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Impact of climate change on tropical Pacific tuna and their fisheries in Pacific Islands waters and high seas areas

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Abstract

A third of the world tuna catch, made up essentially of skipjack, yellowfin and bigeye tuna and South Pacific albacore (hereafter 'albacore'), comes from the Exclusive Economic Zones (EEZs) of the 22 Pacific Island countries and territories (PICTs) in the Western and Central Pacific Ocean (WCPO). We investigated how climate change could affect the distribution and abundance of these tuna species at the Pacific basin scale, and within the EEZs of PICTs. This study relied on the application of the model SEAPODYM to each tuna species, first with a model parameterization phase over the historical period (1980-2010) using a reanalysis of ocean conditions, and then with projections of an ensemble of simulations to explore key sources of uncertainties. Five different atmospheric forcing datasets from Earth System models projected under the ("business as usual") IPCC RCP8.5 emissions scenario were used to drive a coupled physical-biogeochemical model (NEMO-PISCES) first, and then SEAPODYM, over the 21st Century. Additional scenarios were included to explore uncertainty associated with future primary production and dissolved oxygen concentration, as well as possible adaptation through phenotypic plasticity of these tuna species to warmer spawning grounds. The impact of ocean acidification was also included for yellowfin tuna based on results from laboratory experiments. The historical simulations reflect key features of the ecology and behaviour of the four tuna species and match the total historical catch in terms of both weight and size frequency distributions. The projections confirm previous results, showing an eastern shift in the biomass of skipjack and yellowfin tuna over time, with a large and increasing uncertainty for the second half of the century, especially for skipjack tuna. The impact is weaker for bigeye tuna and albacore due to revised parameter estimates, which predict a wider and warmer range of favorable spawning habitat. For albacore, a strong sensitivity to sub-surface oxygen conditions resulted in a very large envelope of projections. Historical fishing pressure was estimated to have reduced the adult stocks of all four tuna species by 30-55 % by the end of 2010, depending on species and region. The effects of fishing on biomass strongly outweighed the decreases attributed to climate change. Thus, fishing pressure is expected to be the dominant driver of tuna population status until at least mid-century. The projected changes in abundance and redistribution of tuna species associated with climate change could have significant implications for the economic development of PICTs, and the management of tuna resources, at basin scale. In particular, larger proportions of the catch of each species is increasingly expected to be made in international waters, making the monitoring and control of the fisheries more difficult.

Introduction

The rich tuna resources of the Western and Central Pacific Ocean (WCPO) supply 60% of the world's tuna. About half of the catch (1.5 Mt; Williams and Terawasi 2015) is extracted from the waters of the 22 Pacific Island countries and territories (PICTs) that span much of this large oceanic region. Four species of tuna dominate the catch; skipjack, yellowfin and bigeye tuna and albacore. Management of these resources by the regional fisheries management organizations1 (RFMOs) depends partly on:

1) understanding the proportions of each of the tuna stocks within the exclusive economic zones (EEZs) of PICTs, Indonesia and the Philippines, and in high seas areas; and

2) estimating catch levels that will optimize the economic and social benefits of tuna fishing for coastal states and distant water fishing nations, while keeping exploitation of tuna resources within safe sustainable limits.

Therefore, much of WCPO tuna management is aimed at assessing the effect of fishing effort on the spawning biomass of each tuna species to establish target and limit reference points for total catches, and harvest control rules. However, because climatic variability influences the distribution and abundance of tropical tuna species (Lehodey et al. 1997), and because climate change is also expected to affect the locations where the best catches are made, reliable projections for the expected changes in tuna catches within the EEZs of PICTs and in high seas areas are now a priority for RFMOs. The sensitivity of stocks to climatic variability also has direct implications for the business planning efforts of all stakeholders in the tuna industry.

Climate change is modifying the physical environment of Pacific tropical tunas. Average sea surface temperature (SST) in the Western Pacific Warm Pool has increased by ~0.7 °C since 1900 (Bindoff et al. 2007, Cravatte et al. 2009) and is expected to continue rising by 1.2–1.6 °C by 2050 relative to 1980-1999, and 2.2–2.7 °C by 2100, under a high emissions scenario (Ganachaud et al. 2011). Increasing temperature also intensifies vertical stratification of the water column, leading to reduced mixing, nutrient inputs from the deeper layer, and transfer of oxygen from the atmosphere in and below the thermocline. Changes in ocean circulation are also projected to impact the mixing and upwelling process on which oceanic primary productivity and the food web for tuna depend. Most biogeochemical models coupled to Earth Climate models to project future changes in primary production under IPCC scenarios

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[1] The Western and Central Pacific Fisheries Commission (WCPFC), the Pacific Islands Forum Fisheries Agency (FFA), the Parties to the Nauru Agreement (PNA), and the Inter-American Tropical Tuna Commission in the Eastern Pacific Ocean.

have predicted a decrease in primary production in tropical and subtropical regions, driven by stratification (Steinacher et al 2010). However, uncertainty is greatest for sub-tropical and tropical regions between 30° N and 30°S in the western Pacific. For example, recent simulations, including some at higher resolutions simulating mesoscale activity, suggest that no change or an increase in primary productivity may occur caused by an intensification of the microbial loop (Laufkötter et al. 2015; Matear et al. 2015). Finally, since the ocean is absorbing a large proportion of additional atmospheric CO_2 derived from anthropogenic activity, the seawater carbonate chemical equilibrium is shifting towards lower pH, i.e., more acidic waters and lower calcium carbonate saturation states (e.g., Caldeira and Wickett 2003; Feely et al. 2004; Barnett et al. 2005). These changes will impact the many calcifying species, e.g., shell-forming marine organisms, but also probably the physiology and respiration of fishes, especially the more vulnerable early life stages (Pörtner et al. 2014).

The potential impact of these long-term environmental changes on the distributions and abundances of fish, and fisheries production, have been explored using 1) retrospective analyses (Perry et al. 2005; Brill 2010; Nye et al. 2009); 2) projections with statistical models based on past correlations with key predictors, typically temperature and primary production (Hazen et al. 2012); 3) and more complex models that integrate interactions and non-linear effects (Cheung et al. 2008, 2010; Anderson et al. 2013; Dueri et al. 2014; Lehodey et al. 2013, 2015). These studies point to a general poleward movement of tropical species, a decrease of fisheries productivity in the low latitudes and possibly an increase at mid and high latitudes. All such studies are affected by various sources of uncertainty related to both the bio-physical variables predicted by climate models, and to the specific model developed for the species or group of species studied. The total uncertainty needs to be quantified to provide a level of confidence in the results. The sources of uncertainty also need to be determined to identify where further research, modelling and observation efforts should be focused.

The partitioning of uncertainty in climate modelling (Hawkins and Sutton 2009), and in modelling of marine living resources (Payne et al., 2016; Cheung et al 2016), has identified structural uncertainty associated with the model design, uncertainty due to initialization, uncertainty generated by the internal variability of the model, parametric uncertainty associated with model parameter values, and uncertainty linked to the scenarios used for projections. Systematic exploration of these different sources of uncertainty leads to a very large ensemble of simulations. Computational limits impose trade-offs during the exploration of these uncertainties. Selection of the most critical sources of uncertainty therefore needs to be based on expert judgement. In general, uncertainty linked to scenarios is considered to increase with time, and initialization uncertainty is thought to dominate at short time-scales and may be ignored at the centennial time-scale used for climate change projections. A well-bounded model with parametrization achieved using abundant observations in a robust statistical framework (e.g., maximum likelihood and Bayesian methods) are considered to need less sensitivity analyses than a model with parameter estimates fixed from limited dataset or not directly observable.

This is certainly the case of the Spatial Ecosystem and Population Dynamics Model (SEAPODYM; Lehodey et al. 2008), which includes a quantitative method to estimate population dynamics, habitats, movements and fisheries parameters with a maximum likelihood estimation (MLE) approach (Senina et al. 2008). SEAPODYM simulates the change in abundance over time and space of a target fish species by age class from larvae to the oldest adults, and can distinguish between the effects of fishing and natural variability (environment and climate). Fish biology and behavior are simulated based on relationships with environmental variables. For instance, the model uses: 1) the distribution of several groups of micronekton (Lehodey et al. 2010, 2015) to drive movement of the tuna feeding on them; 2) oceanic currents to redistribute tuna larvae; 3) water temperature and dissolved oxygen concentration to control the habitat preferences of tuna (changing with age); and, 4) changes in gradient of daylight and other variables to trigger spawning migrations. Based on first biological principles and functional relationships to the environmental variables, SEAPODYM uses a small number of parameters (< 25) to estimate the dynamics of target species, and an additional 3-4 parameters to define the selectivity form and catchability of each fishery added in the simulation. Data used to estimate the parameters typically include catch, fishing effort, length frequencies of target species, and release-recapture tagging data (Senina et al., 2017; *submitted*). The full, spatially-explicit representation of SEAPODYM, using an Eulerian advection-diffusion-reaction framework, allows the use of data in the MLE at the resolution of the grid used to solve the model numerically, e.g., one or two degree square. Therefore, a massive amount of observations (several hundred thousand) can be included in one model optimization.

