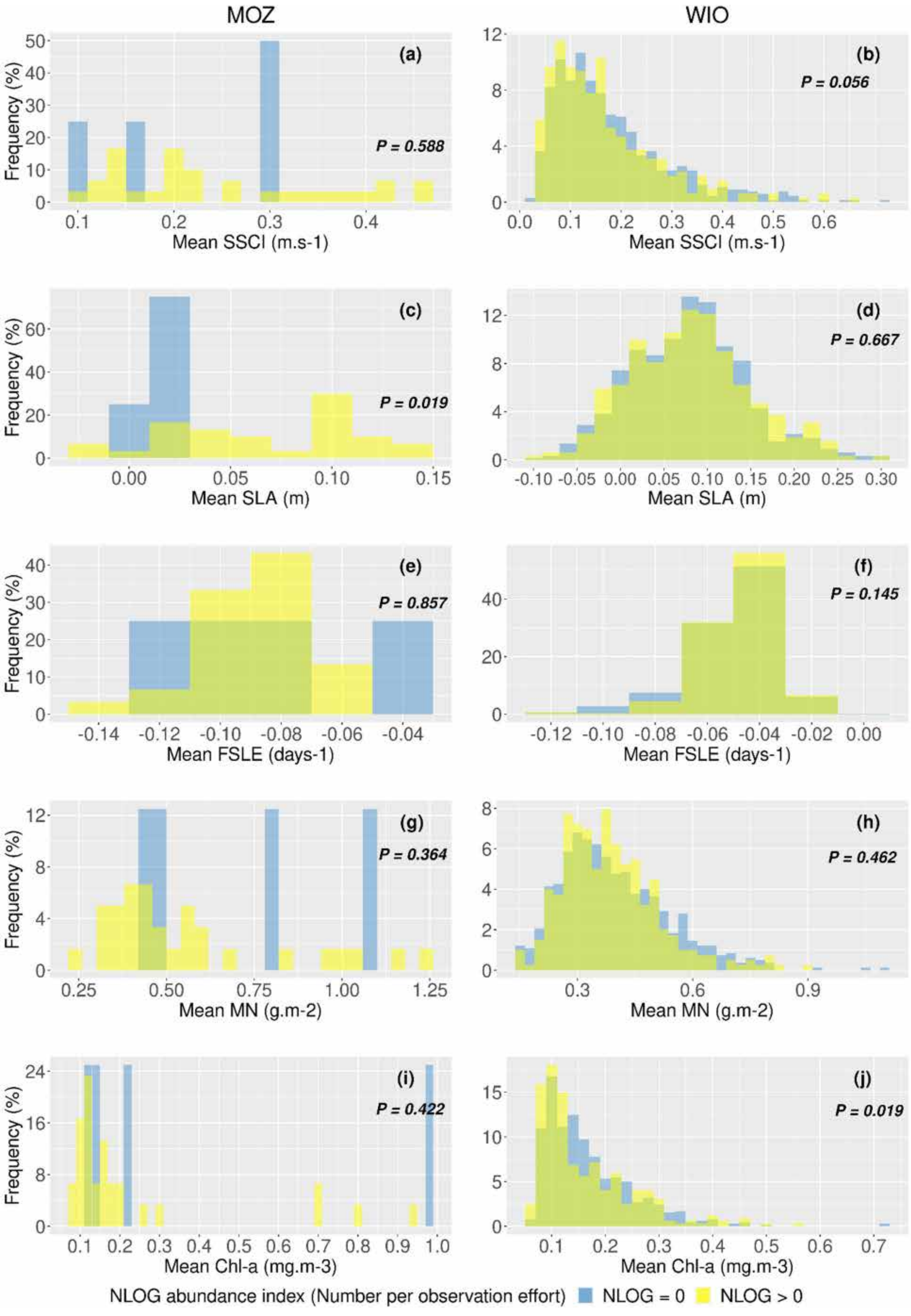
MOZ
WIO
(a)
P = 0.588
Frequency (%)
0 10 20 30 40 50
0.1 0.2 0.3 0.4
Mean SSCI (m.s-1)
(b)
P = 0.056
0 4 8 12
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Mean SSCI (m.s-1)
(c)
P = 0.019
Frequency (%)
0 20 40 60
0.00 0.05 0.10 0.15
Mean SLA (m)
(d)
P = 0.667
0 4 8 12
-0.10 -0.05 0.00 0.05 0.10 0.15 0.20 0.25 0.30
Mean SLA (m)
(e)
P = 0.857
Frequency (%)
0 10 20 30 40
-0.14 -0.12 -0.10 -0.08 -0.06 -0.04
Mean FSLE (days-1)
(f)
P = 0.145
0 20 40
-0.12 -0.10 -0.08 -0.06 -0.04 -0.02 0.00
Mean FSLE (days-1)
(g)
P = 0.364
Frequency (%)
0 4 8 12
0.25 0.50 0.75 1.00 1.25
Mean MN (g.m-2)
(h)
P = 0.462
0 2 4 6 8
0.3 0.6 0.9
Mean MN (g.m-2)
(i)
P = 0.422
Frequency (%)
0 8 16 24
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Mean Chl-a (mg.m-3)
(j)
P = 0.019
0 5 10 15
0.1 0.2 0.3 0.4 0.5 0.6 0.7
Mean Chl-a (mg.m-3)
NLOG abundance index (Number per observation effort) 🟦 NLOG = 0 🟨 NLOG > 0

