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Large-scale distribution of tuna species in a warming ocean — Source link

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Abstract

Tuna are globally distributed species of major commercial importance and a major source of protein in many countries. Tuna are characterized by dynamic distribution patterns that respond to climate variability and long-term change. Here we investigated the effect of environmental conditions on the worldwide distribution and relative abundance of six tuna species between 1958 and 2004 and estimated the expected end-of-the-century changes based on a high carbon dioxide emission scenario (RCP8.5). We created species distribution models using a long-term Japanese longline fishery dataset and two-step Generalized Additive Models. Over the historical period, suitable habitats shifted poleward for 20 out of 22 tuna stocks, based on their gravity centre and/or one of their distribution limits. On average, tuna habitat distribution limits have shifted poleward 6.5 km per decade in the northern hemisphere and 5.5 km per decade in the southern hemisphere. Larger tuna distribution shifts and relative abundance changes are expected in the future, especially by the end-of-the-century (2080-2099). Temperate tunas (albacore, Atlantic bluefin and southern bluefin) and the tropical bigeye tuna are expected to decline in the tropics and shift poleward. In contrast, skipjack and yellowfin tunas become more abundant in tropical areas as well as in most coastal countries' Exclusive Economic Zones. These results provide global information on the potential effects of climate change in tuna populations and might assist countries seeking to minimize these effects via adaptive management.

1. Introduction

Fisheries contribute to subsistence and food security for many countries. They provide wild protein resources, generate employment, promote economic growth, and comprise important renewable resource (Bell *et al.*, 2009; Gillett, 2000). Pelagic species, including both small pelagics and large tunas, consist of the largest proportion of the global marine catches (21%, 19.6 million tons) (FAO, 2016). The annual catch of tuna and tuna-like species reached about 7.7 million tons in 2014 (FAO, 2016) and this is economically important to many nations (Brill & Hobday, 2017). Furthermore, as widely distributed and highly migratory species (Arrizabalaga *et al.*, 2015; FAO, 1994; FAO, 2011), tuna play ecologically important roles in many regions due to their top-down influence on the ecosystem structure (Cox *et al.*, 2002; Sibert *et al.*, 2006). The most economically important tuna species are referred to as principal market tunas, and are caught by industrial pelagic fisheries around the globe (FAO, 2011). These principal market tunas include albacore (*Thunnus alalunga*), Atlantic bluefin tuna (*T. thynnus*), bigeye tuna (*T. obesus*), Pacific bluefin tuna (*T. orientalis*), southern bluefin tuna (*T. maccoyii*), yellowfin tuna (*T. albacares*), and skipjack tuna (*Katsuwonus pelamis*). Catches of principal market tunas reached 4.9 million tons in 2016 (ISSF, 2018) and are considered fully utilized (ISSF, 2018). The total adult biomass of tuna has been estimated to decline by 49% between 1954 and 2006 (Juan-Jordá *et al.*, 2011), and this decline has been attributed to intensified exploitation (Worm & Tittensor, 2011).

Climate change has a significant impact across all marine ecosystems, latitudes and trophic levels (Scheffers *et al.*, 2016) with many studies showing global warming effects on species distribution and abundance (Burrows *et al.*, 2011; Cheung *et al.*, 2013; Pecl *et al.*, 2017; Richardson *et al.*, 2012), as well as phenology (Asch, 2015; Poloczanska *et al.*, 2013; Poloczanska *et al.*, 2016). Climate change may redistribute the global catch potential with a 30–70% increase in high-latitude regions and a 40% decrease in the tropics (Cheung *et al.*, 2009). Increases in the proportion of tropical tuna in sub-tropical regions between 1965 and 2011 were related to ocean warming (Monllor-Hurtado *et al.*, 2017). Due to the socio-economic value of tuna species, understanding and predicting responses to global climate change are a priority for the scientific community to design effective fishery management to ensure the sustainability of tuna populations and, hence, human societies depending on them (Barange *et al.*, 2018; Hobday *et al.*, 2017). Recently, Arrizabalaga *et al.* (2015) described the global habitat preferences of commercially valuable tuna, but did not explore historical or future changes in these distributions. Other regional, single ocean, or single species projections have predicted tuna distribution and tuna population responses to climate change (Bell *et al.*, 2013; Christian & Holmes, 2016; Druon *et al.*, 2017; Dueri *et al.*, 2014; Lehodey *et al.*, 2012; Michael *et al.*, 2017). For example, studies on Pacific Ocean skipjack predict significant changes in their abundance and spatial distribution (reduction in most tropical waters and expansion in higher latitudes) in the future (Dueri *et al.*, 2014; Dueri *et al.*, 2016; Lehodey *et al.*, 2012). It has also been predicted that the distribution of tuna will be affected by changes linked to physiological characteristics. For example, a decrease in oxygen concentration will compress the vertical habitat of tuna in the water column (Mislan *et al.*, 2017).

Despite of the relevance of tuna in the global economy and the future supply of food (Mullon *et al.*, 2017), a global-scale study addressing the historical changes of the tuna habitat and providing future distributions based on climate change projections for all major commercial species is lacking. Here, we investigate the effect of environmental conditions on the worldwide distribution of six tuna species between 1958 and 2004 and estimate the expected changes by the mid and end of the century under climate change. We also analyze changes in tuna habitat within countries' Exclusive Economic Zones (EEZ) to assess the potential impact for those countries.

2. Material and Methods

2.1 Fishery data

Six of the seven most commercial tuna species were considered in this study (the temperate species - albacore, Atlantic and southern bluefin tunas, and the tropical yellowfin, bigeye, and skipjack tunas). Japanese fleet pelagic longline fishing catch and effort data were used in developing the distribution models because of their extended spatio-temporal coverage. Atlantic (AO), Indian (IO) and Pacific (PO) Ocean Japanese longline catch and effort data were obtained from the five relevant tuna Regional Fishery Management Organizations (RFMOs), i.e. International Commission for the Conservation of Atlantic Tunas (ICCAT, www.iccat.int), Indian Ocean Tuna Commission (IOTC, www.iotc.org), Western and Central Pacific Fisheries Commission (WCPFC, www.wcpfc.int), Inter-American Tropical Tuna Commission (IATTC, www.iattc.org) and Commission for the Conservation of Southern Bluefin Tuna (CCSBT, www.ccsbt.org), with the exception of WCPFC where fleet-specific information and skipjack catches were not available (Arrizabalaga *et al.*, 2015). Nominal Catch Per Unit Effort (CPUE, tuna tons per 1000 hooks) between 1958 and 2004 was calculated as the ratio of catch (tons) to the number of hooks, with the exception of SBT as catch data were in number of individuals rather than as biomass and only available from 1965 onwards. CPUE was assumed to be a proxy for fish relative abundance: we acknowledge potential issues with this assumption (e.g. Schirripa *et al.* (2017)), however, it remains the best data source for our analyses. Although the spatio-temporal resolution was heterogeneous between data sources, all CPUE were averaged by season and at 5°x5° spatial resolution.

2.2 Historical and future environmental data

Historical environmental data (1958-2004) were obtained from the PISCES biogeochemical model (Pelagic Interaction Scheme for Carbon and Ecosystem Studies, Aumont and Bopp (2006)). This model is derived from the Hamburg Model of Carbon Cycle version 5 (HAMOCC5) (Aumont *et al.*, 2003) and simulates the lower trophic levels of marine ecosystems (plankton), the biogeochemical cycles of carbon and the main limiting nutrients (Aumont *et al.*, 2015). Based on the analysis of Arrizabalaga *et al.*

(2015), the following variables were used to characterize the environmental preferences of tunas: sea surface temperature (SST in ºC), sea surface salinity (SSS in PSU), sea surface height (SSH, in m) and mixed layer depth (MLD, in m) as abiotic environmental variables, and phytoplankton (log(phyto) in log(mmol/m^3)) as biotic factor. All environmental variables were averaged to the same spatial (5º x 5º) and temporal (season) resolution as the fishery data.