SEAPODYM has been used extensively to study the population dynamics of tropical tunas and the impact of fisheries and environmental variability, including climate change (Lehodey et al. 2010, 2013, 2015; Sibert el al. 2012; Bell et al. 2013; Dragon et al. 2015). However, previous studies on the impact of climate change on tuna were based on one single Earth System Model projection following the IPCC "business as usual" scenario. In addition, they highlighted a problem of coherence between historical and projected environmental forcings. The fish model component of SEAPODYM needs to be parameterized using a realistic historical reanalysis (i.e., one based on a consistent set of atmospheric observations) to drive the coupled physical-biogeochemical model. Such parameterization will allow matching of the observed variability of the large fishing dataset, e.g., changes in fishing grounds due to an El Niño event.

Projection of such parameterization with future environmental conditions predicted from an IPCC-type model can produce spurious results due to errors and biases in these predictions (Lehodey et al. 2013). A tentative method for correcting the most obvious bias (water temperature) has been proposed but it is still necessary to run MLE over the historical period with the climate model environmental forcing to re-estimate the parameters. This approach is not completely satisfactory, however, because other biases that are more difficult to detect (e.g., in the ocean circulation) are also likely to occur. To date, it has not practical to propose an ensemble of simulations to explore the various sources of uncertainty.

We propose a new approach in this study. First, a single best estimate of SEAPODYM parameters is achieved based on historical available data and a realistic reanalysis of ocean conditions. Then, the historical period is prolonged by an ensemble of projections over the 21st Century using atmospheric forcing variables from 5 different Earth System models predicted under the IPCC RCP8.5 scenario ("business as usual") to drive a coupled physical-biogeochemical model (NEMO-PISCES) first, and then SEAPODYM. However, prior to this, a correction is applied to the atmospheric variables of the projections to avoid abrupt changes when switching from an historical to a projected time series. With this approach, the impacts of climate change on skipjack, yellowfin and bigeye tuna and albacore are analyzed with a simulation ensemble focusing on the most critical sources of uncertainty.

Materials and methods

SEAPODYM tuna model optimization

The history of the tuna populations under the combined effects of fishing pressure and natural climate variability, e.g., El Niño Southern Oscillation (ENSO), is predicted by the SEAPODYM model as a result of the optimization phase to estimate the model parameters. The model simulates tuna age-structured population dynamics with different rules changing according to the life stage (Lehodey et al. 2008; www.seapodym.eu). For example, as larvae and juveniles tuna drift with currents but later have autonomous movement, i.e., in addition to the velocities of currents their movement has a component linked to fish size and habitat quality. The model also considers fishing (Figure 1 & *Supp. Mat.*) by accounting for fishing mortality, total catch and size frequencies of the catch. Because the model domain covers the whole Pacific Basin, historical fishing datasets were prepared from the combination of data provided by the Pacific Community to the Western Central Pacific Ocean (WCPO), and by the Inter-American Tropical Tuna Commission for the Eastern Pacific Ocean (EPO).

The fully-explicit modelling of spatial dynamics relies on advection-diffusion-reaction equations, i.e., the density of fish and catch are computed in each cell of a computational grid defined over the model domain. The spatial resolution used for both the optimization and projection was 2° x 2° and the resolution for time and age dimensions was one month. The MLE approach developed for SEAPODYM (Senina et al. 2008) takes advantage of this spatially explicit representation by using the numerous catch/effort data, and length-frequency catch data, available at these resolutions. The recent addition of release-recapture tagging data to the likelihood function also allowed movement and habitat parameters to be estimated (Senina et al. 2017). A series of other changes have also been added to the previous version of SEAPODYM (Lehodey et al. 2008). These changes include spawning habitat defined with prey and predator functions separately instead of using the prey-predator ratio, and an additional parameter associated with each functional group of prey (micronekton) that provides more flexibility in the representation of vertical behavior and access to tuna forage.

Fishing mortality is computed either from fishing effort and estimation of catchability and selectivity of the fishery, or directly from observed catches when fishing effort is not available or too uncertain. Finally, information to constrain the average stock estimate is added to the likelihood function prior to analysis with the objective of identifying the minimum stock size given the spatial distribution predicted by the model that supports all local catch levels. However, to compensate sources of spatial mismatch between the highest observed catch and predicted catch, a local discrepancy of less than 20% is allowed (Senina et al. 2016). Such local errors are inevitable given the coarse spatial resolution of the model, which does not allow prediction of highly heterogeneous density fish distributions.

Each fishery is defined with a selectivity function and a catchability coefficient that is allowed to vary linearly over time. The catchability parameters are estimated, whereas linear trend parameters are calibrated during the model optimization phase using fishing effort to predict the catch. If the catch removal method is preferred for some fisheries, their catchability coefficients are estimated *a posteriori* (as long as the fishing effort data exist) in order to allow the fishing effort scenarios during the projection period. The fit between observations and predictions is used to validate the optimal solutions of the models. We verify that the total catch is well predicted, as it is a primary objective to include all fishing mortality. The fit by fishery is also validated to ensure that there are no regional biases. The fit between observed and predicted catch is also analysed spatially, as well as the fit between observed and predicted size frequency distributions and, when available, tag data.

The necessary input variables to run SEAPODYM are 3D (0~1000m depth), water temperature and currents, dissolved oxygen concentrations, total vertically-integrated primary production, and euphotic depths. They are provided by the NEMO-PISCES coupled model. The additional fields of pH used to investigate the future ocean acidification effects are also standard outputs of the PISCES model (Aumont et al. 2015). The ocean physical model NEMO is driven by the ERA40-INTERIM (1979- 2010) atmospheric reanalysis (atmospheric temperature, zonal and meridional wind speeds, radiative heat fluxes, relative humidity, and precipitation) which has been corrected using satellite data (Dee et al. 2011). All forcing variables are interpolated on the same regular grid and resolution prior to use in SEAPODYM simulations. The physical-biogeochemical forcing is used to simulate the zooplankton and micronekton functional groups (Lehodey et al. 2010a, 2015), before running the tuna dynamics and fisheries parameter estimations.

Once the optimal parameterization is achieved for a given species and validated by statistical fits to the data, one more simulation is produced without fisheries data. In this analysis without fishing mortality, the stocks rapidly increase and reach an equilibrium state in a time that is defined by the life span and the stock-recruitment relationship estimated for the species. We assume that at the end of the 30-year reanalysis, all four stocks are at their virgin (unfished) state and influenced by environmental variability only. The structure of the populations in December 2010, the last time step of the reanalysis is saved to serve as the initial conditions for the projections starting in 2011. The simulation ensembles are produced without fishing and thus highlight the impact of climate change only.

Uncertainties explored in the simulation ensemble

Given the long time-scale of these climate change projections and the robust quantitative method used to estimate SEAPODYM parameters, the largest sources of uncertainty concern their accumulation in generating the forcing variables, the model structure and the (IPCC) scenarios. Due to limited resources for computation, the effort is set on the first two sources of uncertainty and only one IPCC scenario (RCP8.5 ~ "business as usual") is used.

Uncertainty from atmospheric forcings is integrated in the ensemble simulation by selecting outputs from five Earth System models of the CMIP5 inter-comparison project (Taylor et al. 2011) to drive the coupled physical-biogeochemical model NEMO-PISCES (Table 1). These models have been selected because they mimic ENSO cycles in their simulations (Bellenger et al. 2014). However, a procedure of correction has been applied to each forcing. The low frequency trends from the climate model variables were extracted and smoothed with a 31-year wide Hanning filter before being added to three successive cycles of 30 years of the reanalysis variables. The results are 90-year forcing sets that span the period 2010-

2100 and mix the past observed variability with long-term trends due to climate change. Finally, a control simulation (three successive repetitions of the reanalysis) with the coupled physical-biogeochemical model is produced to verify that there is no long-term trend generated internally without climate change forcing.

Population dynamics of tropical tunas have been shown to be sensitive to the projected decrease in primary production in the western equatorial Pacific, and to declines in dissolved oxygen concentration in the eastern equatorial Pacific (Lehodey et al. 2013, 2015). Long-term trends projected with coarse-resolution, coupled physical-biogeochemical models are uncertain for these two variables. Warming-induced increases in phytoplankton growth, intensification of the microbial loop, or stronger mixing not well represented in climate models using coarse resolution, can counter-balance classical expected nutrient limitation due to increased stratification at low latitude (Laufkötter et al. 2015; Matear et al. 2015). Although decreasing trends in dissolved oxygen concentration have been detected from historical datasets (Schmidtko et al. 2017), their origin (observation errors, natural variability or climate change) is not yet clear. Higher resolution in Earth System Models seems necessary to obtain a better representation of observed changes (Duteil et al. 2014; Long et al. 2016). To account for this uncertainty, one additional member in the simulation ensemble includes a gradual increase in primary production in warm waters of the tropics, defined by SST > 27°C, reaching 10% more than in 2010 at the end of the century. Another member of the ensemble is also using climatological distribution of dissolved oxygen concentration instead of model projection.

