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Modelling seasonal environmental preferences of tropical tuna purse seine fisheries in the Mozambique Channel

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ABSTRACT

The spatial-temporal environmental preferences and biomass aggregation of tropical tuna from purse seine fishery in the Mozambique Channel (MZC) have barely been investigated. In this study, tuna biomass volume from Fish Aggregating Devices (FADs) and Free-Swimming Schools (FSC), collected by Spanish fishing logbooks during 2003–2013, were modelled separately as a function of a set of oceanographic variables (sea surface temperature, sea surface height, geostrophic currents, salinity, and chlorophyll-a) using Generalized Additive Models (GAMs). Temporal variables (natural day, month and year), and spatial variables (latitude and longitude) were included in the models to account for the spatio-temporal structure of dynamic biomass of tropical tuna volume gathering. Oceanographic, temporal and spatial effects on aggregated catches differed between fishing modes, even though some common aspects appeared along the area and the period of study. Fishable patches of tuna biomass accumulation were explained by sea surface temperature, productivity, sea surface height, geostrophic currents, and apart from the spatio-temporal variables interactions. Although the models predicted slight differences for tuna fishing spots preferences, both fishing modes partially overlapped. Goodness of fit for selected variables showed that models were able to predict tuna catches assembled patterns in the MZC reasonably well. These results highlight a connection between the biophysical state of the oceans and purse seine tuna catches in the MZC, and ultimately may contribute to the scientific advice for the appropriate management and conservation of the exploited resources by purse seine fleets in the area of MZC.

1. Introduction

The tunas are one of the most ecological and socio-economic valuable fisheries in the Indian Ocean, managed by The Indian Ocean Tuna Commission (IOTC). The three tropical tuna species, skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*), together contribute more than half of the total Indian Ocean tuna catch (Lecomte et al., 2017a), and are the target species of many industrial and small-scale fisheries (Lecomte et al., 2017b; Chassot et al., 2019) caught by both coastal countries and distant fishing nations in the Indian Ocean (Havice and Reed, 2012; Lecomte et al., 2017b). Industrial purse seiners and longliners flagged as EU-France, EU-Spain, and Seychelles reported 34 % of total catches of these species from an overall ~$1050 million tonnes in 2019 (IOTC, 2020).

In the Western Indian Ocean (WIO), the Mozambique Channel (MZC) is a region where tropical tunas are mainly fished by European purse seine vessels from at least the 1980s and by longliners from 1850sand small-scale fisheries have been seeking tuna species throughout history (Miyake et al., 2004). Tuna schools are harvested by European purse seine fleets through two major fishing strategies that result in different species and size composition of the catch, i.e. tuna schools associated with Fish Aggregated Devices (FADs) and on Free Swimming Schools (FSC) (Guillotreau et al., 2011; Dagorn et al., 2013a; Fonteneau and Chassot, 2014; Torres-Irineo et al., 2014; Chassot et al., 2019). Sets on FADs are mostly composed with skipjack and juveniles of yellowfin and bigeye tuna, while sets on FSC targeted large adult yellowfin and bigeye tuna (Dagorn et al., 2013b; Fonteneau and Chassot, 2014). Although large and small-scale fisheries operate in different fishing grounds, interactions between fleet catches of the three main tropical tuna species are common in MZC (POSEIDON, et al., 2014; Lecomte et al., 2017b), leading to fishing pressure on tuna stocks.

Tropical tuna fisheries are the major source of economic profits and

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job provisioning in different segments of production chain (e.g.: extractive fishing, transhipment, fish processing, canning, and trading) in nations around MZC (Campling, 2012; Lecomte et al., 2017b). Therefore, while fishing activities on tropical tunas in developing coastal states, and, in particular, in MZC, contribute to the country's economy growth and supports social livelihood and food security (Obura et al., 2017), they are also the stressors affecting the biomass of tropical tuna and related species due to high catch volume of tuna by various fishing communities (Lecomte et al., 2017b; Chassot et al., 2019).

Availability of tuna schools in the MZC are also often influenced by environmental conditions. Several authors have investigated the effect of environmental effects on tuna distribution (*e.g.* Fraile et al., 2010; Lan et al., 2017; Maunder et al., 2017), and biomass aggregation elsewhere (e.g.:Yen et al., 2016; Lopez et al., 2017a, 2017b; Marsac, 2017) with few studies including the MZC (e.g.:Tew-Kai and Marsac, 2010; Dueri et al., 2014; Marsac, 2017). The oceanographic variables that have been most frequently linked to tuna populations (Song et al., 2009; Fraile et al., 2010; Lan et al., 2017) and other large pelagic species (Maravelias and Reid, 1997; Murase et al., 2009), included sea surface temperature, chlorophyll, sea level anomalies, salinity, sea surface currents, depth, and the space-time scale (Table 1). Effects of these physical-biological conditions in the oceans plays a significant role in influencing the spatio-temporal distribution and abundance of tropical tuna species. Furthermore, the increasing development of FADs purse seine fishing mode of the European fleets in the MZC is also influenced by environmental conditions. This makes the investigation of the dynamics of fish species and biomass aggregation in relation to their marine environments of key importance which could contribute to providing guidelines for fisheries management and conservation measures in the Mozambique Channel.

Analysis of the effect of the physical-biological oceanographic variables on the distribution and biomass density of tuna revealed seasonal change in pelagic fish distributions including tuna in the MZC. For example, during austral winter (March-June), tuna schools seems to peak in MZC (Kaplan et al., 2014; Obura et al., 2018), attracting purse seiners to fish in northern regions of the channel (Davies et al., 2014). The three main tropical tuna species seasonally fished by purse seines in the MZC, are *Katsuwonus pelamis, Thunnus albacares,* and *Thunnus obesus* (Campling, 2012; Kaplan et al., 2014).

Approaches and methods applied to infer the relationship of large pelagic species with specific oceanographic conditions are diverse (e.g.: APECOSM-E, GLM, MaxEnt, randomForest, MARSS). However, generalized additive models (GAM, Wood, 2006), have been recognized as powerful tools to investigate these effects in detail (e. g.: Maravelias, 2001; Murase et al., 2009; Fraile et al., 2010; Lan et al., 2017; Lopez et al., 2017a, 2017b), because of their flexibility to conduct robust regressions and the ability to model non-linear relationships through non-parametric splines (Hastie and Tibshirani, 1990).

There are limited studies in the MZC linking environmental conditions with fish biomass accumulation as well as a scarcity of GAM application to investigate the concentrations of tuna biomass in the study area. This limitation is related to difficulties in obtaining coastal catch data for small-scale fisheries. Spanish purse seine logbooks provide detailed information on catches and effort of tropical tunas in the MZC for the two fishing modes, FADs and FSC. As Spanish purse seine tropical tuna catches represent an important percentage of total catches reported by the WIO this study assesses the relationship between environmental factors and tuna biomass accumulation using data provided by purse seiners in the MZC. The study objectives are to: (i) reveal their temporal dynamics, and (ii) predict the biomass spatial aggregation hotspots in relation to their preferred environmental conditions. As tuna and tuna like species in the study area are under IOTC management (IOTC, 2019), results of this work may help regional management fisheries organizations and decision-makers to improve conservation and management measures while also supporting coastal states around the MZC area wishing to develop commercial and domestic tuna fisheries.

2. Methodology

2.1. Study area

The Mozambique Channel (MZC), is located in the southwestern part of the Indian Ocean, with Mozambique in the west, Madagascar in the east and the Comoros archipelago in the north. MZC is a good natural

Table 1
Review of the importance of the environmental, spatial, and temporal variables on the distribution of tuna. ACS- Acoustic survey BET- Bigeye tuna; BLS- AO-Atlantic Ocean; Chl-chlorophyll-a; D. Expl. - Deviance Explained; DP-depth in the ocean; GC-Geostrophic currents; IO-Indian Ocean; Lat- latitude; LL- longline; Lon- longitude; Mon- Month/Season; PO- Pacific Ocean; PS-purse seine; Sal-salinity; SKJ- Skipjack tuna; Sp-Species; SSH, Sea Surface Height; SST- Sea Surface Temperature; TPT- tropical tuna (BET, SKJ, YFT); WIO- Western Indian Ocean; Yr-year; YFT- Yellowfin tuna. TPO- tropical Pacific Ocean; AO-EQP equatorial Atlantic Pacific Ocean; IO-ENP eastern north pacific Indian ocean; WPO - Western Pacific Ocean.