Projections of oceanographic variables for the reference period (1980-1999), mid (2040-2059) and the end-of-the-21st-century (2080-2099) were extracted from the average of 16 IPCC AR5 (Fifth Assessment Report of the Intergovernmental Panel on Climate Change) models that contain a biological module (hereinafter Ensemble) with a mean ~1º spatial resolution (Cabré *et al.*, 2014). We considered the highest-carbon-emission scenario (RCP8.5 with 936 CO_2 ppm by the end-of-the-century) of the IPCC AR5 (IPCC (2013)). By the end-of-the-century, this scenario projects global average increase of temperature and SSH (2.23ºC and 0.16 m, respectively), and decrease of MLD, SSS and phytoplankton (18.7 m, 0.24 psu and 0.16 mmol/m^3, respectively).

2.3 Tuna distribution models

2.3.1 Generalized additive models

Species distribution models (SDM) associate species occurrence or abundance with environmental conditions (Elith *et al.*, 2006; Guisan & Zimmermann, 2000). SDM of tuna was constructed by modelling tuna CPUEs in relation to environmental conditions using Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990; Wood, 2012; Wood, 2017). GAMs were selected as they enable the fit of non-linear responses for a wide range of statistical distributions. The two-step methodology described in Borchers *et al.* (1997) for horse mackerel (*Trachurus trachurus*) and in (Erauskin-Extramiana *et al.*, in press) for anchovy, was adapted here for tuna catch and effort data. Tuna catch data are problematic for building reliable SDMs because the observed absences (strata with fishing effort but no catches) are restricted to the fishing area. Thus, our adapted methodology includes the generation of pseudo-absences ocean-wide depending on the range of environmental variables (Iturbide *et al.*, 2015). Following the recommendations in Barbet-Massin *et al.* (2012) to produce the most accurate predicted distributions, pseudo-absences were randomly generated ocean-wide excluding the yearly presence locations and balanced with the number of presences in each particular year (Iturbide *et al.*, 2015). In the case of Atlantic bluefin tuna, pseudo-absences were limited to the Atlantic Ocean and the Mediterranean Sea, while in the case of southern bluefin tuna they were limited to the southern hemisphere. Due to the lack of fishery data in the western and central Pacific for skipjack, no pseudo-absences for this species were generated in this area. Then, the first step was to fit the presence/pseudo-absence (PA) model to the tuna occurrence assuming a binomial error distribution with a logit-link function. The second step was to fit the abundance model (AB) for non-zero observations using the log-transformed Catch-Per-Unit-Effort (CPUE) as response variable assuming Gaussian error distribution and identity link. The expected CPUE was calculated as the product of the first and second models (PA * AB) after back-transforming the logarithm of the CPUE from the abundance model to the original CPUE scale. In order to fit unimodal response curves for the environmental variables (according to the ecological niche concept of Hutchinson (1957)) and avoid overfitting, degrees of smoothness ("k" values) were set equal or less than three. GAMs were built using the "mgcv" package in R-language (Wood, 2012) after removing all the records with missing values.

Three fixed factors (Year, Season and Stock) and their interactions were also added to the full model to correct for the spatial and temporal changes in abundance and/or catchability. The Stock factor also corrects for potential differences in the way the tuna RFMOs data are gathered, which might affect average CPUE values (Arrizabalaga *et al.*, 2015; Schirripa *et al.*, 2017).

2.3.2 Model selection and validation

The best model selection was conducted using the *dredge* function of the 'MuMIn' package (Barton, 2016). This function generates a subset of models with different combinations of variables of the global model and selects the one with the lowest AIC (Akaike Information Criterion) (Bruge *et al.*, 2016; Guisan & Zimmermann, 2000; Sakamoto *et al.*, 1986).

The presence/pseudo-absence model was validated using the cross-validation method (Burnham & Anderson, 2003), with *k*-fold equally sized sub-datasets (Hijmans *et al.*, 2013). We used *k*=5, i.e. 80% of randomly selected observations to validate the fit of the remaining (i.e. 20%). We followed the two threshold selection criteria of Jiménez-Valverde and Lobo (2007) to convert the species probability of presence to either presence (above the assigned value) or absence (below the threshold). The first criteria selected the threshold for which the sensitivity (true predicted presences) was equal to the specificity (true predicted absences). The second criteria followed the maximization of the sensitivity plus specificity.

The confusion matrix accuracy assessment (VanDerWal *et al.*, 2012) was used to evaluate how reasonable was the discrimination of the presences and absences in the PA model. Area Under the Curve (AUC) values range between 0.5 (random sorting) to 1 (perfect discrimination) and was estimated over the presences and absences estimated by the model and the presences and pseudo-absences randomly generated. Accuracy in the abundance model was calculated by comparing predictions with observations using the R-squared value and contrasted with the overall explained deviance. A large difference between both values would indicate overfitting (Villarino *et al.*, 2015).

2.4 Historical trend analysis

In order to analyze the tuna species habitats' changes between 1958 and 2004, we predicted the worldwide distribution annually according to the selected model and using the yearly aggregated environmental data for each particular year. The Gravity Center (GC) of the tuna distribution, as the mean location of the stock biomass (Bez & Rivoirard, 2001) and 5, 20, 80 and 95% percentiles (P5, P20, P80 and P95) of the location weighted by the relative abundance were calculated in order to identify changes in the distribution of tunas' populations and their shifts. P5, P20, P80 and P95 provide information of the northern and southern distribution limits in both, past and future. Relative abundance changes were also estimated as the difference between the relative abundance average for the last and first five years of the time series in each latitude.

2.4.1 Distribution and climatic indices

The potential correlations between climatic indices and the distribution GC changes were studied to test the hypothesis that population distribution changes were due to oscillations of global climatic indices instead of climate change. The climatic indices used (from https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/) were: Southern Oscillation Index (SOI), North Atlantic Oscillation (NAO), Pacific/North American teleconnection pattern (PNA), Artic Oscillation (AO), Southern Annular Mode (SAM), Trans Polar Index (TPI), Pacific Decadal Oscillation (PDO), Dipole Mode Index (DMI) and North Pacific Index (NP). The correlation between the GC and the yearly average of each climatic index was calculated in both spatial axes (latitudinal and longitudinal) but only with those indices considered to affect the distribution area of each stock.

2.5 Future projections and changes

To study the future impact of climate change on tuna distribution and relative abundance, GAM predictions for the mid (2040-2059) and the end-of-the-21st-century (2080-2099) were compared with predictions for the reference period (1980-1999). For each species, model projections were performed at each level of each of the fixed factors and then averaged. These averages represent the spatial distribution and relative abundance of tuna at each location, given an average abundance and catchability condition.

2.5.1 Expected changes in Exclusive Economic Zones (EEZs)

The potential relative abundance changes for all the species under future climate change was estimated within the exclusive economic zones (EEZs) for all coastal countries. EEZ data (from http://www.marineregions.org) delimit the 200 nautical miles boundary from each coast (Flanders Marine Institute, 2018). As the spatial resolution in coastal areas was low in projection models, we only analyzed those countries with data in more than the 30% of the grid-cells inside the EEZ. The averaged relative abundance within EEZs was estimated for the reference period as well as the future, and changes were calculated as the difference between both periods.

3. Results

3.1. Tuna distribution models

Selected tuna distribution models explained between 35.5% (southern bluefin tuna) and 62.4% (skipjack tuna) of the deviance during the reference period (S. Table 1). Most of the models included all the environmental and fixed factors but not all fixed factors interactions (S. Table 1, S. Fig. 1a, b). The models showed a good predictive power (S. Table 2) with an AUC between 0.784 (albacore tuna) and 0.838 (Atlantic bluefin tuna) for PA model and R-squared values between 0.34 (Atlantic bluefin tuna) and 0.74 (yellowfin tuna).