Table 1 - Uncertainty explored in the simulation ensembles produced for this study

Uncertainty in atmospheric forcing		**Structural uncertainty in biogeochemical model**	**Structural uncertainty in SEAPODYM**
Code	***CMIP5 model***		
IPSL	IPSL-CM5A-MR (Institut Pierre Simon Laplace, France)	- *Primary production:* Increase of PP by 10% (PP10) in tropical waters (defined by SST >27°C) - *Dissolved Oxyge*n: No change (O2clim) = Use of climatological fields	- *Genetic adaptation:* Regular increase in optimal spawning temperature to reach + 2°C at the end of the Century - *Ocean acidification*: Additional mortality on larvae based on laboratory experiments with low medium and high sensitivity to pH (available only for yellowfin).
MIROC	MIROC-ESM (Model for Interdisciplinary Research on Climate, Japan)		
NorESM	NorESM1-ME (Norwegian Climate Centre, Norway)		
MPI	MPI-ESM-MR (Max Planck Institute for Meteorology, Germany)		
GFDL	GFDL-ESM2G (Geophysical Fluid Dynamics Laboratory, USA)		

Previous studies have shown that the major drivers of tuna population dynamics under climate change simulations are linked to the evolution of spawning grounds and larvae recruitment. The match between environmental conditions and the optimal spawning temperature seems a primary factor to consider. Therefore, we investigate the phenotypic plasticity within the population to better adjust to changing ocean temperatures with one more simulation where the estimated optimal spawning temperature linearly increases to reach two degrees more at the end of the 21st Century, i.e., roughly following the temperature increase in the tropics under the RCP8.5 scenario used in this study. The final potential effect investigated is ocean acidification. Based on laboratory experiments (Frommel et al., 2016), it was possible to include a functional relationship to describe additional larvae mortality due to decreasing pH for yellowfin tuna. The uncertainty associated with the laboratory experiments is integrated through three different parameterizations - low, medium and high impact (see *Supp. Mat.*).

Taken together, these different simulations produce an ensemble of 35 members for yellowfin tuna and 20 members for the three other tuna species (Table 1). Impact of climate change on tuna is analysed by extracting the mean and standard errors of biomass of tuna for the adults and recruits from the simulation ensembles for different areas (EEZs of PICTs, high seas pockets and international waters).

Results

Historical reference simulations (1980-2010)

A. Tuna biology and model optimization

The model optimizations provide realistic estimates of dynamics and distributions of the four species of tuna as known from historical fisheries and catch distributions (Figure 1 and *Supp. Mat.*) and general knowledge on these species (e.g., Sharp and Dizon 1978; Sund et al 1981; Graham and Dickson 2004). Skipjack, yellowfin and bigeye tuna and albacore inhabit a wide range of ecosystems in the epi- and meso-pelagic oceanic layers of the tropical/subtropical Pacific Ocean. Skipjack and yellowfin tuna spend their entire lives in tropical waters, or tropical waters transported into more temperate latitudes by currents (Kuroshio and East Australian Currents). They grow quickly, reach small to medium maximum size, have early age at first maturity and short to medium life spans. In contrast, bigeye tuna and albacore have life-history characteristics that are intermediate between tropical and temperate (e.g., bluefin) tuna. They are distributed both in tropical waters and temperate waters, and characterized by intermediate to maximum size, and slower rates of growth, greater ages at first maturity and longer life spans (>10 years) than skipjack and yellowfin tuna.

Recent studies on the growth of bigeye tuna (Aires-da-Silva et al., 2015; Farley et al. 2017) suggest that mean length-at-age is larger in the EPO than in the WCPO. This new information has been used to revise the growth function for stock assessments provided for the WCPFC (McKechnie et al. 2017), which now have a lower asymptotic length value (around 150 – 160 cm, instead of 184 cm used in the 2014 reference case model). Both past and new growth parameters have been tested with SEAPODYM. The overall fit to data is slightly improved with the new parameters, due to a more diffusive population density. When comparing the fit to catch data from the fishery, there is no real differences between the two simulation outputs. However, the structures of the populations are significantly different. In the "new growth" simulation, lower natural mortality coefficients are estimated in old age classes, allowing a substantial increase in the mean age and biomass of older individuals to compensate for the change associated with lower size (weight) predicted by the growth function. There are also substantial changes in spawning habitat and subsequent recruitment. The different structures allow a similar fit to catch data but result in a degraded fit to spatially-disaggregated size-frequency data of longline fisheries. Therefore, the reference bigeye simulation for the present study retains the growth parameters of the 2014 assessment (Harley et al. 2014).

Sampling at sea indicates that all tuna species spawn in warm waters (mainly with SST > 26 °C) in broad areas of the equatorial and tropical oceans (e.g., Wild and Hampton 1994). Laboratory experiments have identified the optimal range of temperatures for yellowfin tuna larvae as 26° to 31°C (Wexler et al. 2011). The model estimates optimal spawning SST ranges in agreement with these observations, with optimal values between 26.5 and 28.9 °C and standard errors ranging from 1.5 to 3.1°C (*Supp. Mat.*). Combined with larval prey and predator mechanisms included in the definition of spawning habitat, and local density-dependence, stock-recruitment mechanism for larvae, the result is an overlapping but gradually changing average distribution of larval density (Figure 2). For skipjack tuna, the core area of this distribution is the Western Pacific Warm Pool. The pattern for yellowfin tuna is similar but slightly more extended to the central-eastern Pacific, whereas bigeye tuna has a more central distribution and albacore has a sub-equatorial distribution (10°S - 25°S). These general patterns agree with observations based on larval sampling, catch of juveniles, and occurrence of sexually mature adults. The dynamics of these distributions are influenced by ENSO, leading to inter-annual variability in recruitment and stock biomass (Lehodey et al. 2001, 2003, 2017; Senina et al. 2008, 2017).

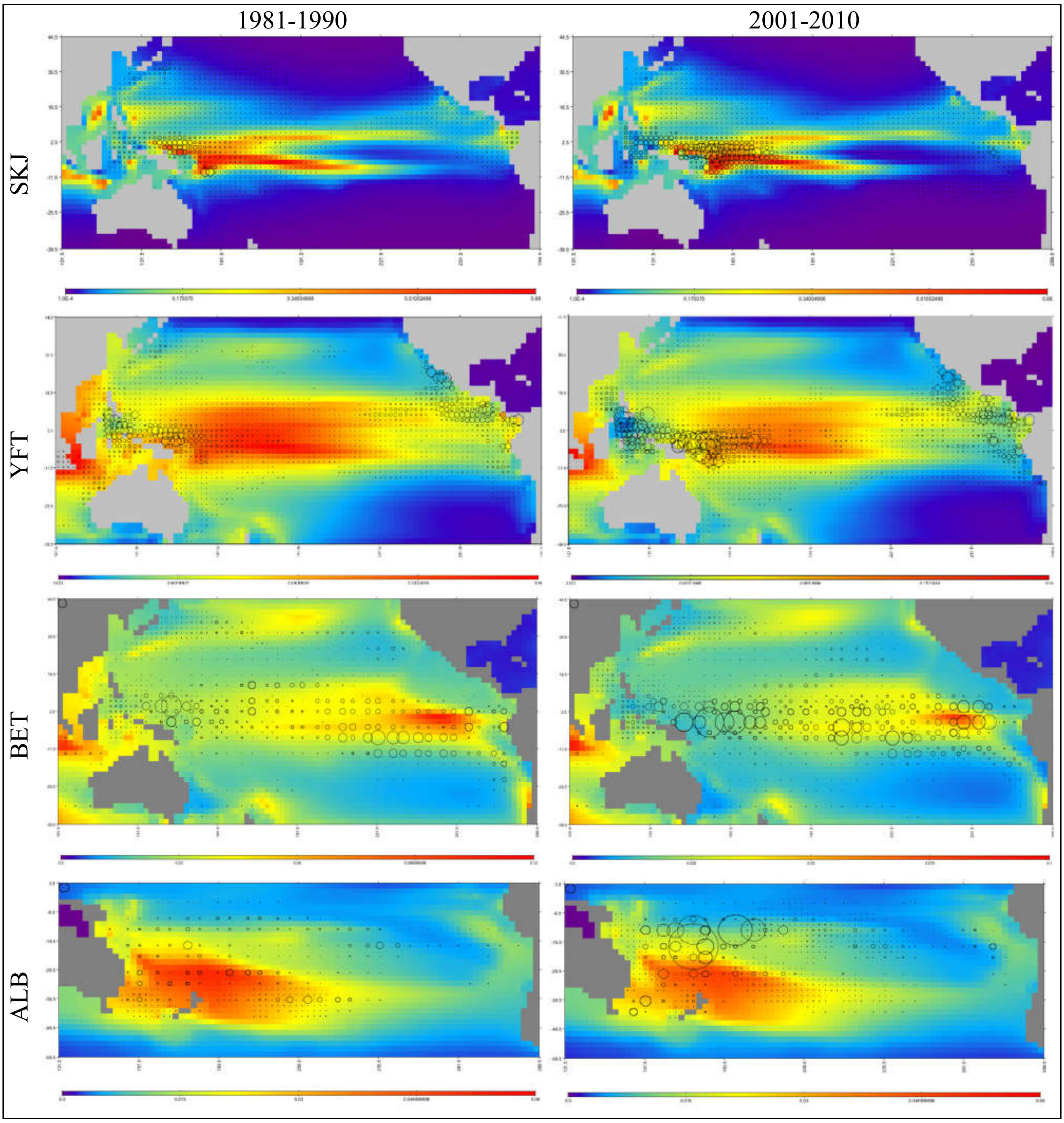

Figure 1: Comparison of predicted distributions for 1st and last decade of the historical time series. Total observed catches are shown, with catch proportional to the size of the circles (same scales between decades).