Area / Habitat	Data Source	Physical-Biological, Temporal and Spatial Variables													Authors
		SST	Sal	GC	SSH	O2	Chl	Lat	Lon	Mon	Yr	DP	Sp	Dev. Expl.	
AO, IO, PO	LL	x	x		x		x			x	x		SKJ	63.7	Arrizabalaga et al., 2015
AO, IO, PO	LL	x	x		x		x			x	x		YFT	50.2	Arrizabalaga et al., 2015
AO, IO, PO	LL	x	x		x		x			x	x		BE	45.3	Arrizabalaga et al., 2015
IO	LL	x		x			x	x		x		x	YFT	*	Dell et al., 2011
WIO	TR	x			x	x	x			x	x	x	SKJ	*	Davies et al., 2014
AO, IO	PS	x	x	x	x	x	x					x	SKJ	*	Druon et al., 2017
AO, IO, PO	LL	x	x		x		x	x	x	x			SKJ	62.4	Erauskin-Extramiana et al., 2019
WIO	PS						x	x	x	x		x	SKJ	40.7	Fraile et al., 2010
WIO	PS						x		x		x	x	YFT	40.3	Fraile et al., 2010
PO	PS/LL	x					x					x	BET	48.6	Houssard et al., 2017
PO	PS/LL	x					x					x	YFT	33.4	Houssard et al., 2017
TPO	LL	x			x		x						YFT	33.60	Lan et al., 2017
WIO	ACS	x	x	x	x		x	x	x				TPT	*	Lopez et al., 2017a
WIO	ACS	x	x	x	x	x	x						TPT	*	Orúe et al., 2020
AO	PS	x	x	x			x					x	YFT	93.0	Maury et al., 2001
IO	LL	x	x	x	x		x						BET	*	Song et al., 2009
WIO		x		x	x		x						TPT	*	Tew-Kai and Marsac, 2010
AO-EQP	LL	x			x		x	x	x	x			YFT	50.73	Zagaglia et al., 2004
IO-ENP	LL	x			x		x	x	x	x			YFT	28.6	Rajapaksha et al., 2013
WPO	PS	x	x	x	x		x	x	x	x		x	SKJ	13	Yen et al., 2016

Deviance explained not provided.

laboratory for investigating species relationship with the environment, due to the complexity of the sea surface circulation, with anti-cyclone and cyclone meso-scale eddies dominating the system (Lutjeharms and Town, 2006; Tew-Kai and Marsac, 2010; Ternon et al., 2014; Ruijter et al., 2015). The current flow in the north of the MZC channel is fed by the warm South Equatorial Currents (SEC), which generate eddies in Comorian basin, propagating south-westward through the channel. In the south, the SEC eddies, merge with eddies generated in the south-east of Madagascar and move westward to form the merged eddies currents trapped by the cold Agulhas Currents (Lutjeharms and Town, 2006; Tew-Kai and Marsac, 2009; Ternon et al., 2014) (Fig. 1 S1). These circulation patterns, and other oceanographic features like sea surface temperature, sea level anomalies, salinity, oceanic fronts, with coupled interactions with nutrient enrichments, and plankton concentrations, play significant role on the marine ecosystem food web, and the consequent aggregation of top predators like tuna (Tew-Kai and Marsac, 2009, 2010; Ternon et al., 2014; Druon et al., 2017; Lopez et al., 2017a, 2017b).

2.2. Fishery data

Scientific estimates of catches and effort data from the Spanish Oceanographic Institute (IEO) were used in the analysis. These estimates are obtained from the logbooks of the Spanish purse seine fleet in the Indian Ocean along the period of February 2003 –June 2013 after composition correction (Pallarés and Petit, 1998); and from detailed fleet data and port sampling. Catch and effort data from logbooks were detailed by set and consist of 3650 sets (7000 FAD and 6650 FSC). Catch information for Katsuwonus *pelamis* (skipjack)*, Thunnus albacares* (yellowfin), and *Thunnus obesus* (bigeye) (Fig. 2 S2) included size category in tonnes for each fishing type (FSC and FAD), fishing hours, date (year, month, and day of the fishing operation), and location (i.e., longitude and latitude). The data was spatially confined to the MZC in the western Indian Ocean, within latitudes of 8 °S to 30 °S and longitudes of 30 °E to 50 °E, and total biomass was aggregated by fishing set per grid cells (Fig. 1). Temporal window of catches was subset to the months between February to August which correspond to the fishing season in the MZC for the time series analysed.

Original logbook data from the tropical Spanish purse seine fishery requires the species composition in total catch of yellowfin, skipjack and bigeye to be corrected for each set (Pallarés and Petit, 1998). This procedure is carried out through a statistical established protocol designed by the Spanish Oceanographic Institute (IEO) and the Institute pour le Reserche and Developpment (IRD) with the program T3 (Tropical Tuna Treatment). The aim of T3 is to reduce the bias among the species composition in catches declared in logbooks, due to species misidentification, mainly among juveniles of bigeye, yellowfin and skipjack tunas. For each set, a weighting factor is applied assigning specific catches depending on the rectangle where the set was located in. Corrected catches are used as the scientific data presented by EU to IOTC secretariat.

2.3. Environmental data

Environmental data for 2003–2013 in the MZC was obtained from the MyOcean-Copernicus EU consortium (marine.copernicus.eu) in netCDF format. Physical and biological environmental data were extracted for each fishing set location of the each date from netCDF files through loop function codes and are the following: sea surface temperature, sea surface temperature gradient derived as the decrease or increase in temperature for each pixel over an 7-day period, sea surface height, eddy kinetic energy (derived from altimetry), sea surface current velocity, heading-direction of the current sea surface, salinity, chlorophyll-a concentration, chlorophyll-a gradient derived as the increase or decrease of chlorophyll amount in each pixel over an 7-day period, and dissolved oxygen concentration (Table 2). Then, environmental variable data were merged with fisheries data by fishing set, (i.e., longitude and latitude, year, month, and day). The spatial and temporal

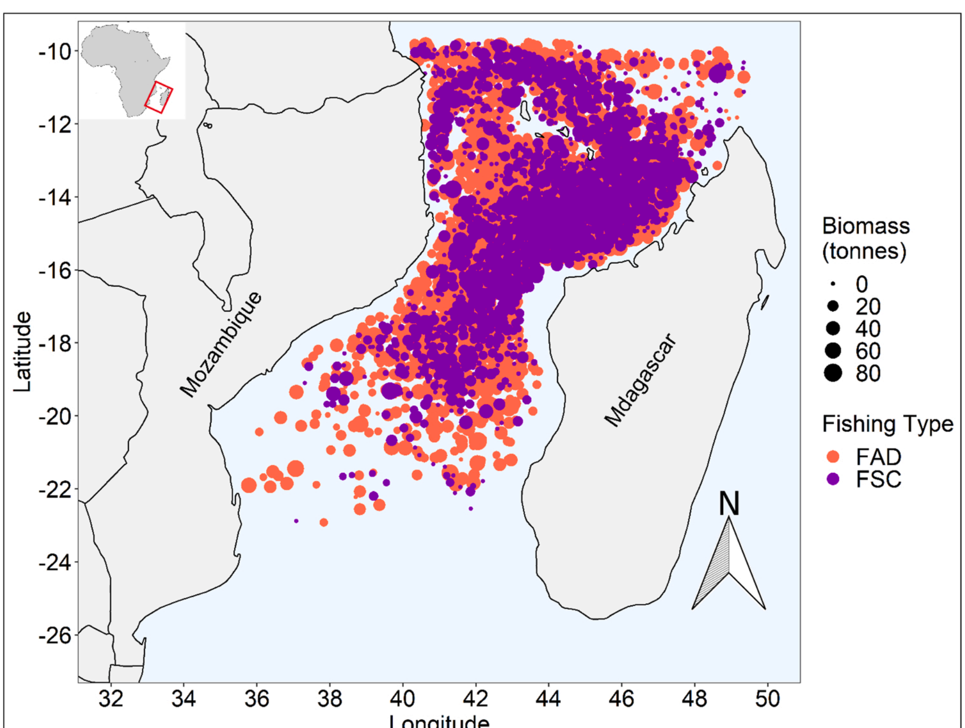

Fig. 1. Total biomass distribution of tropical tuna species in tonnes (Bigeye, Skipjack and Yellowfin tuna) in the Mozambique Channel targeted by Spanish purse seine fleets for the period 2003 - 2013. Catches were monthly aggregated by 0.25° x 0.25° resolution. FSC - free-swimming schools and FAD - fish aggregation around devices.