Global tuna relative abundance is represented in Fig. 1. Albacore tuna was distributed between 60 ºS to 60ºN worldwide with larger relative abundances in the temperate waters of Indian and Pacific oceans. Lower abundances were associated with high productive areas (such as main upwelling zones) or equatorial areas. Atlantic bluefin tuna mainly appeared north of 35ºN in the North Atlantic Ocean and in the Mediterranean Sea. Other areas in the south Atlantic off the west coast of South Africa and Namibia, and in the Southern Ocean show presence. The west Africa area was fished during the first years of the time series (mainly in the 1960's), with the last observation in 1998. Since then, no Atlantic bluefin have been caught with longline in the southern hemisphere. Southern bluefin tuna appeared between 30 and 60ºS with the highest abundances south of Australia, New Zealand, and South America (Chile and Argentina). High abundances were predicted south of the East Pacific Ocean where there was absence of fishery data. Between Australia and some Indo-Pacific islands, where southern bluefin catch data were available, very low abundances were predicted by the model. Yellowfin and bigeye tunas were distributed between the equator and the subtropics in three main oceans (Pacific, Indian and Atlantic) with higher abundances of yellowfin in the equatorial areas and between 20ºS and 20ºN in the Atlantic Ocean for bigeye. Very low or null abundances were predicted in the central Indo-Pacific region. Potential presence of both species was predicted in the Mediterranean Sea although there were no catch data there. Skipjack tuna showed a similar distribution to yellowfin and bigeye tunas.

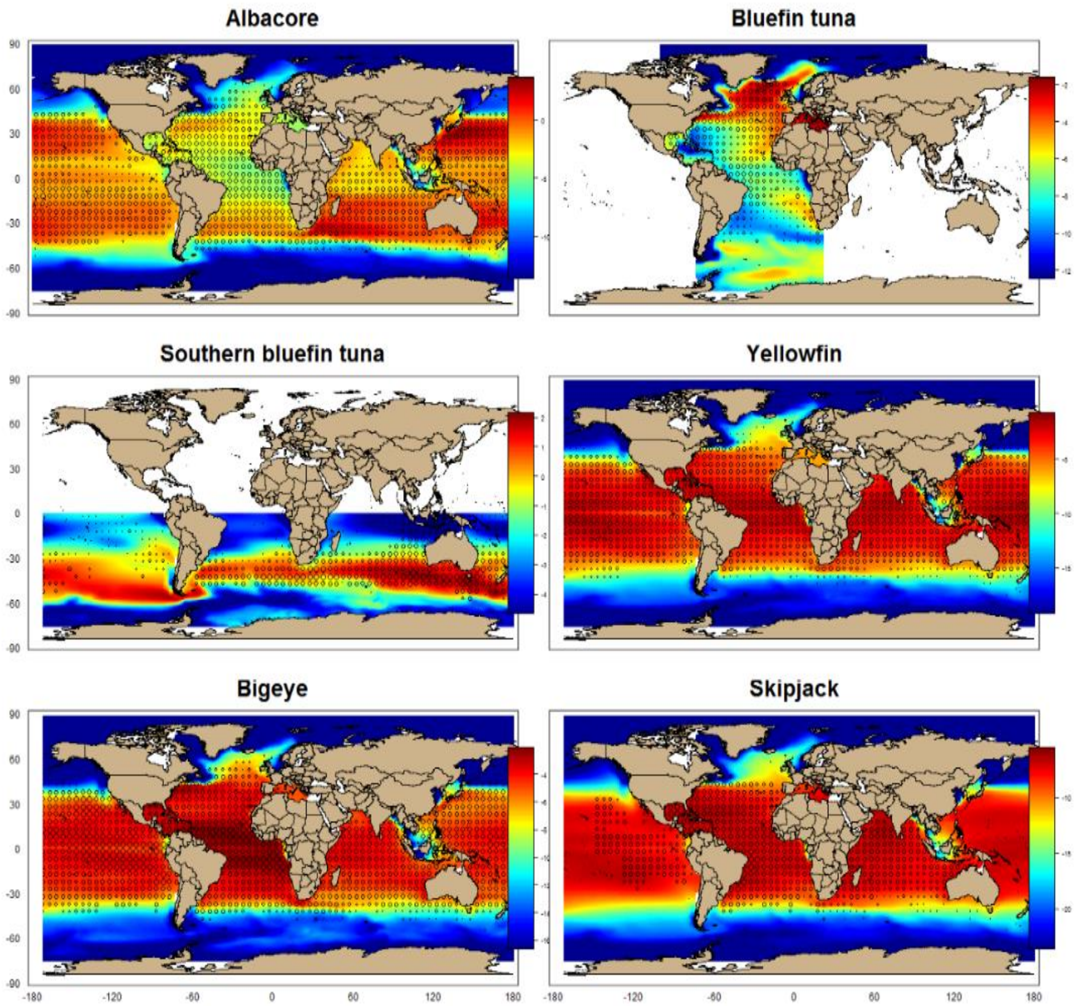

Figure 1: Global distribution of tuna species. a) Albacore tuna, b) Atlantic bluefin tuna, c) Southern bluefin tuna, d) Yellowfin tuna, e) Bigeye tuna and d) Skipjack tuna. Relative abundances (in tons/1000 hooks) are represented in a log-transformed scale. Notice the different scales for different species. The black circles represent the raw log-transformed CPUE data and the size is proportional to the value. Circles are not present in West Pacific due to the lack of catch data.

3.2. Past distribution and trend analysis

Historic tuna habitat and relative abundance showed important changes between 1958 and 2004 (Fig. 2, Fig. 3 and Table 1). Modeled albacore habitat gravity center (GC) showed significant (p-value < 0.05) poleward shifts in all the stocks (Fig. 2a, c, d, h, i, j and Table 1) with the highest change in North Atlantic Ocean (28.8 km per decade). The distribution limits shifted significantly poleward except in the south Pacific and in the Mediterranean Sea, which involves an expansion of the distribution area. Relative abundance in recent years decreased significantly (up to 50%) in the most productive area for longline between 10 and 30º N and slightly between the equator and 25º S (Fig. 3). A smaller increase occurred in the first 10º of the northern hemisphere and in the northern and southern boundaries (30-40º N and 25-35º S). The Atlantic bluefin tuna habitat GC shifted northward significantly in the West Atlantic Ocean (p-value<0.001) but this change was not significant in the East Atlantic Ocean (p-value=0.07) (Fig. 2e, g and Table 1). In both stocks, the northern limit shift further north was highly significant which means that Atlantic bluefin habitat became more suitable at higher latitudes. The relative abundance of bluefin increased slightly in all the northern hemisphere (0-60º N) in recent years (Fig. 3). The southern bluefin tuna habitat GC shifted northward towards the equator significantly (p-value < 0.001) between 1965 and 2004. In the 1960's and 1970's, southern bluefin tuna GC shifted to the pole (southward) and it was not until the 1980's when it started shifting towards the equator (Fig. 2k and Table 1). Both limits (northern and southern) shifted northward and hence, the relative abundance in recent years decreased south of 25ºS (Fig. 3). Yellowfin tuna habitat GC shifted significantly to the south in the Pacific and Indian Oceans (both p-value<0.001) but no trend was found in the Atlantic Ocean (p-value=0.87) (Fig. 2b, f, j, l and Table 1). The largest change occurred in the East Pacific Ocean at a rate of 26.6 km per decade. In general, both limits shifted southward in the Pacific and Indian Ocean but poleward in the Atlantic. The abundance in recent years increased in all latitudes except for a small decrease between 6 and 10ºN (Fig. 3). In contrast to yellowfin, bigeye tuna habitat GC shifted significantly to the north in the Atlantic Ocean (p-value=0.019) and southward in the Indian Ocean. Pacific tuna stocks showed no significant trends (p-values=0.2 and 0.65 for east and west, respectively) (Fig. 2b, l and Table 1). The distribution limits shifted poleward in the Atlantic Ocean (but only significantly in the northern hemisphere), while no trends were found in the Pacific. Bigeye tuna relative abundance increased in recent years through its distribution range, especially between the equator and 60ºN (Fig. 3). Skipjack tuna stocks showed different responses to environmental changes around the world: northward shift in the West Atlantic (p-value=0.006), southward shifts in the east and west Pacific and Indian stocks (p-value=0.046, <0.001 and <0.001 respectively), and no significant shift in the East Atlantic (p-value=0.29) (Fig. 2b, e, g, j, l and Table 1). The distribution limits did not show a trend, with a different pattern depending on the stock. Changes in the mean abundance per latitude were barely noticeable, varying between -4.3e^{-5} to 4.4e^{-5} tons/1000 hooks CPUE change (Fig. 3).