Skipjack and yellowfin tuna are opportunistic spawners, whereas there is noticeable seasonality in the spawning of albacore, which spend most of their lives feeding in subtropical/ warm-temperate waters and migrate to latitudes of 10°S and 25°S to spawn (Ramon and Bailey 1996). Juvenile albacore (age 1 year, ~45 cm FL) are subsequently caught in surface fisheries in New Zealand's coastal waters. The seasonal switch between feeding and spawning migrations is used in the model for albacore and the associated parameters are estimated effectively with the MLE. This is not the case for the three other species of tuna (*Suppl. Mat.*).

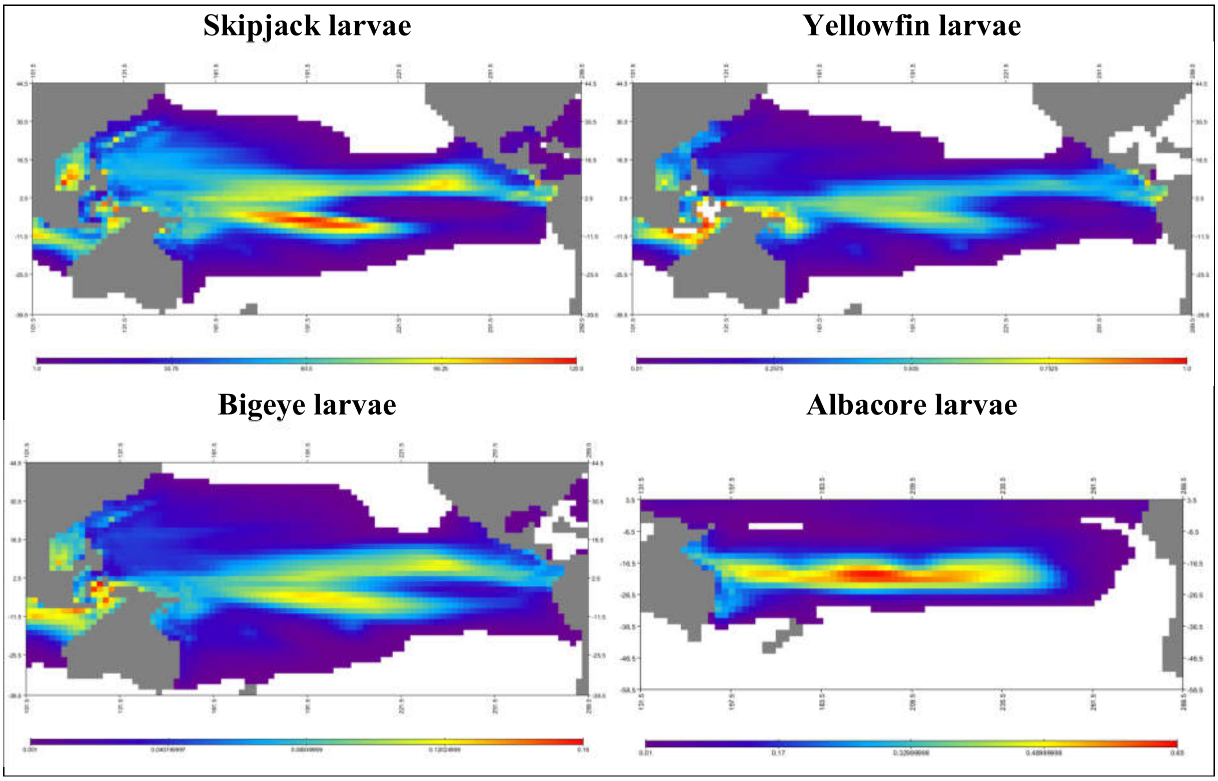

Figure 2: Mean predicted distributions of tuna larvae densities (nb km^{-2}) for 2001-2010.

All four species of tuna are voracious opportunistic predators feeding on micronekton organisms. The feeding habitat of immature and adult tuna is defined by their accessibility to the six functional groups of epi- and mesopelagic micronekton included in the model. The accessibility of micronektonic prey depends on the tolerance of tuna to low oxygenated waters, and the temperature preference of tuna species, which change with age and are weighted by a coefficient for each micronekton group. Parameter estimates are provided in *Supp. Mat.*. With the narrowest estimated thermal habitat (26°- 28.5°C) and the lowest tolerance to low-oxygenated waters (threshold value 3.76 mL L^{-1}), skipjack tuna is mainly limited to epipelagic forage, i.e., either resident epipelagic or highly-migratory mesopelagic micronekton species present in the surface layer at night. The thermal habitat of yellowfin tuna is estimated to be wider (13.3 - 32°C) and the model for this species shows a lack of sensitivity to oxygen with a very low oxygen tolerance threshold value (0.41 mL L^{-1}). The habitat is known to be even wider for bigeye tuna. Adults of this species have well-developed thermoregulation mechanisms and physiological adaptations that confer good tolerance to low levels of dissolved oxygen, allowing them to dive regularly to the deeper lower mesopelagic layer (>400 m depth) (Brill 1994; Schaefer and Fuller 2010). For bigeye tuna, the model estimates a large thermal range with the optimal value at age decreasing from 27°C for the youngest cohorts to 10°C for the oldest. There is also a low threshold oxygen value (0.5 mL L^{-1}), and an increasing contribution of non-migrant lower-mesopelagic micronekton for bigeye tuna compared to the other tuna species. Albacore is much less tolerant to poorly oxygenated waters than bigeye tuna (Sund et al. 1981; Brill 1994) and more limited in its vertical habitat - electronic tagging data indicate that albacore has a preference for the upper mesopelagic layer (Domokos et al. 2007; Williams et al. 2015). Bertrand et al. (2002) reports that 97.5% of all experimental longline albacore catch in the French Polynesian EEZ occurred in waters above 10°C. These observations match well the predicted habitat with a thermal range estimated between 10°C (std. dev. 1.99) and 23.5°C (std. dev. 5.21), a threshold value in dissolved oxygen concentration of 3.43 mL L^{-1} and a noticeable contribution of upper meso-pelagic micronekton groups (*Supp. Mat.*).

Thus, it is remarkable that the relationships to the different functional groups of prey estimated to compute the feeding habitats, agree well with observations on the feeding ecology and vertical behaviour of tuna (e.g., Sund et al. 1981; Dagorn et al. 2000; Bertrand et al. 2002; Domokos et al. 2007; Schaefer et al. 2010; 2011). Skipjack tuna are limited to feeding on the groups present in the epipelagic layer (epipelagic and highly migrant lower mesopelagic); yellowfin tuna to the epipelagic and upper mesopelagic layers, bigeye tuna to the upper and lower mesopelagic layers; and albacore to the non-migrant upper mesopelagic and epipelagic groups. For albacore, however, this habitat is characterized by a marked seasonal change (and thus migration) between the spawning ground in tropical waters and the feeding grounds near Tasmania, New Zealand, and the sub-tropical convergence zone (STCZ) in the central Pacific at about 40°S. This is well simulated by the model with a migration controlled by the seasonal change in day length leading to a gradual shift of the thermal preference window towards the optimal spawning temperature range. The resulting movement of albacore *"tends to correspond with the* *seasonal shift in the 23–28°C sea surface temperature isotherm location*" as inferred from monthly trends in longline catch rates by Langley (2004).

The effective average movement rates are computed by combining estimated theoretical rates with predicted values of habitat (diffusion) or habitat gradients (advection). The highest diffusion rates estimated for albacore are somewhat counter-balanced by the seasonal switch of the spawning migration that creates strong habitat gradients around the peak of the spawning season. This peak is predicted to occur in early November in the Southern Hemisphere (i.e., Julian day 115 for the northern hemisphere), and coincides with the peak observed in the gonad index of female albacore (Farley et al. 2013).

