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Modelling the impacts of climate change on skipjack tuna (Katsuwonus pelamis) in the Mozambique Channel

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Complete List of Authors:	*Nataniel, Anildo Naftal; Eduardo Mondlane University, Escola Superior de Ciencias Marinhas e Costeiras Pennino, Maria Grazia; Instituto Español de Oceanografía, Centro Oceanográfico de Vigo Lopez, Jon; Inter-American Tropical Tuna Commission Soto, Maria; Instituto Español de Oceanografía
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Response letter to reviewers

Dear Dr Steven Bograd,
Chief Editor
Fisheries Oceanography Journal

Please find enclosed the files with the revised version of our original manuscript FOG-21-1693 entitled "Modelling the impacts of climate change on skipjack tuna (*Katsuwonus pelamis*) in the Mozambique Channel" by Nataniel et al. We would like to thank you and the reviewers for all the useful and very constructive comments, which we believe have improved the manuscript significantly. We addressed all the reviewer's concerns, which were carefully considered below. We hope the manuscript is now suitable for publication in Fisheries Oceanography journal. This manuscript was subjected to major changes following reviewers' recommendations (e.g. by combining FAD – Fish aggregating device and FSC-Free Swimming Schools data into a single model) and therefore, significant changes occurred throughout the manuscript, particularly on the material and methods, results, discussion and conclusion sections. Because of the complete transformation, preparing a track change version will be not helpful, and could have even been counterproductive for further revision. This new version of the manuscript is clearer, more concise, and addressed all comments raised by the Reviewers. Please do not hesitate in contacting us for further changes and improvements.

Best regards,

Anildo Naftal Nataniel on behalf of all co-authors

Reviewer #1: Evaluation ms FOG-21-1693

This study investigates the habitat of skipjack (SKJ) tuna in the Mozambique Channel (MZC) from model-based oceanographic variables and purse seine catch of the Spanish tuna fleet. GAMs are used to quantify statistically the combination of variables that would better explain the distribution of SKJ catches in time and space over the study period 2003-2013. The authors then use the component of the model based on sea surface temperature to predict the potential SKJ fishing areas during the 21st century by selecting two IPCC-RCP scenarios (mild and strong emissions of greenhouse gas). The authors conclude that the optimal SKJ habitat may gradually shift to the southernmost region of the MZC. This is an interesting topic and conclusions have the potential to raise awareness that resilient policies must be developed by the riparian countries to mitigate climate change impacts on local fisheries communities. However, I have a number of concerns to express about the data used in the study and the results produced. At this stage, this ms is still far from meeting the standard required for publication in Fisheries Oceanography. Several analyses should be redone from scratch. Therefore, I recommend (very) major revisions.

We are grateful to the Reviewer for this general comment, and we carefully answer point by point the comments below.

Methodology: Firstly, I would say that the word biomass which is used everywhere in the ms is not appropriate. Biomass is the result of different processes such as recruitment, growth and natural/fishing mortality. This is not a quantity that can be estimated directly at a regional scale (at least on tunas). Locally, biomass indicators can be provided by echosounders set on the buoys, but this kind of information in not used in this study. In general, biomass is estimated by stock assessment models. Here, the authors only deal with catch data, so each occurrence of biomass should be deleted and replaced by catch or similar term (including the keywords).

We are grateful to the Reviewer for this comment. We replaced the word "biomass" by "catch" throughout the manuscript as well as in the keywords.

Study area:

In line 89, saying that the Agulhas Current (to be written in singular, not plural) is a cool current is a big mistake! The Agulhas Current is a western boundary current carrying the Mozambique Channel tropical waters in the temperate latitudes. So it is just the opposite to what is stated by the authors.

Thank you so much for highligting this mistake. We correct the words "Agulhas Currents" to "Agulhas Current". We revised the current literature and we updated the explanation about the flow of Agulhas Current as suggested by the Reviewer. Please see lines 81-84 of the revised manuscript.

Stating that March-June are austral winter months is another mistake. Austral winter ranges from June to September. Likewise, the statement that "tuna schools peak in the MZC" is not a correct one, as this perception depends only on fisheries, and obviously, this has limitations. This also applies to the sentence line 94. The tuna fleets operate seasonally in the MZC before moving outside the MZC at the onset of the austral winter towards other highly productive areas such as the Somali Basin. In such a situation.

Thank you so much for pointing this out. We replaced the expression "austral winter" with "at the onset of the austral winter" and redefined the period to March to May to integrate the additional comments by the Reviewer. The mentioned statement "tuna schools peak in the MZC", was re-written as "environmental conditions seems to be more suitable for tuna schools in the MZC (Kaplan et al., 2014; Obura et al., 2018) and, thereby…". Please note that we also say "Skipjack catches by <u>industrial</u> purse seiners in the MZC are rare throughout the rest of the year (Campling, 2012; Kaplan et al., 2014; Chassot et al., 2019)" to improve clarity. Please see lines 86-88 of the revised manuscript.

Fisheries data

The catch sets are stratified between FAD and FSC sets. The distinction is only based on the logbook data. However, it is unclear how a fish school can be assigned as a FSC if it is actually moving freely nearby a FAD, which he may be heading to, or just leaving. I refer the author to the paper by Moreno et al 20161, which discusses such uncertainty: "… *Because of all these inconsistencies, it is contended here that the division of free versus associated schools, although seemingly clear, is actually very difficult to assess and implement while at sea, as it is quite problematic to categorically assert the absence of a floating, semi-submerged or submerged body in the vicinity of a purse seine set*". I am raising this issue as the paper is structured under this partitioning between free and associated schools, with two different models are built for each fishing mode, which to me, does not make sense in terms of ecology, in particular for skipjack tuna."

Thank you so much for the comment. As suggested by reviewer, we considered the paper by Moreno et al., 2016. Based on the information found in the literature, and the comments by the Reviewer, we restructured our manuscript and analysis considering skipjack catches without partitioning in free and associated schools. Therefore, we established a new unique single model to simplify the ecological interpretation of the analysis. We are thankful to the reviewer about these recommendations. Please see the new analysis and the structure of the revised manuscript following their advice.

Line 103. It cannot be stated that the catch data are subset because of seasonality, as there is a single fishing season in the MZC. The core of the fishing season ranges from March to May. The IOTC C/E database (and analysis by Tew-Kai and Marsac 20102) indicate that catches in the MZC in February are scarce (as the fleet is operating in the equatorial region) and catch in June-August are also quite sporadic (with numerous missing years for these months). The authors could consider shortening the length of data set, in terms of months, as the current series includes rare events (especially in June-August) that can affect the robustness of the model.

Thank you so much for the comment. The data were subsetted, and only data from March to May used in the study improve robustness of the model (line 97-98), as suggested by the Reviewer. Please see the new analysis in the revised version of the manuscript.

Environmental data

My feeling is that the authors have taken all data available from the Copernicus Ocean model without conducting a thorough reflection of their ecological relevance in the study. For instance, what does a low or high salinity indicate for tuna, or the EKE? There should be a reason given at this stage to justify the choice of the variables.

Thank you so much for the comment. First, we performed an exploratory analysis in order to identify the most important ecological/environmental variables related to skipjack tuna catches. The explanation of the exploratory analysis conducted is described in lines 139-147 on the "model construction and projection" section. We also did a literature review to help us with the selection of the environmental variables related to the tropical tuna distribution and habitat preferences. The explanation and some examples of the reviewed literature are given in lines 119-127 of the revised manuscript. Additional literature consulted for the variable's selection is provided in Table 2 of the supplementary material. Also, please keep in mind that some variables, such as EkE or SST gradient, have proven to be important for large pelagic fish and marine predators and therefore, we think they should be included to explore their effect in the species we are considering. The relationship between the different environmental variables included and skipjack is discussed in the discussion section, in the light of the results, published literature and their effect on similar species.

Ocean models' products are used. The name of the products must be clearly indicated as CMEMS (Copernicus) gives access to a range of ocean models at various spatial and temporal scales, and for physical and biogeochemical variables.

Thanks for pointing this out. In lines 116-118 we explained that all oceanographic variables were extracted from the product GLOBAL_REANALYSIS_PHY_001_031 except chlorophyl-a concentration and Oxygen, which were downloaded from the product GLOBAL_REANALYSIS_BIO_001_029. Besides, EkE was derived from model. We included a Table S1 in the supplementary material summarizing the information of the environmental variables used in the study, including explicit reference to the name of the products used.

As the MZC is dominated by mesoscale eddies, sea level anomalies (SLA) would better depict these structures than the sea surface height (SSH) used in the study. Indeed, the CMEMS only produces SSH, but the AVISO altimetry products include SLA at 0.25° spatial resolution, which could have been used in the study. See paper by Tew-Kai and Marsac 2010 emphasizing the role of mesoscale eddies, characterized by SLA, on the distribution of tuna schools (and seabirds).

Thank you for the comment. We agree that MZC is dominated by mesoscale eddies, and the exact relationship between tuna and these processes is being investigated by many scientists and fishermen, using both SLA and SSH (Table S2). Tew-Kai and Marsac (2010) argue "*there is a much weaker link* *between tuna school sightings and eddy descriptors*" and Potier et al., (2014) found that "*tuna was associated with low horizontal gradients of sea-level anomalies*". Also, in the MZC, eddy activity is most developed in the central and southern part (16–24°S) but, purse seine tuna catches are mostly aggregated in latitudes <16ºS. As mentioned, SSH has been used in many studies (both in peer reviewed papers and grey literature) to understand tropical tuna habitat preferences, like those listed in Table S2 in the supplementary material, among others. Both SSH and SLA seem to be good proxies for mesoscale eddie processes and thus, we opted to keep SSH for our particular study, for the sake of data availability, time and consistency with some published papers and the CMEMS products we used. Future works will try to access SLA from Aviso, conduct sensitivity analyses and explore the use of the suggested variable.

I do not see the usefulness of considering the current sea surface heading in an area characterized by propagating mesoscale eddies. At one pixel, the current will turn in different directions as the eddy is passing through and this may introduce noise in the analysis. What information in terms of favorable tuna habitat (or fishing conditions) can be drawn from this parameter?

Thank you for the comment. The direction of surface currents (HDG-heading) have been used in scientific studies on tropical tuna and other large pelagic species fairly often and may indicate animals relationship with particular water masses, including waters where micronekton, zooplankton and other preys are driven to concentrate in specific patches, potentially attracting tuna schools to improve feeding success as well as other processes still being investigated (e.g. life-cycle processes, local and regional movements, fine and large scale biological processes). For example, Lopez et al (2017) found that the direction of the currents was significantly impacting the dynamics of tuna schools and bycatch species in the Atlantic Ocean, a process also highlighted by fishermen and other scientists in the Indian Ocean (as stated, for example, in Moreno et al.,2007) and Orue et al 2020). Another study from Huggett (2014) suggests that mesoscale eddy and surface current shelf interactions play a fundamental role in shaping the Mozambique Channel pelagic ecosystem through the concentration, enhanced growth and redistribution of zooplankton communities. The inclusion/exclusion of variables in the final model are decided by a very well-established methodology in the scientific community, where variables that are correlated to each other and do not improve models' descriptive and performance power are not considered. As scientists, it is sometimes difficult to describe in detail the causality of correlated processes from an ecological/biological point of view but they also encourage further analysis and discussion to keep investigating all the processes that are connected to a species, in an obvious manner or not, and in the short, medium and long-term. Lines 319 -329 in the discussion section explicitly mention the need to conduct potential work on additional habitat preference studies in the future.

Sea surface chlorophyll exhibits highly skewed distributions, requiring data to be log-transformed to be used in statistical analyses, in order to give more contrast in the data. This is a very basic point…

Thank you so much for pointing this out. The chlorophyll-a was log-transformed (e.g.: logx+0.01) and used in the statistics modelling analysis, as suggested by the Reviewer (Lines 155-156). An small constant (i.e. 0.01) was added to the variable before transforming to avoid zero values when transforming into logarithmic scale.

The authors do not indicate the depth level of the dissolved oxygen (DO) variable? By default, I assume it is surface which does not have any meaning, as the upper layer is oxygen-saturated (the content only depends on ambient temperature) and is never a constraining variable for tuna habitat in the high seas. Concentrations below 3.6 ml/l are considered as a threshold in oxygen stress for SKJ, and 2.45 to 2.83 ml/l are considered as lethal dissolved oxygen levels. Therefore, to be relevant to tuna ecology, it would have been more appropriate to use the depth of the oxycline, or alternatively, the depth of ~3 ml/l to incorporate oxygen concentration as a pertinent covariate in the model.

Thank you for the comment. As mentioned in the manuscript, the oxygen was removed in the analysis due to the correlation with other more important ecological variables for the species (e.g. SST) and the limited descriptive power of surface dissolved oxygen, as mentioned by the Reviewer (the depth level oxygen was not available for this particular study). Furthermore, when we grouped the fisheries data (FSC and FAD) for the new model suggested by the Reviewer, the exploratory analysis highlighted that the surface dissolved oxygen was not significant.

Eventually, the gradients in SST (SSTGD) and CHL (CHLGD) are calculated by week, whereas the statistical analysis if conducted on a monthly basis. Therefore, it is unclear which value (from the 4 weekly values in a month) is taken in the monthly analysis: maximum weekly gradient in the week, sum, average? What does a gradient mean if it evolves in opposite directions during the month considered and how a biological response (tuna catch) is functionally related to this, in such a case?

Thank you for the comment. In lines 148 -152 in the methodological section, we explain that for each ¼º cell the catches were aggregated as sum while for environmental variables we calculated the mean. For our model, SSTG and CHLGD were averaged for a period of a month, like the other environmental variables. The SST and CHL gradients help to explain the response of tuna aggregation to the increase or decrease of temperature and/or CHL, and help understand the dynamics of the species in relation to those environmental processes. These variables have been widely used by authors investigating the relationship of large pelagic species with the environment. For example, (Lopez et al., 2020) included these variables in a study for silky shark in the Atlantic Ocean and (Bigelow et al., , 1999) (in this journal; Fisheries Oceanography) did the same for swordfish and blue shark in Hawaii.

Model construction

I do not have comments on the method, which is well described. GAMS are now a very popular statistical framework. However, what is the point of building a multi-variable model and finally, use a truncated version of it (using SST only) to project the habitat and catch of SKJ.

Thank you so much for your comment. The main objective of this study is to predict the potential skipjack tuna fishing grounds by 2050 and 2100 under optimistic and pessimistic climate change scenario, where changes of SST are the main driver. Some authors considered SST as one of the best factors to predict the ecological niche of skipjack tuna (e.g.: Mugo et al., 2010; Dueri et al., 2014), influencing species' physiological abilities and migratory behaviour (Graham & Dickson, 2004); affecting optimal feeding forage and growth rates at between ~15ºC and 30ºC (Barkley, Nell, & Gooding, 1978), and limiting spawning aggregation among schools in both northern and southern latitudinal waters where temperatures average >24ºC isotherms (Matsumoto et al., 1984; Schaefer, 2001). Therefore, SST is central for the biology of the species and climate change, and may also be a good proxy for, or be connected to, other environmental variables and processes (e.g. Lali and Parsons, 2006; Mann and Lazier, 2006; Miller and Wheeler, 2012; Gruber, 2011; Popova et al., 2016; Rahmstorf, 2007; Aral et al., 2012; Aral and Guan, 2016). We included this explanation in lines 211-226 of the methodological sections of the revised manuscript. Most importantly, the SST is one of the only environmental variables for which projections are available and have been used in other studies with similar objectives (e.g.: Dueri et al., 2014; Yenet al., 2016; Assis et al., 2018).

2- Results

The model performance is evaluated as good, because the necessary flexibility (knots) was given to the model to improve the fit (higher "wiggliness"). Overall, I have some difficulties to interpret the ecological meaning of several of the relationships. A model can be mathematically excellent and biologically irrelevant.

Thank you so much for the comment. The number of knots (k) were defined as 6, 20 or 50, depending if the variables were included in the model as single main effects, first order interactions, or spatial components in the triple interaction, respectively, following the methodology of several authors in the field (e.g. Cardinale et al., 2009; Giannoulaki et al., 2013; Jones et al., 2014, Wikle et al., 2019). Besides, and as suggested by previous studies (e.g.: Fletcher & Fortin, 2018; Norberg et al., 2019; Wikle et al., 2019), cross-validation was performed to assess the predictive power of the model. All these procedures were taking into account to evaluate the performance and predictive power of the model. From an ecological point of view, our results are discussed in the discussion section, comparing them with previous studies and our knowledge on the species, as well as with other similar works on tropical tuna (table 2 supplementary material). In addition, as now we performed a unique model for all the data following Reviewer's suggestion, some of the potential incongruences in the results are not present anymore.

One main issue is the different responses emerging between the so-called FAD and FSC schools. Why such a difference in the responses to SST and SST gradient, whereas this is the same tuna species (and probably with the same size range). Why is the response to SSS for FAD opposite to that of FSC; as well as for SSH (negative linear for FAD, bell-shaped for FSC)? These differences are not analysed in the discussion.

Thank you so much for pointing this out. However, and following the reviewer suggestion above, we fitted a new model combining both the FAD and FSC data, and thus, the mentioned counterintuitive differences are not present anymore in this manuscript version.

Line 222-23: the authors indicate that SKJ catches are positively correlated with SSS and DOC. I do not see this on Fig 2 where the relationship is negative in the range of SSS 33.5 to 35 (bulk of the observations) and where the response to DOC is a reversed bell-shape curve.

Thank you so much. As we changed the model following the Reviewer's previous suggestion, the mentioned results do not apply anymore. Indeed, DOC and SSS were not selected in the new final combined model.

Line 230: West of 43°E is certainly a mistake

Thank you for pointing this out. This was a mistake. However, our approach combines now both FSC and FAD data into a single model, and thus, this sentence does not exist anymore in the new version of the manuscript.

Line 238: this is certainly not biomass which is projected in these maps.

Thank you for highlighting this. The word "biomass" was replaced by "catch" throughout the manuscript, as suggested by the Reviewer.

Line 240: the authors should indicate what they mean by "skipjack fishable area": is it based on the currently observed fishing areas, or on the habitat where SKJ can live?

Thank you so much. Following this comment by the Reviewer, the expression “skipjack fishable area” was replaced by “skipjack fishing observed area”. Please see line 2~~6~~52 of the revised version of the manuscript.

Table 1 gives the GAM statistics. I think one important statistics, F, should be presented. It indicates the relative importance of each covariate in the model. Only the p-value is in that table, and it is not informative enough in this respect as it is everywhere significant. What is the importance of SST relatively to other variables? What are we missing in the projection where only SST is considered and the other variables are artificially set to zero in the projection model?

Thank you for the comment. We included the F-statistic in Table 1 and also the deviance explained by each covariate in the model. We explained why we used SST in the model projection in lines 211 -226 and the response above. The relative importance of SST is provided in Table 1 as well as for the other covariates selected in the model, which is the second most important, just after the triple spatial-temporal interaction.

Lines 243 to 255. Why is the amount of spatial change quantified by summing losses and gain ? Needs an explanation. To me, subtracting losses to gain would give better metric of the magnitude of spatial change, not the sum. This metric could be compared to the “unchanged” area, and this would provide an overall score of change, towards expansion or contraction. In Line 243, “predicted major changes to skipjack tuna biomass” is not the appropriate wording. It should be replaced with “predicted major changes in size of SKJ habitat” because only the spatial dimension is projected, not the biomass.

Thank you for your comment. The approach presented in the manuscript was conducted following the methodologies of previous published studies that quantify changes in fishing habitats due to climate change/SST changes (e.g.: Lezama-Ochoa et al., 2016). However, following the reviewer suggestions, we also computed the difference by subtracting losses to gain. The sentence “predicted major changes to skipjack tuna biomass” was replaced by “predicted major changes in size of SKJ habitat “(see line 254), as suggested.

Line 261. I do not understand the percentages presented. The color scale on maps of Fig 4 and 5, which represent differences (ratios?) range from -0.1 to +0.7 for FAD and -0.5 to +0.6 for FSC. So what do the losses of 31% and 25% in northern latitudes mean, whereas the shading north of 20°S indicates values of -0.1 (- 10% ?). This needs to be clarified, and this also applies to the FSC results.

Thank you so much. Following the reviewer suggestion, we now have established a single model for skipjack and thus, figures are completely new. The values from -0.22 to 0.34 correspond to the difference of catches in tonnes between future scenarios and RPS. To estimate the percentage of area change (e.g:. ~46% losses in Figure 3a), we calculated the ratio between all cells with negative signs divide by total area over the MZC.

3- Discussion

Line 308 : no cold waters in the Agulhas current

Thank you so much for pointing it out. Corrected as suggested everywhere in the manuscript.

The discussion is developing interesting aspects of the effect of climate change for the coastal countries around the MZC. However, a clear interpretation of the results of the GAMs, especially raising the points that I developed earlier, are totally absent of the discussion, which is not acceptable. What is the justification to conduct separate analyses for FAD and FSC? Why such different responses to the environment between the two fishing modes? What is the link to tuna ecology? What do we miss by projecting SKJ catch/fishable area with a model where only one covariate remains?

Thank you for the comment. The discussion now considers the new combined model and its results. Therefore, these issues related to FAD vs FSC preferences are not present anymore in the revised manuscript.

4- Figures

Figure 1: the map does not represent the distribution of the biomass … only purse seine sets! Because of the use of dots, the reader gest the false impression that FSC and FAD sets distribute in distinct areas. The reality is that both fishing methods coexists in many areas. In the map, the FSC dots hide the FAD dots. I would recommend making a heat map representing the sum the catch by 0.25° or 1°square. This will improve greatly the visibility of the map as well as showing exactly the data used in the study.

Thank you for the suggestion. We produced a new heat map with a ¼º resolution, as suggested by reviewer.

Figures 2 and 3: all panels should be on the same page and letters associated to each panel. Recall the full name of the variable in the caption (SST : sea surface temperature, SSS…)

Thank you so much. Figures were redone and figure captions modified following the reviewer's recommendations. Due to the new combined model, Figure 2-3 have now been merged into a single figure.

Figure 4: the letters indicated in the caption do not refer to the appropriate panels. This has been corrected in the caption of Fig 5 and should be copies in the caption of Fig 4

Thanks for pointing this out. Due to the new combined model, Figure 4-5 have now been merged into a single figure.

Details

- References in the text: for papers with more than two authors, only mention the first authors followed by "et al." . Example in line 46: (Chassot, Bodin, Sardenne, & Obura, 2019) should be (Chassot et al., 2019). This appears several times in the ms.

Thanks for highlighting these details. It was a mistake related to the Mendeley program used for citations and references. We carefully checked and corrected these mistakes in the revised version.

- Line 42 : WIO fishing grounds is too vague. Either you indicate "West of [longitude]" or FAO Area 51

Thank you so much. Changed to "FAO area 51".

- Line 44: IOTC Database 218. There is a new release in 2020 and all catch data (and %) should be updated based on this last version. Same in line 66

Thank you so much. Both references have been updated using the 2020 IOTC Database.

