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Large-scale distribution of tuna species in a warming ocean

Maite Erauskin-Extramiana[1] | Haritz Arrizabalaga[2] | Alistair J. Hobday[3] | Anna Cabré[4] | Leire Ibaibarriaga[1] | Igor Arregui[2] | Hilario Murua[2] | Guillem Chust[1]

[1]AZTI, Marine Research Division, Sukarrieta, Basque Country, Spain
[2]AZTI, Marine Research Division, Pasaia, Basque Country, Spain
[3]Oceans and Atmosphere, Commonwealth Scientific and Industrial Research Organization, Hobart, Tas., Australia
[4]Institute of Marine Sciences, Passeig Marítim, Barcelona, Catalonia, Spain

Correspondence
Maite Erauskin-Extramiana, AZTI, Marine Research Division, Sukarrieta, Basque Country, Spain.
Email: merauskin@azti.es

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Abstract

Tuna are globally distributed species of major commercial importance and some tuna species are 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 world-wide 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-greenhouse gas concentration 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 (GC) 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 changes in abundance 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 are projected to become more abundant in tropical areas as well as in most coastal countries' exclusive economic zones (EEZ). These results provide global information on the potential effects of climate change in tuna populations and can assist countries seeking to minimize these effects via adaptive management.

KEYWORDS
climate change, exclusive economic zone, future projections, poleward shift, species distribution model, tuna

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 pelagic fishes and large tunas, comprise the largest proportion (21%, 19.6 million tons) of global catches (including crustacean, mollusks and freshwater fishes) (FAO, 2016). The annual catch of tuna and tuna-like species reached about 7.7 million tons in 2014 (FAO, 2016) and represents an economically important contribution to many nations (Brill & Hobday, 2017). 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). The total adult biomass of tuna has been estimated to decline by 49% between 1954 and 2006 (Juan-Jordá, Mosqueira, Cooper, Freire, & Dulvy, 2011), and this decline has been attributed to intensive 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, Watson, & Pauly, 2013; Pecl et al., 2017; Richardson et al., 2012), as well as phenology (Asch, 2015; Poloczanska et al., 2013, 2016). Climate change is predicted to lead to a redistribution of 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, Pennino, & Sanchez-Lizaso, 2017). Due to the socioeconomic value of tuna species, understanding and predicting responses to global climate change are a priority for the scientific community to assist in the design of effective fishery management to ensure the sustainability of tuna populations and, hence, the development of the 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 efforts have projected tuna distribution and tuna population responses to climate change (Bell, Reid, et al., 2013; Christian & Holmes, 2016; Druon, Chassot, Murua, & Lopez, 2017; Dueri, Bopp, & Maury, 2014; Lehodey, Senina, Calmettes, Hampton, & Nicol, 2013; Michael, Wilcox, Tuck, Hobday, & Strutton, 2017). For example, studies on Pacific Ocean skipjack project 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, 2016; Lehodey et al., 2013). 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 is expected to compress the vertical habitat of tuna in the water column (Mislan, Deutsch, Brill, Dunne, & Sarmiento, 2017). In general, regional and local studies have used a variety of approaches, with knowledge gaps for most of the large pelagic species, such as critical environmental conditions (Trenkel et al., 2014) making them difficult to compare in the absence of a common baseline (Arrizabalaga et al., 2015). In the case of tunas, habitat studies covering their worldwide distribution are required to address global management issues and facilitate the integration of Ecosystem Approach to Fisheries Management in a consistent way across tuna Regional Fishery Management Organizations (RFMOs) (Arrizabalaga et al., 2015; Juan-Jordá, Murua, Arrizabalaga, Dulvy, & Restrepo, 2018). This is particularly important in the case of tunas because they are widely distributed and highly migratory species (Arrizabalaga et al., 2015; FAO, 2011, 2014) playing ecologically important roles in many regions due to their top-down influence on the ecosystem structure (Cox et al., 2002; Sibert, Hampton, Kleiber, & Maunder, 2006).

Despite 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 projected changes by mid- and end-of-the-century under climate change. We also analyze the changes in tuna habitat within countries' exclusive economic zones (EEZ) to assess the potential impact for those countries. The findings will be relevant for tuna stock management and will contribute to understanding the potential impacts of climate change in fisheries and fishing nations.

2 | MATERIALS 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 spatiotemporal coverage. Atlantic (AO), Indian (IO), and Pacific (PO) Ocean Japanese longline catch and effort data were obtained from the five relevant tuna RFMOs, that is 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 1,000 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 onward. Although the spatiotemporal resolution was heterogeneous between data sources, all CPUE were averaged by season and at 5° × 5° spatial resolution. Our dataset has some limitations. CPUE was assumed to be a proxy for fish relative abundance and we acknowledge potential issues with this assumption (e.g., Schirripa et al. 2017), and that longline gear is not efficient for catching skipjack tuna, as its catchability is very low. However, the longline method catches a wide range of species in a consistent way over a vast spatial scale and time (Arrizabalaga et al., 2015); thus, its main strength is the consistency during time and space for the most commercially valuable tuna species worldwide and it remains the best data source for our analyses. Beyond some data inaccuracies in specific locations, our approach is consistent and the longline fishery data are suited to the objectives of the study, since we use a single fishing gear, which represents a "common baseline" for all the species observations. Other gears (e.g., purse seine or baitboat, which do target skipjack tuna), show a much more limited spatial and temporal distribution. Furthermore, the persistent suitable habitat for longline fishing is contained within the tropical and temperate latitudes which seem consistent with the global latitudinal habitat preferences displayed by the top six tuna target species, which are among the main target species of longliners in the high seas (Ortuño-Crespo et al., 2018).

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, Maier-Reimer, Blain, & Monfray, 2003) and simulates the lower trophic levels of marine ecosystems (plankton), the biogeochemical cycles of carbon and the main limiting nutrients (Aumont, Éthé, Tagliabue, Bopp, & Gehlen, 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 (in °C), sea surface salinity (SSS, in PSU), sea surface height anomaly (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 degree square (5° × 5°) 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 (called Ensemble) with a mean ~1° spatial resolution (Cabré, Marinov, & Leung, 2015). We considered the highest greenhouse gas concentration scenario (RCP8.5 with 936 CO2 ppm by the end-of-the-century) of the IPCC AR5 (IPCC (2013)) among the four scenarios considered; RCP8.5 is usually used as "business as usual" scenario for the purposes of estimating the worst consequences of climate change. We implemented the Precautionary Approach which represents "caution in advance." When assessing risk management responses, given the uncertainty of occurrence of any of the IPCC scenarios, the worst scenario should be an important consideration by policy makers. On the other hand, the results for the rest of the scenarios will be contained in the worst scenario, just with the change attained latter. The RCP8.5 climate scenario projects a global average increase of temperature and SSH (2.23°C and 0.16 m, respectively), and a 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 modeling tuna CPUEs in relation to environmental conditions using generalized additive models (GAMs) (Hastie & Tibshirani, 1990; Wood, 2012, 2017). GAMs were selected as they enable the fit of nonlinear responses for a wide range of statistical distributions. The two-step methodology described in Borchers, Buckland, Priede, and Ahmadi (1997) for horse mackerel (*Trachurus trachurus*) and Erauskin-Extramiana et al. (2019) 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, in our model the pseudo-absences were randomly generated through time and space, only excluding points with the presence data and balanced with the number of presences in each particular year following Barbet-Massin, Jiguet, Albert, and Thuiller (2012), Elith and Leathwick (2009), Guisan and Theurillat (2000), and 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. 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 nonzero observations using the log-transformed 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 to avoid overfitting, degrees of smoothness ("*k*" values) were set equal or less than 3. 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" R-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, Alvarez, Fontán, Cotano, & Chust, 2016; Guisan & Zimmermann, 2000; Sakamoto, Ishiguro, & Kitagawa, 1986).