Table 2
Environmental, spatial and temporal variables used in the study.

Variables	Acronym Used	Unit	Spatial Resolution	Temporal Resolution
Chlorophyll a concentration	CHL	mg m^{-3}	0.25° x0.25°	Daily
Chlorophyll Gradient concentration	CHLGD	mg m^{-3}	0.25° x0.25°	±7 days
Current Heading	HDG	degrees	0.25° x0.25°	Daily
Eddy Kinetic Energy	KE	m^2 s^{-2}	0.25° x0.25°	Daily
Current Velocity	SSC	m s^{-1}	0.25° x0.25°	Daily
Sea Surface Height	SSH	m	0.25° x0.25°	Daily
Oxygen concentration	O_2	mg l^{-1}	0.25° x0.25°	Daily
Sea Surface Salinity	SSS	g kg^{-1}	0.25° x0.25°	Daily
Sea Surface Temperature	SST	°C	0.25° x0.25°	Daily
Sea Surface Temperature Gradient	SSTGD	°C	0.25° x0.25°	±7days
Latitude	Lat	degrees	0.25° x0.25°	Daily
Longitude	Long	degrees	0.25° x0.25°	Daily
Month	Month	–	0.25° x0.25°	Monthly
Natural Day (365 days per Year)	YearDay	–	0.25° x0.25°	Daily
Year (2003–2013)	Year	–	0.25° x0.25°	Yearly

resolution was 1/4° and daily, respectively. Besides oceanographic variables, spatial-temporal variables were included in the analysis to better isolate the effect of the environment and could be misinterpreted as abundance variables or even masking some other environmental processes not included in the model. These spatial-temporal variables were longitude, latitude, year, month, day, and natural day, i.e., from 1 to 365 days (Cortés-Avizanda et al., 2011).

2.4. Data analysis

For the purpose of this analysis, corrected individual species composition in catches was aggregated to define total biomass by set (e.g.: *Biomass* = *BET* + *SKJ* + *YFT)*; where *BET, SKJ, YFT* are the catch of yellowfin, skipjack and bigeye, respectively. Due the differences in catch composition and sizes between the two types of sets (FADs or FSC) this aggregation makes sense to represent biomass of tropical tunas as a group. For FAD sets, the effect of oceanographic variables impacts the aggregation of schools of skipjack, juveniles of bigeye and yellowfin while for FSC sets, catches of adult yellowfin predominate.

All the statistical analyses were conducted in the R software version 3.5.0 (R Core Team, 2018). Exploratory data analysis included a visual checking of the data through the cloud function in the lattice package (Sarkar, 2008) in order to have a general overview of the potential relationships of covariates and the response variable (i.e. tuna biomass) in time and space. The relative effect of covariates on the dependent variable was also explored to gather information on the most important variables effecting tuna biomass and reduce model complexity in further stages (Dell et al., 2011), using randomForest package (Liaw and Matthew, 2002).

Correlation among predictor covariates was tested using pairwise plot and Pearson rank correlation scores, and one covariate between covariates pairs with correlation coefficient ≥ +0.70 and ≤ -0.70 was dropped from the variable selection process (Dormann et al., 2013), based on the relative importance test and the ecological expert knowledge and literature for the species (Zuur et al., 2009). A variance inflation factor analysis was also conducted as an additional measure to test collinearity using a threshold value of 3 (Zuur et al., 2009). Hence, the covariates natural day, oxygen concentration, and current velocity were dropped for further modelling phase due to collinearity and correlation with ecologically more important environmental variables.

Furthermore, boxplots were used to visualize and inspect positive catch distribution, detect and correct outliers. However, some authors (e.g.: Zagaglia et al., 2004; Cortés-Avizanda et al., 2011) suggest that there is no need for the prior assumption of normality and linearity required to fit GAM models. For this analysis normal, lognormal, and gamma distributions were fitted to the response data by fishing mode using the fitdistrplus package (Delignette-Muller and Dutang, 2015), to determine which distribution family should be best used for modelling. For the first step, normality was tested with original response data. Then, as statistic results and graphical inspection shown that the original data did not follow the normal distribution, data were transformed to logarithmic scale and model refitted to meet normality criteria (Underwood, 1997; Wood, 2006; Zuur et al., 2009). Assumption for good distribution model were based on lowest Akaike Information Criterion (AIC), Kolmogorov-Smirnov statistics and graphical inspection (Delignette-Muller and Dutang, 2015). However, for FSC, Kolmogorov-Smirnov statistics was relatively favourable to lognormal distribution, whereas AIC and graphical inspection were indicating the use of normal distribution for the logarithmic scale transformed response variable (set in the exploratory analysis in Section 2.1), as the best distribution to fit the model.

In early stages of the modelling, daily set by set data for each fishing mode was used. However, because of the low performance of the models and the failure to detect the variance changes at this scale, data were monthly aggregated to 1/4° grid cell (such as sum for the biomass and mean for the environmental variables). Details to create different scale grids and raster layers through the raster package can be found in Bivand et al. (2015) and grey literatures.

GAMs were established to examine the effects of environmental variables on the spatio-temporal tuna biomass aggregation for each fishing mode (i.e., FADs and FSC). The logarithmic transformation of total biomass (i.e., *log(Biomass+1)*) was used as the dependent variable to reduce skewness and improve model performance (Wood, 2006). GAMs were fitted using a Gaussian family with identity link function using the gam function from the mgcv statistical package in R (Wood, 2006), following the recommendations for modelling continuous data (e.g: Wood, 2006; Zuur et al., 2009, 2010), and the distribution tests as follows:

$$Y = \alpha + \sum_{j=1}^{n} f_j(x_j) + \varepsilon$$

Where, Y is the response variable, α is a constant, f_j are regression coefficients or smoothing functions, x_j are measured values for predictor variables and ε is the residual. The best GAM for each fishing mode was obtained with a backward stepwise procedure (see details below), starting from an annotation as follows:

$$ln\ (Biomass+1) \sim te(space\text{-}time,\ k = (506),\ d = c(2,1) + s(C_a,\ C_b,\ k = 20) +$$

$$s(C_c,\ k = 6) + \ldots\ c(C_c,\ k = 6) + s(C_z,\ k = 6) + random\mathrm{w}$$

here the function *te* forms the product from the marginal's terms of the space-time triple interactions, *d* is the dimension of each spline in the triple interaction which in our case is two for spatial components and one for temporal term. The *s* is the penalized spline smooth function, for the single interactions, and environmental covariates (C). All interactions were fitted by the tensor product smooth (ts), while the single covariates were fitted with cubic regression spline (*cs*) to model nonlinear relationships. The "*cs*" ensures that a regression spline with shrinkage is applied, a smoother can have zero degrees of freedom, and all smoothers with zero degrees of freedom can be dropped simultaneously from the model (Zuur et al., 2009); *c* specify cyclic cubic regression spline used to illustrate the cyclical behaviour of the sea surface currents direction denoted as heading (Wood, 2006), and the random effect account for inter-annual variability in fishing effort and fleet behaviour (Brodie et al., 2015). Dimension, k, representing the maximum degrees of freedom for each smooth term, was set as $k = 6$ for the main effect, $k = 20$ for the first order interaction (Cardinale et al., 2009; Giannoulaki et al., 2013; Jones et al., 2014). The value of $k = 50$ for spatial components in the space-time triple interaction was found after trial and error selection of k (Wikle et al., 2019), to avoid models overfitting, and to simplify the interpretation of the results.