Reviewer 2

1. The authors used the skipjack catch data based on fishing modes (FADs and FSC). In many cases in the field, there is no significant distance between the spatial distribution of FADs and that of FSC. It would probably be more interesting if the authors use the catch data based on a number of cohorts or size structure of the fish. Since it is most likely that the fish response to the environmental changes is different from the size structure compositions or cohorts.

Thank you so much for the comment. As suggested by reviewer 1, as well as your comment, we restructured our paper and analysis considering only skipjack catches without partitioning in free and associated schools. We build a new unique model to simplify the ecological interpretation of data analysis and the caveats associated to the data, particularly with skipjack. Please, see the new model and results in the revised manuscript.
In addition, the available dataset are total catches by species, and thus no size information is available (note also that the size of the captured skipjack is very similar in this fishery, ~45-50 cm FL, and not significant size changes are expected).

2. It is not clear to me that the main reasons why the predicted potential fishing grounds shift to southward? They are because of increasing surface temperature (ex 1°C and 2°C) or displacement of foraging area distribution. I think the authors need to describe this point.

Thank you so much for your comment. The predicted change in SST projected shifting of skipjack habitat/fishing grounds towards the south. In this revised version, as we fit a new model, the projection also shows displacement of skipjack tuna towards the south. We believe this is mainly related to SST changes, as is the primary driver of the species distribution projection in our methodology. The reasons for skipjack to move southward could not be only physical, and some ecological reasons related to the biology could also exist. We discuss this issue in the discussion section (see lines 307 -329 for a detailed discussion on the skipjack predicted distribution and the potential relationship with the environment, including foraging).

3. The authors showed that the deviances explained by the models were about 23.2% and 32.9 % for FADs and FSC respectively which means that more than 65% variability of the data for both fishing modes could not be explained by the model. The authors need to discuss factors that are not covered by the model prediction.

Thanks for the comment. Following reviewer's suggestion, we added an explanation on this matter in the discussion section, describing this issue and the need to further investigate other factors not present in the model. Please see lines 285 -297 of the revised manuscript. Also, please note that the model has been re-done, combining both FSC and FAD data, as suggested by the Reviewers.

4. I think it is also important for readers to know that among the environmental variables, which one is the most important controlling the movement of fish habitat/biomass to the south of the study area by 2050 and 2100.

Thank you so much. Following the reviewer's suggestion, we included in Table 1 the information about the contribution of each covariate in the model by calculating the deviance explained for each covariate term. We also included the F-statistic, as suggested by Reviewer 1. SST and SST gradient are the most important factors, after the triple interaction spatio-temporal component included.

5. In the discussion section, the authors should explain the role or contribution of each variable to construct the prediction model of the potential fishing ground. For example, current velocity and EKE may explain the ocean circulation pattern and cyclonic/anticyclonic eddy which subsequently enhance the forage area. A combination of oceanographic variables including abiotic ones should support each other to get the main thrust of the paper, defining the potential skipjack fishing ground.

Thank you so much. A more detailed section in this matter has been included in the discussion section, as suggested by reviewer. Please see lines 298 -322 of the revised manuscript. The effect of each variable was discussed in relation to the SST as is the principal driver used to project skipjack fishing ground change in 2050 and 2100.

6. How to determine the accuracy of the model to predict the potential fishing area by 2050 and 2100 since it is hard to make a substantial verification. Perhaps the authors have the idea of short-term verification.

Thank you so much for the comment. In order to assess the predictive performance of our model we applied a cross-validation process, suggested by several studies performing similar works (e.g.: Wood, 2006;; Fletcher & Fortin, 2018; Norberg et al., 2019; Wikle et al., 2019). This procedure and the metrics derived from it (i.e., RMSE and Pearson correlation) validate the model predictions using past data. With respect to the validation of the future (i.e. short-term prediction), we agree with the reviewer that could be something interesting to mention. Periodic revisions of this study could help understand the uncertainty of the projections, for example. Using other environmental projections, if available in the future, could also help explore the sensitivity of using different data products by different remote sensing/climate monitoring agencies. We added a couple of sentences to reflect these ideas in the discussion section (see new lines 323 - 329).

Specific comments:
Line 72 : Patrick Lehodey should be Lehodey et al., 2013

Thank you. References have been carefully checked in the revised document.

Line 99 : The data was should be The data were …….

Thank you so much. It has been corrected accordingly.

Line 309 : I didn't see the Figure 1 S1 in the manuscript

Thank you for the comment. The figure was provided in the supplementary material. We have uploaded again to make sure is available for the Reviewers.

Line 412: Patrick Lehodey et al., 2011 should be Lehodey at al., 2011

Thank you so much, corrected as suggested.

Figure caption 4: It is not clear, the meaning of the latest sentence "Differences depict predicted biomass between layers 2050 and the present in the first column (a and c), and between layers 2100 and 2050 in the second column (b and d)".

Thank you so much. Figure 3 caption has been corrected.

The unit of Biomass of both Figures 4 and 5 should be shown in the legend. Skipjack catch at the Figure 1 also needs a clear legend.

Thank you so much. We included the unit in Figure1 and 3, and Figure 1 was also changed as suggested by the other reviewer.

Table 2. The contribution (percentage) of each predictor to cumulative deviance explained is better to show on the table to see clearly the best variable.

Thank you so much. Table 1 has been revised following Reviewers' suggestions.

Mentioned Refences

Aral, M. M., & Guan, J. (2016). Global sea surface temperature and sea level rise estimation with optimal historical time lag data. *Water (Switzerland)*, *8*(11). https://doi.org/10.3390/w8110519

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Title Page

Running Head: CLIMATE CHANGE AND SKIPJACK IN THE MZC

Title: *Modelling the impacts of climate change on skipjack tuna (Katsuwonus pelamis) in the Mozambique Channel*

Autors

Anildo Nataniel[1], Maria Grazia Pennino[2], Jon Lopez[3], Maria Soto[4]

[1]UEM, Escola Superior de Ciências Marinhas e Costeiras, Av. 1 de Julho, Chuabo Dembe, Quelimane, Mozambique
[2]Instituto Español de Oceanografía (IEO, CSIC), Centro Oceanográfico de Vigo, Subida a Radio Faro, 50-52,36390 Vigo, Spain
[3]Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, 92037 La Jolla, United States
[4]Instituto Español de Oceanografía (IEO, CSIC), Puerto Pesquero s/n, Fuengirola, 29640, Málaga, Spain

Corresponding author:

Anildo Nataniel*

Email address: a.naftal@gmail.com; Telf.: +258842140007

Abstract

Skipjack tuna play a significant role in global marine fisheries and are of particular interest for socio-economy in the tropical waters of the Mozambique Channel. However, human-induced climate change has been leading to a reduction and reallocation of biomass, along with other ecological changes, thereby creating a feedback loop with negative socioeconomic consequences for fisheries-reliant coastal communities. The objective of this study was to predict the potential skipjack tuna fishing grounds by 2050 and 2100. To that end, skipjack tuna catch data were collected from Spanish purse seine fleets and subsequently Generalized Additive Models were used to model these data against a combination of environmental variables and future pathway projections from BIO-ORACLE models under optimistic (RCP2.6) and pessimistic (RCP8.5) scenarios. Both optimistic and pessimistic scenarios by 2050 predicted that the potential fishing grounds will relocate southward from tropical to more temperate waters, with moderate shifts in the potential fishing grounds of purse seines to the latitude >16ºS. Whereas the pessimistic scenario predicted higher displacement catches of purse seines in the southernmost part (>24ºS) and moderate to high catches in northern (>20ºS) of the Mozambique Channel by the end of the century Despite the degree of uncertainty surrounding the climate change impacts on skipjack tuna we argue that fisheries stakeholders, administrators and regional tuna fisheries management organizations should work toward building resilience and ensuring sustainability while reducing or mitigating vulnerability and climate change impacts on local and regional communities and their livelihoods.

Keywords: Climate change impacts, Mozambique Channel, purse seine fisheries, skipjack tuna, predicted skipjack catch, GAM

1. Introduction

Climate change, including increased global warming, ocean acidification, and ocean deoxygenation (Gruber, 2011; Ramírez et al., 2017), is a growing global concern and can lead to changes in the marine physicochemical and biological environments (Ramírez et al., 2017) and thereby modify net primary production, ocean circulation and fish abundance and distribution (Lehodey et al., 2010; Dueri et al., 2014).

In the marine ecosystem of the Western Indian Ocean (WIO), which includes the Mozambique Channel (MZC) climate change is expected to lead to increased temperatures, a slowdown of ocean circulation and a decrease in primary production (Mcclanahan et al., 2011; Popova et al., 2016). Moreover, this increased warming is expected to occur at a faster rate than in other tropical ocean regions (Roxy et al., 2014). With respect to the global distribution of marine species, tuna strictly depend on optimal temperatures, along with other oceanographic and environmental variables (Lopez et al., 2017; Orúe et al., 2020). Thus, considering the predicted changes induced by a warmer climate, it is expected that tuna will migrate from their original habitats to regions of higher latitude, upwellings, deeper waters and near eddies and fronts (Dueri et al., 2014; Marsac, 2017; Lecomte et al., 2017; Marsac, 2017; Monllor-Hurtado et al., 2017). Consequently, ecosystem responses to these climate impacts may lead to changes in catch volumes and, subsequently impact the national economies and livelihoods of WIO coastal states (Sumaila et al., 2011).

Among tropical tuna species the skipjack tuna (*Katsuwonus pelamis*) is the most caught tuna by industrial and small-scale fisheries in the FAO area 51 (POSEIDON et al., 2014; Mukesh et al., 2019). Between 1989 and 2019, the total skipjack catch from FAO 51 fishing grounds was about 9,000,000 tonnes, about 56% were fished by industrial purse seines, 11% by semi-industrial fisheries, and 33% from small-scale fisheries respectively (IOTC, 2020 Database). Over the last decade, skipjack have accounted for about 60% of all tropical tuna catches in the MZC high seas (Chassot, et al., 2019). In the coastal waters around MZC, small-scale skipjack fisheries catches were reported to be ~43 thousand tonnes for the entire period between 2014 and 2019 inclusive (IOTC, 2020 Database). However, this number is thought to be much higher given that statistics from small-scale fisheries were under reported to the regional fisheries management organization: the Indian Ocean Tuna Commission (IOTC) (Chassot et al. 2019). Thus, it is evident that skipjack tuna from industrial, semi-industrial fleets and small-scale fisheries significantly contribute to the economy and livelihoods of WIO states by regularly supplying canneries and supporting local and regional food security (POSEIDON et al., 2014; Lecomte et al., 2017).

Skipjack tuna movement between marine economic exclusive zones within the MZC determines the interests and relationships among countries and industrial and small-scale fisheries. Previous studies carried out by Fonteneau and Hallier (2015), and Chassot et al. (2019) have demonstrated the complex movements of skipjack tuna between the northern MZC toward the south and northernmost areas out of the channel. This migratory behaviour is related to seasonal variations (Campling, 2012; Kaplan et al., 2014) and linked to an environmental habitat suitability dependent on water temperature, feeding forage and oxygen concentration (Lehodey et al., 2013; Dueri et al., 2014). Variables, such as sea surface height, currents (speed, kinetic energy, and direction) and mixed layer depth have also been considered to investigate tuna distribution and habitat preferences (e.g., Mugo et al., 2010; Yen et al., 2016; Lopez et al., 2017; Orúe et al., 2020; Orúe et al., 2020a). However, studies analysing climate change impacts on the area are either scarce or non-existent.

Although the exploitation of skipjack tuna stocks in the Indian Ocean is currently considered to be sustainable (IOTC, Database) skipjack tuna are highly sensitive to environmental conditions and changes (Loukos et al., 2003;Yen et al., 2016; Orúe et al., 2020). Given that climate change impacts will be particularly significant in marine ecosystems any variation in environmental factors may lead to changes in fish distribution and catchability (Dueri et al., 2014). Earlier studies have attempted to project the distribution and abundance of skipjack tuna elsewhere under climate change scenarios using APECOSM-E (Apex-Predator-Ecosystem-Model – Estimation) (Dueri et al., 2014), and catch aggregation, using SEAPODYM (Spatial Ecosystem and Population Dynamics Model) (Lehodey et al., 2013) and Generalized

Additive Models (GAMs; Yen et al., 2016) and their findings suggested that climate change scenarios could lead to significant large scale changes to the distribution and habitats of skipjack tuna.

In this study we attempt to predict the effects of climate change on the distribution of skipjack tuna using GAMs, by analysing Spanish purse seine fisheries in the MZC. Specifically, we intend to (i) identify which biotic or abiotic characteristics most affect skipjack tuna catch distribution; (ii) predict the distributional shifts of skipjack tuna by the years 2050 and 2100 under optimistic and pessimistic climate change scenarios; and (iii) discuss the consequences of changes to species distributions and catch rates.

2. Methodology

2.1. Study area

The MZC is located in the southwestern Indian Ocean, with Mozambique to the west, Madagascar to the east and the Comoros archipelago to the north (Figure 1). The MZC is a particularly good place to investigate the relationship of a species with the environment as the current flows in the north of the channel are fed by warm South Equatorial Currents (SEC), which generate large eddies around the Comorian basin (Lutjeharms and Town, 2006; Ternon et al., 2014). From the narrows area of the channel (~16ºS) mesoscale eddies are formed, and progress from here southward, merging with those eddies generated in south-eastern Madagascar and move westward, where they become trapped by the Agulhas Current ~27ºS, moving southward (de Ruijter et al., 2006; Lutjeharms and Town, 2006; Ternon et al., 2014) (Figure1 S1, supplementary material). The effects of physical and biological oceanographic variables on the distribution of tuna schools appear to be seasonal in the MZC. For example, at the onset of the austral winter months (March-May) environmental conditions seem to be more suitable for tuna schools in the MZC (Kaplan et al., 2014; Obura et al., 2018) and attract purse seiners to fish in the northern part of the channel (Davies et al., 2014). Skipjack catches by industrial purse seines in the MZC are rare throughout the rest of the year (Campling, 2012; Kaplan et al., 2014; Chassot et al., 2019).

2.2. Fisheries Data

Fishing logbooks from Spanish tropical tuna purse seine fisheries were collected by the Spanish Oceanographic Institute for the period February 2003 - June 2013 (hereafter: RPS - Reference Period of the Study). The data were spatially restricted to the MZC, within the latitudes 8ºS to 30ºS and longitudes 30ºE to 50ºE (Figure 1). These data consist of 13,630 fishing set observations (49% in FSC - Free-Swimming Schools and 51% in FAD - Fish Aggregating Devices), with information on catch compositions, fishing hours, date (year, month, and day of the fishing operation), and location (i.e., longitude and latitude). Data were restricted to the months between March and May, which represent the fishing season for industrial purse seiners in the MZC. The distribution of skipjack catches data, shows that both purse seine set types (FAD and FSC) share the fishing grounds over the area (Figure S2 and S3, supplementary material), with high catches records in western side of Madagascar Island and northern of Comoros Islands (Figure 1). Because of the shared fishing grounds and the uncertainty to discriminate between free and associated schools of skipjack (Moreno et al., (2016)), all fisheries data were combined in this study.

2.3. Environmental Data

Environmental data for the MZC for the period 2003-2013 (RPS) was downloaded from the MyOcean-Copernicus EU consortium (CMEMS; marine.copernicus.eu) in netCDF format and extracted for each fishing set location and date through specific codes and routines using functions from the packages netCDF4 (Pierce, 2017), chron (Jame & Hornik, 2013), and lubridate (Grolemund & Wickham, 2011), and other basic functions in version 3.6.0 of R software (R Core Team, 2018). The environmental factors included were: sea surface temperature (SST, ºC); sea surface temperature gradient (SSTGD, ºC), which was derived from the decrease or increase in temperature for each pixel over a 7-day period; sea surface height (SSH, m); eddy kinetic energy (KE, derived from altimetry, $m^2 s^{-1}$); current sea surface heading (HDG, degrees); current sea surface velocity (SSC, $m s^{-1}$): chlorophyll-a concentration (CHL, $mg m^{-3}$); chlorophyll-a concentration gradient (CHLGD, $mg m^{-3}$, derived from the decrease or increase in CHL concentration for each pixel over a 7-day period); sea surface salinity (g Kg^{-1}), and Oxygen concentration (O_2, mg l^{-1}). The spatial and temporal resolutions were 1/4° and daily, respectively (table S1, Supplementary material). All the variables were extracted from the CMEMS product GLOBAL_REANALYSIS_PHY_001_031, except chlorophyll-a and oxygen concentrations which were downloaded from the product GLOBAL_REANALYSIS_BIO_001_029. These variables were assumed to be potentially related to skipjack tuna as several studies already explored or evidenced the importance of these relationships (e.g., Loukos et al., 2003; Lehodey et al., 2013; Mugo et al., 2010; Dueri et al., 2014; Yen et al., 2016). Spatial-temporal variables, such as longitude, latitude, year, month, and natural day, (i.e., from 1 to 365 days) were also incorporated into the models because they can help with spatial-autocorrelation and may explain part of the variability on catches not explained by other environmental variables and spatially structured processes (e.g., other abiotic and biotic factors and processes) not included in this study (Cortés-Avizanda et al., 2011). The oceanographic and spatio-temporal variables considered here have been used by other studies to model tuna and other large marine predators, habitats, environmental preferences or fishing hotspots (Table S2, supplementary material).

Intergovernmental Panel on Climate Change (IPCC) surface temperature projections were used to model future scenarios (IPCC, 2014). Specifically, we accessed the Representative Concentration Pathways (RCP) 2.6 and 8.5 for the years 2050 and 2100 (radiative forcing levels of approximately 2.6 and 8.5 Wm^{-2} by the end of 2100, respectively) for monthly mean sea surface temperature with a spatial resolution of 0.083º x 0.083º grid cells from Bio-ORACLE (http://www.bio-oracle.org). The RCP2.6 (optimistic) emission scenario assumes the least change, with a temperature increase of 1ºC by 2050 and 2º C by 2100 and a salinity increase of 0.5 PSU and 1 PSU units for these same years, respectively. The RCP8.5 (most pessimistic) scenario, by contrast, presumes more severe changes, with a temperature increase of 1.5º C by 2050 and almost 3º C by 2100, and a salinity increase of 1 PSU and 1.5 PSU units for these same years, respectively (Meinshausen et al., 2011; IPCC, 2014).

2.4. Model construction and projection

In an exploratory phase, the relative importance of covariates on skipjack tuna catch was assessed using the randomForest package (Liaw & Matthew, 2002), and the most important covariates were selected to reduce model complexity and redundancy in later fitting stages (Dell et al., 2011). Additionally and following Zuur et al. (2010) correlation among variables was tested using the Pearson correlation rank (rho), and only variables with a *rho* absolute value lower than 0.70 were included simultaneously in the GAMs (Dormann et al., 2013). Finally, a variance inflation factor analysis was also conducted using a threshold value of 3 as a supplementary measure to test collinearity among explicative variables (Zuur et al., 2009). The covariates natural day, current velocity and dissolved oxygen were dropped for further modelling due to collinearity and correlation with ecologically more important environmental variables.

In the first steps of model construction, the daily set by set data were used as response variables. However, the model underperformed and failed to detect the changes in variance at this scale, therefore, data were aggregated by month to a 1/4º grid cell (i.e., the sum of the catches and the mean of the environmental variables). Details to create different scale grids and raster layers through the raster package can be found in Bivand et al. (2015). GAMs (Wood, 2006) were established by using the new positive gridded data to examine the effects of environmental variables on the spatio-temporal skipjack distributions. The logarithmic transformation of skipjack tuna catches (i.e., log (Catch+1)) was used as the dependent variable to reduce skewness and improve model performance (Zuur et al., 2010). The logarithmic transformation was applied also to the covariates CHL and KE to improve contrast and model fitting. GAMs were fitted with a Gaussian family by using the identity link function and applying the *mgcv* package (Wood, 2006), and followed the procedures to model continuous data (Wood, 2006; Zuur et al., 2009) and distribution data tests (Delignette-Muller & Dutang, 2015).

GAMs are semi-parametric extension of Generalized Linear Models (GLMs) (Guisan et al., 2002b) for which the strictly linear predictor:

$$g(\mu(\mathbf{X})) = \beta_0 + \beta_1 X_1 + \cdots + \beta_p X_p,$$

where $\mathbf{X} = (X_1, \ldots, X_p)$ are covariables, $\mu(X) = E(Y|X)$ is the conditional exception of the response variable Y, g is the link function (explained below) and $\beta_0, \beta_1, \ldots, \beta_p$ are the unknown parameters, is replaced by

$$g(\mu(\mathbf{X})) = \beta_0 + f_1(X_1) + \cdots + f_p(X_p),$$

where $f_j(X_j)$ is the unknown smooth partial effect of X_j on the predictor. Hence GAMs avoid the assumption of linear relation between the response variable and the covariables providing a more flexible model. Note that GLMs are an extension of Linear Models for which the distribution of the response variable can be other than gaussian. For this reason, in the previous models a link function g is applied to $\mu(X)$. Using the syntax of the *mgcv* R package, the GAM was fitted as:

$$\ln(\text{Catch}+1) \sim te(\text{space-time, k=(50,6), d=c(2,1)}) + s(C_a, C_b, k=20) + s(C_c, k=6) +$$
$$s(C_d, k=6) + \ldots + s(C_z, k=6) + c(C, k=6) + random$$

where *te* function forms the product from the marginal terms of the space-time triple interactions; *d* is the dimension of each spline in the triple interaction (which in this case is two for spatial components and one for temporal terms); and *s* is the penalized spline smooth function for single interactions and environmental covariates (C). All interactions were fitted by the tensor smooth (ts) product whereas the single covariates were fitted with cubic spline regressions (*cs*) to model nonlinear relationships. Cubic spline regressions ensure that: a regression spline with shrinkage is applied, that a smoother can have zero degrees of freedom, and that all smoothers with zero degrees of freedom can be simultaneously dropped from the model (Zuur et al., 2009). A cyclic cubic regression spline, *c*, was used to illustrate the cyclical behaviour of the terms (e.g., Heading) (Wood, 2006). Finally, a random effect was included (i.e., year) to account for inter-annual variability in fishing effort and fleet behaviour (Brodie et al., 2015; Lopez et al., 2020). Dimension, denoted by *k*, was used to represents the maximum degrees of freedom allowed for each smooth term and was set to 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), and k=50 for spatial components in the space-time triple interaction after trial error (Wikle et al., 2019) to avoid model overfitting and to simplify the interpretation of results. After the first model simulations, 5% of residual data noise was excluded, i.e., 95% of data were absorbed into the model either without or with less outliers (Zuur et al., 2010) to improve model robustness.

The backward selection method with a residual deviance score, a Generalized Cross Validation (GCV) score, an Akaike information criterion (AIC), a residual check (Wood, 2006; Zuur et al., 2009) and a residuals spatial autocorrelation test (Bjørnstad et al., 2001), were the criteria considered to determine the best model .