The presence/pseudo-absence model was validated using the cross-validation method (Burnham & Anderson, 2003), with *k*-fold equally sized sub-datasets (Hijmans, Phillips, Leathwick, & Elith, 2013). We used k = 5, that is 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, Falconi, Januchowski, Shoo, & Storlie, 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) and 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' habitat 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 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 trends in the distribution of tunas' populations and their shifts (considering significant a $p < 0.05$). P5, P20, P80, and P95 provide information of the northern and southern distribution limits in both, past and future. Abundance changes were also estimated as the difference between the relative abundance average for the last and first 5 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 as follows: 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 estimate the future impact of climate change on tuna distribution and relative abundance, GAM projections 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 EEZs

The potential abundance changes (in CPUE, tonnes per 1000 hooks) averaged per grid cell for all the species under future climate change was estimated within the 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 and 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 (Table S1). Most of the models included all the environmental and fixed factors but not all fixed factors interactions (Table S1, Figure S1a,b). The models showed good predictive power (Table 2) with an AUC between 0.784 (albacore tuna) and 0.838 (Atlantic bluefin tuna) for PA model, sensitivity between 0.796 (S. bluefin) and 0.882 (yellowfin), specificity between 0.724 (albacore) and 0.806 (A. bluefin), and *R*-squared values between 0.34 (Atlantic bluefin tuna) and 0.74 (yellowfin tuna).

Global tuna relative abundance is represented in Figure 1. Albacore tuna was distributed between 60°S to 60°N worldwide with larger relative abundances in the temperate waters of Indian and Pacific oceans (Figure 1a). Lower abundances were associated with high-productive areas (such as main upwelling zones) or equatorial areas. Atlantic bluefin tuna mainly appeared north of 35°N in the North Atlantic Ocean and in the Mediterranean Sea (Figure 1b). Other areas in the south Atlantic off the west coast of South Africa and Namibia, and in the Southern Ocean show the presence. The West Africa area was fished during the first years of the time series (mainly in the 1960s), 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 60°S with the highest abundances south of Australia, New Zealand, and South America (Chile and Argentina) (Figure 1c). High abundances

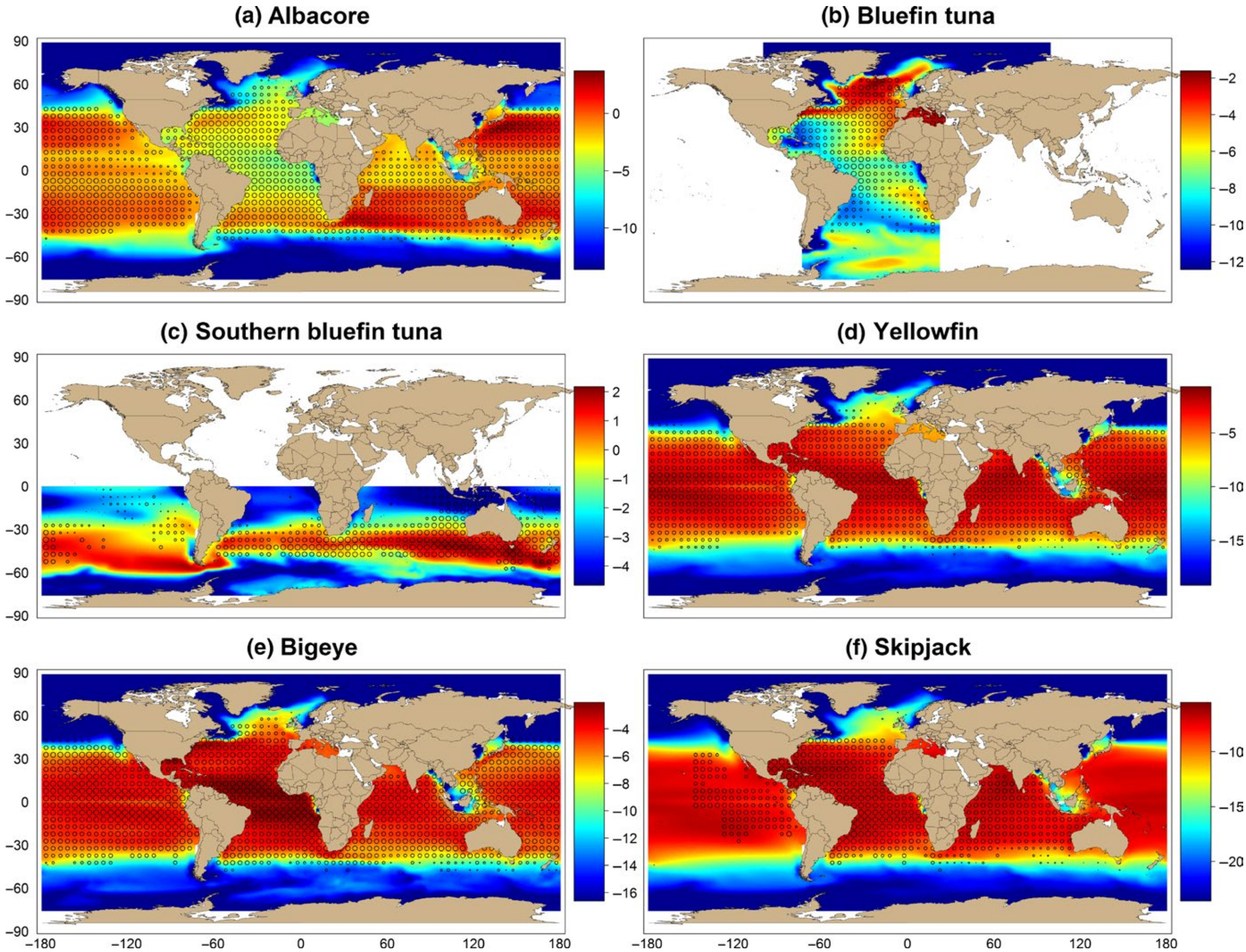

FIGURE 1 Global distribution of tuna species. (a) Albacore tuna, (b) Atlantic bluefin tuna, (c) Southern bluefin tuna, (d) Yellowfin tuna, (e) Bigeye tuna, and (f) Skipjack tuna. Relative abundances (in tons per 1,000 hooks) are represented in a log-transformed scale. Notice the different scales for 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 in skipjack due to the lack of catch data [Colour figure can be viewed at wileyonlinelibrary.com]

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 20°S and 20°N in the Atlantic Ocean for bigeye (Figure 1d,e). Very low or null abundances were predicted in the central Indo-Pacific region. The 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 1f).