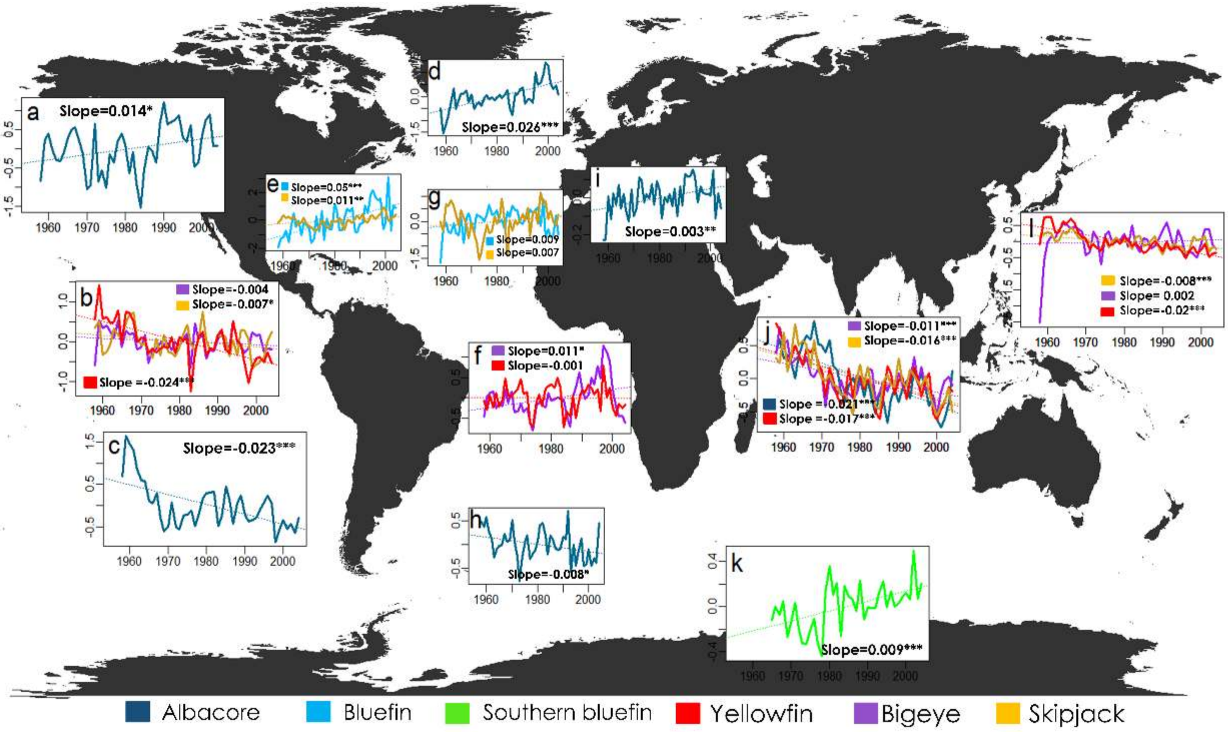

Figure 2: Historical trends for the habitat of 22 tuna stocks' gravity center anomalies (in latitudinal degrees).

In summary, 20 out of 22 stocks have shifted poleward, either their gravity centre and/or one of their distribution limits. All temperate tuna habitats shifted significantly poleward (northward in the northern hemisphere and southward in the southern hemisphere), except southern bluefin tuna which moved to the north. Tropical tunas, distributed around the equator, showed opposing shifts in their distribution limits, hence,

Table 1: Change in Gravity Center (GC, in latitudinal degrees per year), North (N) and South (S) limits estimated with percentiles 95 (P95), 80 (P80), 20 (P20) and 5 (P5) for the six-tuna species between 1958 to 2004 except in the case of S. bluefin tuna which was between 1965 and 2004. P-value < 0.001 is represented by '***', p-value between 0.001 and 0.01 with '**', and p-value >0.01 and < 0.05 by '*'.

Graphic	Species	Stock	Ocean	GC	limN (P80)	limN (P95)	limS (P20)	limS (P95)
a	Albacore	albNP	North Pacific	0.014*	0.027***	0.016*	0.003	-0.03**
b	Bigeye	betEP	East Pacific	-0.004	0.005	0.009	-0.017*	-0.02**
	Skipjack	skjEP		-0.007*	-0.003	0.01	0.003	-0.014*
	Yellowfin	yftEP		-0.024***	-0.015*	0.004	-0.034***	-0.005
c	Albacore	albSP	South Pacific	-0.023***	-0.043***	-0.035**	-0.011	-0.01*
d	Albacore	albNA	North Atlantic	0.026***	0.045***	0.035***	0.013	-0.043***
e	A. bluefin	bftW	West Atlantic	0.05***	0.018***	0.072**	0.036	0.035***
	Skipjack	skjWA		0.011**	0.012**	0.015**	0.017*	0.002
f	Bigeye	betA	Atlantic	0.011*	0.023**	0.017***	-0.002	-0.005
	Yellowfin	yftA		-0.001	0.019**	0.005	-0.013*	-0.042**
g	A. bluefin	bftE	East Atlantic	0.009	0.038***	0.025***	0.003	0.005
	Skipjack	skjEA		0.007	0.037*	0.013*	-0.009	-0.009
h	Albacore	albSA	South Atlantic	-0.008*	0.000	-0.013	-0.012*	0.000
i	Albacore	albM	Mediterranean	0.003**	0.001	0.000	0.007	0.004*
j	Albacore	albI	Indian	-0.021***	-0.023***	-0.011	-0.037***	-0.014**
	Bigeye	betI		-0.011***	-0.002	0.000	-0.011	-0.035***
	Skipjack	skjI		-0.016***	-0.002	-0.001	-0.019**	-0.017**
	Yellowfin	yftI		-0.017***	-0.005	-0.003	-0.022***	-0.037***
k	S. bluefin	sbt	Southern	0.009***	0.009	0.028***	0.006	0.01*
l	Bigeye	betWP	West Pacific	0.002	0.009	-0.029***	0.01	-0.017*
	Skipjack	skjWP		-0.008***	-0.01*	-0.012*	-0.008	-0.006
	Yellowfin	yftWP		-0.02***	-0.011*	-0.03***	-0.013*	-0.004

were less affected in their GC. They generally shifted southward in the Pacific and Indian Oceans but northward in the Atlantic Ocean. Overall, 91% of the stocks shifted poleward during the study period, representing 89% of the temperate and 92% of tropical tunas. On average, the distribution limits (P80) shifted poleward 6.5 km per decade in the northern hemisphere and 5.5 km per decade in the southern hemisphere.