For the three other tuna species, which spawn and feed in tropical waters, the movements are controlled only by the gradient in the feeding habitat. The use of tagging data in the MLE in the application to skipjack tuna (see details in Senina et al. submitted) allows a better estimation of movement, resulting in less diffusion. Note the tagging data were used for bigeye and yellowfin tuna only for the estimation of habitat parameters in the first phases of optimization.

B. Historical fisheries and biomass distributions

Together, skipjack, yellowfin and bigeye tuna and albacore represent >90% of the total catch taken by industrial fleets in the Pacific Ocean. Pole-and-line and longline were the first two main fishing gears used by industrial fleets, with pole-and-line targeting small- to medium-size skipjack and yellowfin tuna in surface waters, and longline targeting larger individual yellowfin and bigeye tuna and albacore in subsurface waters. The surface fishery also includes boats that use trolling gear to target albacore, and small-scale artisanal fisheries using various fishing gears such as handlines and ringnets.

After a development phase in the 1970s, purse-seine fishing expanded rapidly at the expense of the pole-and-line fishery. Since the 1990s, the use of fish aggregating devices (FADs) to attract and temporarily retain schools of tuna, has been widely adopted by purse-seine vessels. Today, half of the total purse-seine catch is taken around FADs. The purse-seine and pole-and-line fisheries in surface waters supply the canning industry, while the longline catch is for fresh or frozen markets, including the valuable sashimi market. A concern associated with the use of FADs is the increasing catch of juvenile bigeye tuna - this species is not the target of the surface fishery and has lower productivity than skipjack and yellowfin tuna.

These fisheries are described and listed in *Supp. Mat*. for each species together with the fit of model predictions to these data (catch and size frequencies of catch). For computational reasons, a compromise is needed between a reasonable number of fisheries and the most homogeneous possible definition according to various criteria (gear, flag, region, period, target species, etc.). Classically, for a given species, the best fits are obtained for fisheries targeting the species over time without switching to a different species and modifying the fishing strategy. For instance, longline fleets targeting bigeye tuna receive a lower score for albacore and yellowfin tuna. Also, since the same purse-seine fishing vessel can fish both on a free school of tuna or a school associated with FADs, the total fishing effort (number of fishing days in a month in the grid cell of the model) needs to be divided between these two different fisheries defined by different catchability and size selectivity. This can result in a noisy fishing effort, especially considering the high spatial resolution of the model. Nevertheless, each fishery is sufficiently well described to achieve very good prediction of total catch by species over the historical period (1980-2010), with correlation coefficients above 0.8 for each series of total catch. This is essential to account for the increasing fishing mortality over the historical period (1980-2010), and to produce accurate initial conditions of the population structures at the beginning of the projection.

Not surprisingly, given the observed trends in fishing effort and catch, the fishing impact is increasing over time (Figure 3). The strongest impact at the end of the time series is on bigeye tuna, with a decrease in adult (spawning) biomass in the range of 50-55% for both the EPO and WCPO, followed by yellowfin tuna (50% and 42% for the EPO and WCPO, respectively), albacore (44%) and skipjack tuna (20-25%). Fishing impact vary spatially, with the strongest decreases occurring in the main fishing grounds (Figure 1).

C. Climate change projections

Without considering the impact of past and future fishing, the projections achieved with the simulation ensembles show average anomalies increasing with time until the end of the century, and with the trends occurring in opposite directions for the EPO and the WCPO (Figure 3). The widest range of uncertainty is for albacore and skipjack tuna in the 2nd half of the century. In the WCPO, trends of biomass are stable until 2050 and then start to decline, with increasing steepness from bigeye tuna to yellowfin tuna to skipjack tuna. The maximum average decrease over the 21st Century is predicted for yellowfin tuna (-40%) and skipjack tuna (-38%), whereas decreases look like they may be limited to -15 % for bigeye tuna. Opposite trends occur in the EPO, with a projected increase of 40% for skipjack tuna compared to the recent period 2000-2010. However, the difference is lower when compared to the period 1980-2000 that was dominated by a higher frequency of strong El Niño events, predicted to be favourable to skipjack recruitment in this region. The projected increase for yellowfin tuna in the EPO is just above 30%, and 20% for bigeye tuna.

For albacore, the ensemble of simulations project a rapid increase in average biomass of 50%, stabilizing after 2035, but with much associated uncertainty. The analysis of uncertainty associated with each specific scenario for albacore (Figure 4) indicates that the rapid projected increase in biomass of albacore is due to the very strong effect of the scenario where no change in dissolved oxygen concentration occurs (SO), resulting in a 3-fold increase in mean biomass. When this scenario is removed, the mean biomass of albacore is predicted to remain stable. By comparison with the reference projection (REF), the SO scenario is also favourable for yellowfin tuna in the EPO. The scenario for a possible underestimation of primary production in the tropical ocean (SP) has a positive effect on all tuna species, but is most pronounced for bigeye and then yellowfin tuna. Under the SP scenario (when primary production increases by 10% in waters above 27°C), the biomass of bigeye tuna increases up to 18% by the end of the century compared to the reference scenario. The scenario testing the effect of a potential adaptation (ST), with optimal spawning temperature increasing in parallel to the projected warming of surface water (>2° by the end of the century), has positive effect only for skipjack tuna in the WCPO (Figure 4) and would be an unfavourable 'adaptation' for all tuna stocks in the EPO. Finally, the ocean acidification scenario (PH), tested only for yellowfin tuna, shows that effects will be strongest in the EPO. Despite ocean acidification causing a relatively small additional mortality for larvae (*Suppl. Mat.*), the average accumulated effect on the yellowfin tuna population in the EPO leads to a biomass decrease of 20% compared to the reference scenario.

In absence of fishing, the population trends in the model are mainly driven by larval recruitment combining with the index value of the spawning habitat and the local density-dependent effect linked to adult (spawning) biomass. Therefore, the changes associated with the oxygen scenarios are mainly driven by the better feeding habitat of adult fish, allowing them to occupy an increasing proportion of the favourable spawning habitat and to eventually reach the maximum potential of the population. For albacore, the density decreased over time in the western part of the southern Pacific Ocean but this was offset by increases in the eastern part (Figure 5). This trend is seen in all simulations with and without oxygen change. For the three other species of tuna, the projected impact of climate change is strongly driven by the spawning habitat through changes in temperature and primary production. For yellowfin tuna in the EPO, the impact is also linked to future oxygen conditions in the adult habitat. Spatial density distributions of skipjack and yellowfin tuna are projected to be the most impacted (Figure 5). The density of skipjack tuna is expected to decrease in the west and slightly increase in the central and east Pacific. Overall, however, total biomass is projected to decline. The biomass of yellowfin tuna projected to be stable at the basin-scale but there is a clear shift in population density from the western to the central and eastern Pacific. The density distribution for bigeye tuna is expected to decrease slightly and homogeneously throughout its habitat, with very few spatial changes compared relative to its present-day distribution.

The projected changes in abundance and distribution of all four species are have potential impacts for the economies of Pacific Islands countries. For example, by 2050, the eastward shift in distribution and decrease in biomass for skipjack and yellowfin tuna could impact Papua New Guinea (PNG), whereas French Polynesia would have a substantial increase in biomass relative to the 2000 decade. In the second half of the century, the decrease in mean percentage biomass will extend to most other EEZs west of 170 °E (FSM, Nauru, Solomon Islands, Palau and Tuvalu), and conversely increase in Vanuatu, Samoa, American Samoa and New Caledonia. The climate change impact on bigeye tuna is predicted to be much lower and significant only by the end of century with a maximum average decrease around 20% in Nauru, Tuvalu and New Caledonia. For albacore, consideration needs to be given to the scenarios with and without projected changes in dissolved oxygen concentration (Figure 5; Table 1). With projected changes in oxygen, the largest increases in mean biomass occur in the EEZs of PICTs to the west (Palau, PNG, FSM and Nauru) but decreases of around 15% are expected to occur in the EEZs of Fiji, New Caledonia and Vanuatu by at the end of the century. If no change in dissolved oxygen concentration occurs, large and widespread increases in biomass are expected, with the maximum increase (~200%) shifted slightly to the western-central region in the EEZs of Palau, Marshall Islands, Kiribati and FSM.