3.2 | Past distribution and trend analysis

Historic tuna habitat and relative abundance showed important changes between 1958 and 2004 (Figures 2 and 3 and Table 1). Modeled albacore latitudinal habitat GC (GClat) showed significant ($p < 0.05$) poleward shifts in all the stocks (Figure 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 30°N and slightly between the equator and 25°S (Figure 3). A smaller increase occurred in the first 10° of the northern hemisphere and in the northern and southern boundaries (30–40°N and 25–35°S). The longitudinal shifts (GClon) were less pronounced (Table 1). North Atlantic and Mediterranean stocks shifted eastward while in the South Atlantic shifts were to the west. The Atlantic bluefin tuna habitat GClat shifted northward significantly in the West Atlantic Ocean ($p < 0.001$) but this change was not significant in the east Atlantic Ocean ($p = 0.07$) (Figure 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 and had not significant shift

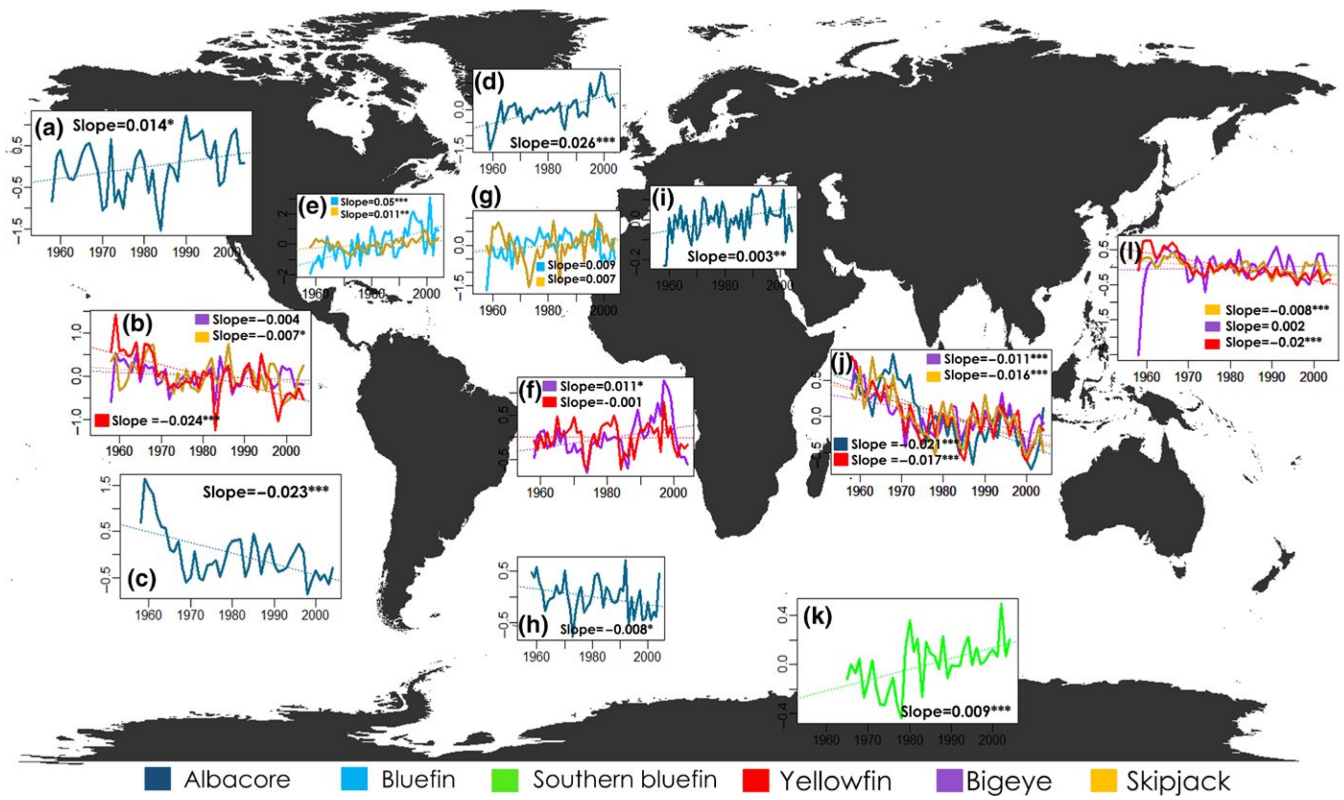

FIGURE 2 Historical trends for the habitat of 22 tuna stocks' gravity center anomalies (in latitudinal degrees) [Colour figure can be viewed at wileyonlinelibrary.com]

in longitude. The relative abundance of bluefin increased slightly in all the northern hemisphere (0–60°N) in recent years (Figure 3). The southern bluefin tuna habitat GC shifted northward toward the equator significantly ($p < 0.001$) between 1965 and 2004. In the 1960s and 1970s, southern bluefin tuna GC shifted to the pole (southward) and it was not until the 1980s when it started shifting toward the equator (Figure 2k and Table 1). Both limits (northern and southern) shifted northward and hence, the relative abundance in recent years decreased south of 25°S (Figure 3). Yellowfin tuna habitat GClat shifted significantly to the south in the Pacific and Indian Oceans (both $p < 0.001$) but no trend was found in the Atlantic Ocean ($p = 0.87$) (Figure 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. A significant westward shift was found in the east Pacific stock, the opposite of the eastward shift of the west Pacific stock. The abundance in recent years increased in all latitudes except for a small decrease between 6 and 10°N (Figure 3). In contrast to yellowfin, bigeye tuna habitat GClat shifted significantly to the north-west in the Atlantic Ocean ($p = 0.019$) and south-west in the Indian Ocean. Pacific tuna stocks showed no significant trends ($p = 0.2$ and 0.65 for east and west, respectively) (Figure 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 60°N (Figure 3). Skipjack tuna stocks showed different responses to environmental changes around the world: north and east shifts in the West Atlantic, southward shifts in the east and west Pacific and Indian stocks ($p = 0.046$, <0.001 and <0.001 respectively), and no significant shift in the east Atlantic ($p = 0.29$) (Figure 2b,e,g,j,l and Table 1). An eastward shift is also found in the west Pacific. The distribution limits did not show a trend, with a different pattern depending on the stock. Changes in the mean abundance per latitude were minor, varying between $-4.3e^{-5}$ and $4.4e^{-5}$ tons per 1,000 hooks CPUE change (Figure 3).