A k-fold cross-validation was applied (James et al., 2014), which consists of randomly splitting observations into k groups, (in this study k was set to 10 folds) to validate and assess model performance. The first fold was treated as a test dataset to validate the prediction of schools aggregation in fishing grounds and the model was fitted to the remaining $k - 1$ folds, which was treated as a training dataset (James et al., 2014). Next, the root mean square error rate (RMSE), Pearson correlation score (rho) and Schoener similarity index D (Zhang, 2016) between predicted and observed values, were computed to measure the accuracy and predictive performance of the model on the held-out fold validation data.

Finally, the model was built with environmental data and used to project skipjack tuna catch distribution into the future (2050 and 2100) according to the RCP2.6 and RCP8.5 climate change scenarios (Assis et al., 2017). The RCP2.6 and RCP8.5 climate change scenarios predict the lowest and highest rises in global temperatures from greenhouse gas concentrations respectively (Moss et al., 2010; Meinshausen et al., 2011). The climate variables available in BiO-ORACLE were used to predict future scenarios (i. e. sea surface temperature-SST) whereas the remaining variables used to construct the model were set to zero given that the goal was to predict based on SST changes - the main proxy for climate change intensity scenarios. SST has been considered one of the best factors to predict the ecological niche of skipjack tuna (e.g.: Mugo et al., 2010; Dueri et al., 2014), as it influences skipjack physiological abilities and migratory behaviour (Graham & Dickson, 2004), affects optimal feeding forage and growth rates (Barkley et al.,

1978) and limits spawning aggregation among schools in both northern and southern latitudinal waters where temperatures average >24ºC isotherms (Matsumoto et al., 1984; Schaefer, 2001). Besides, SST is a good proxy for, or is connected to, other environmental variables and processes (e.g.: Lali and Parsons, 2006; Mann and Lazier, 2006; Miller and Wheeler, 2012; Gruber, 2011; Popova et al., 2016; Rahmstorf, 2007; Aral et al., 2012; Aral and Guan, 2016). Furthermore, SST data from Bio-ORACLE have been widely used to predict the potential distribution of marine species under different climate change scenarios (e.g., Tyberghein et al., 2012; Duffy et al., 2016). Changes to skipjack distribution was assessed by estimating the differences in spatial predictions of each ¼º square cell between projected future and reference period scenarios (e.g., Dueri et al., 2014; Yen et al., 2016). All analyses were conducted using R version 3.6 (R Core Team, 2018).

3. Results

3.1. Model performance

The relationships between skipjack tuna catches and the environmental parameters examined in this study are summarized in Table 1 along with model parameters (estimated degrees of freedom -EDF, explained deviance, AIC and GVC scores) the proportion explained by model terms and the statistical significance of covariates. All variables selected in the model where highly significant (p-values < 0.01). The k-fold cross validation statistics, i.e., accuracy metric measure (RMSE), Pearson correlation (rho) and similarity index (D) between predicted and observed values, were reasonably good (RMSE ~ 0.08, rho ~ 0.37, D=0.88), which suggests good model performance. Furthermore, the goodness-of-fit for model met the basic criteria as confirmed by residual checking, i.e., residual graphic inspections using spline correlograms did not display spatial autocorrelation. Also, residual of histogram normal distribution, homogeneity of variance, and the straight linearity between fitted values and response criterions were met (Figure S4 supplementary material).

3.2. Environmental effects

The effects of all environmental factors on skipjack tuna catches are shown in Figure 2. The spatial-temporal interactions (Longitude x Latitude x Month), shows that skipjack tuna aggregated more in west coast of Madagascar at the latitude <18ºS whereas in the Mozambique coast the effects of the spatio-temporal interactions depicted negative catches at the areas <40.5E/16ºS between March-April and at the longitudes <39ºE in May (Figure 2). The fishing cores were predicted at the section >42ºE and <17ºS, mostly in the west tip of Madagascar. This was the most important term in the model, contributing to about 10% out of ~16% of the total model deviance (65% of the total). The interaction SST x SSTGD was the second most important term (contributed to ~2.40% in model deviance, 15% of the total). Skipjack tuna tends to aggregate more in warm waters (SST >27ºC) particularly where temperatures changed by ±1ºC over a week period. Sea surface current direction (HDG) with ~1.20% of contribution in model deviance (8% of the total), is the third most important ecological variable. The shape of functional forms for HDG revealed that skipjack tuna was most caught when the currents were moving in southward and northwest directions (Figure 2) which could be related to the anti-cyclone gyres generated around Comoro Islands. Skipjack catches shown high variance at the lowest and highest chlorophyll concentration values and an optimum range at medium levels (Figure 2). The shape of functional forms indicated an increase in skipjack tuna at sea surface height values between 0.5-0.6 m. Skipjack tuna catches were positively correlated with KE especially at medium levels (Figure 2). Together, CHL, SSH, and KE account with ~1.8% in the model deviance (11% of the total) (i.e. each covariate contributes with less than 1%).

3.3. Projected skipjack tuna distribution in future scenarios

Table 2 summarizes the percentage of changes to the areas where skipjack tuna distribution is projected under the future climate change scenarios. Current skipjack fishing observed areas covered ~25% of the Mozambique Channel whereas the overall projected area changes for skipjack tuna aggregation is ~84%.

Model results for the RCP2.6 scenario (Table 2) predicted major changes in size of SKJ habitat from the RPS to 2050 i.e., the fishing areas would change (sum of loss and gain) by about ~93% in the MZC (+1.5% of absolute gain). Between the RPS and 2100 the models also revealed major area changes, by ~90% (+4.3 of absolute gain). However, for the period 2050-2100 the models projected that the fishing areas for skipjack tuna would minor to 10% (-9.3 of absolute gain).

The area changes to skipjack tuna schools predicted by the RCP8.5 scenario (Table 2) between the RPS and 2050 were about 90% (+3.7 of absolute gain) whereas from the RPS to 2100 changes were projected to ~88% (+79.7 of absolute gain). However, between 2050 - 2100 continuous change was predicted, i.e., >92% of all areas (+60.1 of absolute gain) were projected to see a shift in skipjack schools' distribution or displacement over the area of the Mozambique Channel.

When projected using skipjack catch model the differences between future and current scenarios under the RCP2.6 and RCP8.5 climate change scenarios predicted catch losses (negative signs), no changes (zero values) and/or catches gains (positive signs) within the MZC (Figure 3). Specifically, RCP2.6 predicted skipjack catch losses of ~ 46% and ~43% in northern latitudes (< 20ºS) from the RPS to the ends of 2050 and 2100 respectively (Figure 3a-b). Positive expansion of ~ 47% toward southern latitudes (> 20ºS) was projected by the end of both 2050 and 2100 (Figure 3a-b). Whereas between 2050 and 2100 no changes to skipjack tuna catches were predicted in ~91% of fishing grounds (Figure 3c).

With respect to the RCP8.5 scenario, by 2050 catches losses (~ 43%) and positive spreading (47%) were projected in latitudes both below and above 20ºS (Figure 3d). By 2100, the model predicted positive displacement of positive anomalies (84%) recovery of tuna catches at the latitude <20ºS and these were projected to increase in the southern areas of the MZC, with particularly high aggregation of tuna schools above 24ºS (Figure 3e). A loss and unchanged on tuna catches were predicted at the narrow area between 20ºS and 24ºS covering an area of ~16%. A comparison between the 2050 and 2100 future projections (Figure 3f) reveals that skipjack catches would be lost or unchanged around 20ºS-25ºS (~24%). By contrast, in the areas <20ºS and >25ºS the positively catch anomalies (~76%) were projected, with most accumulated in the north part of the MZC. The projections show displacement characterized by catch recovering (<20ºS) and expansion above 25ºS.

4. Discussion

The GAM used in this study to model skipjack catches performed well and had a reasonable level of predicting power (RMSE < 10%). As suggested in previous studies for selection of good predictive ecological models (e.g.: Fletcher & Fortin, 2018; Norberg et al., 2019; Wikle et al., 2019) we fit a small set of models showing complementary performance, and then apply a cross-validation procedure. The low deviance explained (~16%) could be related to the exclusion of other factors or processes in the model such as fine and large scale environmental processes, inherent biological and behavioural factors, processes related to the life-cycle of the species, as well as issues related with catchability and fishing operations (e.g.: Torres-Irineo et al., 2014; Lopez et al., 2014; Lopez & Scott, 2014; Moreno et al., 2016b). For example the complex bio-physical processes dominated by eddy circulation in the MZC (e.g.: Béhagle et al., 2014; Huggett, 2014), as well as details on the biology or the behaviour of the species (e.g. school fragmentation, density dependant behaviour) are hard to detect, quantify and integrate in traditional modelling exercises and could effect model performance. Further studies should explore the use of additional or complementary environmental and biological factors to investigate model performance, as well as descriptive and predictive power of models in relation to covariate selection. Similarly, periodic revisions of the current model, as well as the use of alternative projections for environmental data could help understand in the short-term the accuracy of the model and the sensitivity of using different data products by different climate-monitoring agencies.

The relationship between environmental variables and skipjack catches has previously been modelled using GAMs (e.g., Mugo et al., 2010; Yen et al., 2016), the SEAPODYM model (e.g., Loukos et al., 2003; Lehodey et al., 2013), and the APECOSM-E model (e.g., Dueri et al., 2012; Dueri et al., 2014). The relationship between environmental variables and other tropical tuna species have also previously been modelled (e.g., Arrizabalaga et al., 2015; Druon et al., 2017; Lopez et al., 2017; Monllor-Hurtado et al., 2017). However, previous studies have rarely modelled this relationship in the MZC. Among the oceanographic variables selected in the above cited studies, SST has been considered one of the best drivers to predict the ecological niche for many pelagic species (Hobday & Pecl, 2014) including skipjack tuna (Mugo et al., 2010; Dueri et al., 2014).

Changes to SST have been considered to influence skipjack physiological abilities and migratory behaviour (Graham & Dickson, 2004). Moreover, SST can affect optimal feeding forage and growth rates of the species below 15ºC and above 30ºC (Barkley et al., 1978) and limit spawning aggregation among schools in both northern and southern latitudinal waters where temperatures average >24ºC isotherms (Matsumoto et al., 1984; Schaefer, 2001). SST may also be a good proxy for other environmental processes as well. For instance, ocean warming could modify the circulation of currents by changing water density, decreasing primary production (low chlorophyl concentration) in the surface layer and displace essential nutrients in euphotic zones by stratifying water mass thereby affecting several trophic levels (Lali and Parsons, 2006; Mann and Lazier, 2006; Miller and Wheeler, 2012). Similarly, rising of SST could induce ocean deoxygenation (Gruber, 2011; Popova et al., 2016) along with continuous sea level rise (Rahmstorf, 2007; Aral et al., 2012; Aral and Guan, 2016). Alternately increasing warming could be positively correlated with motion intensification from cyclonic or anticyclonic eddies (Matyas, 2015) shifting the redistribution of trophic level and tuna species (Potier et al., 2014). The direction of surface currents (HDG-heading) may indicate where micronekton, zooplankton and other prey are driven by surface currents and concentrated in specific patches, potentially attracting tuna schools. Béhagle et al., (2014) found that the mesoscale features in the Mozambique Channel, either cyclonic and anticyclonic, exhibited greater micronekton density. Another study from Huggett (2014) suggest that mesoscale eddy and shelf interactions play a fundamental role in shaping the Mozambique Channel pelagic ecosystem through the concentration, enhanced growth and redistribution of zooplankton communities. The present study found significant relationship with several of the environmental variables mentioned above including SST and

SST gradient, CHL, KE, SSH and direction of the currents. However, further ecological or habitat analysis are needed to better understand the effects of environmental variables on the species of interest including tuna and other important species to support economic and food security in the region.

The effects of climate change on marine ecosystems, particularly on tropical tuna species have become of general concern in recent years (Lehodey et al., 2013; Dueri et al., 2014; Monllor-Hurtado et al., 2017; Erauskin-Extramiana et al., 2019). In the MZC, skipjack tuna catches exhibited distribution trends that follow the general tendencies of climate change scenarios. More specifically, skipjack tuna under the RCP2.6 scenario are expected to move from the warm waters in the north injected by the SEC to the intermediate waters in the south fed by Agulhas Current (AC). Thus, following the trajectory circulation of cyclones and anti-cyclone eddies in the area (Figure S1). Similarly the RCP8.5 scenario indicated a potential southward displacement projection by 2050 in agreement with current and future potential eddy and water circulation (e.g.: Lutjeharms & Town, 2006; Swartet al., 2010; Ternon et al., 2014). In contrast comparisons between 2100 and RPS, and 2010-2050 projected recovering trends of skipjack catches in the area <20ºS, where warming is predicted to happen faster (Roxy et al., 2014). Perhaps, the complex mechanism of water mass circulation in the MZC such as the suggested possible dilution and mixing among the northward currents (e. g.: cold North Atlantic Deep Water – NADW and Antarctic Intermediate Water - AAIW), and southward currents (e.g.: Red Sea Water -RSW and North Indian Deep Water – NIDW) and South Equatorial Currents (SEC) within the Comorian basin (e.g.: Ullgrenet al., 2012; Collins et al., 2016; Charles et al., 2020). This coupled with the effects of cyclone and anti-cyclone eddies which exchange the water mass could probably explain the displacement with restoration trend in northern of MZC. Also, Warm water (SST ~28ºC - 30ºC) is also related to tropical cyclone formation and storm intensification (Suzuki et al., 2004; Matyas, 2015) promoting high evaporation and contributing to increase precipitation in the region which could act in favour of skipjack suitable habitat. Constant monitoring and investigation of the impacts of climate change in the oceanography of the area are necessary to better assess, understand and mitigate the potential environmental consequences in MZC waters and associated habitats for species of interest. Understanding the potential habitat distribution of a species like skipjack tuna could provide important information about future oceanic and coastal fishing grounds, and contribute to designing and implementing spatially-explicit management plans.

The Intergovernmental Panel on Climate Change (IPCC) has projected ocean warming in the top 100m at between 2ºC and 3ºC by the end of the twenty-first century depending on the severity of predictive scenarios (M. Collins et al., 2013). Pelagic species, such as skipjack tuna, may respond to climate change by shifting their geographical or bathymetric distribution and the intensity of school aggregations (e.g., Cheung et al., 2013; Barange et al., 2014; Monllor-Hurtado et al., 2017). The present study was conducted in the Mozambique Channel, which is considered to be one of the most important "warming hotspot" regions in the world (Hobday & Pecl., 2014; Popova et al., 2016). Model projections for both the optimistic and pessimistic climate scenarios suggest that climate change will redistribute skipjack tuna from the traditional areas in the north towards areas in the southern part of the Mozambique Channel by 2050 and 2100 (Figure 3). These results are aligned with findings from other regions of the Pacific Ocean, suggest potential catch may increase in waters that are currently cold (Dueri et al., 2014; Yen et al., 2016). Interestingly, the results showed by RCP8.5 scenarios for the period between 2100-RPS and 2100-2050 project catch restoration in areas predicted to warm significantly (Roxy et al., 2014; Popova et al., 2016). However previous studies have predicted that warm equatorial habitats will become less favourable for tuna (e.g., Loukos et al., 2003; Lehodey et al., 2013; Dueri et al., 2014; Lehodey et al., 2015; Monllor-Hurtado et al., 2017). Therefore additional analyses are desirable in the future to test and investigate in detail potential differences and robustness of projections of skipjack tuna using different climate scenarios and data sources.

The results of our study show that under a low greenhouse gas emissions scenario (RCP 2.6) an increase in the potential distribution of skipjack catches will be favoured towards the southern waters of the MZC with relatively high favourable fishing grounds predicted to gain ~ +1.5% and ~4.3% by 2050 and 2100, and minor loss in total fishing grounds l between 2100 - 2050 of about 9%. Similar patterns of catch anomalies at the start and the end of the century have been found in other regions of the Indian Ocean for skipjack as well (Dueri et al., 2014; Marsac, 2017). Whilst the change would be of limited impact and may not generate major stress for skipjack tuna under the optimistic scenario (Marsac, 2017) purse seine fleets may continue to fish skipjack across the predicted suitable habitats if the operations are economically viable. However, studies investigating the effects of climate change on fishing behaviour and the socio-economic implications on industrial and non-industrial fleets operating in the region should be promoted to guarantee that coastal and oceanic fisheries adaptation and resiliency plans are developed on time.

Changes to the distribution of tuna are expected to be more pronounced in the pessimistic climate scenario (RCP8.5) with an expansion of skipjack catches from the fastest warming northern area of the Mozambique Channel to the south (Roxy et al., 2014; Popova et al., 2016) by 2050 with gained habitat almost to +4% relative to lost area. The redistribution pattern of skipjack fishing grounds (Moss et al., 2010; Meinshausen et al., 2011; O'Neill et al., 2016) could be a major stress and may dramatically change skipjack fisheries and species' dynamics in the MZC. The fishing grounds where skipjack are expected to accumulate by the middle of the century have previously been predicted to be industrial tuna purse seine fishing grounds (Dueri et al., 2014; Marsac, 2017). However, by the end of the century positive anomalies of fishing ground displacement were predicted, with >60% relative to the lost, suggesting that fishing grounds will be located in northern of MZC (>20ºS). Under RCP8.5 (Figure 3d-f) model predictions locations may respond to the complex hydrographic water mass dilution and mixing around Comorian basin, and elsewhere in MZC (e.g.:Ullgren et al., 2012; Collins et al, 2016; Charles et al., 2020). These could include, cyclone formation, storm intensification, evaporation and heavy rainfall (Suzuki et al., 2004; Matyas, 2015), and can contribute to water mass mixing, nutrient recycling, heat flux exchange, and redistribution of dissolved oxygen These and other processes could make the northern of MZC a productive and favourable area for skipjack.

Climate change also interacts with other non-climate stressors such as overfishing, habitat disruption, illegal, unreported and unregulated fishing and marine pollution (Brander, 2008; Daw et al., 2009; Benkenstein, 2013).Thus it is one of the many stressors in marine socio-ecological systems impacting fisheries (Perry et al., 2010). Human and social systems could adapt to these unintended changes in several ways. For example by exploiting previously unfished resources, fishing in previously unfished locations or seasons (Brander, 2008), diversifying income sources, and/or developing policies and governing mechanisms to facilitate or promote resilience (e.g., Badjeck et al., 2010; Grafton, 2010; Kalikoski et al., 2010). Some communities in the northern area could be significantly impacted however communities in the central and southern areas of the Mozambique channel could benefit from the redistribution of skipjack resources. This disparity has previously been documented by Allison et al. (2009), who suggested that climate change could positively impact some communities in specific locations while harming others. Climate change is also expected to create socio-ecological uncertainties in coastal states (Badjeck et al., 2010; Grafton, 2010; Hanna, 2011). Besides the uncertainty surrounding the effects on bio-physical processes and how those effects flow through ecosystem services (Dulvy et al., 2011) and fish availability (Lehodey et al., 2011) climate effects may also change fish production costs associated with locating, harvesting, processing, storing and transporting catches (Hanna, 2011). The degree of uncertainty when it comes to the negative impacts of climate change on future distribution of tuna catches could potentially effect the economy and social well-being or livelihood of small-scale fisheries communities located in northern Mozambique Channel. On a regional scale the coastal states surrounding the MZC (e.g., the Comoros Islands, Madagascar, Mozambique, and Mayotte) could also suffer an impact on their economic revenues as a result of climate variability (Hanna, 2011; Dey et al., 2016), as industrial fleets with tuna access agreements reassess their fishing strategies and move toward the more temperate areas that are projected to have more favorable tuna fishing areas (Grafton, 2010; Perry et al., 2010; Hanna, 2011; Hobday and Pecl, 2014). Thus, long-term climate effects may impact existing fishing agreements between the Mozambique Channel coastal states and distant water fishing nations (Havice & Reed, 2012) with potential negative impact on socio-economic incomes for some African coastal states.

According to Allison et al.(2009) coastal nations along the MZC have a moderate to high dependence on fishing relative to their national economies, export revenues, and fish consumption. This and other investigations found MZC coastal state nations vulnerability to climate impacts to be high and adaptive capacity to be low (Allison et al., 2009; Daw et al., 2009; Benkenstein, 2013). Therefore fishers, fisheries managers, and decision-makers around the Mozambique Channel are encouraged to take measures to make them more resilient and adapt to the socio-ecological and socio-economic uncertainty shift associated with climate change. Given that many small-scale fishers have been targeting tuna and tuna-like species in the northern part of the Mozambique Channel (Mutombene et al., 2017; Chassot et al., 2019) which is an area that is predicted to be significantly impacted by the year 2050 (e.g., Roxy et al., 2014; Popova et al., 2016),they will have to adapt to this new reality by targeting multiple species, shifting their fishing seasons or fishing sites and/or developing new fishing strategies (e.g., FAO, 2006; Benkenstein, 2013; Wanyonyi et al., 2016; Mutombene et al., 2017). For fishers with strong attachments to their communities, who are either unable or unwilling to move closer to these new fishing grounds may have to adopt more diversified and flexible livelihoods (Blythe, 2015; Lindegren and Brander, 2018). By contrast industrial fleets may respond to climate impacts by investing in advanced technical and innovative fishing technologies (Allison et al., 2009; Grafton, 2010; Perry et al., 2010; Hanna, 2011) in order to continue fishing the original target species.

The dilemma for fisheries stakeholders is when and how to adapt or be resilient when challenged with the uncertainties of marine resources and the effects of inevitable climate change. Thus, fisheries stakeholders operating in the Mozambique Channel should develop precautionary fisheries management plans to reduce the vulnerability of fishing communities even if these adaptation plans do not take effect for several years (Grafton, 2010). Climate change adaptation and mitigation strategies will vary according to the fishery as the degree of exposure, sensitivity, vulnerability and adaptative capacity differs according to marine ecological ecosystem, targeted species, operational characteristics of the fleet, and social groups (Daw et al., 2009; Grafton, 2010; Lindegren and Brander, 2018). Approaches to enhance the resilience of the fishing sectors, such as adaptative co-management or inclusive Marine Spatial Planning (MSP) (Pennino et al., 2021), which have been proposed to address uncertainty and harness the knowledge and commitment of fisheries resources at multiple scales, may be a good place to start. This study will contribute to increased awareness of the impacts of climate change on high ecological and socio-economic value fisheries, such as skipjack tuna fisheries in the MZC.

5.Conclusion

Our findings show that biophysical variables affect the distribution of skipjack tuna catches in the MZC and that species distribution will be affected by climate change with potential implications on local and international fishing communities. This will be especially acute in the northern part of the MZC.

The model projected the distribution of skipjack tuna under optimistic (RCP2.6) and pessimistic (RCP8.5) climate change scenarios. The optimistic scenario projected that skipjack tuna catches would shift toward the southern part of Mozambique Channel, between latitudes 19ºS and 25ºS, by 2050, and that the distribution change would be either minor or unchanged from 2050 to 2100. In the worst-case scenario (RCP8.5) the potential fishing grounds were projected at latitudes >20ºS by 2050, and positive anomalies were projected to likely occur at latitudes < 20ºS between 2050 and 2100. By the end of the century, signs of high catch distributions are expected outside of the MZC at latitudes >25ºS toward temperate regions. Given that climate change is projected to impact skipjack fisheries in the MZC this may lead to socioeconomic challenges for fishing communities. Coastal states in the MZC area should strengthen governance and promote policies to build resilience and increase the adaptive capacity of local, national and regional fisheries to reduce their vulnerability to climate impacts. The present study contributes to an understanding of the effects of climate change by stakeholders and demonstrates a need to develop more participatory climate mitigation and adaptation strategies., It is suggested that adaptative co-management or inclusive MSP are supported to address uncertainty and connect knowledge with commitments that offer and develop alternatives to increase the resilience and adaptive capacity at both socio-ecological and socio-economic scales.