Table 3 Summary table of models: (a) $\mathrm{GAM_{WIO\_obs}}$ and $\mathrm{LM_{MOZ\_obs}}$ based on observer's data and (b) $\mathrm{GAM_{WIO\_sim}}$ and $\mathrm{GAM_{MOZ\_sim}}$ based on simulations' data. Significant p.values are in bold

	Explanatory variable	Significance (*p*.value)	Estimate	Model's R^2
(a)				
$\mathrm{GAM_{WIO\_obs}}$	Chla	$\mathbf{1.4 \times 10^{-3}}$	see Fig. 3	$R^2 = 0.06$
	SLA	$\mathbf{6.5 \times 10^{-5}}$	see Fig. 3	
$\mathrm{LM_{MOZ\_obs}}$	SLA	0.10	0.26	$R^2 = 0.06$
(b)				
$\mathrm{GAM_{WIO\_sim}}$	Chla	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	$R^2 = 0.104$
	SLA	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
	MN	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
	SSCI	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
	FSLE	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
$\mathrm{GAM_{MOZ\_sim}}$	Chla	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	$R^2 = 0.279$
	SLA	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
	MN	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
	SSCI	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	
	FSLE	$\mathbf{< 2 \times 10^{-16}}$	see Fig. 3	

observers' data with a higher observation effort threshold ($T = 10$, i.e., at least 10 days at sea observations per month to consider a grid cell), Chla and SLA were considered significant in the WIO area, but the low R^2 of the model (0.08) also indicate poor explanatory power (Table A4). With $T = 10$, no variable was significant and selected for linear model in the MOZ zone (Table A4).

Discussion

Although formulated more than 30 years ago (Hall 1992), the indicator-log hypothesis has not yet been tested for tropical tunas, due to the difficulty of assessing the presence and abundance of NLOGs in the open ocean. The Western Indian Ocean is a major fishing ground for tropical tuna, where the majority of industrial tuna purse seiners operate (IOTC 2024). This study leverages a large dataset of NLOGs observations, recorded by observers onboard purse seine vessels, along with a recently-developed Lagrangian model of NLOG drifts, to examine the relationship between the presence of natural floating objects and environmental variables that serve as proxies for habitat preference and suitability for tropical tunas in the Western Indian Ocean. The results reveal no conclusive evidence of a consistent relationship between the presence and abundance of natural floating objects and these environmental variables in oceanic regions. Both field data and simulated NLOG densities provided consistent results, at two different resolutions: NLOG abundance was found to correlate (but weakly) to environmental variables only in coastal areas such as the Mozambique Channel, while there was weak to no correlation between NLOG abundance and environmental variables in oceanic areas (WIO), thus challenging the indicator-log hypothesis which is supposed to be valid across the entire ocean.

According to this hypothesis, the presence of NLOGs indicates productive areas but their absence does not give information on the area's productivity. Therefore, significant differences should be expected in the values of environmental variables recorded between areas where NLOGs are present and those where they are absent. However, the distribution of monthly means of the environmental variables recorded over 2° cells was not significantly different whether measured in the presence or absence of NLOG observations, which is not consistent with the indicator-log hypothesis. Furthermore, NLOG abundance derived from observers' data was correlated only with SLA (Kendall $\tau = -0.102$) in the WIO and did not display any other significant correlation with other environmental variables, including relevant habitat preference and suitability characteristics such as micronekton or Chlorophyll-a. The GAM and LM models confirmed these results, showing poor performances and few significant environmental variables in both subregions (WIO and MOZ, respectively). Sensitivity analyses performed with a larger threshold of observation effort confirmed them all (see Tables A1-A3-A4).