Covariate selection was performed applying a backward stepwise elimination procedure based on the following criteria: (i) the approximate 95 % confidence band for the smooth term included zero everywhere; (ii) Generalized Cross Validation (GCV) score drop when the term was dropped (Wood, 2001); and (iii) Akaike Information Criterion (AIC) score decreased when the term was deleted (Akaike, 1974). Final models with lowest GCV and AIC scores were selected.

The goodness-of-fit of the models was assessed by examining and considering diagnostics checks, the percent of deviance explained, lowest AIC and GCV scores, the graphical inspection of the residuals to access normality and homogeneity, and the straight linearity between fitted values and response (Hastie and Tibshirani, 1990; Wood, 2006; Zuur et al., 2009). Furthermore, residuals spatial autocorrelation was tested with the *spline.correlog* function from the ncf package (Bjørnstad et al., 2001).

Four temporal term candidates were tested (i.e., month as a factor, month as cubic spline, space-time triple interaction, and natural day). The default GCV was chosen as the best smooth selection parameter over the Restricted Maximum Likelihood (REML) and Marginal Likelihood (ML), as GVC select optimal smooth parameters (i.e. low prediction error as the sample size tend to infinite) (Wood, 2011).

Model validation was based on the k-fold cross validation, consisting on randomly split observations on k groups, which in this case k was set to 10 folds. The first fold was treated as a validation set, and the model was fitted on the remaining $k - 1$ folds (James et al., 2014). Then, root mean square error rate (RMSE) was computed as metric measure accuracy to evaluate model prediction on the held-out fold observation data. Also, similarity index between observed and predicted data was estimated (Warren et al., 2008), through niche Overlap function in the dismo package (Hijmans and Elith, 2016), and Pearson correlation test (r^2) between predicted and observed biomass were estimated through cor.test function in the base stats package (R Core Team, 2018).

3. Results

Table 3 summarizes the goodness-of-fit criteria and the statistics of the response variable distribution considered in our analysis as recommended for continuous data. The analysis showed that normal distribution of the logarithmic scale transformed response data were the best fit distributions for both FAD and FSC fishing mode data. Biomass of about 197,078.30 tonnes of tropical tuna aggregated in northward of MZC over the study period, accounted with 68 % of the total biomass for FADs, while for FSC was about 32 % of total biomass.

Table 3
Statistics summary for testing the best fitted distribution to the data. AIC-Akaike Information Criterion; FAD-fishing around aggregating devices; FSC- free swimming schools; KSS- Kolmogorov-Smirnov statistic; Normal log(x+1) - refer to the response data transformed to logarithm scale. p-value of Kolmogorov-Smirnov statistic help to indicate that sample follow (p-value >0.05) or not (p-value<0.05) the normal distribution.

Data Model Fit Statistic	FAD			FSC		
	AIC	KSS	p-value	AIC	KSS	p- value
Normal	35424.03	0.1854	<0.0001	15718.31	0.2381	<0.0001
Gamma	31885.42	0.0557	<0.0001	13595.77	0.0699	<0.0001
Normal log (x+1)	9274.67	0.0212	0.1249	4325.83	0.0341	0.1238

Table 4
Selected GAM models for seasonal and spatial biomass distribution for tropical tuna species. All models were fitted with gaussian distribution with identity link. EDF: effective degree of freedom; FADs: fishing aggregating devices; FSC- fishing on free swimming schools; SSH - sea surface height; CHL - chlorophyll-a; SST - sea surface temperature; SSTGD- sea surface temperature gradient; SSS - sea surface salinity; CHLGD -: chlorophyll-a gradient; HDG - heading (sea surface currents direction); VEL - sea surface current velocity; KE - Kinetic energy; Long - Longitude in degree; Lat - Latitude in degree.

Parameters	Model Fitted with Gaussian Family Identity Link			
	FAD		FSC	
Adjusted R2	0.20		0.27	
Dev. Explained. (%)	22.60		32.60	
AIC score	6790.28		3137.36	
GCV score	0.60		0.78	
n	2925		1217	
EDF	106.35		100.00	
Residual df.	2818.65		1124.93	
Covariates	EDF	p-value	EDF	p-value
CHL	–	–	4.78	<0.001
CHLGD	–	–	–	–
HDG	3.57	<0.001	–	–
KE	4.75	<0.001	–	–
MONTH	–	–	–	–
SSH	1.95	<0.01	3.35	<0.001
SSS	4.37	<0.01	4.39	<0.001
SST	–	–	–	–
SSTGD	–	–	–	–
VEL	–	–	–	–
Year			0.11	<0.001
Natural day	–	–	–	–
CHL x CHLGD	8.70	<0.05	–	–
SST x SSTGD	11.48	<0.001	12.42	<0.001
Long x Lat x Month	70.52	<0.001	73.95	<0.001

Table 4 summarizes final spatio-temporal GAM models. Models with triple interactions were finally selected based on performance scores. Covariate selection differed between FAD and FSC fishing, although the space-time triple interaction was the most significant terms in both fishing modes. The shapes of the functional forms for the selected covariates for both FAD and FSC models were plotted (Fig. 2 and 4). Both FAD and FSC models displayed non-linear responses to the covariates. The predicted relative tuna biomass assembled by fishing mode also exhibited different spatial distribution patterns in the area. The performance scores of the models, including deviance explained, AIC and GCV scores, effective degree of freedom (EDF) and variables significance can be found in Table 4.

3.1. FAD model

The final GAM for FADs explained 22.60 % of the deviance with an adjusted R^2 score of 0.20 (Table 4). The spatial correlograms showed non-significant residual autocorrelation, and model residual check displayed histograms close to the normal distributions, and the variance met homogeneity criteria (Fig. 3 S3). The selected variables were, ordered according to the variable significance (i.e., p-value): interactions longitude - latitude - month (Fig. 2a), SST - SSTGD, CHL −CHLGD, single covariates such as KE, HDG, SSH, and SSS (Fig. 2b and Table 4). The top panel in Fig. 2a, shows that tuna biomass was high along the Mozambique coast at the latitude 18 °S and 24 °S in February and early March. In late March up to May, tuna biomass was more aggregated in west coast of Madagascar at latitude 12 °S and 17 °S, and from June to August the biomass was relatively accumulated in northern area of the MZC below 12 °S. It seems that for the period of June to August, model suggest that purse seiners quit fishing in the Mozambique Channel.