In summary, 20 out of 22 stocks have shifted poleward, as represented by their GC 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, 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.

3.2.1 | Relation with climatic indices

The analyses between latitudinal GC changes in tuna stocks and climatic indices showed very few significant correlations (Table S3).

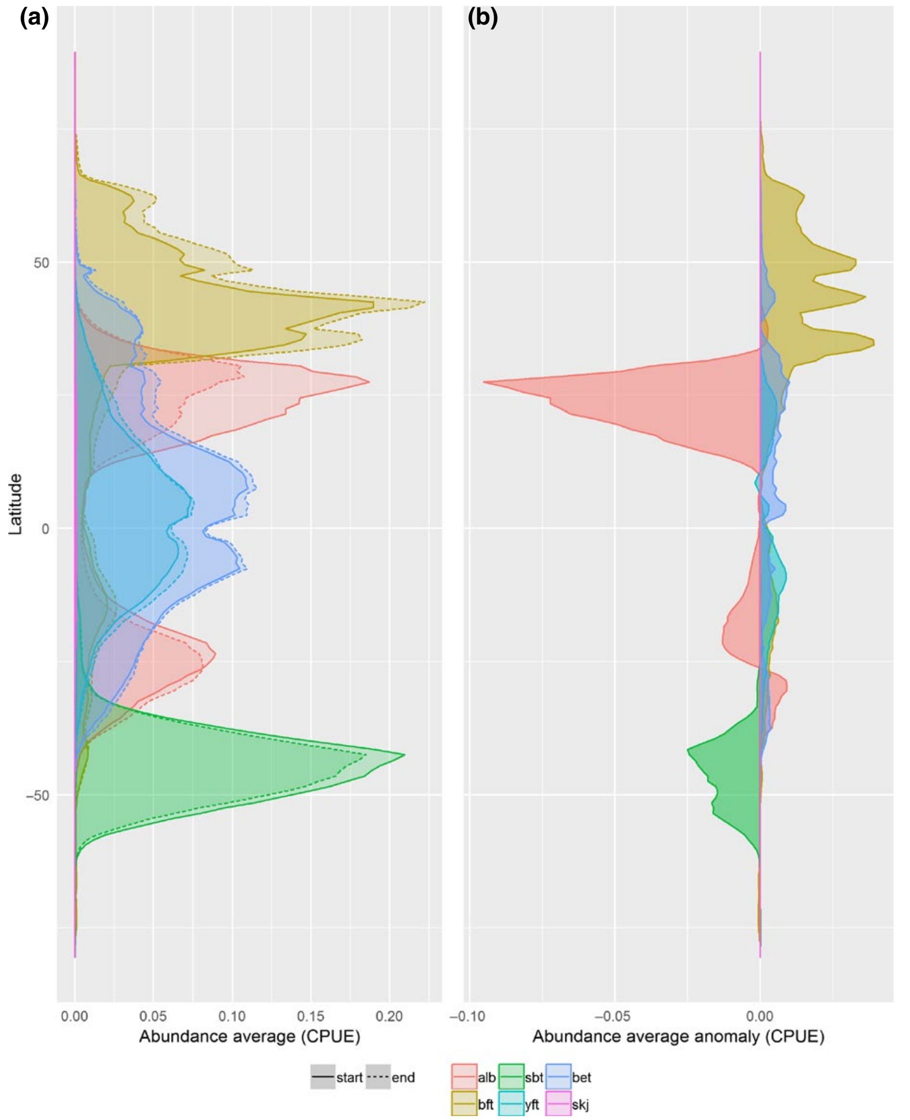

FIGURE 3 Changes in abundance (in tons per 1,000 hooks and 10 inds per 1,000 hooks in the case of S. bluefin) between past (1958–1963 and 1965–1970 for S. bluefin) and recent (1999–2004) period. (a) Average abundance per latitude for the two periods; (b) abundance anomalies estimated as the difference 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 [Colour figure can be viewed at wileyonlinelibrary.com]

Only 20.5% of the latitudinal changes were related to climatic indices, and only 10.3% in the case of longitudinal shifts.

3.3 | Future tuna projections

3.3.1 | Distribution and changes in abundance

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 our results projected higher changes 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 (Figure 4a–c,e) while tropical tunas as skipjack and yellowfin are projected to increase abundance in their core tropical areas and eastward in the Pacific Ocean (Figure 4d,f). However, a decrease in abundance in the most western equatorial Pacific for both skipjack and yellowfin tuna is projected.

Our results projected that 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 (Figure 4a,b). The GC 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 (Figure 4a,b). In all the stocks, an eastward shift is projected by 2100 (with the highest rate in the North Atlantic) except in the Mediterranean Sea (Table 2). 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 (Figure 4c,d). 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

TABLE 1 Change in Gravity Center (GClat, in latitudinal and GClon in longitudinal 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 and 2004 except in the case of southern bluefin tuna (S. bluefin) which was between 1965 and 2004. ****p* < 0.001, ***p*-value between 0.001 and 0.01, **p*-value >0.01 and <0.05

Graphic	Species	Stock	Ocean	GClon	GClat	limN (P80)	limN (P95)	limS (P20)	limS (P5)
a	Albacore	albNP	North Pacific	0.038	0.014*	0.027***	0.016*	0.003	−0.03**
b	Bigeye	betEP	East Pacific	−0.005	−0.004	0.005	0.009	−0.017*	−0.02**
	Skipjack	skjEP	East Pacific	0.001	−0.007*	−0.003	0.01	0.003	−0.014*
	Yellowfin	yftEP	East Pacific	−0.021**	−0.024***	−0.015*	0.004	−0.034***	−0.005
c	Albacore	albSP	South Pacific	0.01	−0.023***	−0.043***	−0.035**	−0.011	−0.01*
d	Albacore	albNA	North Atlantic	0.036***	0.026***	0.045***	0.035***	0.013	−0.043***
e	A. bluefin	bftW	West Atlantic	−0.007	0.05***	0.018***	0.072**	0.036	0.035***
	Skipjack	skjWA	West Atlantic	0.016***	0.011**	0.012**	0.015**	0.017*	0.002
f	Bigeye	betA	Atlantic	−0.011*	0.011*	0.023**	0.017***	−0.002	−0.005
	Yellowfin	yftA	Atlantic	−0.014	−0.001	0.019**	0.005	−0.013*	−0.042**
g	A. bluefin	bftE	East Atlantic	−0.017	0.009	0.038***	0.025***	0.003	0.005
	Skipjack	skjEA	East Atlantic	0.003	0.007	0.037*	0.013*	−0.009	−0.009
h	Albacore	albSA	South Atlantic	−0.018**	−0.008*	0.000	−0.013	−0.012*	0.000
i	Albacore	albM	Mediterranean	0.008*	0.003**	0.001	0.000	0.007	0.004*
j	Albacore	albI	Indian	−0.031**	−0.021***	−0.023***	−0.011	−0.037***	−0.014**
	Bigeye	betI	Indian	−0.021***	−0.011***	−0.002	0.000	−0.011	−0.035***
	Skipjack	skjI	Indian	−0.005	−0.016***	−0.002	−0.001	−0.019**	−0.017**
	Yellowfin	yftI	Indian	−0.003	−0.017***	−0.005	−0.003	−0.022***	−0.037***
k	S. bluefin	sbt	Southern	0.011	0.009***	0.009	0.028***	0.006	0.01*
l	Bigeye	betWP	West Pacific	0.023	0.002	0.009	−0.029***	0.01	−0.017*
	Skipjack	skjWP	West Pacific	0.016*	−0.008***	−0.01*	−0.012*	−0.008	−0.006
	Yellowfin	yftWP	West Pacific	0.046***	−0.02***	−0.011*	−0.03***	−0.013*	−0.004