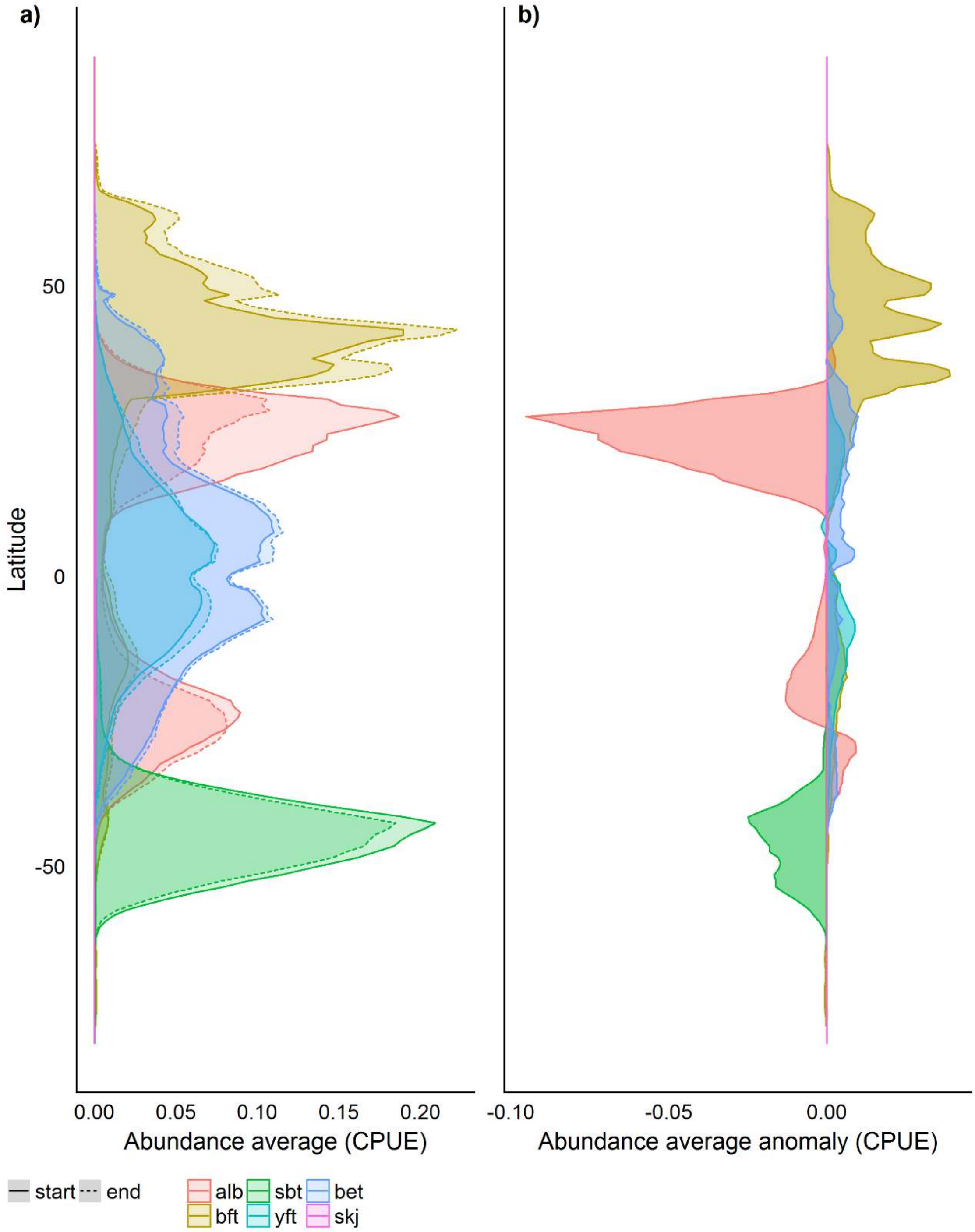

Figure 3: Relative abundance changes (in tons/1000 hooks and 10 inds/1000 hooks in the case of S. bluefin) between past (1958-1963 and 1965-1970 for S. bluefin) and recent (1999-2004) period. a) Average abundance per latitude for the two periods; b) Abundance anomalies estimated as the difference between past and recent periods for six tuna species: alb=albacore tuna, bft=A. bluefin tuna, sbt=S. bluefin tuna, yft=yellowfin tuna, bet= bigeye tuna and skj=skipjack tuna.

3.2.1. Relation with climatic indices

The analyses between latitudinal GC changes in tuna stocks and climatic indices showed very few significant correlations (S. Table 3). Only 20.5% of the latitudinal changes were related to climatic indices, and the percentage was reduced to 4.6% in the case of longitudinal shifts.

3.3. Future tuna projections

3.3.1. Distribution and relative abundance changes

Future projections of tuna habitat under the RCP8.5 climate change scenario showed similar patterns for the mid- and the end-of-the-century but with higher changes expected by 2080-2099, with respect to the reference period (1980-1999). In general, most of the species are projected to expand their northern and southern boundaries (Table 2) increasing the relative abundance in the limits of their distribution (Fig. 4) while tropical tunas as skipjack and yellowfin are expected to increase abundance in their core tropical areas and eastward in the Pacific Ocean.

The relative abundance of albacore tuna increases in the distribution limits of the Indian and Pacific Oceans, but decrease in temperate areas around South Africa, south of Japan and Taiwan and northeast of Australia (Fig. 4). The gravity center for the future moves southward for the southern hemisphere stocks (South Atlantic, South Pacific and Indian) and northward for the northern hemisphere stocks (North Atlantic and North Pacific), except in the Mediterranean Sea where albacore do not show a clear trend (Table 2). Albacore tuna expand their northern and southern limits and decrease in temperate areas (Fig. 4). Atlantic bluefin tuna decrease in most of the current North Atlantic distribution area and increase slightly in the most northern areas of the Atlantic Ocean such as around Svalbard and Jan Mayen Islands. The western Atlantic bluefin stock is impeded by land masses with regard to expansion northward, but the eastern bluefin stock extends its northern distribution limit by the end-of-the-century. The model also projects that the habitat improves in high southern latitudes, where no occurrences have been observed, shifting the West Atlantic bluefin stock southward.

Table 1: Gravity Center anomalies (GC, in latitudinal degrees), North (N) and South (S) limits estimated with percentiles 95 (P95) and 5 (P5) for the six-tuna species for mid- (2040-2059) and the end-of-the-century (2080-2099).

			Mid-cent (2040-2059)			End-end (2080-2099)		
Stock	**Species**	**Ocean**	**GC**	**N**	**S**	**GC**	**N**	**S**
albI	Albacore	Indian	-2.44	-3.00	-1.50	-4.78	-6.50	-2.50
albM		Mediterranean	-0.65	-0.38	-1.87	0.39	-0.50	1.40
albNA		North Atlantic	1.97	2.98	1.50	3.20	4.84	2.23
albNP		North Pacific	1.67	1.50	3.50	2.74	1.50	5.50
albSA		South Atlantic	-2.50	-5.28	-1.00	-4.45	-9.28	-1.50
albSP		South Pacific	-2.84	-5.00	-2.00	-4.98	-10.00	-3.00
betA	Bigeye	Atlantic	0.42	1.50	-2.21	-0.11	1.79	-2.75
betEP		East Pacific	-0.41	1.85	-1.16	-1.74	2.30	-2.05
betI		Indian	-1.14	-0.11	-1.74	-2.49	-0.89	-0.55
betWP		West Pacific	-0.34	2.46	-2.34	-2.57	2.11	-3.01
bftE	A. bluefin	East Atlantic	-3.14	1.03	-14.74	-14.28	6.38	-33.46
bftW		West Atlantic	-10.67	-0.35	8.01	-47.29	12.43	4.40
sbt	S. bluefin	Southern	-0.63	-1.00	0.00	2.29	3.00	0.50
skjEA	Skipjack	East Atlantic	1.51	5.20	-3.90	0.15	8.95	-6.99
skjEP		East Pacific	-0.04	43.89	-3.33	-0.75	35.46	-6.92
skjI		Indian	-0.81	-0.65	-3.33	-1.20	3.17	-7.38
skjWA		West Atlantic	0.68	-18.08	-4.59	1.02	-11.92	-9.46
skjWP		West Pacific	-0.18	5.68	-2.28	-1.21	-29.94	-5.48
yftA	Yellowfin	Atlantic	-0.27	0.08	-0.41	-1.13	-3.42	-0.05
yftEP		East Pacific	0.18	0.50	0.30	0.38	1.39	-0.04
yftI		Indian	0.23	0.06	-0.44	0.50	0.06	-0.46
yftWP		West Pacific	-0.09	0.50	-0.50	-0.88	1.50	-1.50