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Conflict of interest

We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere. All authors have approved the manuscript and agree with submission to *Fisheries Oceanography Journal*. We have read and abided by statements of ethical standards for manuscripts submission to Fisheries Oceanography Journal. The authors have no conflicts of interest to declare.

Data Availability Statement

The data that support the findings of this study are available from third party. Restrictions apply to the availability of these data, which were used under authorization for this study. Fishery data are available from Maria Ruiz Soto [maria.soto@ieo.es] with the permission of Spanish Oceanography Institute. Environmental Oceanography data are available from Jon Lopez [jlopez@iattc.org], and accessible from [marine.copernicus.eu], while climate data were derived from public domain resources [Bio-ORACLE - http://www.bio-oracle.org] [marine.copernicus.eu], while climate data were derived from public domain resources [Bio-ORACLE - http://www.bio-oracle.org**].**

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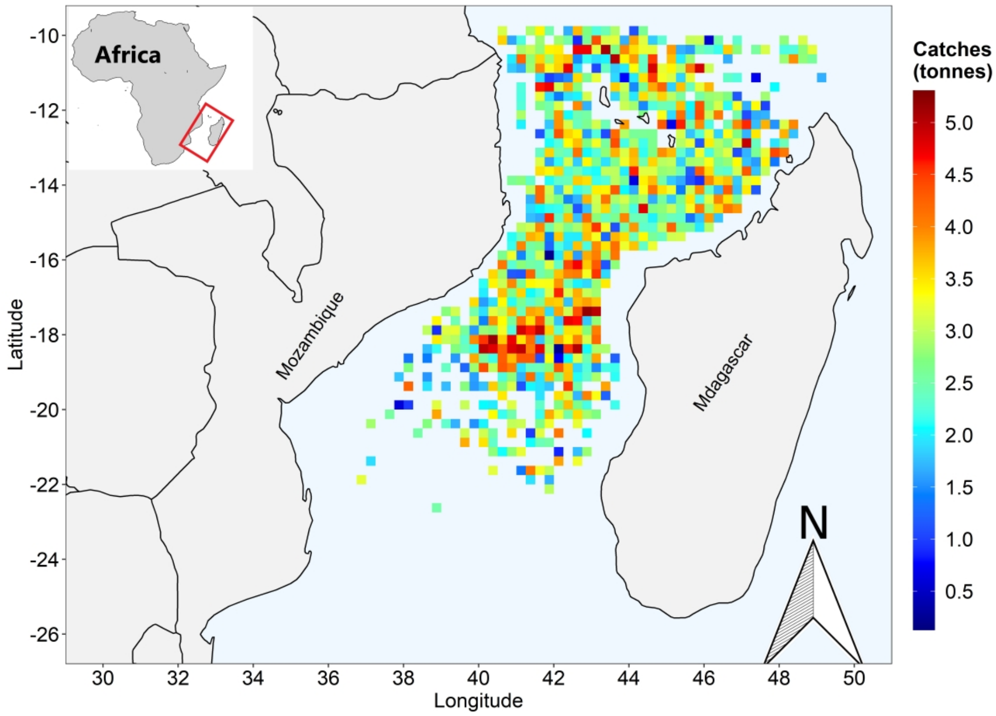

Figure 1 - Skipjack tuna catches (tonnes) distribution in the Mozambique Channel targeted by Spanish purse seine fleets for the period 2003 - 2013 (RPS). Catches aggregated were monthly by 0.25º x 0.25º resolution and displayed in the map at the logarithmic scale.

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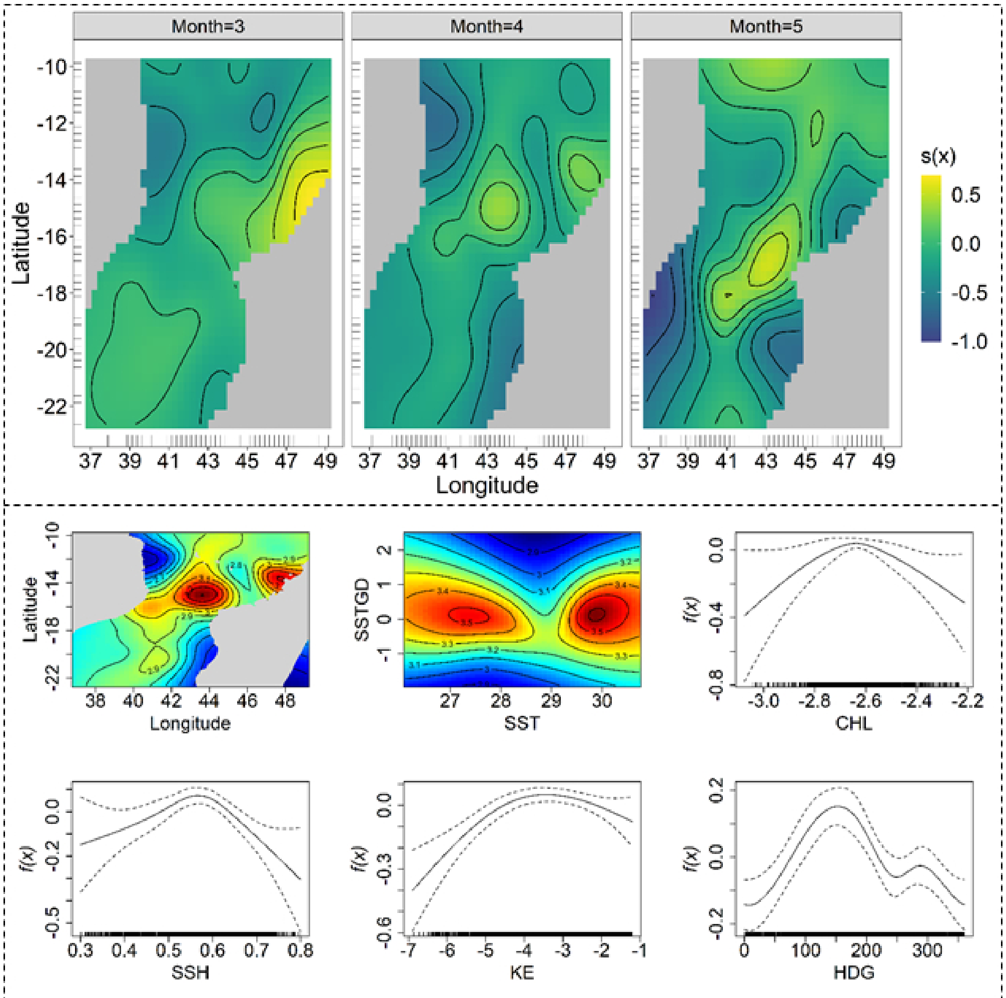

Figure 2 - Partial effects of environmental factors on the skipjack tuna catches of the Spanish purse seine fleets in the Mozambique Channel. The top panel displays the space-time effects, and the bottom panel displays the oceanography variable effects. Tick marks on the x-axis represent the observed data. The y-axes, denoted as f(x), represent the relative importance of the model's predictor variables. Dashed lines indicate the lower and upper 95% confidence intervals of the smooth plot.

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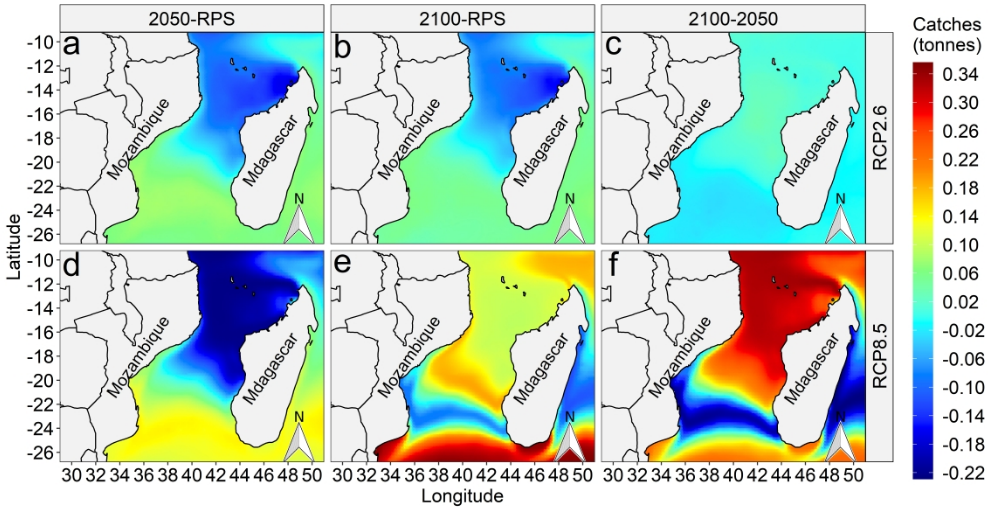

Figure 3 - Projected differences in skipjack tuna catches (tonnes) targeted by purse seine around free and associated schools between the RPS (2003-2013) and future (2050 and 2100) under the BIO-ORACLE RCP2.6 and RCP8.5 climate change scenarios. The first column (panel a and d) depicts the anomalies of predicted catches between layers 2050 and the RPS. The second column (panel b and e) show anomalies between layers 2100 and RPS, and the third column (panel b and e), display the anomalies between layers 2100 and 2050.

1874x997mm (96 x 96 DPI)

Table 1 - Selected GAM model of skipjack tuna distribution in the Mozambique Channel. Models were fitted with Gaussian distributions with identity links. EDF: effective degrees of freedom, SSH: sea surface height, CHL: chlorophyll-a, SST: sea surface temperature, SSTGD: sea surface temperature gradient, HDG: heading (sea surface currents direction), KE: kinetic energy. Long: Longitude in degrees. Lat: Latitude in degrees. Dev. Covariate: is deviance explained by each covariate term in the model. Dev. Explained is the deviance explained by all covariates in the model, AIC Akaike Information Criterion. F-Statistic: give the ratio between deviance explained and not explained by covariate.

Parameters	**Mode output fitted by Gaussian family identity link function**			
Adjusted R^2	0.13			
Dev. Explained. (%)	15.60			
AIC score	8188.00			
GCV score	0.69			
n	3328			
EDF	88.88			
Residual df.	3239.12			
Covariates	***EDF***	***p-value***	**Dev. Covariate**	**F-Statistic**
CHL	2.70	<0.01	0.37	2.41
HDG	3.61	<0.001	1.22	8.52
SSH	3.17	<0.001	0.69	4.25
KE	2.64	<0.001	0.73	4.90
Year	0.02	<0.001	0.13	0.69
SST x SSTGD	11.70	<0.001	2.39	4.13
Long x Lat x Month	64.03	<0.001	10.44	1.70

Table 2 - Percentage of projected area changes for skipjack tuna catches accumulation under future climate change scenarios, by fishing mode. Unchanged areas (%) indicated by values around zero (0) anomalies; lost areas indicated by negative anomalies, and gained areas indicated by positive anomalies and correspond to the locations with skipjack catches aggregation. RPS - reference period of the study corresponding to 2003 - 2013.

RCP	**Year**	**Projection (%)**				
		Unchanged	**Loss**	**Gain**	**Gain + Loss**	**Gain - Loss**
RCP2.6	2050 - RPS	6.71	45.87	47.41	93.28	+1.5
	2100 - RPS	9.99	42.86	47.15	90.01	+4.3
	2100 - 2050	90.66	9.34	0	9.34	-9.3
RCP8.5	2050 - RPS	9.96	43.17	46.87	90.04	+3.7
	2100 - RPS	11.65	4.35	84.01	88.36	+79.7
	2100 - 2050	7.51	16.21	76.28	92.49	+60.1

Supplementary Material

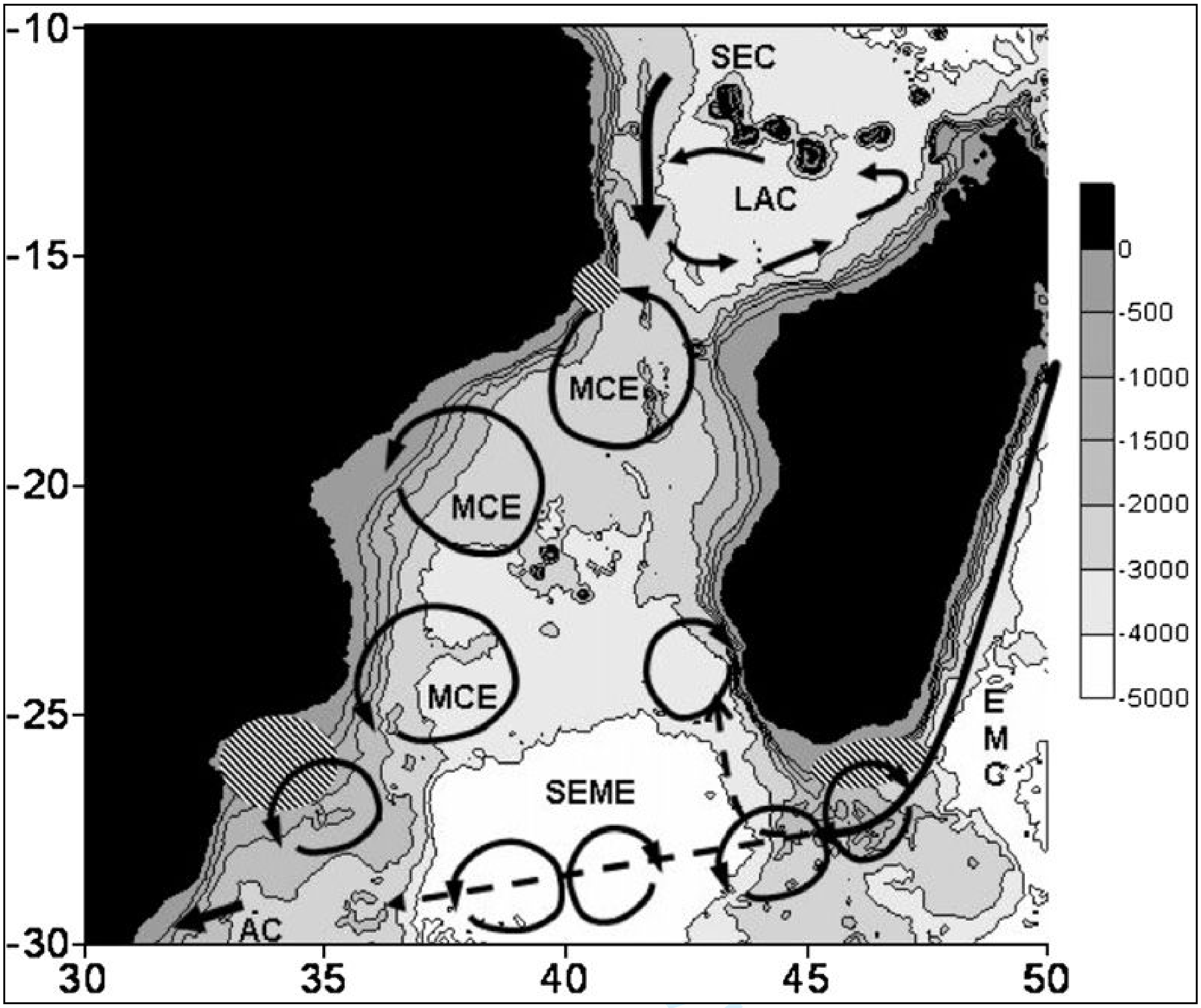

Figure S1. Major circulatory features in the Mozambique Channel with bathymetry. The main current and the mesoscale features are schematically shown. Hatched areas denote upwelling. In the north of the channel, the coastal current shown is fed by the South Equatorial Current (SEC) and later depicts a large anticyclonic cell (LAC) in the Comoro basin. The white area with black points represents the lee eddy off Angoche. In the west, along Mozambique coasts, mesoscale eddies (MCE) move in a southwesterly direction. In the east coast of Madagascar, the feature shown is the East Madagascar Current (EMC) and in the south, the south east Madagascar dipolar eddies (SEME) moving westward and little north ward. The mesoscale eddies from the Mozambique channel and the dipolar structures from the south of Madagascar reach the Agulhas Current (AC). (author: Tew-Kai and Marsac, 2009).

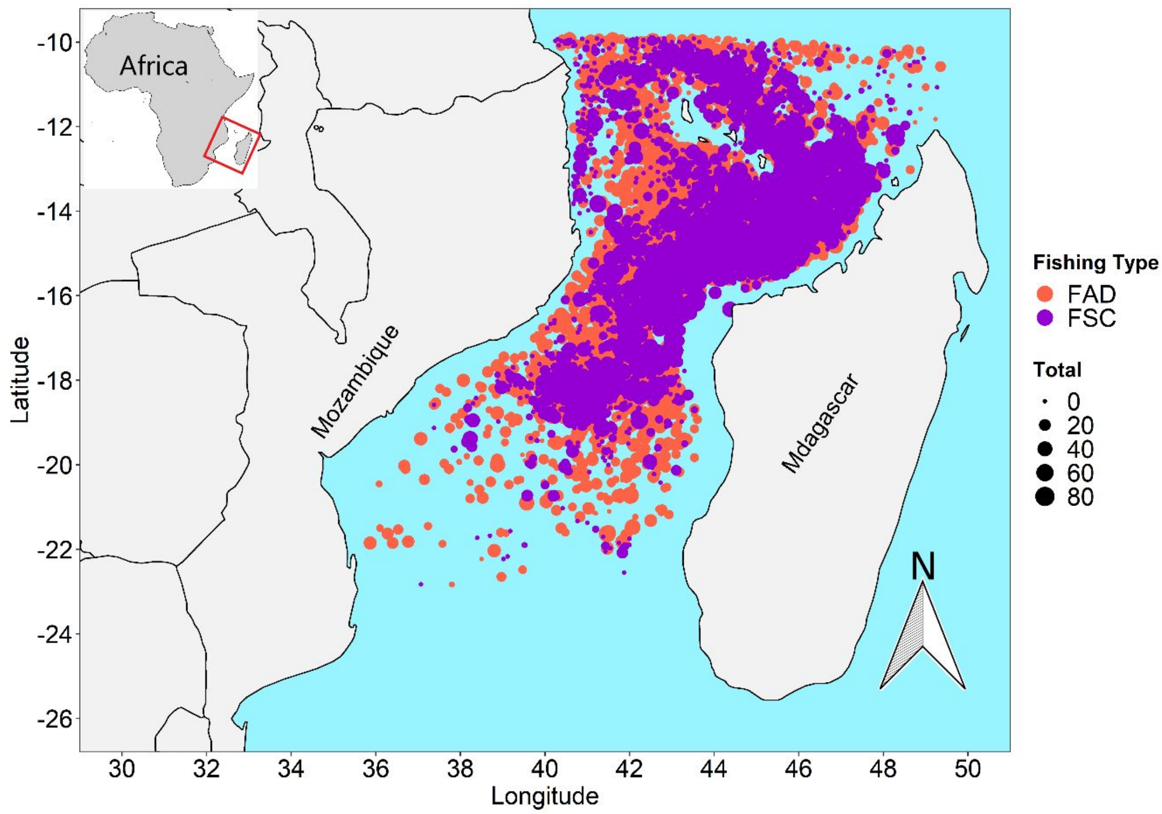

Figure S2 - Catches distribution of Skipjack tuna in the Mozambique Channel targeted by Spanish purse seine fleets for the period 2003 - 2013 (RPS). Catches were aggregated monthly by 0.25º x 0.25º resolution. FSC - Free-Swimming Schools; FAD - Fish Aggregating Devices.

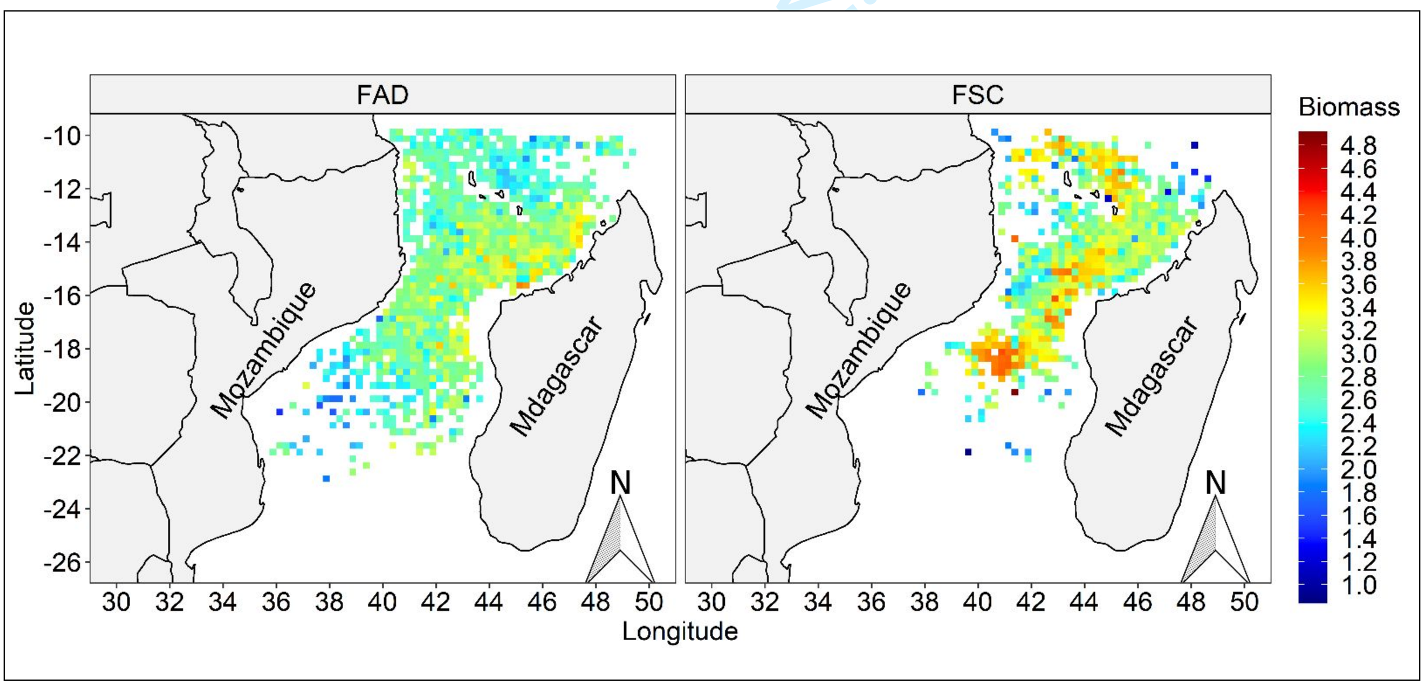

Figure S3. Predicted spatial distribution of skipjack tuna catches~~biomass~~ density caught in FADs (left panel) and FSC (right panel) fishing mode in the Mozambique Channel for the period 2003-2013 (RPS), gridded by 0.25º x 0.25º spatial resolution, and transformed to natural logarithm scale for better performance in GAM modelling.