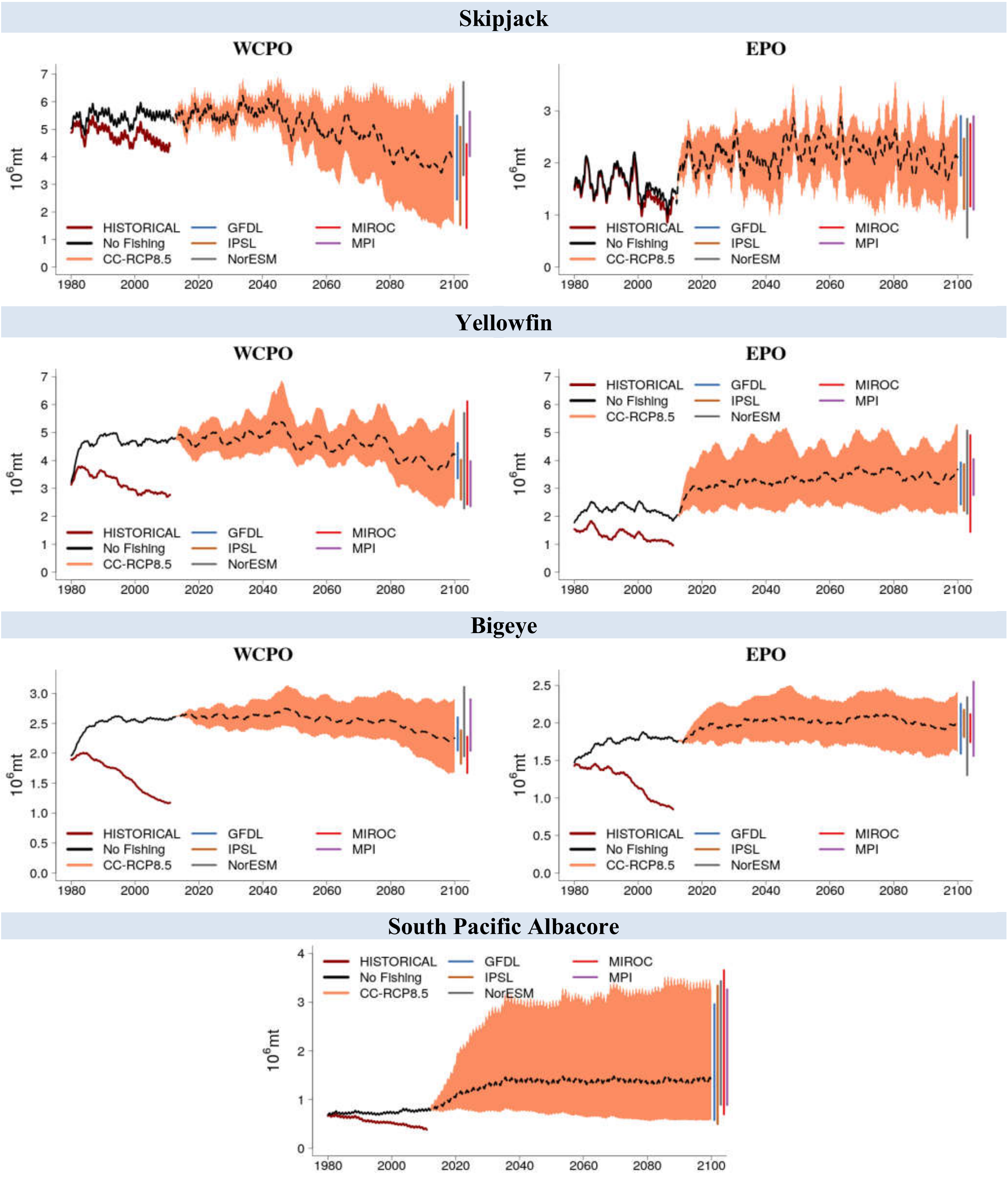

Figure 3: Envelope of predictions computed from simulation ensembles under IPCC RCP8.5 scenario for the western central (WCPO) and eastern (EPO) Pacific Ocean. The change in total biomass is presented with the average (dotted line) and its envelope bounded by the 5% and 95% quantile values of the simulation ensembles.

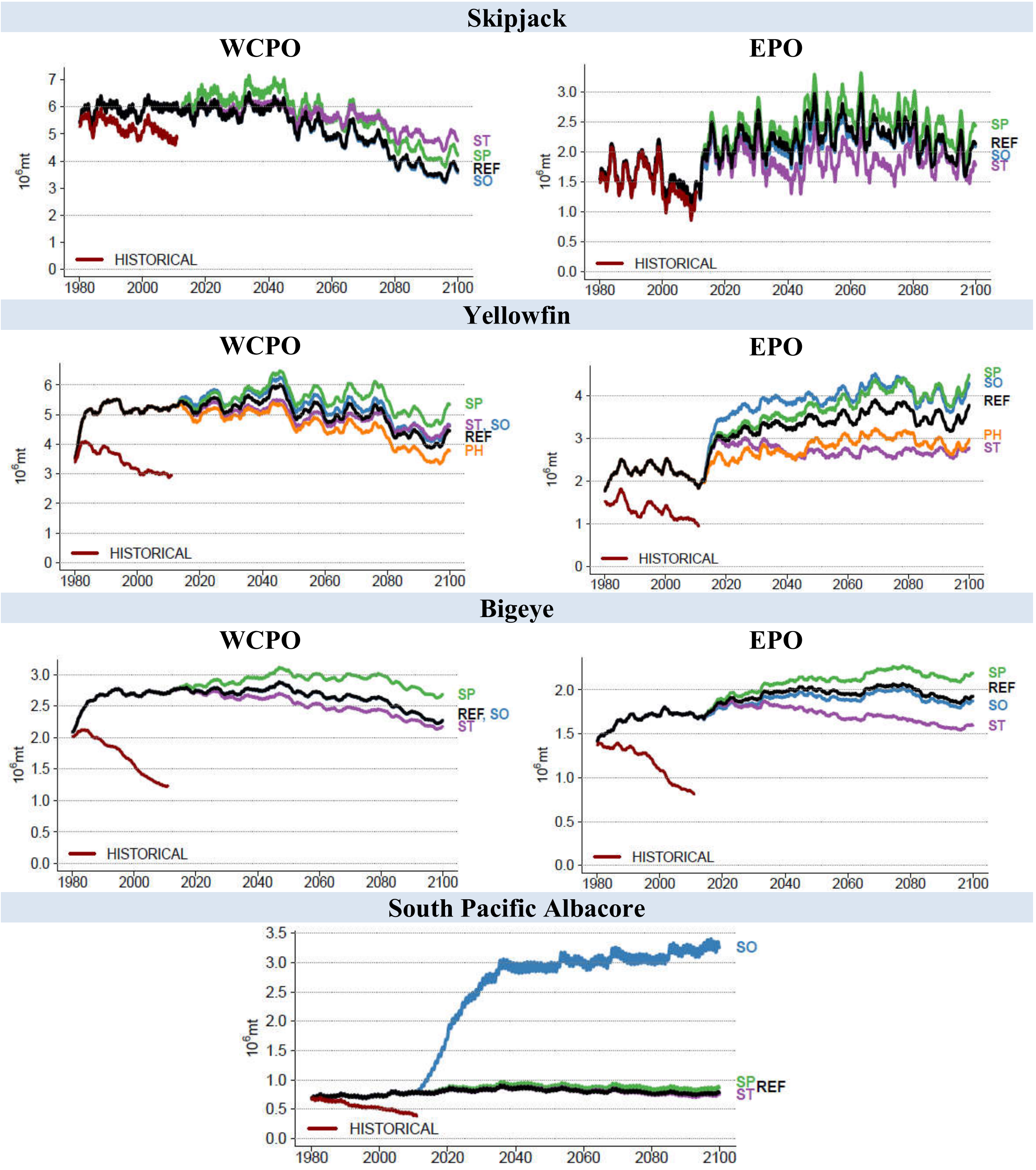

Figure 4: Mean projection (5 forcings) by scenario exploring uncertainty in primary production (SP), change in optimal spawning temperature (ST), no change in dissolved oxygen concentration (SO) and ocean acidification scenario (PH) compared to the reference projection (REF).