end-of-the-century. Both stocks shift eastward with a higher rate in the eastern Atlantic. 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.

The relative abundance of the southern bluefin tuna increases toward their southern limit by mid-century but it decreases in most of the historical distribution area (Figure 4e,f). 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 latitudinal GC shifts slightly southward by mid-century and northward by the end-of-the-century. For both time periods, a westward shift is projected. 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 (Figure 4g,h). However, the abundance is projected to decrease north of Papua New Guinea and east of the Philippines. The yellowfin tuna GClat shifts southward in the west Pacific and Atlantic, while northward in the east Pacific and Indian Oceans. Overall, both, the yellowfin and bigeye tuna shift eastward except in the Indian Ocean where a westward shift is projected for both periods (2040–2059 and 2080–2099). The spatial distribution of bigeye tuna is projected to change most in the Atlantic Ocean and less so in the Pacific and Indian Oceans (Figure 4i,j). 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 GClat 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 (Figure 4k,l). 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 areas are projected to occur by the mid-century. A contraction of the distribution is projected for the western Atlantic and western Pacific stocks by the end-of-the-century. Most of the stocks shift to the east except in the Indian Ocean and the west Atlantic.

3.3.2 | Tuna abundance changes in the EEZ

Our results projected important changes in tuna abundance in EEZs in the future (Figure 5, Table 3, and Table S4). All species except albacore have the same trend for mid- and the end-of-the-century,

TABLE 2 Gravity Center anomalies (GClat, in latitudinal and GClon in longitudinal 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) related to the reference period

Species	Stock	Ocean	GClon	GClat	N	S	GClon	GClat	N	S
Albacore	albI	Indian	0.38	−2.44	−3	−1.5	1.42	−4.78	−6.5	−2.5
	albM	Mediterranean	3.12	−0.65	−0.38	−1.87	−0.97	0.39	−0.5	1.4
	albNA	North Atlantic	3.34	1.97	2.98	1.5	7.49	3.2	4.84	2.23
	albNP	North Pacific	0.48	1.67	1.5	3.5	1.77	2.74	1.5	5.5
	albSA	South Atlantic	1.09	−2.5	−5.28	−1	2.65	−4.45	−9.28	−1.5
	albSP	South Pacific	0.32	−2.84	−5	−2	1.12	−4.98	−10	−3
Bigeye	betA	Atlantic	1.64	0.42	1.5	−2.21	3.47	−0.11	1.79	−2.75
	betEP	East Pacific	0.5	−0.41	1.85	−1.16	1.82	−1.74	2.3	−2.05
	betI	Indian	−0.28	−1.14	−0.11	−1.74	−0.16	−2.49	−0.89	−0.55
	betWP	West Pacific	1.98	−0.34	2.46	−2.34	4.08	−2.57	2.11	−3.01
A. bluefin	bftE	East Atlantic	11.65	−3.14	1.03	−14.74	14.36	−14.28	6.38	−33.46
	bftW	West Atlantic	0.51	−10.67	−0.35	8.01	6.87	−47.29	12.43	4.4
S. bluefin	sbt	Southern	−2.58	−0.63	−1	0	−5.93	2.29	3	0.5
Skipjack	skjEA	East Atlantic	1.65	1.51	5.2	−3.9	0.76	0.15	8.95	−6.99
	skjEP	East Pacific	0.21	−0.04	43.89	−3.33	0.83	−0.75	35.46	−6.92
	skjI	Indian	−0.93	−0.81	−0.65	−3.33	−1.58	−1.2	3.17	−7.38
	skjWA	West Atlantic	−0.44	0.68	−18.08	−4.59	−0.84	1.02	−11.92	−9.46
	skjWP	West Pacific	1.53	−0.18	5.68	−2.28	3.56	−1.21	−29.94	−5.48
Yellowfin	yftA	Atlantic	1.33	−0.27	0.08	−0.41	3.28	−1.13	−3.42	−0.05
	yftEP	East Pacific	0.06	0.18	0.5	0.3	0.99	0.38	1.39	−0.04
	yftI	Indian	−1.44	0.23	0.06	−0.44	−2.65	0.5	0.06	−0.46
	yftWP	West Pacific	1.83	−0.09	0.5	−0.5	3.96	−0.88	1.5	−1.5

with greater magnitude by the end. Albacore is projected to increase by 6% by 2050 then decrease by 6% by 2100, relative to the reference period. The relative abundance of albacore tuna decreases in most EEZs, except for some countries located close to its distributional limit. Both bluefin species (Atlantic and Southern) are projected to have the greatest depletion, reaching 60% in the case of Atlantic bluefin tuna by the end-of-the-century. Northern countries such as Norway, Greenland, Iceland, Canada, the United Kingdom, and Ireland have the greatest projected 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 is projected to decrease. Bigeye tuna is projected to decrease in all EEZs, except in EEZs for 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 is projected to slightly increase. Skipjack and yellowfin tunas are the only species that are projected to significantly increase in the future (yellowfin is the most favored species almost doubling its relative abundance by 2100), despite projected decrease in EEZs of a few countries such as Indonesia, Malaysia, Micronesia, Palau, Philippines, and Taiwan.

4 | DISCUSSION

Tuna habitat, as modeled here, has shifted poleward over the 1958–2004 period and is projected to continue shifting under climate change, with potential important consequences for fisheries in coastal states and the countries that depend on them. We estimated a poleward shift in the suitable habitat of 89% of the temperate and 92% of the tropical tuna stocks between 1958 and 2004. Southern bluefin tuna was an exception as it shifted equatorward after 1980. For the same period, a decrease in the relative abundance of albacore was found between 10 and 40°N and 5 and 25°S. Southern bluefin also decreased its relative abundance in most of the latitudes.