Supplementary Material 3: S3

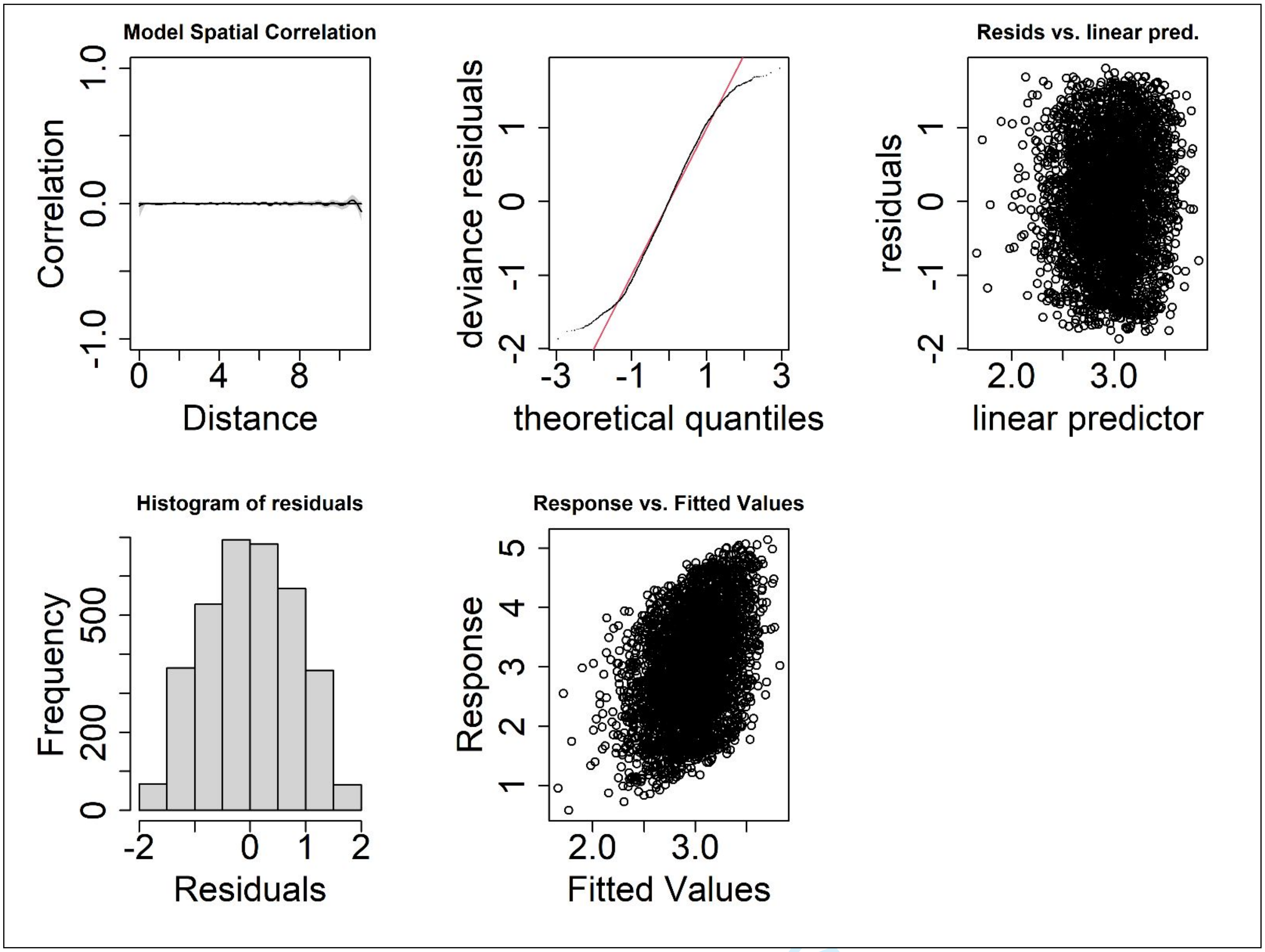

Figure S4 - Display the goodness-of-fit for GAM in FSC. Top left panel depict spatial correlogram showing no spatial correlation, i.e., residual with non-significant autocorrelation. The mid panel in left sketched the homogeneity of variance, and the bottom left is closely to strait line. The two-right figures in the panel (qq-plot and histogram) shows residual close to normal distribution.

Table S1 - Environmental, spatial and temporal variables used in the study

Variables	Acronym Used	Unit	Spatial Resolution	Temporal Resolution	Product identifier
Chlorophyll a concentration	CHL	mg m^{-3}	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_BIO_001_029
Chlorophyll Gradient concentration	CHLGD	mg m^{-3}	0.25º x0.25º	±7 days	GLOBAL_REANALYSIS_BIO_001_029
Current Heading	HDG	degrees	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_PHY_001_031
Eddy Kinetic Energy	KE	m^2 s^{-2}	0.25º x0.25º	Daily	Derived from model
Current Velocity	SSC	m s^{-1}	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_PHY_001_031
Sea Surface Height	SSH	m	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_PHY_001_031
Oxygen concentration	O_2	mg l^{-1}	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_BIO_001_029
Sea Surface Salinity	SSS	g kg^{-1}	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_PHY_001_031
Sea Surface Temperature	SST	ºC	0.25º x0.25º	Daily	GLOBAL_REANALYSIS_PHY_001_031
Sea Surface Temperature Gradient	SSTGD	ºC	0.25º x0.25º	±7days	GLOBAL_REANALYSIS_PHY_001_031
Latitude	Lat	degrees	0.25º x0.25º	Daily	-
Longitude	Long	degrees	0.25º x0.25º	Daily	-
Month	Month	-	0.25º x0.25º	Monthly	-
Natural Day (365 days per Year)	YearDay	-	0.25º x0.25º	Daily	-
Year (2003 -2013)	Year	-	0.25º x0.25º	Yearly	-

Table S2- 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., 2017
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	*	Songet 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
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Supplementary Material 2

Manuscript Copy with Track Changes

Abstract

Skipjack tuna play a significant role in global marine fisheries and are of particular interest for socio-economy in the tropical waters of the Mozambique Channel. However, human-induced climate change has been leading to a reduction and reallocation of biomass, along with other ecological changes, thereby creating a feedback loop with negative socioeconomic consequences for fisheries-reliant coastal communities. The objective of this study was to predict the potential skipjack tuna fishing grounds by 2050 and 2100. To that end, skipjack tuna catch data were collected from Spanish purse seine fleets who use one of two fishing modes (FADs - fishing around aggregating devices, and FSC- free swimming schools) and, subsequently, Generalized Additive Models, were used to model these data against a combination of in-situ environmental variables and future pathway projections from BIO-ORACLE models under optimistic (RCP2.6) and pessimistic (RCP8.5) scenarios. Both scenarios predicted that the potential fishing grounds will relocate southward from tropical to more temperate waters, with moderate shifts in the potential fishing grounds of purse seines to the latitude >16ºS.. The optimistic scenario projected moderate shifts in the potential fishing grounds of purse seines to the latitude 17ºS - 24ºS by mid-century, whereas the pessimistic scenario predicted higher catches of purse seines in the southernmost part (>24ºS) of the Mozambique Channel. Despite the degree of uncertainty surrounding the climate change impacts on skipjack tuna, we argue that fisheries stakeholders, administrators, and regional tuna fisheries management organizations should work toward building resilience and ensuring sustainability while reducing or mitigating vulnerability and climate change impacts on local and regional communities and their livelihoods.

Keywords: Climate change impacts, Mozambique Channel, purse seine fisheries, skipjack tuna biomass, predicted skipjack biomass, GAM

1. Introduction

Climate change, including increased global warming, ocean acidification, and ocean deoxygenation (Gruber, 2011; Ramírez et al., 2017), is a growing global concern and can lead to changes in the marine physicochemical and biological environments (Ramírez et al., 2017) and, thereby, modify net primary production, ocean circulation, and fish abundance and distribution (Lehodey et al., 2010; Dueri et al., 2014).

In the marine ecosystem of the Western Indian Ocean (WIO), which includes the Mozambique Channel (MZC), climate change is expected to lead to increased temperatures, a slowdown of ocean circulation and a decrease in primary production (Mcclanahan et al., 2011; Popova et al., 2016). Moreover, this increased warming is expected to occur at a faster rate than in other tropical ocean regions (Roxy et al., 2014). With respect to the global distribution of marine species, tuna fish strictly depend on optimal temperatures, along with other oceanographic and environmental variables (Lopez et al., 2017; Orúe et al., 2020). Thus, considering the predicted changes induced by a warmer climate, it is expected that tuna will migrate from their original habitats to regions with higher latitude, upwellings, deeper waters, and near eddies and fronts (Dueri et al., 2014;Marsac, 2017) Lecomte et al., 2017; Marsac, 2017; Monllor-Hurtado et al., 2017). Consequently, ecosystem responses to these climate impacts may lead to changes in catch volumes and, subsequently, impact the national economies and livelihoods of WIO coastal states (Sumaila et al., 2011).

Among tropical tuna species, the skipjack tuna (*Katsuwonus pelamis*) is the most caught by industrial and small-scale fisheries in the WIO region (POSEIDON et al., 2014; Mukesh et al., 2019). Between 1989 and 2019, the total skipjack catch from FAO 51 fishing grounds was about 9,000,000 tonnes, about 56% were fished by industrial purse seines, 11% by semi-industrial fisheries, and 33% from small-scale fisheries respectively (IOTC, 2020 Database). ~~For 30 years, between 1985 and 2015, total skipjack catches from WIO fishing grounds amounted to about 8,000,000 tonnes, whereby about 55% were fished by~~

industrial purse seines, 34% by semi-industrial fisheries, and 11% from small-scale fisheries and longlines, respectively (IOTC, 2018 Database). Over the last decade, skipjack have accounted for about 60% of all tropical tuna catches in the MZC high seas (Chassot, Bodin, Sardenne, & Obura, 2019). In the coastal waters around MZC, small-scale skipjack fisheries catches were reported to be ~430 thousand tonnes for the period between 2014 and 20189 (IOTC, 2020 Database). However, this number is thought to be much higher given that statistics from small-scale fisheries were under reported to the regional fisheries management organization: the Indian Ocean Tuna Commission (IOTC) (Chassot et al. 2019). Thus, it is evident that skipjack tuna from industrial and semi-industrial fleets, and small-scale fisheries significantly contribute to the economy and livelihoods of WIO states by regularly supplying canneries and supporting local and regional food security (POSEIDON et al., 2014; Lecomte et al., 2017).

Skipjack tuna movement between marine economic exclusive zones within the MZC determines the interests and relationships among countries and industrial and small-scale fisheries. Previous studies carried out by Fonteneau and Hallier (2015), and Chassot et al. (2019) have demonstrated the complex movements of skipjack tuna between the northern MZC toward the south and northernmost areas out of the channel. This migratory behaviour is related to seasonal variations (Campling, 2012; Kaplan et al., 2014) and linked to an environmental habitat suitability dependent on water temperature, feeding forage and oxygen concentration (Lehodey et al., 2013; Dueri et al., 2014). Variables, such as sea surface height, currents (speed, kinetic energy, and direction), and mixed layer depth, have also been considered to investigate tuna distribution and habitat preferences (e.g., Mugo et al., 2010; Yen et al., 2016; Lopez et al., 2017; Orúe et al., 2020; Orúe et al., 2020a). However, studies analysing climate change impacts on the area are either scarce or non-existent.

Although the exploitation of skipjack tuna stocks in the Indian Ocean is currently considered to be sustainable (IOTC, 2018), skipjack tuna are highly sensitive to environmental conditions and changes (Loukos et al., 2003;Yen et al., 2016; Orúe et al., 2020). Given that climate change impacts will be particularly significant in marine ecosystems, any variation in environmental factors may lead to changes in fish distribution and catchability (Dueri et al., 2014). Earlier studies have attempted to project the distribution and abundance of skipjack tuna under climate change scenarios elsewhere using APECOSM-E (Apex-Predator-Ecosystem-Model – Estimation) (Dueri et al., 2014), and biomass aggregation using SEAPODYM (Spatial Ecosystem and Population Dynamics Model) (Patrick Lehodey et al., 2013) and Generalized Additive Models (GAMs; Yen et al., 2016), and their findings suggested that climate change scenarios could lead to significant large scale changes to the distribution and habitats of skipjack tuna.

~~Within this context,~~ in this study we attempt~~aim~~ to predict the effects of climate change on the distribution of skipjack tuna using GAMs, by analysing Spanish purse seine fisheries in the MZC. Specifically, we intend to (i) identify which biotic or abiotic characteristics most affect skipjack tuna catch ~~biomass~~ distributions; (ii) predict the distributional shifts of skipjack tuna by the years 2050 and 2100 under optimistic and pessimistic climate change scenarios~~investigate the distributional shifts of skipjack tuna by the years 2050 and 2100 under optimistic and pessimistic climate change scenarios~~; and (iii) discuss the consequences of changes to species distributions and catch rates.

2. Methodology

2.1. Study area

The MZC is located in the southwestern Indian Ocean, with Mozambique to the west, Madagascar to the east and the Comoros archipelago to the north (Figure 1). The MZC is a particularly good place to investigate the relationship of a species with the environment as the current flows in the north of the channel are fed by warm South Equatorial Currents (SEC), which generate large eddies ~~in the~~around the Comorian basin ~~and propagate south-westward~~ (Lutjeharms and Town, 2006; Ternon et al., 2014). From the narrows area of the channel (~16ºS) mesoscale eddies are formed, and progress from here southward, merging with those eddies generated in south-eastern Madagascar and move westward, where they become trapped by the Agulhas Current ~27ºS, moving southward (de Ruijter et al., 2006; Lutjeharms and Town, 2006; Ternon et al., 2014) (Figure1 S1, supplementary material).~~In the south, the SEC eddies merge with those generated in south-eastern Madagascar and move westward, where they become trapped by the cool Agulhas Currents (Lutjeharms and Town, 2006; Ternon et al., 2014) (Figure~~

~~S1, supplementary material)~~. The effects of physical and -biological oceanographic variables on the distribution of tuna biomass appear to be seasonal in the MZC. For example, ~~during~~ at the onset of the austral winter months (March-~~June~~JMay environmental conditions seem to be more suitable for tuna schools in the MZC (Kaplan et al., 2014; Obura et al., 2018) and attract purse seiners to fish in the northern part of the channel (Davies et al., 2014)~~), tuna schools peak in the MZC (Kaplan et al., 2014; Obura et al., 2018) and, thereby, attract purse seiners to fish in the northern part of the channel (Davies, Mees, & Milner-Gulland, 2014)~~. Skipjack catches by purse seines in the MZC are rare throughout the rest of the year (Campling, 2012; Kaplan et al., 2014; Chassot et al., 2019).

2.2. Fisheries Data

Fishing logbooks from Spanish tropical tuna purse seine fisheries were collected by the Spanish Oceanographic Institute for the period February 2003 - June 2013 (hereafter: RPS - Reference Period of the Study). The data was spatially restricted to the MZC, within the latitudes 8ºS to 30ºS and longitudes 30ºE to 50ºE (Figure~~.~~ 1). These data consist of 13,630 fishing set observations (49% in FSC - Free-Swimming Schools and 51% in FAD - Fish Aggregating Devices), with information on catch compositions, fishing hours, date (year, month, and day of the fishing operation), and location (i.e., longitude and latitude). Data were restricted to the months between March and May, which represent the fishing season for industrial purse seiners in the MZC. The distribution of skipjack catches data, shows that both purse seine set types (FAD and FSC) share the fishing grounds over the area (Figure S2 and S3, supplementary material), with high catches records in western side of Madagascar Island and northern of Comoros Islands (Figure 1). Because of the shared fishing grounds and the uncertainty to discriminate between free and associated schools of skipjack (Moreno et al., (2016)), all fisheries data were combined in this study. ~~Because of seasonality, catches were subset to the months between February and August.~~

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2.3. Environmental Data

Environmental data for the MZC for the period 2003-2013 (RPS) was downloaded from the MyOcean-Copernicus EU consortium (marine.copernicus.eu) in netCDF format and extracted for each fishing set location and date through specific codes and routines using functions from the packages netCDF4 (Pierce, 2017), chron (Jame & Hornik, 2013), and lubridate (Grolemund & Wickham, 2011), and other basic functions in version 3.6.0 of R software (R Core Team, 2018). The environmental factors included were: sea surface temperature (SST, ºC); sea surface temperature gradient (SSTGD, ºC), which was derived from the decrease or increase in temperature for each pixel over a 7-day period, sea surface height (SSH, m); eddy kinetic energy (EKE, derived from altimetry, m^2 s^{-1}); sea surface current velocity (SSC, m s^{-1}); current sea surface heading (HDG, degrees); salinity (SSS); chlorophyll-a concentration (CHL, mg m^{-3}); chlorophyll-a gradient (CHLGD, mg m^{-3}), which was derived from either the increase or decrease in the amount of chlorophyll in each pixel over a 7-day period; and ~~dissolved~~ oxygen concentration (O_2, mg l^{-1}~~DOC, mmol m^{-3}~~) (Table 1 S1). All the variables were extracted from the CMEMS product GLOBAL_REANALYSIS_PHY_001_031, except chlorophyll-a and oxygen concentrations which were downloaded from the product GLOBAL_REANALYSIS_BIO_001_029.~~The spatial and temporal resolutions were 1/4° and daily, respectively~~. These variables were assumed to be potentially related to skipjack tuna as several studies already explored or evidenced the importance of these relationships ~~distributions and biomass densities~~ (e.g., Loukos et al., 2003; Lehodey et al., 2013; Mugo et al., 2010; Dueri et al., 2014; Yen et al., 2016). Spatial-temporal variables, such as longitude, latitude, year, month, and natural day (i.e., from 1 to 365 days) were also incorporated into the models because they can help with spatial-autocorrelation and may explain part of the variability in biomass not explained by other environmental variables and spatially structured processes ~~not included in this study~~ (Cortés-Avizanda et al., 2011). The oceanographic and spatio-temporal variables considered here have been used by other studies to model tuna and other large marine predators, habitats, environmental preferences or fishing hotspots (Table S2, supplementary material).

Intergovernmental Panel on Climate Change (IPCC) surface temperature projections were used to model future scenarios (IPCC, 2014). Specifically, we accessed the Representative Concentration Pathways (RCP) 2.6 and 8.5 for the years 2050 and 2100 (radiative forcing levels of approximately 2.6 and 8.5 Wm^{-2} by the end of 2100, respectively) for monthly mean sea surface temperature with a spatial resolution of 0.083º x 0.083º grid cells from Bio-ORACLE (http://www.bio-oracle.org). The RCP2.6 (optimistic) emission scenario assumes the least change, with a temperature increase of 1ºC by 2050 and 2º C by 2100 and a salinity increase of 0.5 and 1 units for these same years, respectively. The RCP8.5 (most pessimistic) scenario, by contrast, presumes more severe changes, with a temperature increase of 1.5º C by 2050 and almost 3º C by 2100, and a salinity increase of 1 and 1.5 units for these same years, respectively (Meinshausen et al., 2011; IPCC, 2014).

2.4. Model construction and projection

In an exploratory phase, the relative importance of skipjack tuna ~~biomass~~ catch was~~variables were~~ assessed using the randomForest package (Liaw & Matthew, 2002), and the most important covariates were selected to reduce model complexity in later fitting stages (Dell, Wilcox, & Hobday, 2011). Additionally, and following Zuur et al. (2010), correlation among variables was tested using the Pearson correlation rank (rho), and only variables with an rho absolute value lower than 0.70 were included simultaneously in the GAMs (Dormann et al., 2013). Finally, a variance inflation factor analysis was also conducted using a threshold value of 3 as a supplementary measure to test collinearity (Zuur et al., 2009). The covariates natural day, and current velocity ~~or kinetic energy~~ dissolved oxygen were dropped for further modelling due to collinearity and correlation with ecologically more important environmental variables.

In the first steps of model construction, the daily set by set data for each fishing mode were used as response variables. However, the model underperformed and failed to detect the changes in variance at this scale, therefore, data were aggregated by month to a 1/4º grid cell (i.e., the sum of the biomass and the mean of the environmental variables). Details to create different scale grids and raster layers through the raster package can be found in Bivand et al. (2015). GAMs (Wood, 2006) were established by using the new positive gridded data to examine the effects of environmental variables on the spatio-temporal skipjack ~~biomass~~ distributions ~~according to each fishing mode (i.e., FADs and FSCs)~~. The logarithmic transformation of skipjack tuna ~~biomass~~ catches (i.e., log (~~Biomass~~Catches+1)) was used as the dependent variable to reduce skewness and improve model performance (Zuur et al., 2010). The logarithmic transformation was applied also to the covariates CHL and KE to improve contrast and model fitting. GAMs were fitted with a Gaussian family by using the identity link function and applying the *mgcv* package (Wood, 2006), and followed the procedures to model continuous data (Wood, 2006; Zuur et al., 2009) and distribution data tests (Delignette-Muller & Dutang, 2015).

GAMs are semi-parametric extension of Generalized Linear Models (GLMs) (Guisan et al., 2002b) for which the strictly linear predictor:~~The complete models were fitted as:~~

$$g(\mu(\mathbf{X})) = \beta_0 + \beta_1 X_1 + \cdots + \beta_p X_p,$$

where $\mathbf{X} = (X_1, \ldots, X_p)$ are covariables, $\mu(X) = E\,(Y\,|X)$ is the conditional exception of the response variable Y, g is the link function (explained below) and $\beta_0, \beta_1, \ldots, \beta_p$ are the unknown parameters, is replaced by

$$g(\mu(\mathbf{X})) = \beta_0 + f_1(X_1) + \cdots + f_p(X_p),$$

where $f_j\,(X_j)$ is the unknown smooth partial effect of X_j on the predictor. Hence GAMs avoid the assumption of linear relation between the response variable and the covariables providing a more flexible model. Note that GLMs are an extension of Linear Models for which the distribution of the response variable can be other than gaussian. For this reason, in the previous models a link function g is applied to $\mu(X)$. Using the syntax of the *mgcv* R package, the GAM was fitted as:

$$\ln(\text{Catch}+1) \sim te(\text{space-time}, k=(50,6), d=c(2,1) + s(C_a, C_b, k=20) + s(C_c, k=6) +$$
$$s(C_d, k=6) + \ldots + s(C_z, k=6) + c(C, k=6) + random$$

~~FAD: ln(Biomass+1) ~ *te*(space-time, k=(30,6), d=c(2,1) + *s*(C_a, C_b, k=20) + *s*(C_e, k=6) + *s*(C_d, k=6)+ …+ *s*(C_z, k=6)+ *c*(Heading, k=6) + (Year)$_{random}$~~

~~FSC: ln(Biomass+1) ~ *te*(space-time, k=(30,6), d=c(2,1) + *s*(C_x, C_y, k=20) + *s*(C_a, k=6) + *s*(C_b, k=6)+ …+ *s*(C_z, k=6)~~

where the *te* function forms the product from the marginal terms of the space-time triple interactions; *d* is the dimension of each spline in the triple interaction (which in this case is two for spatial components and one for temporal terms); and *s* is the penalized spline smooth function for single interactions and environmental covariates (C). All interactions were fitted by the tensor smooth (ts) product, whereas the single covariates were fitted with cubic spline regressions (*cs*) to model nonlinear relationships. Cubic Spline regressions ensure that: a regression spline with shrinkage is applied, that a smoother can have zero degrees of freedom, and that all smoothers with zero degrees of freedom can be simultaneously dropped from the model (Zuur et al., 2009). A cyclic cubic regression spline, *c*, was used to illustrate the cyclical behaviour of the terms (e.g., Heading) (Wood, 2006). Finally, a random effect was included (i.e., year) to account for inter-annual variability in fishing effort and fleet behaviour (Brodie et al 2015). Dimension, denoted by *k*, was used to represents the maximum degrees of freedom allowed for each smooth term and was set to 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), and k=30 for spatial components in the space-time triple interaction (Wikle, Zammit-Mangion, & Cressie, 2019) to avoid model overfitting and to simplify the interpretation of results. After the first model simulations, 5% of residual data noise was excluded, i.e., 95% of data were absorbed into the model either without or with less outliers (Zuur et al., 2010) to improve model robustness.