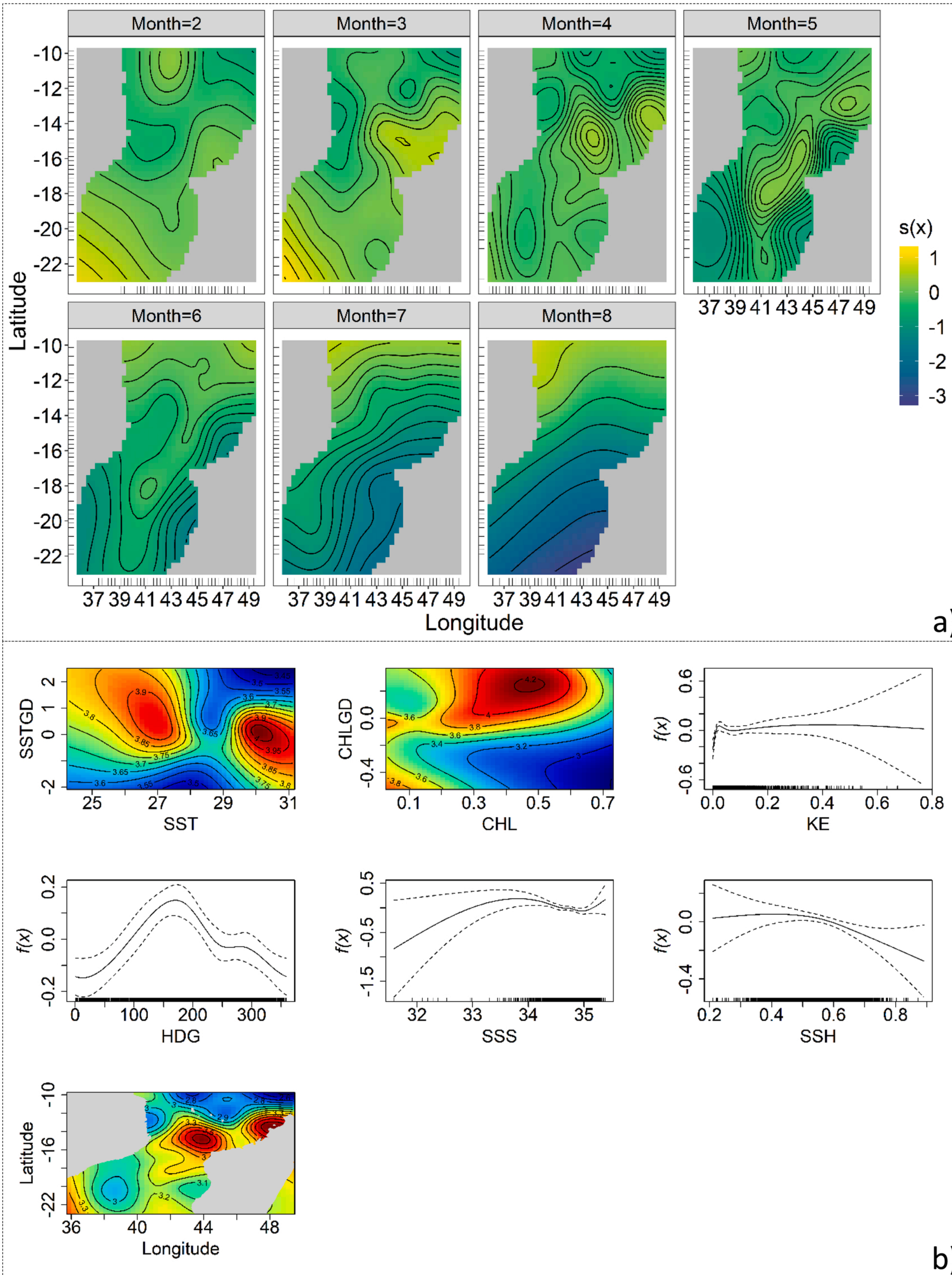

Fig. 2. Smoothed fits of covariates from GAM, modelling biomass of tuna catches in FAD. Top panel is partial effect of the tri-dimensional interaction longitude x latitude x month in surface plot. Bottom panel are partial effect of the two-dimensional terms (SST - SSTGD, and CHL –CHLGD), partial effects of each covariate (Ke, HDG, SSH, and SSS) plotted as smoothed fits, and contour map of catches distribution. Tick marks on the *x*-axis are the observed data. The *y*-axis represents the smooth terms contribution to the model on the scale of linear predictors. y-axes, denoted as f(x), reflects the relative importance of predictor variable of the model. Dashed lines indicate the lower and upper 95 % confidence of the smooth plotted lines.

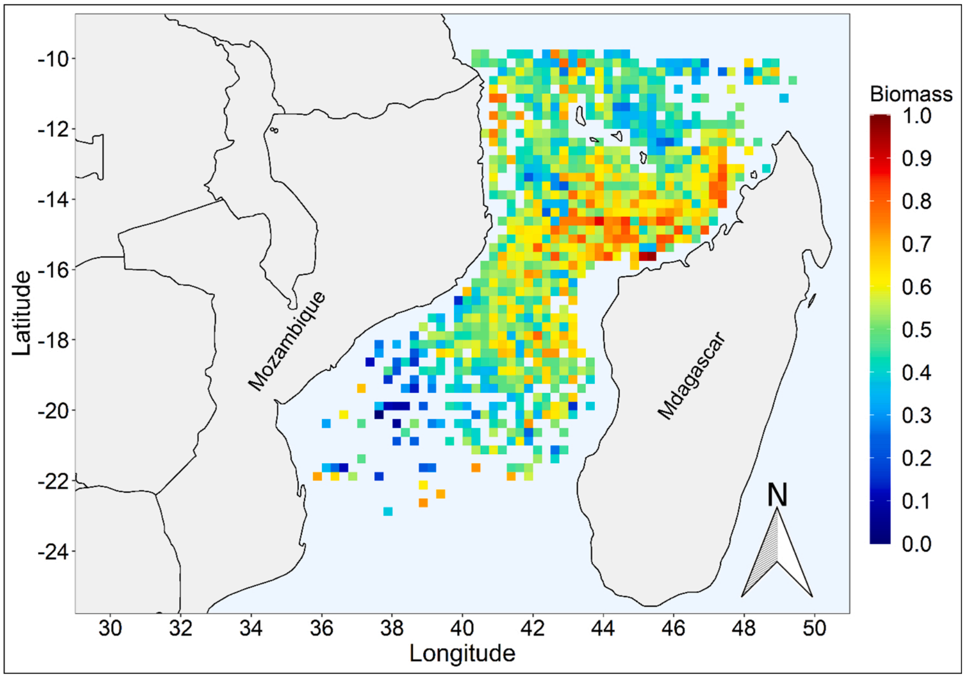

Fig. 3. Predicted spatial distribution of normalized tuna biomass density caught in FADs fishing mode in the Mozambique Channel area. Data are tuna biomass for the period 2003-2013, gridded by 0.25° x 0.25° spatial resolution, and transformed to natural logarithm scale for better performance in GAM modelling.

Tuna biomass revealed two distinct groups, i.e., schools with preference in waters where temperature changed by ±2 °C in a week period from 24 °C up to 28 °C, and waters above 29° where temperature changed between ±2 °C. Those waters were characterized by patches where chlorophyll concentration changed between ±0.2 mg Kg^{-1} in a week period. The shape of functional forms in the patches where tuna biomass aggregated exhibits relative flattened trend with KE intensity, increasing in waters moving toward west-southward. Higher biomass of tuna was related to salinity waters ranged between 32 gkg^{-1} to 34.5 gkg^{-1}, where SSH elevation was below 0.6 m. Contour map from GAM, revealed two hotspots of tuna biomass located in northern west tip of Madagascar between the latitude 12 °S and 16 °S (Fig. 2b).

Fig. 3 displays predicted biomass aggregated around FADs along the Mozambique Channel. The maps for the area of the Mozambique Channel illustrated that tuna biomass density is high in northern Mozambique Channel, with the core observed in north-west coast of Madagascar Island at the longitude 42 °E to 47 °E, and latitude12 °S to 20 °S. GAM predicted tuna biomass density decreased west-southward and west-northward along the Mozambique Channel, surrounding Mayotte and Comoros Island waters (Fig. 3). Low biomass density was expected at the latitude above 20 °S, falling to zero nearest Mozambique cost. There was no predicted biomass at high latitudes above 23 °S in the study area. GAM predicted tuna biomass aggregation in MZC similarly to the observed biomass around FADs, i.e., RMSE was 0.09, Schoener similarity index "D" was about 0.90, and Pearson correlation test was about r^2 =0.44.

3.2. FSC model

Final FSC model for the tuna biomass explained 32.60 % of the deviance with an adjusted R^2 score of 0.27 (Table 4). The spatial correlograms displayed non-significant residual autocorrelation, and model residual check followed homogeneity criteria, and histogram close to the normal distributions. Covariates selected for the final model, in order of significance, were (Table 4, Fig. 4): interactions longitude - latitude - month (Fig. 4a), SST - SSTGD, single terms such as SSS, SSH, and CHL (Fig. 4b). Fig. 4a depicted that in February tuna biomass density was located north of the Mozambique Channel. High biomass was observed in April and May, and similarly to the FAD strategy, GAM detected that FSC seiners start to leave Mozambique Channel to other fishing ground between June and August. However, between June and August the records of biomass were relatively high, the frequency of sets was very low, revealing departure time of seiners to other fishing patches (Fig. 4a). Higher biomass density was associated with waters of SST above 26 °C, where SSTGD was changing between ±1.5 °C in a week period (Fig. 4b). In relation to salinity, tuna exhibited flattened trend at relatively low SSS water, and a peak in waters where salinity was around 34.5−35 g Kg^{-1}. Furthermore, tuna biomass was positively related with SSH values 0.4−0.6 m, while in relation to the CHL, a relative decreasing trend with increasing chlorophyll-a concentration was found (Fig. 4b). Contour map depicted fishing hotspots for FSC seiners at the west tip of Madagascar at the latitude 14 °S to 16 °S, another hotspot in northern part of the Channel, reaching Mozambique coast at the latitude below 12 °S (Fig. 4b).