The relative abundance of the southern bluefin tuna increases in the southern limit by mid-century but it decreases in most of the reference distribution area. By the end-of-the-century (2080-2099), the relative abundance decreases in most of the distribution area compared to the reference period. As a consequence of these changes, the GC shifts slightly southward by mid-century and northward by the end-of-the-century. The southern boundary shifts northward by 2080-2099. Yellowfin tuna increase in most of their distribution area, with the highest changes projected for the equatorial areas of the Atlantic, Indian and Central Pacific Oceans. However, the abundance is expected to decrease north of Papua New Guinea and east of the Philippines. The yellowfin tuna GC shifts southward in the West Pacific and Atlantic, while northward in the East Pacific and Indian Oceans. The spatial distribution of bigeye tuna is projected to change most in the Atlantic Ocean and less so in the Pacific and Indian Oceans. The relative abundance decreases in the equatorial and tropical areas, but increases in the subtropical zones, especially in the Northeast Atlantic and in the Southeast Atlantic off South Africa and Namibia. The GC for all bigeye stocks, except in the Atlantic Ocean in 2040-2059, shifts to the south and all the stocks expand their distribution areas. The relative abundance of skipjack tuna increases in most of the distribution area, especially in the West Atlantic Ocean, the Caribbean Sea, and the Bermuda region, similar to yellowfin. Southward shifts occur in the Pacific and Indian Oceans and northward in the Atlantic Ocean. Expansions of the eastern Pacific, western Pacific, Indian, and Eastern Atlantic stocks distribution area are projected to occur by the mid-century. A contraction of the distribution is predicted for the western Atlantic and western Pacific stocks by the end-of-the-century.

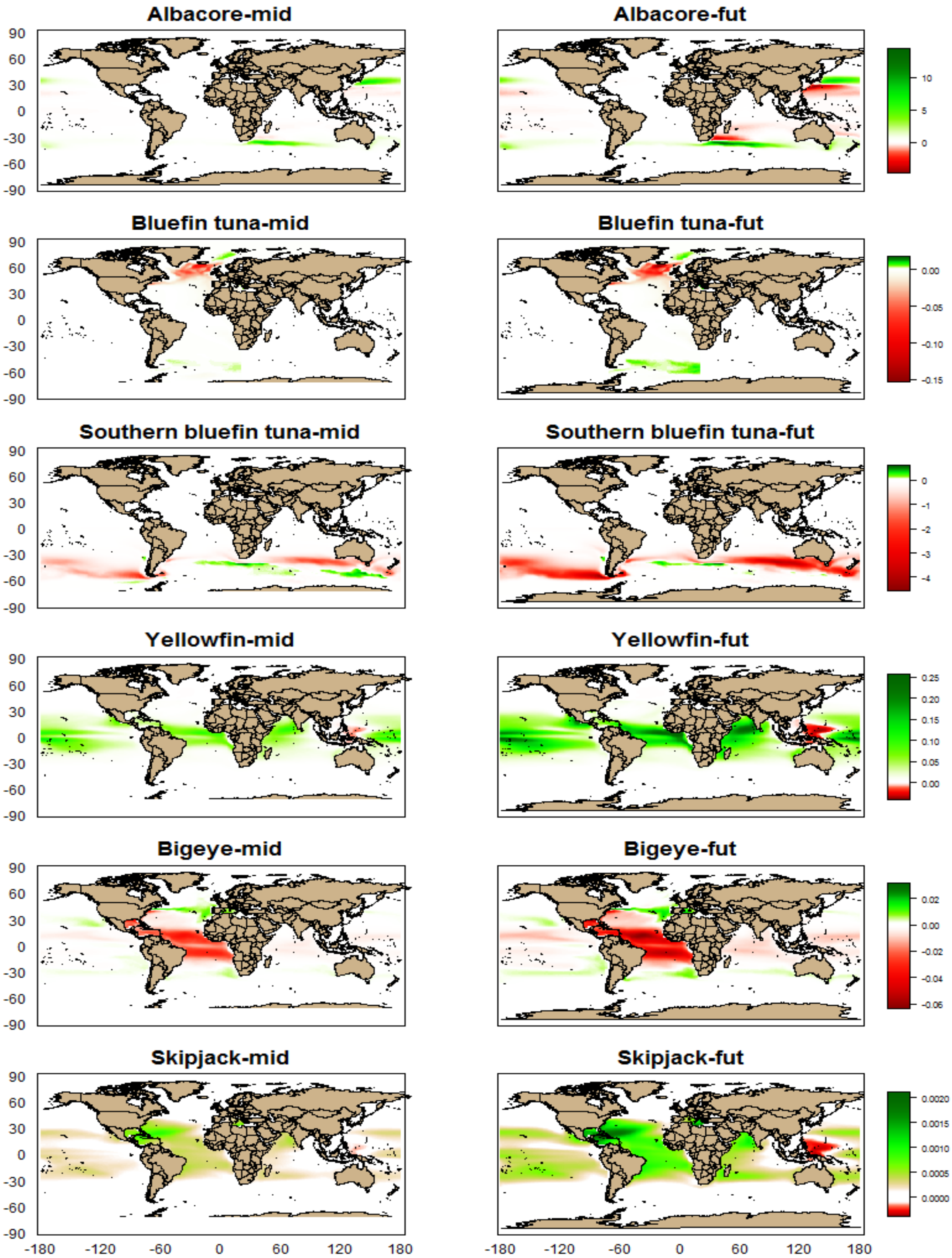

Figure 4: Gains and losses of relative abundance (in tons/1000 hooks, except for SBT, in number of individuals/1000 hooks) for mid- (left column) and end-of-the-century (right column).

3.3.2. Tuna abundance changes in the Exclusive Economic Zones (EEZ)

Important changes in tuna abundance are expected in EEZs in the future (Fig. 5). It is expected that northern countries such as Norway, Greenland, Iceland, Canada, United

Kingdom, and Ireland have the greatest depletion in Atlantic bluefin tuna abundance in the future, with higher decreases by the end-of-the-century. Similarly, the abundance of southern bluefin tuna in the southern hemisphere countries EEZ decreases, with Chile and Argentina being the countries with the highest losses. Bigeye tuna decreases in all the countries EEZ, except in a few high latitude northern and southern hemisphere countries such as Norway, Iceland, Canada, Argentina, Chile, New Zealand, South Africa, and some Northeast Atlantic countries (e.g. Portugal, Spain, France) where the abundance