The backward selection method with a residual deviance score, a Generalized Cross Validation (GCV) score, an Akaike information criterion (AIC), a residual check (Wood, 2006; Zuur et al., 2009), and a residuals spatial autocorrelation test (Bjørnstad, Falck, Barbara, & State, 2001), were the criteria considered to determine the best models for the skipjack tuna biomass aggregation in both set types.

A k-fold cross-validation was applied (James, Witten, Hastie, & Tibshirani, 2014), which consists of randomly splitting observations into k groups, (in this study k was set to 10 folds) to validate and assess model performance. The first fold was treated as a test dataset to validate the prediction of schools aggregation~~biomass accumulation~~ in fishing grounds, and the model was fitted to the remaining $k-1$ folds, which was treated as a training dataset (James et al., 2014). Next, the root mean square error rate (RMSE) and the Pearson correlation score (rho) and Schoener similarity index D (Zhang, 2016) between predicted and observed values, were computed to measure the accuracy and predictive performance of the model on the held-out fold validation data.

Finally, skipjack tuna biomass models were built with environmental data and used to project skipjack tuna biomass distribution into the future (2050 and 2100) according to the RCP2.6 and RCP8.5 (climate change scenarios (Assis et al., 2017). The RCP2.6 and RCP8.5 climate change scenarios predict the lowest and highest rises in global temperatures from greenhouse gas concentrations, respectively (Moss et al., 2010; Meinshausen et al., 2011). The climate variables available in the BiO-ORACLE surface layer were used to predict future scenarios (i.e.~~,g.,~~ sea surface temperature-SST)~~,~~ whereas the remaining variables used to construct the model were set to zero given that the goal was to predict based on SST changes - the main proxy for climate change intensity scenarios. SST has been considered one of the best factors to predict the ecological niche of skipjack tuna (e.g.: Mugo et al., 2010; Dueri et al., 2014), as it influences skipjack physiological abilities and migratory behaviour (Graham & Dickson, 2004), affects optimal feeding forage and growth rates (Barkley et al., 1978) and limits spawning aggregation among schools in both northern and southern latitudinal waters where temperatures average >24ºC isotherms (Matsumoto et al., 1984; Schaefer, 2001). Besides, SST is a good proxy for, or is connected to, other environmental variables and processes (e.g.: Lali and Parsons, 2006; Mann and Lazier, 2006; Miller and Wheeler, 2012; Gruber, 2011; Popova et al., 2016; Rahmstorf, 2007; Aral et al., 2012; Aral and Guan, 2016). Furthermore, SST data from Bio-ORACLE have been widely us. Furthermore, SST data from Bio-ORACLE have been widely used to predict the potential distribution of marine species under different climate change scenarios~~The use of Bio-ORACLE data to model the distribution of marine species is well known~~ (e.g., Tyberghein et al., 2012; Duffy et al., 2016). Changes to skipjack ~~biomass~~ distributions ~~and aggregations in marine habitats~~ wasere assessed by estimating the ~~overlapping~~ differences in spatial predictions between projected future and- reference period ~~present~~ scenarios (e.g., Dueri et al., 2014; Yen et al., 2016). All analyses were conducted using R version 3.6 (R Core Team, 2018).

3. Results

3.1. Model performance

The relationships between skipjack tuna catches and the environmental parameters examined in this study for both fishing modes (FAD and FSC) are summarized in Table 1, along with model parameters (estimated degrees of freedom -EDF, explained deviance, AIC and GVC scores) the proportion explained by model terms and the statistical significance of covariates~~and the statistical significance of each variable~~. All variables selected in the model where highly significant (p-values < 0.01). ~~had P-values < 0.01 for both fishing mode models~~. The k-fold cross validation statistics, i.e., accuracy metric measure (RMSE) and Pearson correlation (rho), and similarity index (D) between predicted and observed values, were reasonably good (RMSE ~ 0.08, rho ~ 0.37, D=0.88), which suggests good model performance ~~were reasonably good for both FAD (RMSE ~ 0.08, r ~ 0.34) and FSC (RMSE ~ 0.09, r ~ 0.39),~~ which suggests good model performance. Furthermore, ~~in both models (FAD and FSC)~~ the goodness-of-fit for model met the basic criteria as confirmed by residual checking, i.e., residual graphic inspections using spline correlograms did not display spatial autocorrelation. Also, residual of histogram normal distribution, homogeneity of variance, and the straight linearity between fitted values and response criterions were met (Figure S4 supplementary material~~Figure 5 and 6 in S3~~).

3.2. Environmental effects

The effects of all environmental factors on ~~FAD~~ skipjack tuna catches are shown in Figure 2. The spatial-temporal interactions (Longitude x Latitude x Month), shows that skipjack tuna aggregated more in west coast of Madagascar at the latitude <18ºS whereas in the Mozambique coast the effects of the spatio-temporal interactions depicted negative catches at the areas <40.5E/16ºS between March-April and at the longitudes <39ºE in May (Figure 2). The fishing cores were predicted at the section >42ºE and <17ºS, mostly in the west tip of Madagascar. This was the most important term in the model, contributing to about 10% out of ~16% of the total model deviance (65% of the total). The interaction SST x SSTGD was the second most important term (contributed to ~2.40% in model deviance, 15% of the total). Skipjack tuna tends to aggregate more in warm waters (SST >27ºC) particularly where temperatures changed by ±1ºC over a week period. Sea surface current direction (HDG) with ~1.20% of contribution in model deviance (8% of the total), is the third most important ecological variable. The shape of functional forms for HDG revealed that skipjack tuna was most caught when the currents were moving in southward and northwest directions (Figure 2) which could be related to the anti-cyclone gyres generated around Comoro Islands. Skipjack catches shown high variance at the lowest and highest chlorophyll concentration values and an optimum range at medium levels (Figure 2). The shape of functional forms indicated an increase in skipjack tuna at sea surface height values between 0.5-0.6 m. Skipjack tuna catches were positively correlated with KE especially at medium levels (Figure 2). Together, CHL, SSH, and KE account with ~1.8% in the model deviance (11% of the total) (i.e. each covariate contributes with less than 1%).

~~had positive effects between February and June in practically all the central MZC, whereas from July to August the positive effects were depicted at the latitude below 16º S (Figure 2-a). Sea surface temperature (SST) influenced skipjack tuna to aggregate more in warm waters (SST >27ºC), particularly where temperatures changed by ±1ºC over the period of a week. Those waters are characterized by low chlorophyll concentrations (CHL<0.5 mg m^{-3}), with week to week positive changes of 0.3 mg m^{-3} (Figure 2-b). Skipjack tuna catches were positively correlated with salinity (SSS) and dissolved oxygen concentrations (DOC), whereas they presented a negative relationship with sea surface height (SSH) (Figure 2-b). The shape of functional forms indicated an increase in skipjack tuna biomass with a relative increase in slow sea surface currents (SSC < 0.2 m s^{-1}) with southward and northwest directions (Figure 2-b).~~

~~Figure 3 illustrates the environmental effects on FSC skipjack tuna catches. The top panel shows the space-time interaction with relative positive effects everywhere from February to June, whereas in July and August the model predicted positive catches in the southern area of MZC and west of 43ºE (Figure 3-a). In this model, Skipjack tuna were positively related with SST temperatures below 28ºC and negative changes of ~1.5ºC in a weeklong period. In those waters, skipjack tunas were positively related to low chlorophyll-a concentrations (CHL) (<0.07 mg m^{-3}) (Figure 3-b). Salinity revealed a flattened trend, with a positive relationship at values around 34.5-35 units, whereas SSH depicted positive effects below ~0.6m and negative effects above ~0.6m, respectively (Figure 3-b). EKE was inversely related to skipjack tuna biomass (Figure 3b).~~

3.3. Projected biomass distribution in future scenarios

Table 2 summarizes the percentage of changes to the areas where skipjack tuna distribution is projected ~~biomass accumulation is projected~~ under the future climate change scenarios. Current skipjack fishing observed ~~fishable~~ areas covered ~~~13~~25% of the Mozambique Channel, whereas the overall projected area changes for skipjack tuna aggregation is ~84%. ~~for FAD and ~11% for FSC, respectively. The overall projected area changes for skipjack biomass aggregation were estimated to be ~87% for FAD and 89% for FSC, respectively.~~

Model results for the RCP2.6 scenario (Table 2) predicted major changes ~~to~~ in size of SKJ habitat from the RPS to 2050 i.e., the fishing areas would change (sum of loss and gain) by about ~93% in the MZC (+1.5% of absolute gain). Between the RPS and 2100 the models also revealed major area changes, by ~90% (+4.3 of absolute gain). However, for the period 2050-2100 the models projected that the fishing areas for skipjack tuna would minor to 10% (-9.3 of absolute gain).

~~skipjack tuna biomass from the RPS to 2050, specifically that FAD fishing areas would change (sum of loss and gain) by about ~85% in the MZC, whereas FSC fishing areas would shift (loss plus gain) by 80%. Between the RPS and 2100, the models also revealed major area changes to both fishing strategies, by~~

about 80%. However, for the period 2050-2100 the models projected that the fishing areas for both FAD and FSC fishing tactics would minor to 20% in the study areas.

The area changes to skipjack schools predicted by the RCP8.5 scenario (Table 2) between the RPS and 2050 were about 90% (+3.7 of absolute gain) whereas from the RPS to 2100 changes were projected to ~88% (+79.7 of absolute gain). However, between 2050 - 2100 continuous change was predicted, i.e., >92% of all areas (+60.1 of absolute gain) were projected to see a shift in skipjack schools' distribution or displacement over the area of the Mozambique Channel.tuna biomass aggregations predicted by the RCP8.5 scenario (Table 2) between the RPS and 2050 were about 90% for FADs and 80% for FSC, respectively. The highest changes were projected from the RPS to 2100, which indicates that skipjack tuna biomass around FADs will shift completely with positive expansion, whereas with FSCs the spatial skipjack biomass aggregation shift was projected at ~95% of the total area for both fishing modes. However, between 2050 - 2100 continuous change was predicted, i.e., >85% of all areas were projected to see a shift in skipjack biomass accumulation in both fishing modes.

When projected using skipjack catch model the differences between future and current scenarios under the RCP2.6 and RCP8.5 climate change scenarios predicted catch losses (negative signs), no changes (zero values) and/or catches gains (positive signs) within the MZC (Figure 3). Specifically, RCP2.6 predicted skipjack catch losses of ~ 46% and ~43% in northern latitudes (< 20ºS) from the RPS to the ends of 2050 and 2100 respectively (Figure 3a-b). Positive expansion of ~ 47% toward southern latitudes (> 20ºS) was projected by the end of both 2050 and 2100 (Figure 3a-b). Whereas between 2050 and 2100 no changes to skipjack tuna catches were predicted in ~91% of fishing grounds (Figure 3c).

With respect to the RCP8.5 scenario, by 2050 catches losses (~ 43%) and positive spreading (47%) were projected in latitudes both below and above 20ºS (Figure 3d). By 2100, the model predicted positive displacement of positive anomalies (84%) recovery of tuna catches at the latitude <20ºS and these were projected to increase in the southern areas of the MZC, with particularly high aggregation of tuna schools above 24ºS (Figure 3e). A loss and unchanged on tuna catches were predicted at the narrow area between 20ºS and 24ºS covering an area of ~16%. A comparison between the 2050 and 2100 future projections

(Figure 3f) reveals that skipjack catches would be lost or unchanged around 20ºS-25ºS (~24%). By contrast, in the areas <20ºS and >25ºS the positively catch anomalies (~76%) were projected, with most accumulated in the north part of the MZC. The projections show displacement characterized by catch recovering (<20ºS) and expansion above 25ºS.

~~3.3.1. FAD model projection~~

~~When projected using the FAD-based model, the differences between future and current scenarios under the RCP2.6 and RCP8.5 climate change scenarios predicted biomass losses (negative signs), no changes to biomass (zero values) and/or biomass gains (positive signs) within the MZC (Figure 4). Specifically, RCP2.6 predicted skipjack biomass losses of ~ 31% and ~ 25% in northern latitudes (< 20ºS) from the RPS to the ends of 2050 and 2100, respectively. Positive expansion of ~ 54% toward southern latitudes (> 20ºS) was projected by the end of both 2050 and 2100 (Figure 4a-b), whereas no changes to skipjack tuna biomass accumulation were predicted in ~84% of fishing grounds between 2050 and 2100 (Figure 4c).~~

~~With respect to the RCP8.5 scenario, by 2050 biomass losses (~ 39%) and positive spreading (50%) were projected in latitudes both below and above 20ºS (Figure 4d). By 2100, the model predicted positive biomass anomalies (100%) and these were projected to increase in the southern areas of the MZC, with particularly high biomass accumulation above 24ºS (Figure 4e). A comparison between the 2050 and 2100 future projections (Figure 4f) reveals that that there is less area where skipjack biomass would be unchanged or lost around 20ºS-25ºS (~16%). By contrast, in the areas <20ºS and >25ºS the positively biomass anomalies (~84%) were projected, with most accumulated in the southernmost part of the MZC.~~

~~3.3.2. FSC model projection~~

As was the case with the FAD projection, the FSC RPS and future scenarios predicted biomass aggregation change and non-change areas. In the RCP2.6 scenario, biomass aggregation losses of ~30% were predicted at latitudes <19ºS between the RPS and 2050, whereas biomass increases were projected between 16ºS and 24ºS, and the northern tip of Madagascar (>44ºE / <12ºS). The projected gain in suitable habitats was around 50% (Figure 5a). Finally, there was barely any shift in about 20% of fishable areas, which suggests that the southward movement may mostly occur by 2050 (Figure 5a). From RPS to 2100 (Figure 5b) the maps display similar patterns of biomass displacement like this shown in Figure 5a. The areas projected with biomass positive shifting is about 49%, negative anomalies around 31%, whereas unshifted areas ~ 20% (Table 2). Despite the similarities between figures 5a and 5b for the period between 2050-2100, major skipjack biomass areas were projected to remain unchanged (81%) in both northern (<19ºS) and southern latitudes >24ºS (Figure 5c). Whereas a loss of ~19% of skipjack biomass from the half to the end of the century was predicted between the latitudes 16ªS - 24ºS, and an increase of ~3% was predicted to be scattered elsewhere in the Channel (Figure 5c).

The projections under the RCP8.5 scenario predicted different skipjack tuna biomass distributions in future scenarios (Figure 5d-f). This scenario predicted that by 2050 biomass would increase from the north to the south, with the most significant aggregation expected at around 20ºS - 24ºS. This zone (20ºS - 24ºS). and the northern tip of Madagascar (>44ºE / <12ºS), accounted with positive anomalies covered an area of 45% (Figure 5d). However, a total of 36% and 19% areas were predicted to either observe a loss of skipjack tuna biomass or remain unchanged, respectively between the RPS and 2050 (Figure 5d). From the RPS to 2100 an area equivalent to about 35% of the MZC from the northern part of the channel to 18ºS, predicted loss of biomass, except the area >44ºE / <12ºS which depicted positive anomalies. Moreover, between 18ºS-19ºS, sub-layers of ~5% of extent were projected to go unchanged and above 19ªS positive southward skipjack biomass anomalies were expected to increase (Figure 5e) and cover an area of ~60% of the MZC (Table 2). The difference between 2100 and 2050 is most likely what is driving the increased north-southward skipjack tuna biomass trend, however, the projections displayed biomass losses of ~ 45% below the latitude 20ºS, and biomass gains of ~40% at latitudes above 22ºS. Areas that were projected to see no

~~change in biomass aggregation (15%) were found at latitudes 20ºS - 22ºS and in the area >44ºE / <12ºS along the northern coast of Madagascar (Figure 5f).~~

4. Discussion

5. The GAM used in this study to model skipjack catches performed well and had a reasonable level of predicting power (RMSE < 10%). As suggested in previous studies for selection of good predictive ecological models (e.g.: Fletcher & Fortin, 2018; Norberg et al., 2019; Wikle et al., 2019) we fit a small set of models showing complementary performance, and then apply a cross-validation procedure. The low deviance explained (~16%) could be related to the exclusion of other factors or processes in the model such as fine and large scale environmental processes, inherent biological and behavioural factors, processes related to the life-cycle of the species, as well as issues related with catchability and fishing operations (e.g.: Torres-Irineo et al., 2014; Lopez et al., 2014; Lopez & Scott, 2014; Moreno et al., 2016b). For example the complex bio-physical processes dominated by eddy circulation in the MZC (e.g.: Béhagle et al., 2014; Huggett, 2014), as well as details on the biology or the behaviour of the species (e.g. school fragmentation, density dependant behaviour) are hard to detect, quantify and integrate in traditional modelling exercises and could effect model performance. Further studies should explore the use of additional or complementary environmental and biological factors to investigate model performance, as well as descriptive and predictive power of models in relation to covariate selection. Similarly, periodic revisions of the current model, as well as the use of alternative projections for environmental data could help understand in the short-term the accuracy of the model and the sensitivity of using different data products by different climate-monitoring agencies.

~~In general, skipjack tuna biomass projections for both fishing modes (FAD and FSC) exhibited distribution trends that follow the general circulation of currents in the Mozambique Channel. More specifically, skipjack tuna is expected to move from the warm waters in the north, injected by the SEC, to~~

~~the cold waters in the south, fed by Agulhas Currents (AC), thereby following the trajectory circulation of cyclones and anti-cyclone eddies (Figure 1 S1).~~

~~The effects of fishing pressure and climate change on marine ecosystems, particularly on tropical tuna species, have become a general concern in recent years (Lehodey et al., 2013; Dueri et al., 2014; Monllor-Hurtado et al., 2017; Erauskin-Extramiana et al., 2019). In this study, skipjack tuna biomass was modelled and projected under different future climate change scenarios using GAMs as a function of spatio-temporal and environmental variables for each fishing mode (FAD and FSC). Species distribution models (Loukos et al., 2003) can predict the potential habitats where biomass can be (re)distributed. Understanding the potential habitat distribution of a species like skipjack tuna could provide important information about future oceanic fishing grounds, and contribute to designing and implementing spatially-explicit management plans.~~

The relationship between environmental variables and skipjack catches has previously been modelled using GAMs (e.g., Mugo et al., 2010; Yen et al., 2016), the SEAPODYM model (e.g., Loukos et al., 2003; Lehodey et al., 2013), and the APECOSM-E model (e.g., Dueri et al., 2012; Dueri et al., 2014). The relationship between environmental variables and other tropical tuna species have also previously been modelled (e.g., Arrizabalaga et al., 2015; Druon et al., 2017; Lopez et al., 2017; Monllor-Hurtado et al., 2017). However, previous studies have rarely modelled this relationship in the MZC. Among the oceanographic variables selected in the above cited studies, SST has been considered one of the best drivers to predict the ecological niche for many pelagic species (Hobday & Pecl, 2014) including skipjack tuna (Mugo et al., 2010; Dueri et al., 2014).

Changes to SST have been considered to influence skipjack physiological abilities and migratory behaviour (Graham & Dickson, 2004). Moreover, SST can affect optimal feeding forage and growth rates of the species below 15ºC and above 30ºC (Barkley et al., 1978) and limit spawning aggregation among schools in both northern and southern latitudinal waters where temperatures average >24ºC isotherms (Matsumoto et al., 1984; Schaefer, 2001). SST may also be a good proxy for other environmental processes as well. For instance, ocean warming could modify the circulation of currents by changing water density, decreasing primary production (low chlorophyl concentration) in the surface layer and displace essential nutrients in euphotic zones by stratifying water mass thereby affecting several trophic levels (Lali and Parsons, 2006; Mann and Lazier, 2006; Miller and Wheeler, 2012). Similarly, rising of SST could induce ocean deoxygenation (Gruber, 2011; Popova et al., 2016) along with continuous sea level rise (Rahmstorf, 2007; Aral et al., 2012; Aral and Guan, 2016). Alternately increasing warming could be positively correlated with motion intensification from cyclonic or anticyclonic eddies (Matyas, 2015) shifting the redistribution of trophic level and tuna species (Potier et al., 2014). The direction of surface currents (HDG-heading) may indicate where micronekton, zooplankton and other prey are driven by surface currents and concentrated in specific patches, potentially attracting tuna schools. Béhagle et al., (2014) found that the mesoscale features in the Mozambique Channel, either cyclonic and anticyclonic, exhibited greater micronekton density. Another study from Huggett (2014) suggest that mesoscale eddy and shelf interactions play a fundamental role in shaping the Mozambique Channel pelagic ecosystem through the concentration, enhanced growth and redistribution of zooplankton communities. The present study found significant relationship with several of the environmental variables mentioned above including SST and SST gradient, CHL, KE, SSH and direction of the currents. However, further ecological or habitat analysis are needed to better understand the effects of environmental variables on the species of interest including tuna and other important species to support economic and food security in the region.