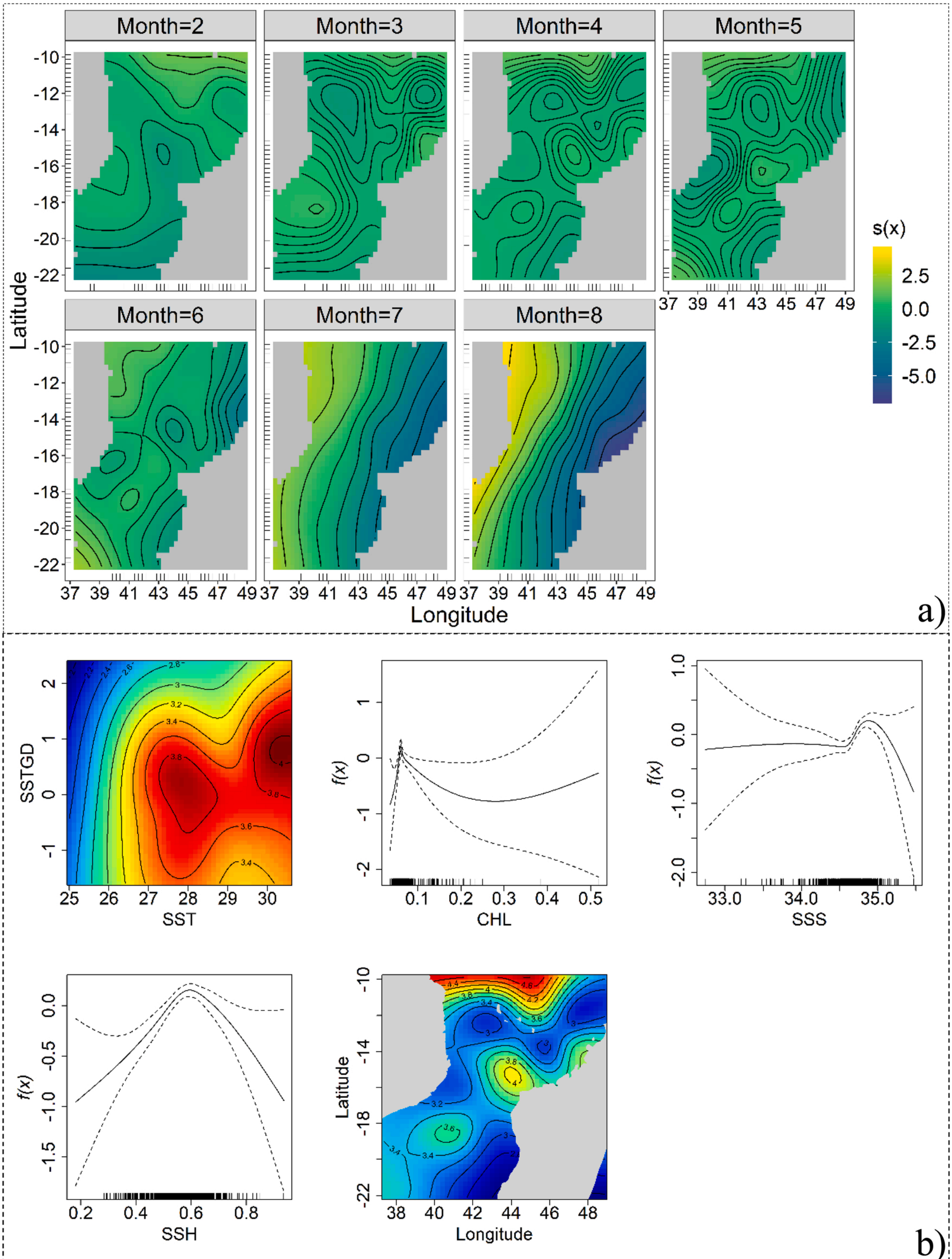

Fig. 4. Smoothed fits of covariates from GAM, modelling biomass of tuna catches in FSC. Top panel a) is partial effect of the tri-dimensional interaction longitude x latitude x month in surface plot. Bottom panel are partial effect of the two-dimensional terms (SST - SSTGD), partial effects of each covariate (SSS, SSH, and CHL) plotted as smoothed fits, and contour map of catches distribution. Tick marks on the *x*-axis are the observed data. The *y*-axis represents the smooth terms contribution to the model on the scale of linear predictors. y-axes, denoted as f(x), reflects the relative importance of predictor variable of the model. Dashed lines indicate the lower and upper 95 % confidence bunds of the smooth plotted.

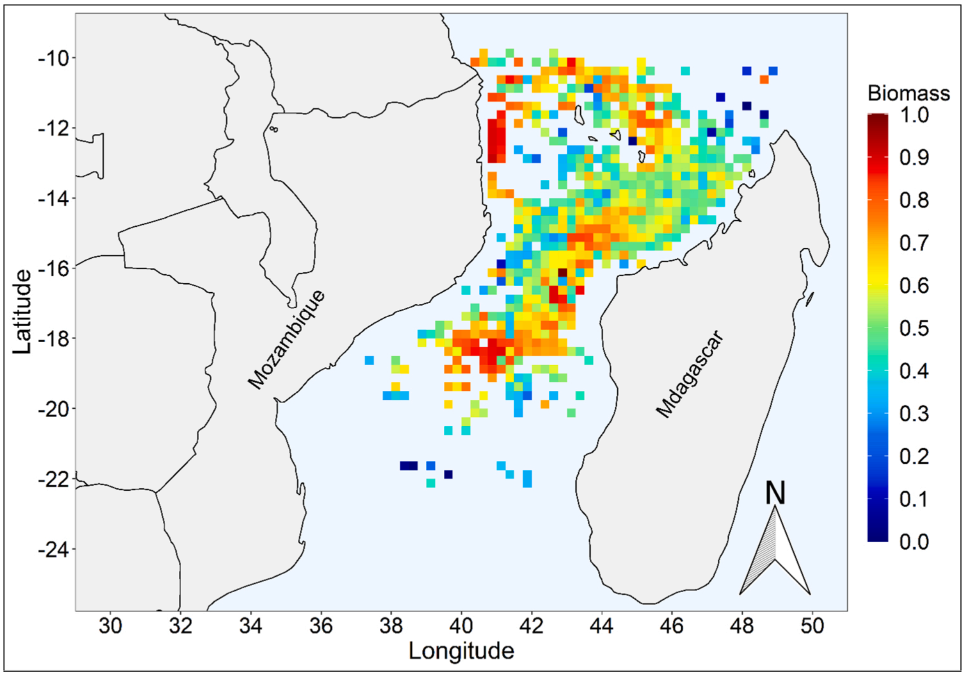

Fig. 5. Predicted spatial distribution of normalized tuna biomass density caught in FSC fishing mode in the Mozambique Channel area. Data are tuna biomass for the period 2003-2013, gridded by 0.25° x 0.25° spatial resolution, and transformed to natural logarithm scale for better performance in GAM modelling.

Fig. 5 shows tuna biomass prediction for FSC in the Mozambique Channel. The sketched maps show that the expected tuna biomass density was high in northern of Mozambique Channel, with core in north-west coast of Madagascar Island at the longitude 40 °E to 46 °E, and latitude10 °S to 20 °S. From the core, GAM predicted high biomass density around northern part of Mayotte and Comoros Island waters (Fig. 5), and southward along the Madagascar coast. Low biomass density was predicted at the Mozambique coast, and there was no expected biomass accumulated above 22 °S. GAM predicted biomass accumulation in the MZC similarly to the observed biomass from FAD set types, with RMSE accuracy of 0.09, Schoener "D" similarity index was about 0.89, with Pearson correlation test $r^2 = 0.52$.

Difference between FAD and FSC predicted biomass is shown in Fig. 6. FAD associated biomass dominates the north-west coast of Madagascar, whereas, values of FSC were much high mostly in the northern of the Mayotte and Comoros Islands, crossing anticlockwise to the Mozambique coast, and between latitude 17 °S and 19 °S. Areas with no difference on catches between the two fishing modes, were randomly predicted, covering many fishing grids along the Mozambique Channel. However, the variable selected by GAM differed between the two fishing modes, there was partial overlapped fishing ground predicted for both fishing strategy.