We used Japanese longline fleet data because they have 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 projected very small differences between tropical, subtropical, and temperate waters habitat for skipjack. Moreover, the Japanese longline fleet mostly catch the large fish of all species and the projected distributions should thus be considered as a proxy for the adult population.

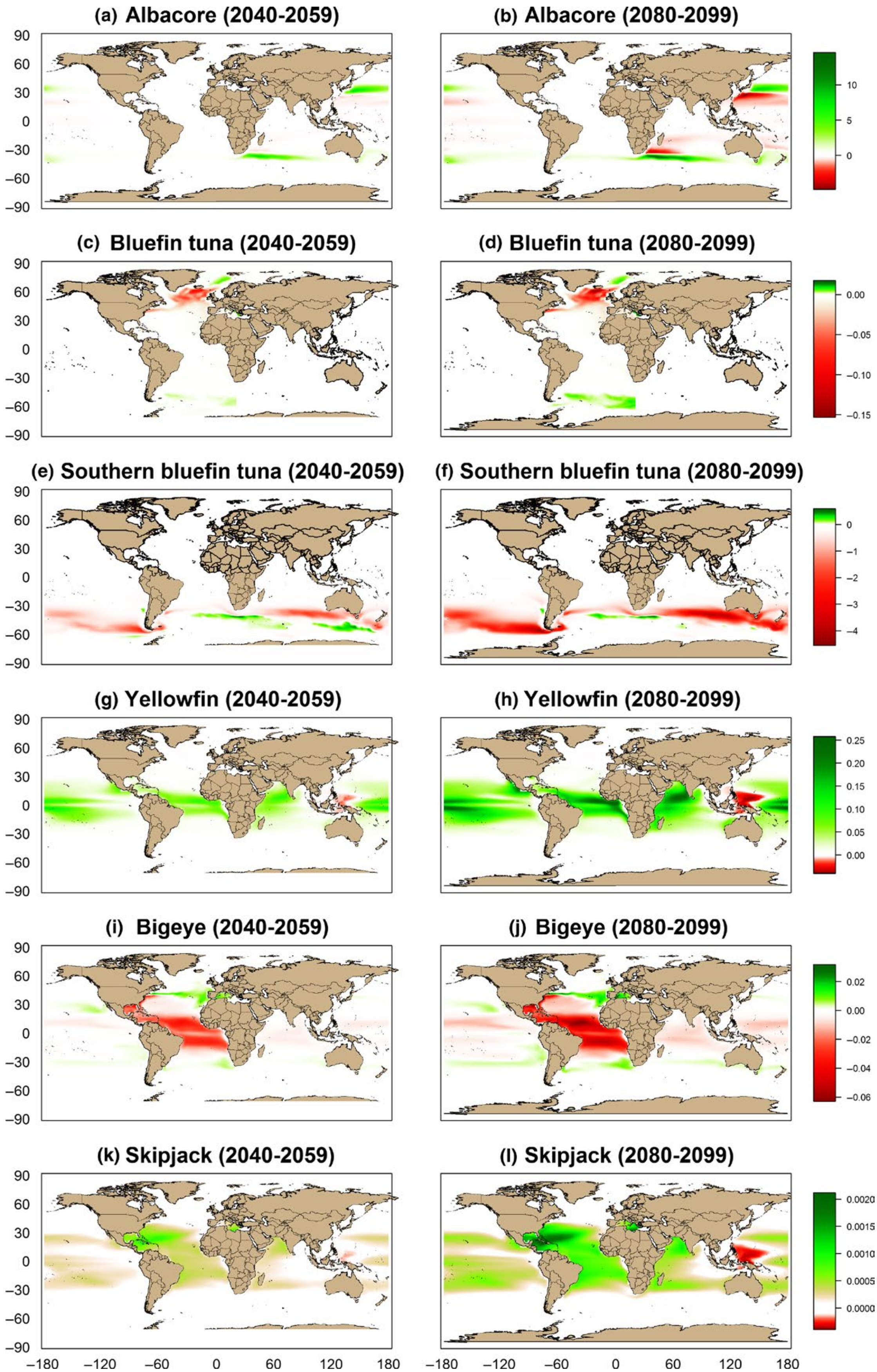

FIGURE 4 Gains and losses of abundance (in tons per 1,000 hooks, except for SBT, in number of individuals per 1,000 hooks) for mid- (left column, a, c, e, g, i and k) and end-of-the-century (right column, b, d, f, h, j, l) [Colour figure can be viewed at wileyonlinelibrary.com]