The GAMs used in this study to model both FAD and FSC fishing modes performed reasonably well and had a reasonable level of predicting power (RMSE < 10% for both models) for skipjack tuna. The relationship between environmental variables and skipjack biomass has previously been modelled using GAMs (e.g., Mugo et al., 2010; Yen et al., 2016), the SEAPODYM model (e.g., Loukos et al., 2003; Lehodey et al., 2013), and the APECOSM-E model (e.g., Dueri et al., 2012; Dueri et al., 2014). Moreover, the relationship between environmental variables and other tropical tuna species have also previously been modelled (e.g., Arrizabalaga et al., 2015; Druon et al., 2017; Lopez et al., 2017; Monllor-Hurtado et al., 2017). However, rarely have previous studies modelled this relationship in the MZC. Among the oceanographic variables selected in the above cited previous models, SST has been considered one of the best drivers to predict the ecological niche for many pelagic species (Hobday & Pecl, 2014), including skipjack tuna schools (Mugo et al., 2010; Dueri et al., 2014). Indeed, changes to SST have been considered to influence skipjack physiological abilities and migratory behaviour (Graham & Dickson, 2004). Moreover, SST can affect optimal feeding forage and growth rates at between ~15ºC and 30ºC (Barkley, Nell, & Gooding, 1978), and limit spawning aggregation among schools in both northern and southern latitudinal waters where temperatures average >24ºC isotherms (Matsumoto et al., 1984; Schaefer, 2001). Furthermore, SST may be a proxy for other environmental processes. For instance, ocean warming could modify the circulation of currents by changing water density, decreasing primary production in the surface layer, and stratifying essential nutrients in euphotic zones and, thereby affect several trophic levels (Lali and Parsons, 2006; Mann and Lazier, 2006; Miller and Wheeler, 2012). Similarly, ocean deoxygenation could also occur (Gruber, 2011; Popova et al., 2016), along with continuous sea level rise (Rahmstorf, 2007; Aral et al., 2012; Aral and Guan, 2016).

The effects of climate change on marine ecosystems, particularly on tropical tuna species have become of general concern in recent years (Lehodey et al., 2013; Dueri et al., 2014; Monllor-Hurtado et al., 2017; Erauskin-Extramiana et al., 2019). In the MZC, skipjack tuna catches exhibited distribution trends that follow the general tendencies of climate change scenarios. More specifically, skipjack tuna under the RCP2.6 scenario are expected to move from the warm waters in the north injected by the SEC to the intermediate waters in the south fed by Agulhas Current (AC). Thus, following the trajectory circulation of cyclones and anti-cyclone eddies in the area (Figure S1). Similarly the RCP8.5 scenario indicated a potential southward displacement projection by 2050 in agreement with current and future potential eddy and water circulation (e.g.: Lutjeharms & Town, 2006; Swartet al., 2010; Ternon et al., 2014). In contrast comparisons between 2100 and RPS, and 2010-2050 projected recovering trends of skipjack catches in the area <20ºS, where warming is predicted to happen faster (Roxy et al., 2014). Perhaps, the complex mechanism of water mass circulation in the MZC such as the suggested possible dilution and mixing among the northward currents (e. g.: cold North Atlantic Deep Water – NADW and Antarctic Intermediate Water - AAIW), and southward currents (e.g.: Red Sea Water -RSW and North Indian Deep Water – NIDW) and South Equatorial Currents (SEC) within the Comorian basin (e.g.: Ullgrenet al., 2012; Collins et al., 2016; Charles et al., 2020). This coupled with the effects of cyclone and anti-cyclone eddies which exchange the water mass could probably explain the displacement with restoration trend in northern of MZC. Also, Warm water (SST ~28ºC - 30ºC) is also related to tropical cyclone formation and storm intensification (Suzuki et al., 2004; Matyas, 2015) promoting high evaporation and contributing to increase precipitation in the region which could act in favour of skipjack suitable habitat. Constant monitoring and investigation of the impacts of climate change in the oceanography of the area are necessary to better assess, understand and mitigate the potential environmental consequences in MZC waters and associated habitats for species of interest. Understanding the potential habitat distribution of a species like skipjack tuna could provide important information about future oceanic and coastal fishing grounds, and contribute to designing and implementing spatially-explicit management plans.

The Intergovernmental Panel on Climate Change (IPCC) has projected ocean warming in the top 100m of the ocean deepest at between 2~~0.6~~ºC and 3~~2~~ºC by the end of the twenty-first century, depending on the severity of predictive scenarios (Collins et al., 2013). ~~Thus, P~~pelagic species, such as skipjack tuna, may respond to climate change by shifting their geographical or bathymetric distributions and the intensity of school aggregations (e.g., Cheung et al., 2013; Barange et al., 2014; Monllor-Hurtado et al., 2017). The present study was conducted in the Mozambique Channel, which is considered to be one of the most important "warming hotspot" regions in the world (Hobday and Pecl, 2014; Popova et al., 2016)~~, with sub-areas characterized by warm waters in the north and cold waters in the south (Lutjeharms and Town, 2006;Ternon et al., 2014)~~. In this context, model projections for both optimistic and pessimistic climate scenarios ~~(i.e., RCP2.6 and RCP8.5)~~ suggest that climate change will redistribute skipjack tuna from the traditional areas in the north toward areas in the southern part of the Mozambique Channel by 2050 and 2100 (Figure~~s~~ 3 ~~4 and 5~~). These results are aligned with findings for other regions of the Pacific Ocean, suggest potential catch may increase in waters that are currently cold ~~where potential biomass accumulation~~

~~may occur in waters that are currently colder~~ (Dueri et al., 2014;Yen et al., 2016). Interestingly, the results showed by RCP8.5 scenarios for the period between 2100-RPS and 2100-2050 project catch restoration in areas predicted to warm significantly (Roxy et al., 2014; Popova et al., 2016). However previous studies have predicted that warm equatorial habitats will become less favourable for tuna (e.g., Loukos et al., 2003; Lehodey et al., 2013; Dueri et al., 2014; Lehodey et al., 2015; Monllor-Hurtado et al., 2017). Therefore, additional analyses are desirable in the future to test and investigate in detail potential differences and robustness of projections of skipjack tuna using different climate scenarios and data sources.

~~Previous studies have also projected potentially suitable habitats for tropical tuna toward temperate and polar regions. By contrast, previous studies have predicted that warm equatorial habitats will become less favourable for tuna (e.g., Loukos et al., 2003; Lehodey et al., 2013; Dueri et al., 2014; Lehodey et al., 2015; Monllor-Hurtado et al., 2017)~~.

~~Overall, t~~The results of our study show that under a low greenhouse gas emissions scenario (RCP 2.6), an increase in the potential distribution of skipjack catches will be favoured towards the southern waters of the MZC with relatively high favourable fishing grounds predicted to gain ~ +1.5% and ~4.3% by 2050 and 2100, and minor loss in total fishing grounds l between 2100 - 2050 of about 9%. Similar patterns of catch anomalies at the start and the end of the century have been found in other regions of the Indian Ocean for skipjack as well (Dueri et al., 2014; Marsac, 2017). ~~biomass on FADs will be favoured towards the southern waters of the MZC.~~ By contrast, in latitudes <19ºS the effects will be negative, i.e., a decrease in skipjack biomass (Figure 4a-b).

Whilst the change would be of limited impact and may not generate major stress for skipjack tuna under the optimistic scenario (Marsac, 2017) purse seine fleets may continue to fish skipjack across the predicted suitable habitats if the operations are economically viable. However, studies investigating the effects of climate change on fishing behaviour and the socio-economic implications on industrial and non-industrial fleets operating in the region should be promoted to guarantee that coastal and oceanic fisheries adaptation and resiliency plans are developed on time.

~~Moreover, biomass anomalies were predicted to remain unchanged between 2050 and 2100 in major areas (~85%), with less decreasing, and no expansion of biomass anomalies to the new habitats (Figure 4c). Likewise, the effects of the RCP2.6 scenario on FSCs showed similar patterns of biomass anomalies and displacement (Figures 5a-c). However, the anomalies in FSC were mostly positive and generally twice as high as those observed on FADs. Similar patterns of biomass anomalies at the start and the end of the century have been found in other regions of the Indian Ocean for skipjack as well (Dueri et al., 2014; Marsac, 2017). Whilst the change would be of limited impact and may not generate major stress for skipjack tuna under the optimistic scenario (Marsac, 2017), purse seine fleets may continue to fish skipjack across the predicted suitable habitats in the Mozambique Channel in the future if the operations are economically viable. Thus, there is a need to investigate the effects of climate change on fishing behaviour and the socio-economic implications of it on industrial and non-industrial fleets.~~

~~As illustrated by the GAMs, c~~Changes to the distribution of tuna are expected to be more pronounced in the pessimistic~~substantial in the worst-case~~ climate scenario (RCP8.5), with an expansion of skipjack ~~biomass~~ catches from the fastest warming northern area of the Mozambique Channel to the south (Roxy et al., 2014; Popova et al., 2016) by 2050 with gained habitat almost to +4% relative to lost area. The redistribution pattern of skipjack fishing grounds~~biomass,~~ (Moss et al., 2010; Meinshausen et al., 2011; O'Neill et al., 2016) ~~will~~ could be a major stress and may dramatically change skipjack fisheries and species' dynamics in the MZC. The fishing grounds where skipjack are expected to accumulate by the middle of the century have previously been predicted to be industrial tuna purse seine fishing grounds~~habitats where skipjack biomass are expected to accumulate by the middle and end of the century have previously been predicted to be future industrial tuna purse seine fishing grounds~~ (Dueri et al., 2014; Marsac, 2017).

However, by the end of the century positive anomalies of fishing ground displacement were predicted, with >60% relative to the lost, suggesting that fishing grounds will be located in northern of MZC (>20ºS). Under RCP8.5 (Figure 3d-f) model predictions locations may respond to the complex hydrographic water mass dilution and mixing around Comorian basin, and elsewhere in MZC (e.g.:Ullgren et al., 2012; Collins et al, 2016; Charles et al., 2020). These could include, cyclone formation, storm intensification, evaporation and heavy rainfall (Suzuki et al., 2004; Matyas, 2015), and can contribute to water mass mixing, nutrient recycling, heat flux exchange, and redistribution of dissolved oxygen These and other processes could make the northern of MZC a productive and favourable area for skipjack.

In the worst-case scenario, major habitat gains (>50%) were projected for skipjack tuna biomass, targeted by FADs, while in FSC predicted expansion of skipjack tuna biomass were less than 50%. Moreover, in the worst-case scenario, the percentage of area either lost or gained was predicted to remain relatively steady until 2050, and then expand (≥60%) to the southernmost part of the MCZ by 2100. The same redistribution patterns of skipjack tuna found in this study under the worst case scenario have also previously been found in previous studies (e.g., Marsac, 2017; Monllor-Hurtado et al., 2017), which suggests that climate effects could drive tropical tuna to redistribute to temperate and polar regions. These possible fishing areas, wherebiomass is likely to accumulate, match the projected trajectories of mesoscale eddies in the area (Lutjeharms and Town, 2006; Swart et al., 2010), which are common features of water circulation in the Mozambique Channel. Although, the SST layers used for future scenario projections were subset from a model with a global scale coverage (Assis et al., 2018), and the SST layer do not account for particular oceanographic dynamics like those observed in the MCZ, our predictions seemed to follow the circulation of eddies predicted to exist by the end of the century.

The SST used in this study is projected to increase by 3ºC by the end of the century in the RCP8.5 scenario, with maximum temperatures reaching 31ºC. The optimal ecological niche for skipjack tuna is between 25ºC - 29ºC and, thus, an increase in SST could affect its spawning rates, larvae survival (Schaefer, 2001; Marsac, 2017), physiology, feeding behaviour, and growth rates (Barkley et al., 1978; Graham and Dickson, 2004). In such a scenario, tuna fish could be forced to leave their current habitats in the northern Mozambique Channel, which is currently the main fishing environment for industrial purse seines and local artisanal fisheries (e.g.: Dueri et al., 2014; Marsac, 2017; Chassot et al., 2019).

Climate change also interacts with other non-climate stressors, such as overfishing, habitat disruption, illegal, unreported and unregulated fishing, and marine pollution (Brander, 2008; Daw et al., 2009; Benkenstein, 2013).~~, and, t~~Thus, it is one of the many stressors in marine socio-ecological systems which impact fisheries (Perry et al.,~~, Ommer, Barange, & Werner,~~ 2010). Human and social systems could adapt to these unintended changes in several ways.~~,~~ F~~f~~or example by exploiting previously unfished resources, fishing in previously unfished locations or seasons (Brander, 2008), diversifying income sources, and/or developing a policies and governing mechanisms to facilitate or promote resilience (e.g., Badjeck et al., 2010; Grafton, 2010; Kalikoski et al., 2010). ~~However,~~Some communities in the northern area could be significantly impacted, however communities in the central and southern areas of the Mozambique channel could benefit from the redistribution of skipjack resources.~~central and southern areas of the Mozambique channel could benefit from the projected redistribution of tune, given that tuna is expected to occur there in the future~~. This disparity ~~The latter~~ has previously been documented by Allison et al. (2009), who suggested that climate change could positively impact some communities in specific locations while harming others.

Climate change is also expected to create socio-ecological uncertainties in coastal states (Badjeck et al., 2010; Grafton, 2010; Hanna, 2011). Besides the uncertainty surrounding the effects on bio-physical processes and how those effects flow through ecosystem services (Dulvy et al., 2011) and fish availability (Patrick Lehodey et al., 2011), climate effect may also change fish production costs associated with the extra fuel consumption needed to search for fish schools, and to harvest, process, store and transport the catches (Hanna, 2011). The degree of uncertainty when it comes to the negative impacts of climate change (e.g., the future distribution of tuna biomass) could potentially and primarily affect the economy and social well-being or livelihood for small-scale fisheries communities located in north of the Mozambique Channel. On a regional scale, the coastal states surrounding the MZC (e.g., the Comoros Islands, Madagascar, Mozambique, and Mayotte) could suffer an impact on their economic revenues as a result of climate variability (Hanna, 2011; Dey et al., 2016), as industrial fleets with tuna access agreements reassess their fishing strategies and move toward the more temperate areas that are projected to have more suitable fishing habitats (Grafton, 2010; Perry et al., 2010; Hanna, 2011; Hobday and Pecl, 2014). Thus, long-term climate effects may impact existing fishing agreements between the Mozambique Channel coastal states and distant water fishing nations (Havice & Reed, 2012), with potential consequences on declining socio-economic incomes for some African coastal states.

According to Allison et al.(2009), coastal nations along the MZC have a moderate to high dependence on fishing when it comes to their national economies, export revenues, and fish consumption. This and other investigations found ~~Moreover, with regard to fisheries in~~ MZC coastal state nations, ~~specifically, this same study found~~ vulnerability to climate impacts to be high and adaptive capacity to be low (Allison et al., 2009; Daw et al., 2009; Benkenstein, 2013). Therefore, fishers, fisheries managers, and decision-makers around the Mozambique Channel are encouraged ~~need~~ to take measures to make them more resilient and adapt to the socio-ecological and socio-economic uncertainty shift associated with climate change. Given that many small-scale fishers have mainly been targeting tuna and tuna-like species in the northern part of the Mozambique Channel (Mutombene et al., 2017; Chassot et al., 2019), which is an area that is predicted to become unsuitable for fishing (e.g., Roxy et al., 2014; Popova et al., 2016), they will have to adapt to this new reality by~~, for example,~~ targeting multiple species, and shifting their fishing seasons to target specific species and fishing sites. (e.g., FAO, 2006; Benkenstein, 2013; Wanyonyi et al., 2016; Mutombene et al., 2017). For fishers with strong attachments to their communities, who are ~~thus~~ either unable or unwilling to move closer to these new fishing grounds, they may have to adopt more diversified and flexible livelihoods, such as including other activities or sources of incomes other than fishing (Blythe, 2015; Lindegren and Brander, 2018). By contrast, industrial fleets may respond to climate impacts by investing in advanced technical and innovative fishing technologies (Allison et al., 2009; Grafton, 2010; Perry et al., 2010; Hanna, 2011) in order to continue fishing the original target species.

The dilemma for all fisheries stakeholders is when and how to adapt or be resilient when challenged with the uncertainties of marine ~~ecosystems~~ resources and the effects of inevitable climate change. Thus, fisheries stakeholders operating in the Mozambique Channel should develop precautionary fisheries management plans to reduce the vulnerability of fishing communities, even if these adaptation plans do not take effect for several years (Grafton, 2010). Climate change adaptation and mitigation strategies will vary according to the fishery given that the degree of exposure, sensitivity, vulnerability and adaptative capacity differs according to marine ecological ecosystem, targeted species, operational characteristics of the fleet, and social groups (Daw et al., 2009; Grafton, 2010; Lindegren and Brander, 2018). Approaches to enhance the resilience of the fishing sectors, such as adaptative co-management or inclusive Marine Spatial Planning (MSP) (Pennino et al., 2021), which haves been proposed to address uncertainty and harness the knowledge and commitment of fisheries resources at multiple scales, may be a good place to start. This study will contribute to increased awareness of the impacts of climate change on high ecological and socio-economic value fisheries, such as skipjack tuna fisheries, in the MZC. Moreover, this study will contribute to discussions on the biophysical, socio-ecological and socio-economic implications of climate change on fisheries and communities, and foster conversations at local and international scales.

5.6. Conclusion

Our findings suggest show that biophysical variables affect the distribution of skipjack tuna biomass catches in the northern part of the MZC and that species distribution will be affected by climate change, with potential implications on local and international fishing communities. This will be especially acute in the northern part of the MZC.

The model projected the distribution of skipjack tuna under optimistic (RCP2.6) and pessimistic (RCP8.5) climate change scenarios. The optimistic scenario projected that skipjack tuna biomass would shift toward the southern part of Mozambique Channel, between latitudes 19ºS and 25ºS, by 2050, and that the distribution change would be either minor or unchanged from 2050 to 2100 for both FADs and FSC. In the worst-case scenario (RCP8.5), the potential fishing habitats ground were projected on FADs at latitudes >20ºS by 2050, and positive anomalies were projected to likely occur at latitudes < 20ºS between 2050 and 2100. By the end of the century, signs of high catch distributions are expected outside of the MZC at latitudes >25ºS toward temperate regions., with high biomass distribution expected outside of the MZC at latitudes >25ºS. For FSC, positive skipjack tuna biomass anomalies were projected from the north to the

~~south with the main core expected between 17ºS-24ºS. However, the model predicted that by 2100 suitable skipjack would be accumulated in the southernmost part of the MZC.~~

Given that climate change is projected to impact skipjack fisheries in the MZC, and this may lead to~~to occur in the~~ MZC and lead to uncertain consequences on fisheries, it may lead to socioeconomic challenges for fishing communities. Coastal states in the MZC area should strengthen governance and promote policies to build resilience and increase the adaptive capacity of local, national and regional fisheries to reduce their vulnerability to climate impacts. The present study will contribute to both an increased awareness of climate change among stakeholders and demonstrates a need to develop more participatory climate mitigation and adaptation strategies.~~,~~ It is suggested that ~~such as adaptative~~ co-management or inclusive MSP are supported ~~, in order~~ to address uncertainty and connect knowledge with commitments that offer and develop alternatives to increase the resilience and adaptive capacity of the fisheries sector at both socio-ecological and socio-economic scales.

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Conflict of interest

We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere. All authors have approved the manuscript and agree with submission to *Fisheries Oceanography Journal*. We have read and abided by statements of ethical standards for manuscripts submission to Fisheries Oceanography Journal. The authors have no conflicts of interest to declare.

Data Availability Statement

The data that support the findings of this study are available from third party. Restrictions apply to the availability of these data, which were used under authorization for this study. Fishery data are available from Maria Ruiz Soto [maria.soto@ieo.es] with the permission of Spanish Oceanography Institute. Environmental Oceanography data are available from Jon Lopez [jlopez@iattc.org], and accessible from [marine.copernicus.eu], while climate data were derived from public domain resources [Bio-ORACLE - http://www.bio-oracle.org] [marine.copernicus.eu], while climate data were derived from public domain resources [Bio-ORACLE - http://www.bio-oracle.org**].**

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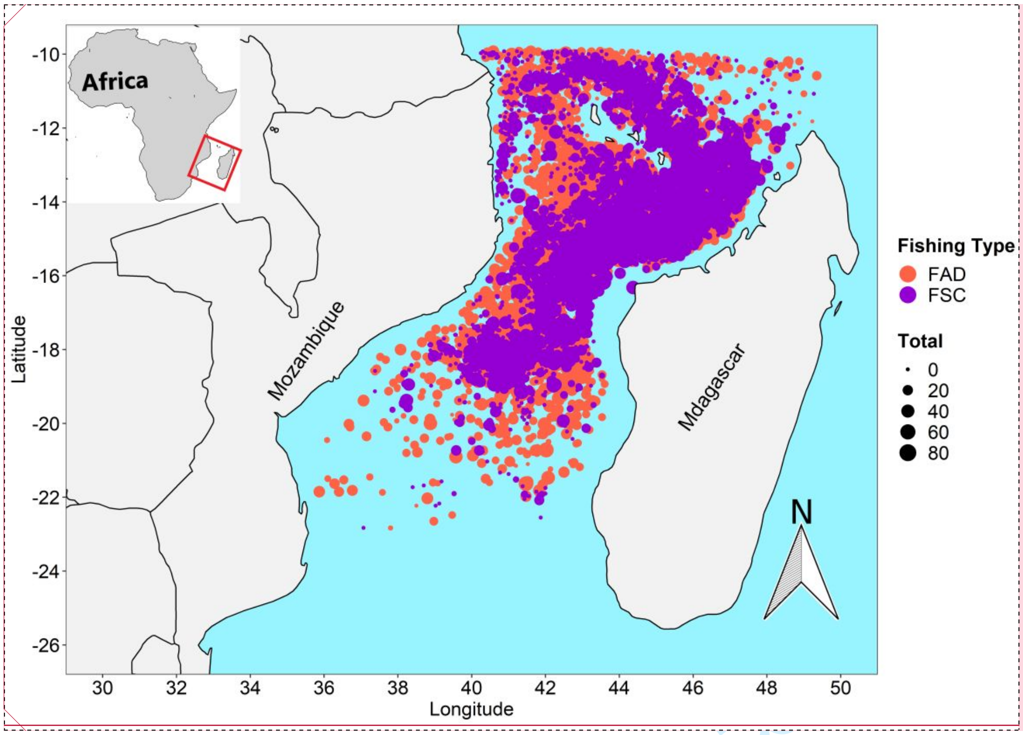

Figure 1 - Biomass distribution of Skipjack tuna in the Mozambique Channel targeted by Spanish purse seine fleets for the period 2003 - 2013 (RPS). Catches were aggregated monthly by 0.25º x 0.25º resolution. FSC - Free-Swimming Schools; FAD - Fish Aggregating Devices.