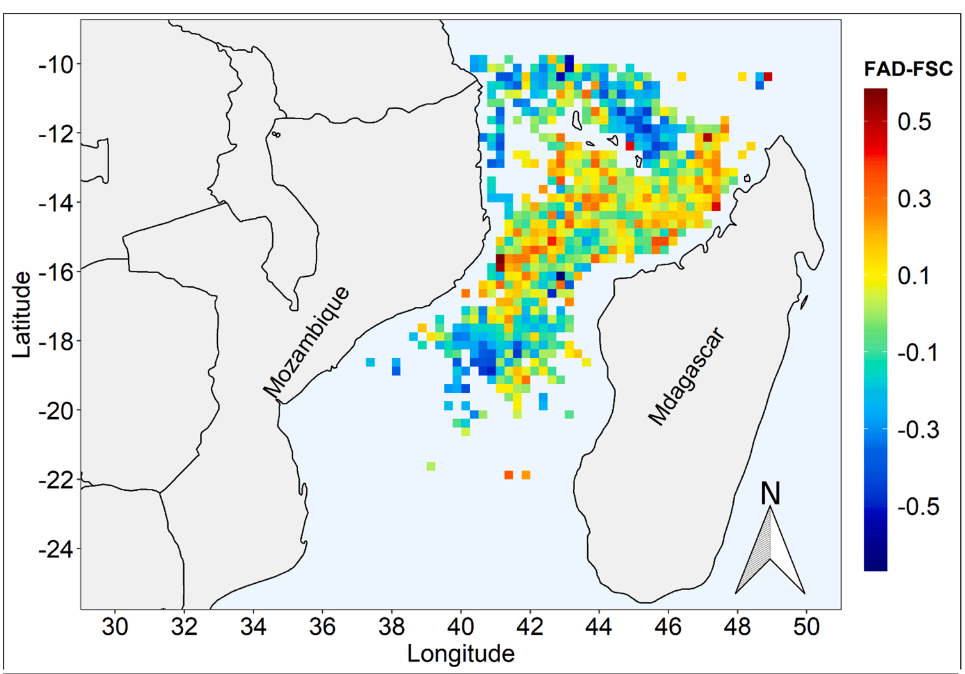

Fig. 6. Map displaying the difference between normalized biomass predicted from FAD and FSC in the Mozambique Channel for the period 2003 to 2013. Colours rank scores below zero indicate regions where the biomass of FSC was expected high, colours rank scores above zero correspond to the areas for high biomass density of FAD (green yellow-dark red grids), and areas indicated no difference (light green colours) on expected biomass density between the two-fishing strategy was record zero score.

4. Discussion

This study presents the evidence for different relationships between tropical tuna biomass accumulation and environmental data for tuna biomass associated with FADs and FSC in the MZC. These relationships have been identified through GAMs, confirming that additive models are adequate to model oceanographic and biomass data. The best fit of the GAM model for FAD explained 22.60 % of the deviance and $R^2 = 0.20$, whereas for FSC the deviance explained was about 32.60 % and $R^2 = 0.27$. This difference could be related to marked environmental preferences for each group, especially FSC tuna (Maury et al., 2001; Druon et al., 2017). It is widely recognized that FSC tuna are usually more strongly related to certain environmental conditions that shape the availability of schools in the area (Maury et al., 2001; Fonteneau et al., 2008; Druon et al., 2017). On the other hand, the known effects of FADs on changes in tuna species behavior, interactions with other species, and tuna schools driven to inappropriate habitats in marine ecosystem (Hallier and Gaertner, 2008), could explain the lower deviance comparable to FSC. GAM were evaluated through cross-validation, with better model accuracy RMSE ~ 9% (James et al., 2014; Wikle et al., 2019;), for both FAD and FSC. Schoener similarity index "D", between predicted and observed biomass aggregation was 0.91 for FAD and 0.89 for FSC, showing that GAM was capable to predict tuna biomass aggregation in MZC (Warren et al., 2008), and Pearson correlation was reasonably good for FAD and FSC close to 44 %, and 52 % respectively. The spatial correlograms showed non-significant residual autocorrelation, suggesting that models are adequately capturing spatial residual and variance patterns (Bjørnstad et al., 2001). Furthermore, goodness-of-fit of the models met the basic criteria through residual checking (Wood, 2006; Zuur et al., 2009).

Regarding the temporal component, in both fishing type models, GAM revealed certain seasonality of tuna biomass in the Mozambique Channel. This is also confirmed by the presence of purse seiners in the area (Campling, 2012; Davies et al., 2014; Kaplan et al., 2014) where fleets start fishing in February-March, up to June, with the highest activity seen around April-May (Figs. 2a and 4 a). It seems that purse seiners quit fishing in the MZC in late June, following tuna migration, probably to the Somali coast during summer upwelling monsoon, and other fishing habitats in Indian Ocean (Tew-Kai and Marsac, 2010; Campling, 2012; Kaplan et al., 2014; Ternon et al., 2014; Orúe et al., 2020). The seasonality of tuna biomass could be related to the variation of the physical driving force of the primary production (Tew-Kai and Marsac, 2009, 2010; José et al., 2014), and the subsequent shift of prey density (Dell et al., 2011), influenced by the seasonal and interannual dynamics of the environment.

Relating to the spatial component, GAMs have also been proven to be powerful tools to account for environmental changes in the spatial domain (e.g. Maravelias, 2001; Mourato et al., 2008; Murase et al., 2009; Brodie et al., 2015; Lan et al., 2017). For tuna biomass around FADs, GAM results suggest that tuna biomass accumulated weekly in water temperature changes by ±2°, however, two distinct groups of tuna in relation to SST preference were observed. One group preferred habitat between 25 °C–27 °C whereas a second school prefers waters about 29 °C–31 °C (Fig. 2b). These findings support earlier studies which documented that tuna inhabit warm pools and may accumulated in cold water fronts with prey enrichments for feeding (Fiedler and Bernard, 1987a, 1987b; Watson et al., 2018). The preferred range of SST is between 25 °C -, 31Cº found in FAD models are the typical values shown by tropical tuna in the Indian Ocean (Rajapaksha et al., 2013; Arrizabalaga et al., 2015; Druon et al., 2017; Duffy et al., 2017). The current research found tuna biomass around FADs was associated with patches where CHL concentrations changes around ±0.4 mg. l^{-1} over a one week period. Possibly, sea surface currents (kinetic energy and heading) played significant role on tuna biomass associated with FADs. The effect of oceanic currents on the redistribution of plankton, micronekton, heat, oxygen and nutrients fluxes has been widely recognized (Fu, 1986; DiMarco et al., 2002; Bryden and Beal, 2001; Anilkumar et al., 2006; José et al., 2014), their detrimental role to set up suitable ecological niche of marine living resources including top predators like tuna. For example, our results show that low kinetic energy values (<0.1 m^2s^{-2}) or sluggish currents, seems to influence tuna biomass (Fig. 2b), and low effect in values > 0.1 m^2 s^{-2}. The flattened trend of tuna biomass depicted, even at the strong eddy kinetic energy, could be related to the directions of the south-west surface currents (heading), which possible drove FADs and tuna associated species to aggregating tuna biomass along the eddies periphery, mainly in the continental shelf of Madagascar coast (hotspots of tuna biomass shown in Fig. 2b bottom left). This finding is in contrast with dispersal effect of kinetic energy and current heading for marine organism (Peters and Marrase, 2000; Reigada et al., 2003), and corroborated with Dell et al. (2011) and Tew-Kai and Marsac (2010), whose found positive relationship between eddy kinetic energy and tuna biomass. The west-southward currents significantly impacted tuna accumulation. Influenced by circulation in the Mozambique Channel, subjected to anti-cyclone and cyclone eddies with origin in the northern part of the channel, propagating west-southward (de Ruijter et al., 2002; Lutjeharms and Town, 2006; Swart et al., 2010), all contribute to the foraging behaviour of tuna through FAD driving or by accumulating and diffusing preys, and shaping the availability of food in the area (Chassot et al., 2019). Salinity, where tuna biomass was associated around FADs, ranged from 31 g Kg^{-1} to 35 g Kg^{-1}, in concordance with previous studies for tropical tuna species (Druon et al., 2017; Arrizabalaga et al., 2015). Tuna biomass accumulated around FADs at low values of sea surface height, usually is related with low intensity of mesoscale eddies (Tew Kai and Marsac, 2009; José et al., 2014), which is known to effect attracting top predatory like tuna to the eddy periphery (Fonteneau et al., 2008; Tew Kai and Marsac, 2010).