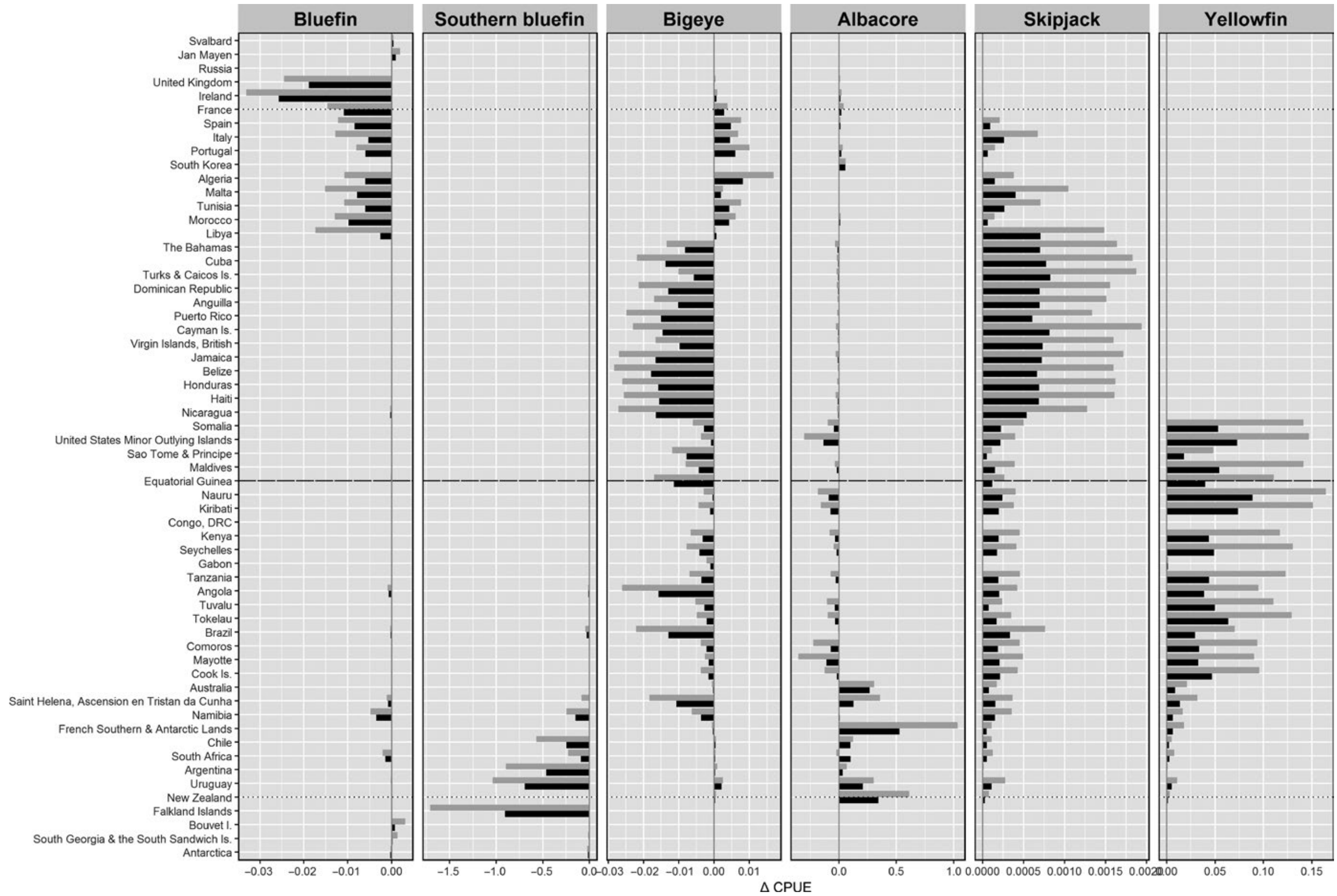

FIGURE 5 Changes in abundance (in CPUE units, tons per 1,000 hooks or individuals per 1,000 hooks in the case of southern bluefin tuna) for the main 10 countries or territories per species with the highest projected changes in the EEZs for mid-century (2040–2059) compared with the reference period (1980–1999). In order to reduce the number of locations such that names can be read, and the latitudinal patterns of changes can be visualized, a set of 10 unique countries with the highest change was selected for each species. If a country was already selected for one species, the next highest unique country for that species was selected and so on, until a unique top 10 list was selected. Across the six species, a total of 60 countries are shown here. Countries are ordered per mean latitude of the EEZ and dotted lines represent the equator (0°) and both 45° parallels (north and south). Numerical values for all countries are shown in Table S4

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 slightly lower than in Arrizabalaga et al. (2015) due to the limitation that we imposed to the degree of smoothness ($k = 3$). Our method has improved the SDMs where the presence data were not available (e.g., in areas where fish were not observed such as close to the poles).

TABLE 3 Change in abundance (%) within EEZs for the mid- and the end-of-the-century in relation to the reference period for each tuna species

Species	Mid-century (2040–2059)	End-century (2080–2099)
Albacore	6.58	−6.38
Bluefin tuna	−42.62	−62.62
Southern bluefin tuna	−22.87	−45.9
Yellowfin	43.37	92.12
Bigeye	−18.4	−34.84
Skipjack	27.05	57.36

4.1 | Tuna distribution models and their reliability

In recent decades, SDMs have been improved and 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. For instance, predictive modeling of species distribution relies entirely on the assumption of environmental equilibrium between the biotic entities and the physical characteristics of their environment (Guisan & Theurillat, 2000). Our approach also assumes such equilibrium. Nevertheless, most studies that use SDMs neglect the time dimension to construct the model, thus, the cases where there is nonequilibrium in the environment triggers a direct bias in the species response curve. We used a long-time series dataset (47 years of tuna catch and effort data), therefore, the model covers a wide range of situations between environment and species occurrence, which improves the reliability of species response curve. 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 × 5 degree), coastal results need to be interpreted carefully in our global study. We partially avoided this problem by including results only for those countries with more than 30% of the cells with data within their EEZs. Only longline catch data were included in our model, so an important part of tuna catches is not represented in our models, especially for skipjack tuna that are caught largely by purse seine and, to a lesser extent, pole and line gears (Arrizabalaga, Murua, & Majkowski, 2012). 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 in response to ocean warming (Dueri et al., 2014; Dulvy et al., 2008; Perry, Low, Ellis, & Reynolds, 2005). Although the reliability of our models is high (deviances explained vary between 34.5% and 74.1% and AUC values of 0.784 and 0.838), the projections assume only the relationship between environmental variables and adult tuna distribution. Not all possible environmental variables which may affect tuna distribution were included in the model. For example, other variables such as oxygen (Gilman, Allain, Collette, Hampton, & Lehodey, 2016; Lehodey et al., 2011; Mislan et al., 2017), pH (Lehodey, Senina, Calmettes, Hampton, & Nicol, 2017; Lehodey et al., 2011; Nicol et al., 2016; Yokoyama et al., 2004), or currents (Lehodey et al., 2011) are potential influences on the cellular physiology, survival or condition during early life stages. Nevertheless, the geographic distribution of the species depends not only on their environmental tolerance, but also on their thermoregulatory capacity (Brill, 1994; Lehodey et al., 2011), dispersal capacity and biological interactions (Peterson et al., 2011) such as predation (Guisan & Thuiller, 2005), intraspecific or interspecific competition, trophic relationships, and population dynamics. In addition, different responses to climate change impacts can desynchronize ecological interactions (Thackeray et al., 2016). Furthermore, the mortality due to fishing, and recruitment process may have an important impact on the total biomass of the species—such mechanisms have been included in some regional models (e.g., Lehodey et al. [2013, 2018], Senina et al. [2016, 2018]). At a global scale, fishing and recruitment mechanisms are more complicated to include, and remain a subject for future analysis when modeling the population shifts due to climate change.

4.2 | Past distribution and abundance changes

We found a poleward shift in the suitable habitat of 20 out of 22 tuna stocks between 1958 and 2004. Some 89% of temperate tuna stocks shifted poleward but southern bluefin tuna was the 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 subtropical waters from 1965 to 2011 due to a poleward shift in response to ocean warming. Atlantic bluefin tuna was captured in waters of east of Greenland in 2012, likely due to a combination of warm temperatures and mackerel immigration (MacKenzie, Payne, Boje, Høyer, & Siegstad, 2014). The prevailing influence of the Atlantic Multidecadal Oscillation (AMO) over the distribution and abundance of this species has also been recently demonstrated (Faillettaz, Beaugrand, Goberville, Kirby, 2019). For many other fish species, the movement of the populations in the last decades has been associated with the latitudinal shift of their habitats (Beare et al., 2004; Bruge et al., 2016; Montero-Serra, Edwards, & Genner, 2015; Perry et al., 2005). Consistent with this movement, the species composition in 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 (Worm & Tittensor, 2011).

Fewer tuna stocks shifted longitudinally (10 out of 22), moving westward in the Indian, East Pacific and South Atlantic oceans and eastward in the north, west, and east Atlantic, Mediterranean and West Pacific. Some studies related the longitudinal shift of skipjack with climatic indices such as El Niño Southern Oscillation (ENSO) in the Pacific (Lehodey, 2001; Lehodey, Bertignac, Hampton, Lewis, & Picaut, 1997) and a long-term eastward shift is projected to the central-eastern Pacific (Bell, Ganachaud, et al., 2013). Our study considered the six species at global scale, which may explain the low correlation between longitudinal stock shifts and climatic indices (see section 2.4.1) such as El Niño in the Pacific.