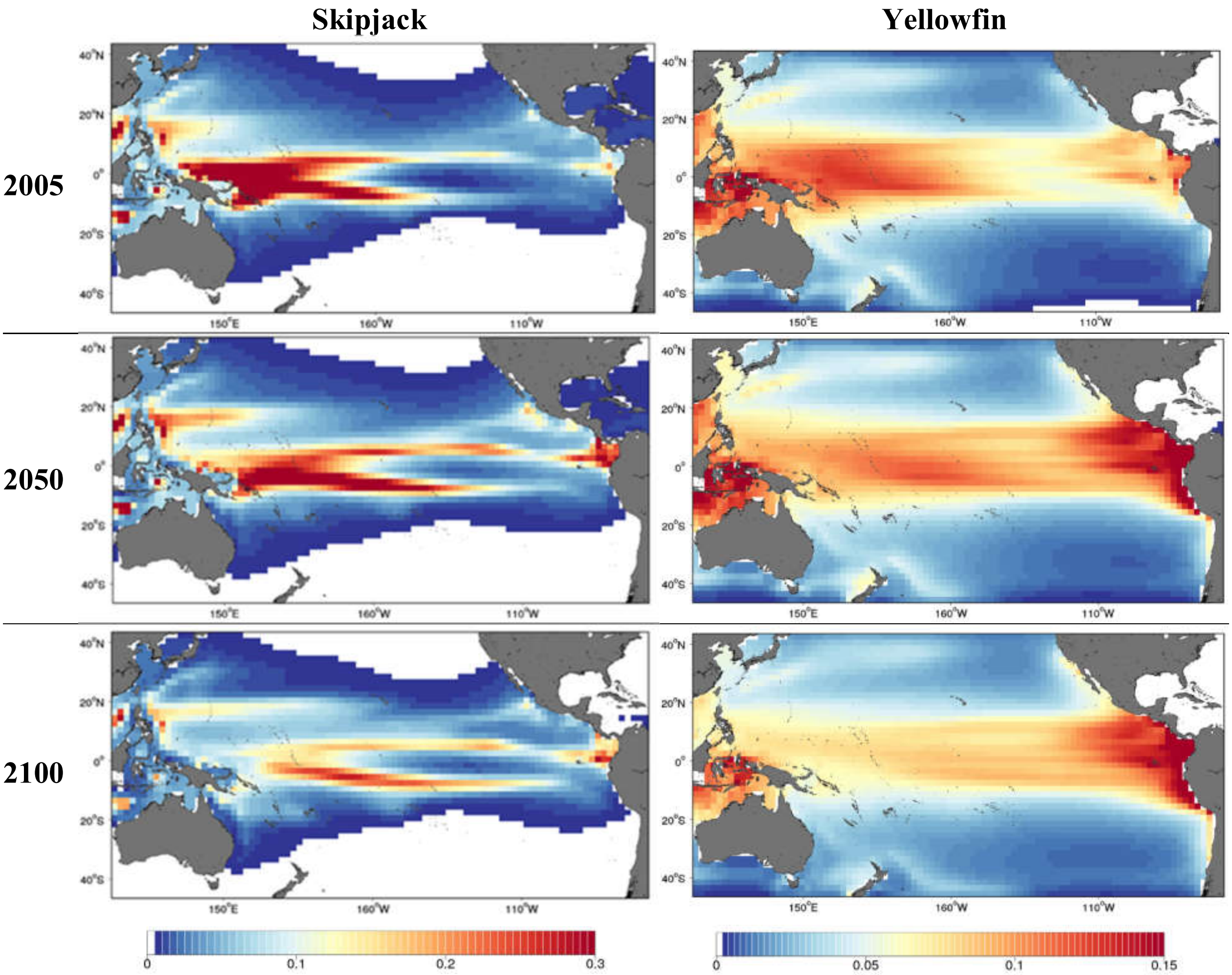

Figure 5: Projected mean distributions of skipjack and yellowfin tuna biomass across the tropical Pacific Ocean under a high emissions scenario (IPCC AR8.5) for 2005 and from the simulation ensembles in the decades centred on 2045 and 2095 including projected average percentage changes for the outlined areas east and west of 150°W.

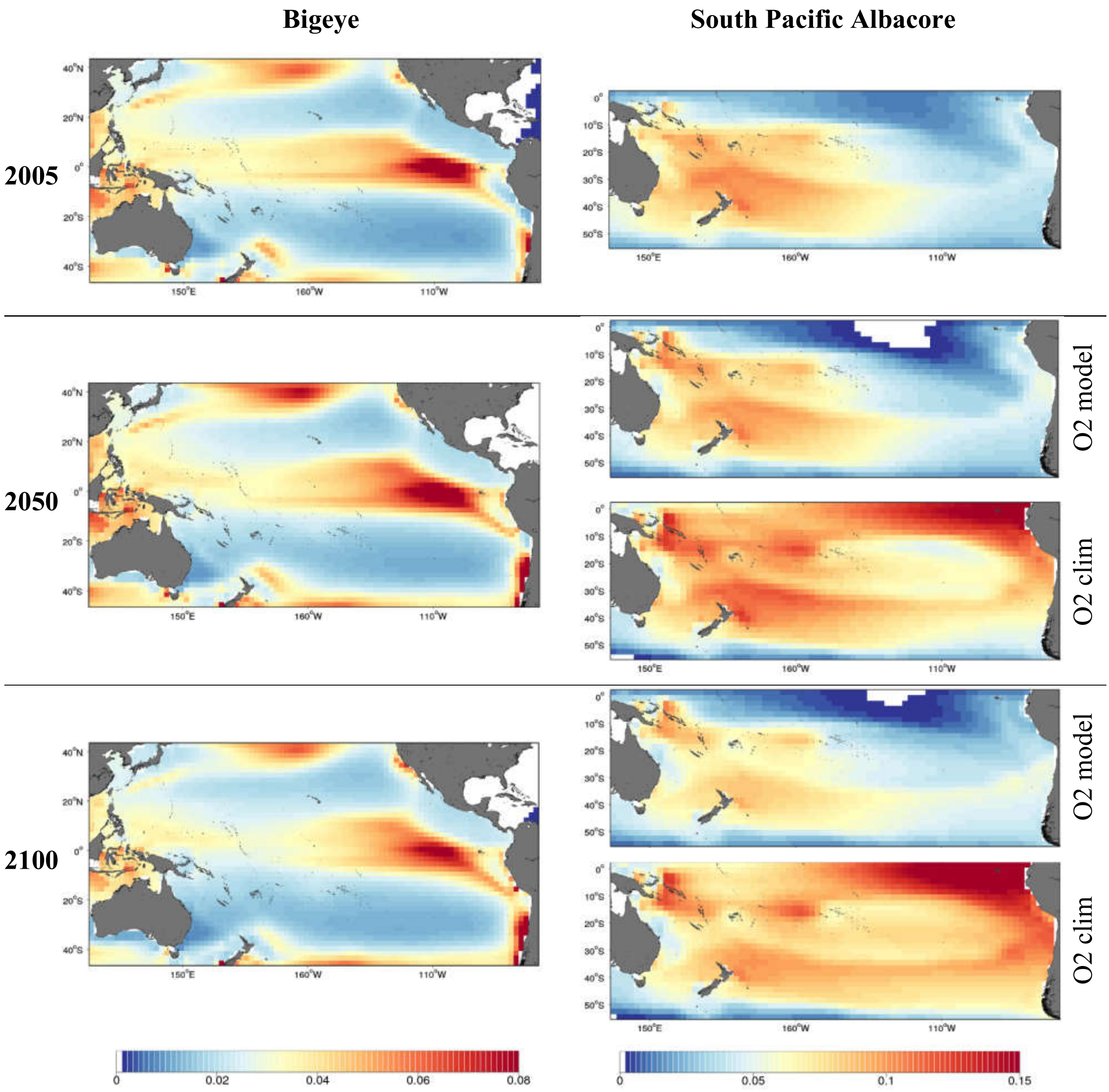

Figure 5 (cont.): Projected mean distributions of bigeye (left) and South Pacific albacore (right) tuna biomass across the tropical Pacific Ocean under a high emissions scenario (IPCC AR8.5) for 2005 and from the simulation ensembles in the decades centred on 2045 and 2095. For the South Pacific albacore two mean distributions are shown with and without the climatological oxygen scenario.

Table 1: Mean biomass change (%) by EEZ for the decades 2046-2055 (2050) and 2091-2100 (2100) relative to 2001-2010 average. CNMI = Commonwealth of Northern Mariana Islands; FSM = Federated States of Micronesia.

Area	**Virgin biomass**							
	SKJ		***YFT***		***BET***		***ALB***	
	2050	2100	2050	2100	2050	2100	2050 (-SO)	2100 (-SO)
West of 170°E								
CNMI	48	8	-1	-14	4	-5	-	-
FSM	-29	-55	-19	-37	3	-6	196 (32)	188 (22)
Guam	-5	-30	-16	-30	2	-3	-	-
Marshall Islands	-17	-31	-12	-31	-3	-12	216 (20)	211 (6)
Nauru	-8	-51	-16	-44	-4	-23	170 (31)	143 (6)
New Caledonia	8	49	-9	-25	-5	-18	14 (0)	-3 (-16)
Palau	-28	-54	-12	-29	4	-6	226 (58)	209 (48)
Papua New Guinea	-43	-72	-21	-42	-4	-16	72 (35)	64 (28)
Solomon Islands	-17	-37	-9	-30	-2	-14	62 (24)	46 (8)
East of 170°E								
Vanuatu	21	82	-2	-20	-1	-13	20 (4)	2 (-14)
American Samoa	42	61	23	9	4	-7	41 (9)	36 (-2)
Cook Islands	16	29	28	18	3	-7	47 (5)	39 (-7)
Fiji	14	14	6	-14	-1	-16	21 (1)	3 (-16)
French Polynesia	97	99	43	45	7	0	60 (4)	59 (-6)
Kiribati	18	-21	7	-17	1	-15	200 (14)	181 (-7)
Niue	24	15	20	6	3	-9	31 (6)	20 (-6)
Pitcairn Islands	60	41	55	72	10	7	68 (11)	85 (11)
Samoa	39	46	20	4	3	-8	36 (7)	29 (-4)
Tokelau	-14	-24	14	-7	-1	-17	92 (11)	69 (-10)
Tonga	15	3	13	-5	1	-14	25 (4)	14 (-9)
Tuvalu	-12	-45	3	-23	-2	-21	93 (13)	66 (-10)
Wallis and Futuna	26	21	14	-5	2	-11	39 (9)	28 (-6)