The utility of GAM using environmental and spatio-temporal variables to predict the seasonality of tuna biomass hotspots in this study was also demonstrated for FSC sets. Tuna showed preference for waters changing their temperature by ±1.5 °Cover a week period, although FSC seems to prefer waters of 27 °C–31 °C, being relatively close to productivity areas, where they can feed (Fiedler and Bernard, 1987a, 1987b; Mugo et al., 2014; Duffy et al., 2017).These results are consistent with previous studies, which have demonstrated that tropical tuna prefer moderately warm waters; (Zagaglia et al., 2004; Lee et al., 2005; Lan et al., 2011; Rajapaksha et al., 2013; Mugo et al., 2014; Arrizabalaga et al., 2015). Primary production, as reflected in chlorophyll concentration shows that in FSC, tuna biomass aggregation was negatively related with production. This is because top predators like tunas do not directly consume primary production but feed on micronekton aggregations sustained by them (Potier et al., 2004, 2007). Productivity of this water can be influenced through sea surface height generated from eddy circulations, which the positive effects have been recognized in previous studies (Fonteneau et al., 2008; Fraile et al., 2010; Tew-Kai and Marsac, 2010; Brodie et al., 2015), by attracting tuna to eddy periphery or fronts (Fonteneau et al., 2008; Tew-Kai and Marsac, 2010), which in our results were between 0.3 m to 0.8 m. The tuna species targeted by FSC, aggregated biomass in water with salinity between 33 and 35 g Kg^{-1}, these salinity values are in concordance with previous studies for tropical tuna species (Druon et al., 2017; Arrizabalaga et al., 2015).

In contrast to the FADs sets, where the hotspots of tuna biomass are located in west coast of Madagascar, for FSC sets, GAM detected the hotspots of tuna biomass in northern tip of the MZC below 12 °S. Difference between FADs and FSC fishing mode revealed partial overlapped of tuna biomass, which could be attributed to oceanographic features such as surface currents (kinetic, velocity, heading), and eddy circulation due their effect on driving and aggregating plankton and prey. Also, it should be noted that purse seiners operate opportunistically on FADs or FSC mode irrespective the location.

Previous studies (Tew-Kai and Marsac, 2009) found that the seasonal productivity was more evident in north of 16 °S and south of 24 °S parts of the MZC, whereas the central area was less related to seasonal cycles, due to mesoscale dynamics. African river run-off, mesoscale cyclone and anti-cyclone eddies circulation also control the chlorophyll concentration and productivity dynamics in the MZC (Tew-Kai and Marsac, 2009; Omta et al., 2009; José et al., 2014), by injecting nutrients in the marine surface from continental coast or deep sea regions. Chlorophyll enrichment increases energy flows in marine ecosystem through trophic pathways, and significantly influences distribution of marine species of any trophic level (Lali and Parsons, 2006; Tew-Kai and Marsac, 2009; Omta et al., 2009). Because of that, CHL concentration has been considered as a good proxy for prey availability in an area. Patches where the dynamics of phytoplankton bloom occur have been detected through remote sensing and documented in the literature as good areas for large pelagic fish abundance (Tew-Kai and Marsac, 2010; Chassot et al., 2011; Abdellaoui et al., 2017). This information has been exploited by fishermen who use remote sensing data to identify potential hotspots or fishing grounds (Fonteneau et al., 2008), mainly for FSC sets attracted through trophic level. The role of oceanic currents on the redistribution of plankton, micronekton, heat, oxygen and nutrients fluxes has been widely recognized (Fu, 1986; DiMarco et al., 2002; Bryden and Beal, 2001; Anilkumar et al., 2006; José et al., 2014). Dell et al. (2011) and Tew-Kai and Marsac (2010) with a positive relationship between eddy kinetic energy and tuna biomass. However, it seems that the west-southward currents impacted the bulk of tuna biomass observed in west side of Madagascar for FADs sets. Probably, the circulation in the Mozambique Channel, subjected to anti-cyclone and cyclone eddies with origin in the northern part of the channel, propagating west-southward (de Ruijter et al., 2002; Lutjeharms and Town, 2006; Swart et al., 2010), was the driving force for the hotspots of tuna biomass detected by GAM around FADs.

GAM was able to predict with reasonable accuracy patches where tuna biomass was accumulated in the Mozambique Channel for FADs and FSC set types, threw non-linear relationship with environmental variables. Because of that, GAM is known as powerful tools to predict fish distribution and biomass aggregations in marine habitats (e.g.: Maury et al., 2001; Murase et al., 2009). However, improvement of GAM to include additional environmental variables, such as oxygen concentration due to it collinearity with others important variables (Zuur et al., 2010; Dormann et al., 2013), and inclusion of other parameters like depth, front indices, zooplankton and micronekton indices would likely improve current models and provide complementary information. Availability of oxygen and zooplankton has been considered as key parameters for large pelagic species, including tuna (Stramma et al., 2011; Huggett, 2014; Potier et al., 2014). Dissolved oxygen depletion and vertical expansion of the oxygen minimum zone has been identified as one of the most important factors necessary to maintain current species distributions as it may restrict foraging habitat for tuna as well as the usable habitat (Stramma et al., 2011). Thus, future studies should consider specific analysis on this issue to better understand the implications of dissolved oxygen in the area and its relationship with tuna.

The results obtained in this study can be used as a first step to better understand the relationship between tuna and environmental parameters in the very dynamic MCZ area. Characterization of hotspots of FADs and FSC fishing regions could contribute to development of better conservation and management measures of the exploited species by purse seine fleets in the area to assure short, medium and long-term sustainability of the species and the fishery. Differences obtained between FADs and FSC modes in environmental models reinforce the necessity to incorporate oceanographic information in the assessment and management processes for tropical tuna fisheries. Species have been traditionally managed using static non-adaptive measures. However, models identifying fishable hotspots where biomass accumulates, like the one presented in this document, can be used to develop more adaptive and dynamic management approaches. Some examples of that can already be seen in large pelagic fisheries of Australia (Hobday et al., 2011) and the California Current (Hazen et al., 2018). Further research should consider detailed analysis on the use of similar approaches for the tropical tuna fisheries worldwide, and particularly, in the WIO region.

5. Conclusion

This study used medium-term time series (eleven years) logbook catch data, to show that the dynamic effect of the environmental oceanographic variables on tropical tuna biomass accumulation along the Mozambique Channel varies according to the fishing mode. The models predicted suitable habitats for FAD associated fish between 10 °S to 18 °S, with the core, in general, in the north-western coast of Madagascar. Predictions for FSC suitable habitat shows that the core is principally found in the northern part of the Mozambique Channel, and also close to Mozambique coast between 10 °S to 16 °S. In this research, sea surface temperature and its variability, productivity, sea surface height, and the interactions of spatial and temporal variables were significant for both fishing types. However, geostrophic currents, showed significant effect for FAD biomass accumulation only. The results obtained in this investigation highlight a connection between the biophysical state of the oceans and purse seine tuna fisheries in the MZC. This may contribute to the knowledge base required for the appropriate conservation of the exploited resources in the area, and support science-based decision making and management in a constantly changing oceanic ecosystem like the Mozambique Channel.

CRediT authorship contribution statement

Anildo N. Nataniela.: Involved in conceptualization, methodology design, application of statistical analysis, investigation process writing original draft of the paper -including pre-publication stages, acquisition of the financial for the project research. Worked also to incorporate the suggestion recommended by reviewers. **Jon Lopez:** The main role was related on conceptualization, methodology development and design, programming, implementation of computer coders in R software, verification of model results, specifically critical review of paper writing. Helped to verify if the recommendation suggested by reviewers were properly included in the manuscript.

Maria Soto Ruiz: Her role included fisheries data provisioning, methodology development and design, statistical data analysis, validation of model results, supervision, leadership responsibility for the research activity planning and execution and paper review

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Declaration of Competing Interest

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

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