For cells where at least one NLOG observation was recorded by observers, the lack of positive correlation between NLOG abundance and environmental variables was unexpected, especially for Chla, FSLE and MN. Indeed, Chla is considered a good proxy for the presence of preys (Druon et al. 2017; Zainuddin et al. 2017) and the possible time lag between chlorophyll blooms and prey arrivals was implicitly accounted for by the monthly scale used (Mondal et al. 2021). In addition, eddies, here estimated using FSLE, are areas rich in forage species and associated top predators searching for food, such as tunas (Tew Kai et al. 2009) but no correlation was found with NLOG abundance indices derived from observers' data. It is likewise for micronekton, a very important variable in indicating the productivity of an area since they are the prey of these top predators (Young et al. 2010).

Observers data are inherently non-random, as they are collected in the fishing grounds chosen by captains, potentially leading to preferential sampling. Purse-seine vessels activities in the Indian Ocean exhibit seasonal patterns since they visit different areas at different seasons (Maufroy et al. 2017). Furthermore, captains are constantly searching for "good locations" that are favourable for tunas. Sampled locations could then be considered to correspond to favourable environmental conditions. Such a preferential sampling could impact the estimated NLOG abundance, but its impact on inferences made on NLOG-environmental

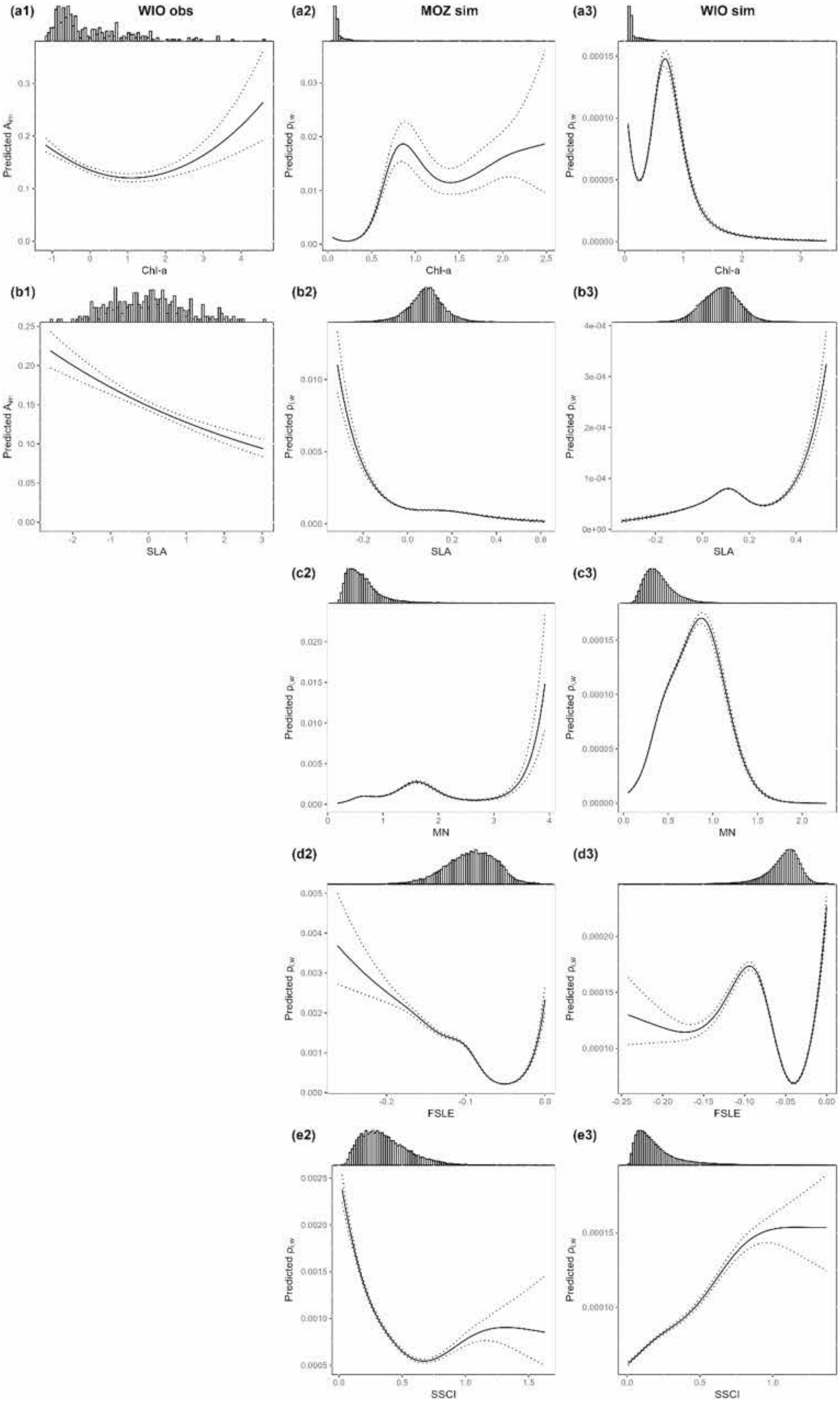

Fig. 3 GAM partial effect plots. The first column (a1) – (b1) shows the two significant explanatory variables for the GAM_{WIO_obs} model fitted to observers' data; The second column (a2) – (e2) shows results for the GAM_{MOZ_sim} model and the third column (a3) – (e3) the GAM_{WIO_sim} model, both fitted to Lagrangian simulations data, with five significant explanatory variables. Histograms on top of the panels represent the data distribution. Dotted lines delimit the standard error on the smooths. Explanatory variables are Chla (a), SLA (b), MN (c), SSCI (d), FSLE (e)

variables relationships should still be limited (Diggle et al. 2010; Conn et al. 2017). To investigate the impact of this preferential sampling, for each area, a set of environmental variables was randomly sampled from 2°/monthly cells showing an observation effort below the threshold ($T<6$; Appendix B). In the MOZ area, no difference were found between the environmental variables from the cells used in the study and those from the random cells. In the WIO zone, some significant differences were observed in the distribution of SLA, MN and Chla. These results alert on a potential inhomogeneous coverage in the WIO area. However, the range of environmental values observed in the sampled cells is similar to that observed in the random cells (Fig. B1). This suggests that any preferential sampling bias resulting from the observers' NLOG sampling is likely minimal. Observers record the presence of NLOGs both when tuna are present (when fishers are performing a set) and when NLOG are randomly encountered throughout the cruise. As a result, preferential sampling bias is expected to have only a modest impact.