The SDMs can predict occurrence probability in areas where the species has not been observed or caught. For example, favorable habitat is projected for Atlantic bluefin tuna in the South Atlantic Ocean (below 45°S), and likewise for yellowfin and bigeye tunas in the Mediterranean Sea. This suggests that the environmental conditions (limited to those studied in this analysis) 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 a species has been observed due to low-longline CPUE (e.g., southern bluefin tuna) or where the model 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 the 1960s (Grewe, Elliott, Innes, & Ward, 1997) which could have affected the relationship between the environment and subsequent habitat suitability projections 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). Additional climate change investigation for this species is warranted.

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 habitat 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 occurred in the 1970s due to the expansion of global fisheries and the development of new offshore fishing grounds (FAO,2011). The improvement in 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., 2013), the changes in predator-prey relationships, the impacts on human services and fisheries (Bell, Reid, et al., 2013; Cheung et al., 2009, 2013; 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. These components are important since they can amplify the warming signal throughout the food web (Chust et al., 2014; Kwiatkowski, Aumont, & Bopp, 2018). We only projected changes in tuna habitat for the 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 projections 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, Horrocks, Harvey, & Hamilton, 2011). In addition, and according to the IPCC AR5 (IPCC, 2013), all RCP scenarios are equally likely to occur. The confidence of a projected variable is related with the variable or parameter studied and the period which the projections are made rather than with the climate change scenario chosen. In addition, as an average of 16 models is used for our projections (ensemble), a homogenization of the species distribution pattern can occur relative to using only one model or focusing in one ocean, which may also reduce apparent relationships to climate drivers such as ENSO.

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 projections, showing that skipjack potential habitat will increase in the future, partially agree with Senina et al. (2016), who projected different future situations depending on the model (from a 50% decrease to no change in abundance due to the compensation between the increasing biomass in the tropics and decreasing biomass in the equatorial warm pool). Recent work by Senina et al. (2018) projected an overall decrease in yellowfin and skipjack in many Pacific Islands EEZs by 2050, while our results suggest an increase in most EEZs. This disagreement is likely explained by the differences in the modeling approaches in both studies, such as: (a) the number of IPCC ensembled models used for projections (16 in our model vs. 4 in Senina et al. 2018), (b) selected environmental parameters considered in the models (i.e., oxygen and pH were not considered in our models), (c) the source of fishery data used in the models (only longline, focused mostly on large individuals, in our model vs. various fishing gears targeting a wider range of sizes), (d) modeled variable (CPUE in our model vs. biomass), and (e) the spatial resolution (oceanwide in our model vs. Pacific basin scale in Senina et al. 2018). However, our results are in agreement with Lehodey et al. (2013) and Dueri et al. (2014) who projected a slight increase in skipjack abundance in the Western Central Pacific Ocean until 2050 followed by a decrease after 2060. They also projected 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, which agrees with our results. According to our analysis, Atlantic bluefin tuna abundance is projected 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. (2017) who projected temperature-induced reductions in tropical and sub-tropical Atlantic and an improvement in subpolar habitat suitability. This redistribution has implications for spawning and migratory behaviors, and availability to fishing fleets (Muhling et al., 2017). This northward shift might allow fishing in more northern latitudes (MacKenzie et al., 2014) but also the southern Atlantic habitat is projected to improve. In the past, this species occurred also in the southern Atlantic, until the "habitat bridge" linking both hemispheres was interrupted in the late 1960s (Briscoe et al., 2017; Fromentin, Reygondeau, Bonhommeau, & Beaugrand, 2014). The projected improvement in southern Atlantic habitat might only result in Atlantic bluefin tuna reappearance if 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 tuna 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; Barange et al., 2014, 2018). The greatest impacts are projected over the nations of South and Southeast Asia, Southwest Africa (from Nigeria south to Namibia), Peru, and some tropical small-island developing states (Barange et al., 2014). These fisheries-dependent developing nations rely on their fisheries sector in terms of wealth, food, and employment, and they have limited capacity to invest in climate adaptation (Allison et al., 2009; Barange et al., 2014). Changes in catch potential and composition 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). Efforts to adapt to climate change should be planned, including adaptation to possible redistribution and decrease/increase in abundance of target species. Additional measures or actions taken in response to climate change should complement and strengthen the overall governance and sustainable use of marine resources (Barange et al., 2018). Tuna is an important source of protein in many countries and the expected increase in their abundance for Pacific nations, as well as other countries, is a possible solution to fill the anticipated gap in protein (Allison et al., 2009; Bell et al., 2015; Gillett, McCoy, Rodwell, & Tamate, 2001). However, other studies such as Senina et al. (2018) project that climate change will both positively and negatively affect tuna abundance in Pacific Islands EEZs' by 2050, with decreasing abundance in the west and slightly increasing abundance in the east Pacific. The catch decreasing would result in less revenue from license fees for the Pacific Island countries (unless practical ways can be found to increase the value of catches, Bell, Allain, et al.2018). Nevertheless, the tuna catches in those countries might be enough for domestic food security, especially if management plans are oriented to reallocate more of the tuna caught within the EEZ for supplying local consumption.

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. However, a large amount of tuna catches corresponds to high seas, which by 2012 and together with billfishes, represented 9.3% of global annual marine fisheries catches (FAO, 2014; Juan-Jordá et al., 2011). In addition, persistent suitable habitat for longline occurs within the tropical and temperate latitudes in the high seas, which is consistent with the global latitudinal patterns of the six tuna species (Ortuño-Crespo et al., 2018). Nevertheless, high seas catches affect different fleets and our analysis was limited to countries EEZ. Our results are consistent with Bell, Reid, et al. (2013), with 82.4% agreement in the trend in skipjack abundance within EEZs of Pacific Island countries and territories (PICTs) (Table S5). The level of agreement with skipjack tuna abundance changes in PICTs projected by Senina et al. (2018) is lower (67.5%), probably due to the differences between the models and data sets as explained above (Table S5). They estimated changes for 2050 and 2100 relative to the 20 years average from 1980 to 2000 under the A2 emissions scenario (slightly lower emissions levels than the RCP8.5 in IPCC AR5, Rogelj, Meinshausen, and Knutti 2012). We projected a decrease in skipjack tuna in the Palau EEZ for both periods, while Bell, Reid, 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, Reid, et al. (2013) projected a decrease. Changes in catch potential estimated by Cheung et al. (2009) based on 1,066 species showed similar latitudinal patterns 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, Cisneros-Montemayor, 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 those 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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ORCID

Maite Erauskin-Extramiana https://orcid.org/0000-0003-0684-2711

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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