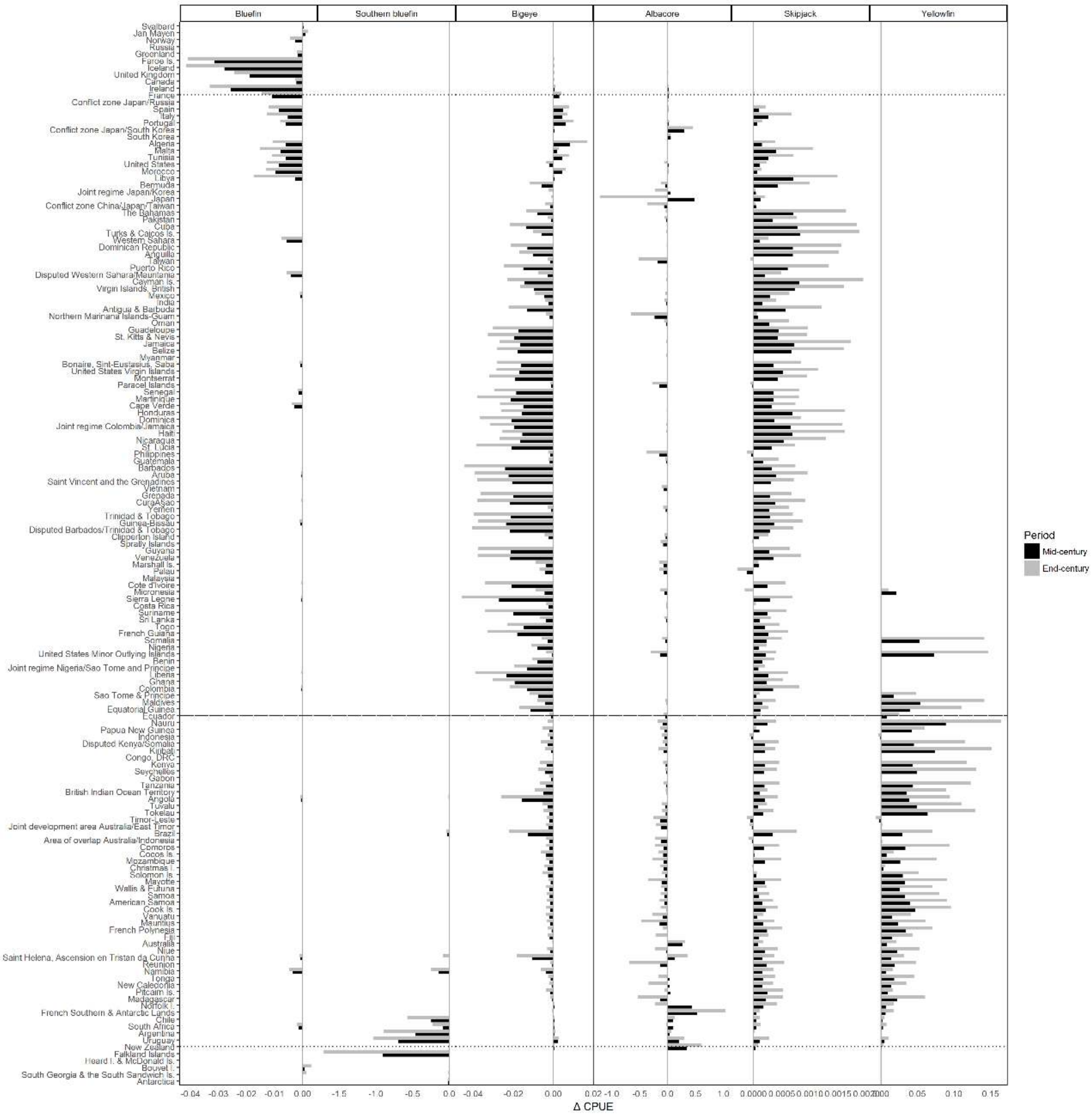

Figure 5: Relative abundance changes (in CPUE units, tons per 1000 hooks or individuals per 1000 hooks in the case of southern bluefin tuna) in different countries EEZs for mid- (2040-2059) and end-of-the-century (2080-2099) compared with the reference period (1980-1999). Countries are ordered per mean latitude of the EEZ and dotted lines represent the equator (0º) and both 45º parallels (North and South).

increases marginally. Similar to bigeye tuna, the abundance of albacore tuna decreases in most EEZs, except for some countries located around its distributional limit. Skipjack and yellowfin tunas are the only species that are projected to significantly increase in the future, despite decreasing in a few countries such as Indonesia, Malaysia, Micronesia, Palau, Philippines, and Taiwan.

4. Discussion

Tuna habitat as modelled here, has shifted poleward over the 1958-2004 period and is projected to continue to shift under climate change, with potential important consequences for coastal fisheries and the countries that depend on them. We used Japanese longline fleet data because it has been the most consistent fleet fishing in all the oceans for the longest period of time. However, the catchability and availability of skipjack tuna for the Japanese fleet is very low, as seen in the low CPUE values, hence our model predicted very small differences between tropical, subtropical and temperate waters habitat for skipjack. Moreover, the Japanese longline fleet catch mostly large fish of all species and the predicted and projected distributions should thus be considered as a proxy for the adult population.

Our method, based on the combination of presence/pseudo-absence and abundance models (AB), improved the prediction of the tuna habitat distribution and the relative abundances worldwide compared to the previous method by Arrizabalaga *et al.* (2015) although the deviance explained in the AB model is always a bit lower than in Arrizabalaga *et al.* (2015) due to the limitation that we imposed to the degree of smoothness (k=3). Particularly, our method has improved the species distribution models where presence data were not available (e.g. in areas where fish were not observed as poles).

4.1. Tuna distribution models and their reliability

In recent decades, the increased use and species distribution model development has been applied to ecological problems on many species at different spatial and temporal scales (Robinson *et al.*, 2011). However, there are still some limitations in the development of SDM. In order to avoid the assumption of a pseudo-equilibrium between the species and the environment in the short term studies (Guisan & Theurillat, 2000) and, hence, to be able to detect long-term variations (Reygondeau *et al.*, 2012), we used a long time-series dataset (47 years of tuna catch and effort data). Fixed factors and their interactions were included in the CPUE model to correct for changes in abundance and/or catchability of tuna by the Japanese fleet (Arrizabalaga *et al.*, 2015). As in the study by Reygondeau *et al.* (2012), where tuna and billfishes were found rarely on continental shelves due to low spatial resolution (5 x 5 degree), coastal results need to be interpreted carefully in our worldwide study. We partially avoided this problem by using only those countries with more than 30% of the cells with data within their EEZs. In addition, our model is two-dimensional because it does not incorporate the depth distribution changes which could be important as fishes could change their vertical distribution, moving to deeper waters to adapt to ocean warming (Dueri *et al.*, 2014; Dulvy *et al.*, 2008; Perry *et al.*, 2005). Although the reliability of our models is high (deviance explained vary between 34.5 and 74.1% and AUC values of 0.784 and 0.838), the predictions assume only the relationship between environmental variables and adult tuna distribution. Nevertheless, the geographic distribution of the species does not only depend on their environmental tolerance, but also on dispersal capacity and biological interactions (Peterson *et al.*, 2011) such as predation (Guisan & Thuiller, 2005), intraspecific or interspecific competition, trophic relationships and population dynamics. Furthermore, different responses to climate change impacts can desynchronize ecological interactions (Thackeray *et al.*, 2016).

4.2. Past distribution and abundance changes

We found a poleward shift in the suitable habitat of 89% of the temperate tuna stocks between 1958 and 2004. Southern bluefin tuna was an exception as it shifted equatorward after 1980. In the same period, 92% of the tropical tunas shifted poleward to the south in the Pacific and Indian Oceans and poleward to the north in the Atlantic Ocean, except for yellowfin and eastern skipjack where no significant trends were observed. Similarly, Monllor-Hurtado *et al.* (2017) observed that tropical tunas (bigeye, yellowfin and skipjack) longline catches decreased significantly in tropical waters and increased in sub-tropical waters from 1965 to 2011 due to a poleward shift in response to ocean warming. For many other fish species, the latitudinal shift of their habitat in the last decades has been associated with the movement of the population (Beare *et al.*, 2004; Bruge *et al.*, 2016; Montero-Serra *et al.*, 2015; Perry *et al.*, 2005). The species composition in worldwide marine fisheries has changed due to climate change; the dominance of warmer water species has increased at higher latitudes and the proportion of subtropical species has decreased in the tropics (Cheung *et al.*, 2013). Range contractions and abundance declines have also been recorded for larger tuna and billfish species such as bluefins (Worm & Tittensor, 2011).