Commented [ANN1]: Replaced according to the reviewer suggestion for combining data from FAD and FSC fishing strategies

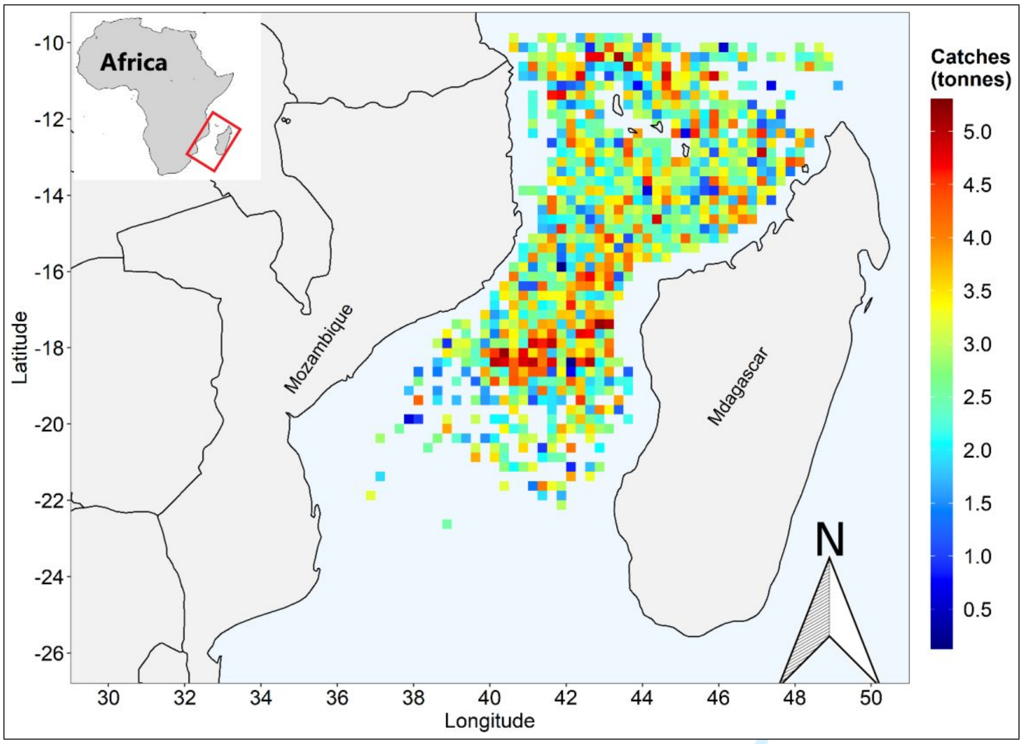

Figure 1 - Skipjack tuna catches (tonnes) distribution in the Mozambique Channel targeted by Spanish purse seine fleets for the period 2003 - 2013 (RPS). Catches aggregated were monthly by 0.25º x 0.25º resolution and displayed in the map at the logarithmic scale.

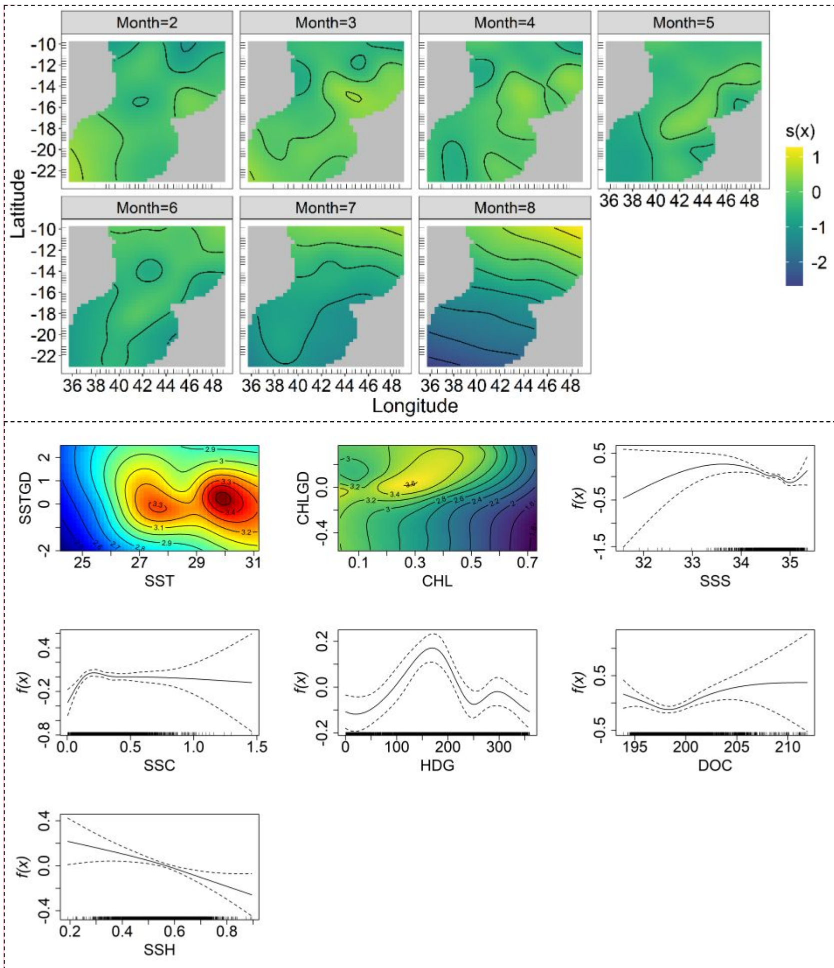

Figure 2 - Partial effects of environmental factors on the biomass of skipjack tuna of the Spanish purse seine fleets in the Mozambique Channel in the FAD fishing mode. The top panel (a) displays the space-time effects, and the bottom panel (b) displays the oceanography variable effects. Tick marks on the *x*-axis represent the observed data. The y-axes, denoted as f(x), represent the relative importance of the model's predictor variables. Dashed lines indicate the lower and upper 95% confidence intervals of the smooth plot.

Commented [ANN2]: Replaced according to the new results from single model

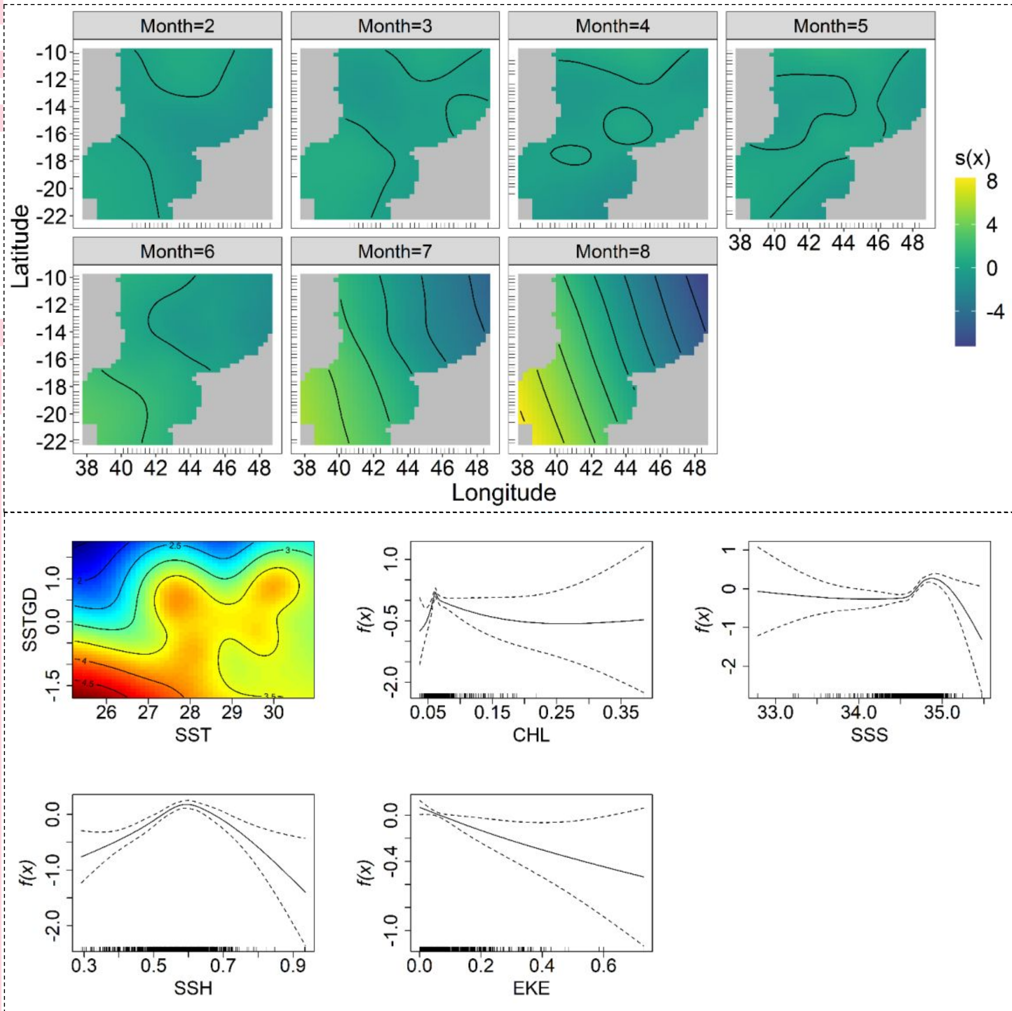

Figure 3 – Partial effects of environmental factors on the biomass of skipjack tuna in Spanish purse seine fleets in the Mozambique Channel in the FSC fishing mode. Top panel (a) displays the space-time effects, and the bottom panel (b) displays the oceanography variable effects. Tick marks on the *x*-axis are the observed data. The y-axes, denoted as f(x), reflect the relative importance of the predictor variable of the model. Dashed lines indicate the lower and upper 95% confidence intervals of the smooth plot.

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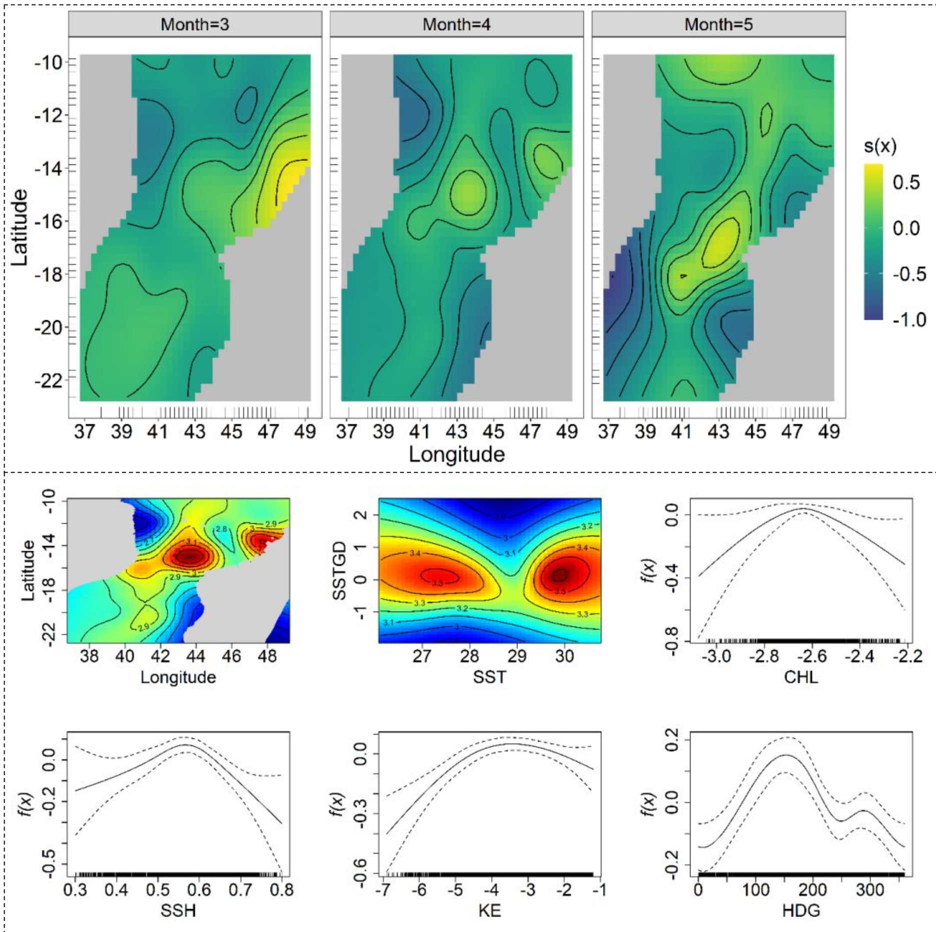

Figure 2 - Partial effects of environmental factors on the skipjack tuna catches of the Spanish purse seine fleets in the Mozambique Channel. The top panel displays the space-time effects, and the bottom panel displays the oceanography variable effects. Tick marks on the *x*-axis represent the observed data. The y-axes, denoted as f(x), represent the relative importance of the model's predictor variables. Dashed lines indicate the lower and upper 95% confidence intervals of the smooth plot.

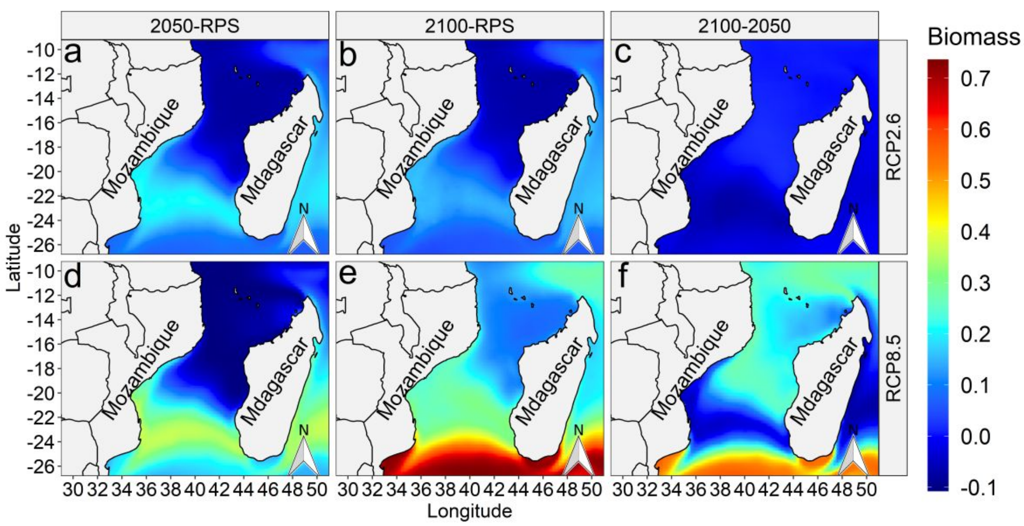

Figure 4 - Projected differences in skipjack tuna targeted around FADs between the RPS (2003-2013) and future (2050 and 2100) under the BIO-ORACLE RCP2.6 and RCP8.5 climate change scenarios. Differences depict predicted biomass between layers 2050 and the present in the first column (a and c), and between layers 2100 and 2050 in the second column (b and d).

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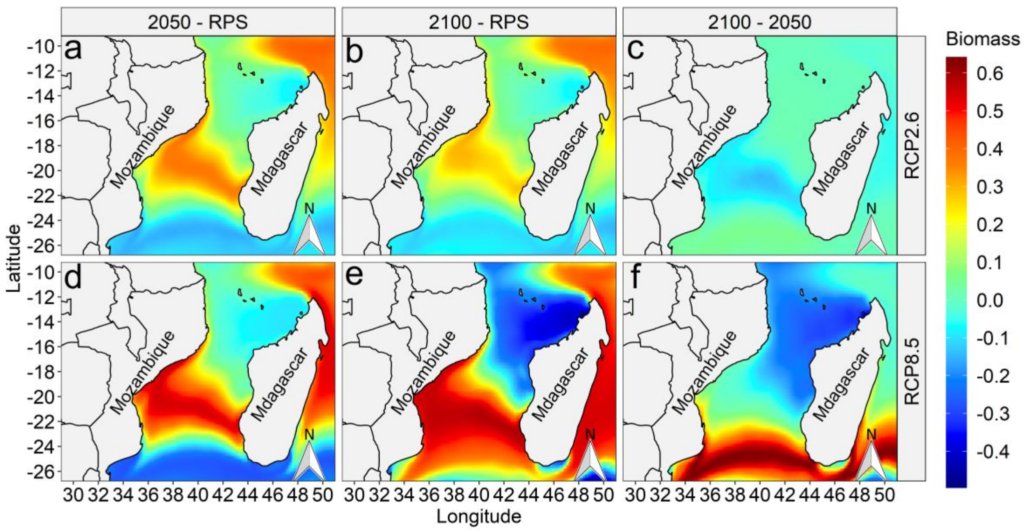

~~Figure 5 - Projected differences in skipjack tuna biomass targeted around FSC between the RPS (2003-2013) and future (2050 and 2100) under the BIO-ORACLE RCP2.6 and RCP8.5 climate change scenarios. Differences depict predicted biomass between layers 2050 and the RPS in first column (a and d), and the layers 2100 and 2050 in subsequent columns (b-e and c - f).~~

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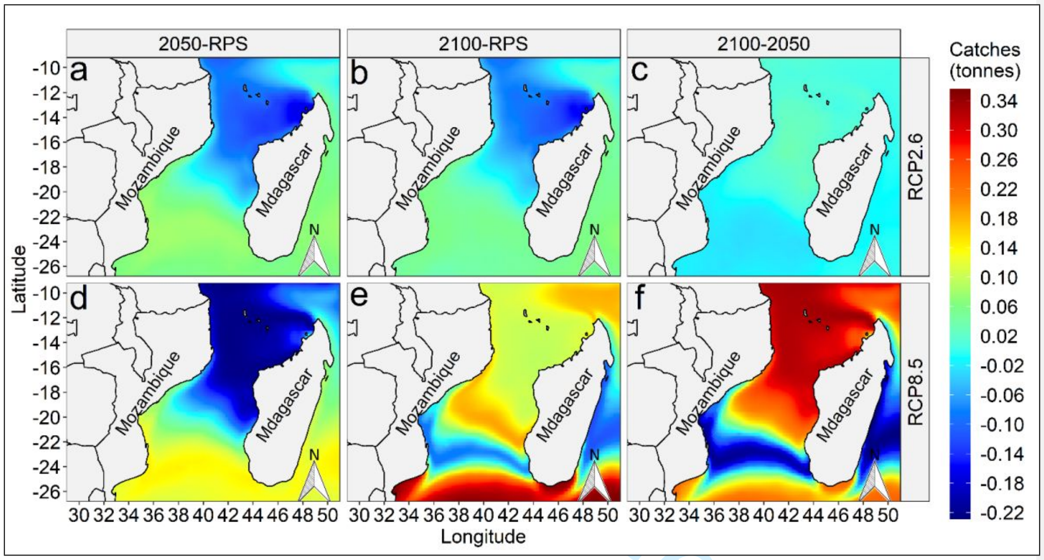

Figure 3 - Projected differences in skipjack tuna catches (tonnes) targeted by purse seine around free and associated schools between the RPS (2003-2013) and future (2050 and 2100) under the BIO-ORACLE RCP2.6 and RCP8.5 climate change scenarios. The first column (panel **a** and **d**) depicts the anomalies of predicted catches between layers 2050 and the RPS. The second column (panel **b** and **e**) show anomalies between layers 2100 and RPS, and the third column (panel b and e), display the anomalies between layers 2100 and 2050.

Table 1 - Selected GAM models for seasonal and spatial biomass distributions of tropical tuna species. All models were fitted with Gaussian distributions with identity links. EDF: effective degrees 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. EKE: eddy kinetic energy. Long: Longitude in degrees. Lat: Latitude in degrees.

Parameters	**Model fitted with gaussian family identity link**			
	FAD		**FSC**	
Adjusted R^2	0.20		0.28	
Dev. Explained. (%)	23.20		32.90	
AIC score	6617.77		2871.39	
GCV score	0.59		0.79	
n	2864		1108	
EDF	107.60		83.56	
Residual df.	2756.40		1024.44	
Covariates	***EDF***	***p-value***	***EDF***	***p-value***
CHL	-	-	4.84	<0.001
HDG	3.83	0.001		
SSH	1.40	<0.001	3.48	<0.001
SSS	4.69	<0.001	4.41	<0.001
SSC	4.25	<0.001		
EKE			0.77	0.01
Year	-	-	-	-
Oxy	3.42	<0.001		
CHL x CHLGD	9.47	<0.01		
SST x SSTGD	11.99	<0.001	14.18	<0.001
Long x Lat x Month	67.42	<0.001	51.89	<0.001

Commented [ANN1]: Replaced according to the new results from single model

Table 1 - Selected GAM model of skipjack tuna distribution in the Mozambique Channel. Models were fitted with Gaussian distributions with identity links. EDF: effective degrees of freedom, SSH: sea surface height, CHL: chlorophyll-a, SST: sea surface temperature, SSTGD: sea surface temperature gradient, HDG: heading (sea surface currents direction), KE: kinetic energy. Long: Longitude in degrees. Lat: Latitude in degrees. Dev. Covariate: is deviance explained by each covariate term in the model. Dev. Explained is the deviance explained by all covariates in the model, AIC Akaike Information Criterion. F-Statistic: give the ratio between deviance explained and not explained by covariate.

Parameters	**Mode output fitted by Gaussian family identity link function**			
Adjusted R^2	0.13			
Dev. Explained. (%)	15.60			
AIC score	8188.00			
GCV score	0.69			
n	3328			
EDF	88.88			
Residual df.	3239.12			
Covariates	***EDF***	***p-value***	**Dev. Covariate**	**F-Statistic**
CHL	2.70	<0.01	0.37	2.41
HDG	3.61	<0.001	1.22	8.52
SSH	3.17	<0.001	0.69	4.25
KE	2.64	<0.001	0.73	4.90
Year	0.02	<0.001	0.13	0.69
SST x SSTGD	11.70	<0.001	2.39	4.13
Long x Lat x Month	64.03	<0.001	10.44	1.70

Table 2 - Percentage of projected area changes for skipjack tuna biomass accumulation under future climate change scenarios, by fishing mode. Unchanged areas (%) indicated by values around zero (0) anomalies; lost areas indicated by negative anomalies, and gained areas indicated by positive anomalies and correspond to the locations with skipjack biomass aggregation. RPS - reference period of the study corresponding to 2003 - 2013.

RCP	Year	FAD			FSC		
		Unchanged	Loss	Gain	Unchanged	Loss	Gain
RCP2.6	2050 - RPS	14.75	30.66	54.49	19.93	30.30	49.77
	2100 - RPS	20.29	25.89	53.83	20.24	31.21	48.55
	2100 - 2050	84.31	15.69	-	81.08	15.88	3.04
RCP8.5	2050 - RPS	10.76	39.06	50.19	19.32	35.59	45.08
	2100 - RPS	-	-	100	4.96	35.36	59.63
	2100 - 2050	14.06	2.1	83.77	14.60	44.84	40.56
Current Fishable Area		13.42			10.77		
Overall Change		**86.58**			**89.23**		

Table 2 - Percentage of projected area changes for skipjack tuna catches accumulation under future climate change scenarios, by fishing mode. Unchanged areas (%) indicated by values around zero (0) anomalies; lost areas indicated by negative anomalies, and gained areas indicated by positive anomalies and correspond to the locations with skipjack catches aggregation. RPS - reference period of the study corresponding to 2003 - 2013.

RCP	**Year**	**Projection (%)**				
		Unchanged	**Loss**	**Gain**	**Gain + Loss**	**Gain - Loss**
RCP2.6	2050 - RPS	6.71	45.87	47.41	93.28	+1.5
	2100 - RPS	9.99	42.86	47.15	90.01	+4.3
	2100 - 2050	90.66	9.34	0	9.34	-9.3
RCP8.5	2050 - RPS	9.96	43.17	46.87	90.04	+3.7
	2100 - RPS	11.65	4.35	84.01	88.36	+79.7
	2100 - 2050	7.51	16.21	76.28	92.49	+60.1

Commented [ANN2]: Replaced according to the new results from single model