Lagrangian simulations allowed overcoming the limited coverage of observers' data, providing fisheries-independent pictures of NLOG densities across the full study area, at a finer spatio-temporal scale. Significant correlations between all environmental variables and NLOG abundance were found. However, this result can be mainly explained by the magnitude of the dataset (209,040 cells at a resolution of 1°/week obtained for the simulated NLOG densities versus 871 cells obtained at a resolution of 2°/month from observers' data) and, globally, the Kendall τ values showed moderate to weak correlations for all variables. The fitted GAM models highlighted significant relationships between simulated NLOG densities and all environmental variables. In the Mozambique channel, the GAM model (GAM_{MOZ_sim}) explained 28% of the NLOG abundance with five environmental variables, signalling that NLOG can be related to environmental features in river-influenced coastal environments. In this area, the GAM models provided consistently increasing NLOG densities for areas characterized by higher productivity (i.e., higher Chla and MN values), upwelling (i.e., lower SLA values) and lower current intensities (i.e., lower SSCI values). Non-monotonic trends were found for the FSLE, which is a proxy of mesoscale features, with a minimum at intermediate values in contrast with expectations of higher productivity for higher values of the FSLE. In the WIO the GAM model predictions were weaker (10% deviance explained, Table 3; Fig. 3). Globally, the predicted trends of NLOG abundance with oceanic variables appeared to be less consistent (non-monotonous trends with Chla and MN, decreasing NLOG densities in upwelling areas - i.e., for lower SLA). A non-monotonous trend with a minimum of NLOG abundance at intermediate FSLE values was also observed, similarly to the MOZ area. Overall, the poor predictions found in the WIO highlight that no clear relationship between NLOG abundance and habitat preference and suitability indices for tropical tuna can be demonstrated in oceanic regions. Namely, our analyses suggest that the hypothesis that floating objects constitute valuable environmental cues of suitable habitats for tropical tunas cannot be validated across the Western Indian Ocean. NLOGs appear to consistently correlate to relevant environmental variables in coastal productive areas (MOZ), but do not clearly appear to indicate habitat richness in oceanic regions further away from the coast (WIO). Consequently, the association of tunas with floating objects to reach and remain in areas suitable for their fitness cannot be a valid explanation of this behavior, since this hypothesis is supposed to be valid across all regions.