The species distribution models can predict occurrence probability in areas where the species has not been observed or caught. For example, a favorable habitat is predicted for Atlantic bluefin tuna in the South Atlantic Ocean (below 45º S), and likewise for yellowfin and bigeye tunas in the Mediterranean Sea. This suggests that the environmental conditions (limited to those studied in this paper) in these areas are favorable for those species, but for some reason they do not occupy them. In contrast, the

SDM models can also predict low occurrence or absence where species has been observed due to low longline CPUE (e.g. southern bluefin tuna) or cannot discriminate between areas of high/low habitat suitability due to low contrast in the CPUE signal (e.g. low skipjack catchability of the Japanese longline). In the case of southern bluefin tuna, for example, there has been little Japanese longline fishery in the spawning ground in tropical waters of south of Java and off the northwest coast of Australia since 1960s (Grewe *et al.*, 1997) which could have affected the relationship with the environment and subsequent habitat suitability predictions of the model (i.e. low suitability or absence whereas some catches are observed). We also found a poleward shift between 1965 and 1979 for southern bluefin tuna and a subsequent northward shift that is difficult to explain, as it is not related to climate variability (i.e. climate indices).

Concerning habitat changes, less suitable habitat was found mainly for albacore and southern bluefin tunas over the last 50 years. Juan-Jordá *et al.* (2011) found the highest population declines for temperate tunas throughout the period 1954-2006 and these changes were attributed to their high exploitation level. However, the habitat losses described in this paper might have also contributed to these declines. We found an increase in suitable habitat for yellowfin, bigeye and Atlantic bluefin tunas and a small change in skipjack tuna between 1958 and 2004. Some studies estimated that the tropical tunas are fished down to approximately maximum sustainable levels, which prevents further sustainable expansion of catches in these fisheries (Juan-Jordá *et al.*, 2011). However, a significant increase in tuna fisheries mainly occurred in the 1970's due to the expansion of the fisheries and the development of new offshore fishing grounds (FAO, 2011), and the improvement of the suitable habitat during the last decades for these species might have also partially contributed to this expansion.

4.3. Future projections and implications for fishing countries

Future projections under different climate change scenarios are crucial to anticipate the impacts on populations of target species (Dueri *et al.*, 2014; Lehodey *et al.*, 2012), the changes in predator-prey relationships, the impacts on human services and fisheries (Bell *et al.*, 2013; Cheung *et al.*, 2013; Cheung *et al.*, 2009; Dueri *et al.*, 2016), and to identify the most vulnerable nations (Allison *et al.*, 2009; Barange *et al.*, 2018).

Although models are useful tools to project future trends and expected impacts, they also have limitations. We are estimating future potential distribution and relative abundances solely due to environmental change, but other processes that are not included in the model such as population and fisheries dynamics and trophic interactions also shape their distribution. These components are important since they can amplify the warming signal throughout the food web (Chust *et al.*, 2014). We only predicted changes in tuna habitat for RCP8.5 IPCC AR5 climate change scenario, but changes for other scenarios (RCP 2.6, 4.5 and 6.0) are expected to be similar until around 2050 when they diverge (Hoegh-Guldberg *et al.*, 2014; IPCC, 2013). Tuna habitat predictions for the end-of-the-century for other climate scenarios are likely to be between the values estimated for mid- and end-of-the-century in our models (Smith *et al.*, 2011).

Temperate tunas and bigeye are expected to decrease at low latitudes and shift poleward. Tropical tunas such as yellowfin and skipjack are projected to increase in relative abundance in the equatorial areas of the main oceans. Our results are in agreement with Lehodey *et al.* (2012) and Dueri *et al.* (2014) who predicted a slight increase of skipjack abundance in the Western Central Pacific Ocean until 2050 followed by a decrease after 2060. They also predicted that the habitat becomes more favorable in the Eastern Pacific Ocean and in higher latitudes, while the western equatorial warm pool would become less favorable for spawning.

According to our analysis, Atlantic bluefin tuna abundance is predicted to decrease across most of its geographical range and to expand northward by the end-of-the-century. This is in agreement with (Muhling *et al.*, 2016) who predicted temperature-induced reductions in tropical and sub-tropical Atlantic and an improvement in subpolar habitat suitability, with implications for spawning and migratory behaviors, and availability to fishing. This northward shift might allow fishing in more northern latitudes (McKenzie et al 2014). In addition, the southern Atlantic habitat is predicted to improve. In the past, this species occurred also in the southern Atlantic, until the "habitat bridge" through the western equatorial Atlantic linking both hemispheres was interrupted in the late 1960's (Briscoe *et al.*, 2017; Fromentin *et al.*, 2014). The predicted improvement in southern Atlantic habitat might only result in Atlantic bluefin tuna reappearance the tropical habitat bridge is restored. Similarly, southward shifts are expected for 14 other large pelagic species (including tunas) for the east and west Australian coast for the end-of-the-century with a decrease in their distribution area (Hobday, 2010).

These shifts have implications for fishing countries. A redistribution of global catch potential is expected under climate change scenarios, increasing on average 30–70% in high-latitude regions and decreasing up to 40% in the tropics (Cheung *et al.*, 2009). The strong interactions between fishing and climate require management to adapt the fishing mortality to guarantee sustainable populations, stabilize catches and profits, and reduce collateral impacts on marine ecosystems (Brander, 2007; Juan-Jordá *et al.*, 2011). This occurs when only abundance is expected to decline in the future, but when future projections involve changes in distribution (with gains and losses in suitable habitat areas), there is also potential for increases in population size (Hobday, 2010). Many of the countries that are more vulnerable to the impacts of climate change on their fisheries are also the poorest and are located in the tropics (Allison *et al.*, 2009). Catch composition and catch potential changes have direct implications for coastal fishing communities and this emphasizes the need to develop adaptation plans to minimize the impacts of global climate change on the economy, local fisheries and food security in many countries (Barange *et al.*, 2018; Cheung *et al.*, 2013). Tuna are an important source of protein in many countries and the increasing availability for Pacific nations is a possible solution to fill the future gap of protein-rich food availability (Allison *et al.*, 2009; Bell *et al.*, 2015; Gillett *et al.*, 2001).

The average catches for all the temperate tuna species (albacore, Atlantic and southern bluefin) and the tropical bigeye are expected to decrease in the future in tropical EEZs, but to increase in the countries located in the boundaries of the suitable area. In contrast, catches for other tropical tuna species (yellowfin and skipjack) are expected to increase in most of the tropical EEZs. Our results support Bell *et al.* (2013), with 82.4% agreement in the results of the Pacific Island countries and territories (PICTs) having a change in skipjack catch within their EEZ (S. Table 4). They estimated changes for 2050 and 2100 relative to the 20-years average from 1980-2000 under the A2 emissions scenario (slightly lower emissions levels than the RCP8.5 in IPCC AR5, Rogelj *et al.* (2012)). We projected a decrease in skipjack tuna in Palau EEZ for both periods, while Bell *et al.* (2013) expected an increase by 2050 and a decrease by 2100. The other exceptions were Solomon Islands and Papua New Guinea where our model projected an increase in abundance and Bell *et al.* (2013) foresaw a decrease. Changes in catch potential estimated by Cheung *et al.* (2009) based on >1000 species showed similar latitudinal patterns found for temperate tunas and bigeye in our study. They expected gains in some high-latitude countries/regions in the northern hemisphere while losses in many tropical and subtropical countries/regions. The highest catch potentials were projected for the northern Atlantic Ocean countries such as Norway, Greenland and Iceland with an increase of 18–

45%, followed by the northern Pacific Ocean (Alaska and Russia) with 20%. In contrast, the catch potential from most other EEZ countries (most of them in tropical and subtropical regions) diminish, with the largest decrease projected in Indonesia (Cheung *et al.*, 2009).

Changes in the distribution of tuna in different countries may have implications for global food security and strongly impact many tropical communities, which are strongly dependent on local fishing resources (Allison *et al.*, 2009; Bell *et al.*, 2018; Cheung *et al.*, 2009). Thus, the generation of knowledge on the most vulnerable countries to climate change is an important research task. Further analysis should focus on the local impacts that the distribution and abundance changes of tunas have on small fisher communities and the adaptation mechanisms needed to diminish the impacts. Such adaptation strategies could involve shifts in fishing areas, changes in target species, and/or changes in fishing agreements (Barange *et al.*, 2018) and must be developed in partnership with affected nations.

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