Marsac et al. 2000 suggested that FADs could act as an ecological trap by altering tuna natural movements and bringing them to or retaining them in areas they would usually avoid or leave, thus affecting their fitness, growth and survival. The ecological trap is an evolutionary concept developed more than 50 years ago by Dwernychuk and Boag (1972) that hypothesises the possible consequences of an environmental change on the behavior of animals and subsequently on other aspects of their biology and ecology, which may result in a reduction in their fitness. This concept implies a environmental change, often attributed to anthropogenic activities (Schlaepfer et al. 2002; Battin 2004), where environmental cues used by animals do not constitute anymore a proxy of habitat quality. Individuals then settle in poor habitats that appear to be the same or preferable to more favourable ones instead of settling in other available and normally favoured habitats (Battin 2004; Robertson and Hutto 2006; Gilroy and Sutherland 2007). The ecological trap concept has then been broadened to the evolutionary trap concept, to include any behavioral and life-history decision and not only habitat-related decisions (e.g. when to migrate, what to eat) that becomes maladaptive because of a sudden environmental change (Schlaepfer et al. 2002).

NLOGs are not always found in areas of high productivity, implying that tuna do not use them as environmental cues for identifying suitable habitats. Hence, our results also imply that the addition of FADs in the open ocean do not particularly "trap" tunas, by retaining/attracting them into areas that are unfavourable for their fitness. The same conclusion was drawn by Dupaix et al. (2023) who found no evidence of an ecological trap for yellowfin tuna in the Western Indian Ocean.

However, our results should not overshadow that FADs can impact the ecology of tunas in a variety of ways. On average, 1.176 million tons of tuna were caught annually by purse seiners representing about 44% of total catches from 2018 to 2022 (ISSF 2025), indicating that tuna associative behavior impact their fitness through an increase of fishing mortality (Dupaix et al. 2024a). Other hypotheses seek to explain the associative behavior of tunas with floating objects and further lead to indirect ecological impacts of FAD. The meeting-point hypothesis, for example, considers that tunas associate with floating objects to form larger schools (Fréon and Dagorn 2000). Under the meeting-point hypothesis, an increase in FAD density could impact schooling behavior by fragmenting schools. Schooling behavior is seen as an evolutionary trade-off, that would lead to the apparition of an optimal school size, which depends on predation pressure and prey availability (Brock and Riffenburgh 1960; Ioannou 2017; Maury 2017). By disturbing the mechanisms through which schools are forming, FADs could strongly impact tunas fitness. Hence, a consequence of this study is the potential rejection of the ecological trap hypothesis as originally formulated (i.e. based on the indicator-log hypothesis), in the area and on the spatio-temporal scale considered, other ecological impacts of FADs remain to be assessed.

Conclusion

In conclusion, based on a 9 year-long time-series, this study indicates that, in the Western Indian Ocean, the indicator-log hypothesis cannot be validated. In other words, if NLOGs are not always found in areas that are favourable for tunas, this means that tunas do not use them as a proxy of a productive area. Consequently, and in the context of this hypothesis, our results bring new evidence suggesting that FADs would not result in an ecological trap for tunas. However, it should not detract from the fact that FADs have numerous ecological impacts. Identifying the indirect impacts of FADs on tuna ecology relies on a better understanding of the behavioral hypotheses underlying tuna association with floating objects. Hence, it is important to continue efforts aiming at better observing and understanding tuna associative behavior.

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Author contributions MC did the study conception and design. Data analysis were performed by all authors. The first draft of the manuscript was written by JG and AD and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data and code availability Observer data are available upon request to the IRD's Ob7 ("*Observatoire des Ecosystèmes Pélagiques Tropicaux Exploités*"). All the environmental data were retrieved from the EU's Copernicus maritime service with the exception of the FSLE that was processed by SSALTO/DUACS and distributed by AVISO+ (see URLs in the Materials and Methods section). NLOG densities from Lagrangian simulations can be obtained from Dupaix et al. (2025). Aggregated datasets and all the scripts used to perform the study are available on GitHub (https://github.com/jeanneguibert/Questioning_the_indicator-log_hypothesis-; https://doi.org/10.5281/zenodo.7418060: v2.0).

Declarations

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

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