Discussion

The modifications to SEAPODYM done during this project has improved the ability of the model for describing the spawning mechanisms, the accessibility to micronekton (prey) functional groups, and seasonal spawning migrations of tropical Pacific tuna and fisheries compared to previous optimizations of SEAPODYM (e.g., Senina et al. 2008; Lehodey et al. 2010, 2013, 2015). Importantly, substantial effort has also been devoted to 1) a quantitative method to estimate parameters with the integration of conventional tagging data in the Maximum Likelihood Estimation approach (Senina et al. 2017, submitted), and 2) an alternative method to use catch directly in the likelihood function when fishing effort is not available or not reliable. A priori information on total biomass was also added in the likelihood to force the model to reach the best compromise between minimal biomass and a good fit to observations. Together with a more realistic environmental forcing and spatially disaggregated fishing data sets revised to match the total declared catch, these evolutions have permitted better estimates of model parameters with a better fit to data, and improved and consistent distributions and dynamics of these important tuna species. The emergence of key features known from the ecology and behaviour of the tuna species is particularly remarkable, such as the relationships between each species and the different vertical layers of the water column and their associated functional groups of prey, and/or the predicted spawning grounds and larval distributions. The results for albacore are also notable, given the more complex life cycle of this sub-tropical species, involving seasonal migrations of adults between feeding and spawning grounds.

The convergence in biomass estimates with independent stock assessment studies (McKechnie et al. 2016, 2017; Tremblay-Boyer et al. 2017; Harley et al. 2014, 2015) provides further confidence in the utility of SEAPODYM to simulate the dynamics of tuna populations under both the fishing pressure and environmental variability that control the abundances and spatial distributions of the four tuna species. This validation over the historical period is a necessary condition for projecting the future of tuna dynamics under the impact of strong environmental changes using IPCC scenarios. The agreement between predicted spawning grounds and larval distributions using existing data and knowledge is also essential because the early life stages are the most sensitive to variability in oceanographic conditions, and thus more vulnerable to the impact of climate change. Nevertheless, it is also necessary to consider ocean acidification. At present this is difficult because the effects of lower pH on the four tuna species, and the prey organisms that support them, are still largely unknown and were not included nor needed in the historical simulation. However, he results of recent laboratory research for yellowfin tuna larvae (Bromhead et al. 2015; Frommel et al. 2016) enabled us to include this effect in the model for this species for the first time. The simulations for yellowfin tuna indicate that ocean acidification has an additional impact on larvae. In the worst scenario, mortality of larvae in the EPO could increase by of 10 to 15% at the end of the century. Over time, this accumulation of the effect of this additional mortality would be expected to produce a significant decrease of the total stock of yellowfin tuna.

In comparison to previous studies (Lehodey et al. 2010, 2013, 2015; Bell et al. 2013, 2018), the conclusions about the impact of a high greenhouse gas (GHG) emissions scenario on skipjack and yellowfin tuna remain unchanged, confirming an eastern shift in biomass of both species over time. However, the envelope of projections becomes very wide for skipjack after mid-century. The improvements to SEAPODYM during this study indicate that the impact of a high GHG emissions scenario on bigeye tuna are likely to be lower than previously determined. This is essentially due to the revised parametrization of the spawning habitat. With this new optimization, estimates for the spawning temperature function produce a wider and warmer range of favourable spawning habitat for bigeye tuna. For albacore, the sensitivity to oxygen detected in previous work is clearly confirmed. However, the expected shift in the spawning ground of albacore to the south identified during a previous study was not confirmed. This is due to the new estimated temperature spawning function, which points to a warmer optimal temperature.

As mentioned in the Section B of the Results, the new simulations indicate that the projected impacts of climate change on tropical Pacific tuna species are likely to have strong implications for the economic development of Pacific Island countries, and the management of tuna resources at basin scale. Although fishing scenarios still need to be used to project the changes in catch by EEZ, an eventual decrease in catch for fleets targeting skipjack and yellowfin tuna with surface fishing methods in the EEZs of countries east of 170°E is likely. Such decreases in catch would result in less revenue from licence fees for the Pacific Island countries (unless practical ways can be found to increase the value of catches, Bell et al. 2018). Larger proportions of each these species are also expected to become accessible in international waters (high seas areas), making the monitoring and control of industrial tuna fisheries more difficult. Therefore, these results argue for the reinforcement of fisheries monitoring and the eradication of illegal fishing at basin scale.

The historical fishing pressure is estimated to have reduced the adult stocks of the tuna species by 30-55% by the end of 2010, depending on species and region. The level of fishing has certainly increased since then and may be closer to, or higher than, the optimal sustainable target of -60% (-50% for skipjack tuna) proposed by the regional fisheries management organizations. The reduction in biomass due to fishing is much more than the reductions expected to occur due to climate change in the decades ahead.

Thus, the effects of fishing are expected to continue to be the dominant driver of tuna population sizes until at least mid-century.

Nevertheless, the rapid, progressive improvements in the development and validation of Earth Climate models should be used to regularly revisit these conclusions and the uncertainty included in the results. In addition, more elaborate methodology needs to be developed to correct the climate model forcings before running the coupled physical-biogeochemical model. Given the sensitivity of the results to the processes controlling the suitability of spawning habitat, and larval survival, a strong research effort (including *in situ* observations and laboratory experiments) should be dedicated to defining the effects of optimal range of spawning temperature and the effect of pH on the simulations. Better monitoring and modeling of future trends in dissolved oxygen concentration and pH will also be essential to reducing the uncertainty associated with this study.

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Supplementary Material

A. Datasets used for model optimization and fishing mortality estimates

Catch data used in optimization of SEAPODYM are monthly spatially-disaggregated catch data at resolution varying from 1 degree (typically for surface gears as purse seine and pole and line) to 5 degrees squares. Size frequencies of catch are aggregated on quarterly time steps at resolutions of 1, 5, 10 or 20 degree squares. For tagging data, only the recapture data available since 2008 are used. A summary of datasets used in the four tuna models are presented here. More details on the optimization approach and these datasets can be found in Senina et al. (2015, 2016, and 2017) and Lehodey et al. (2014, 2017).

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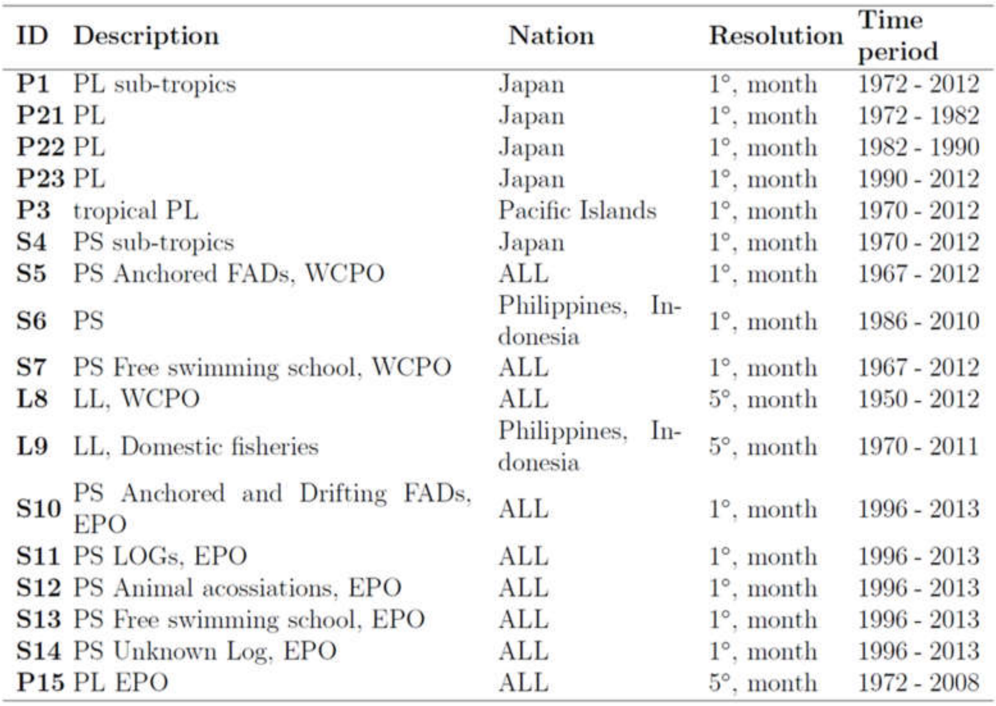
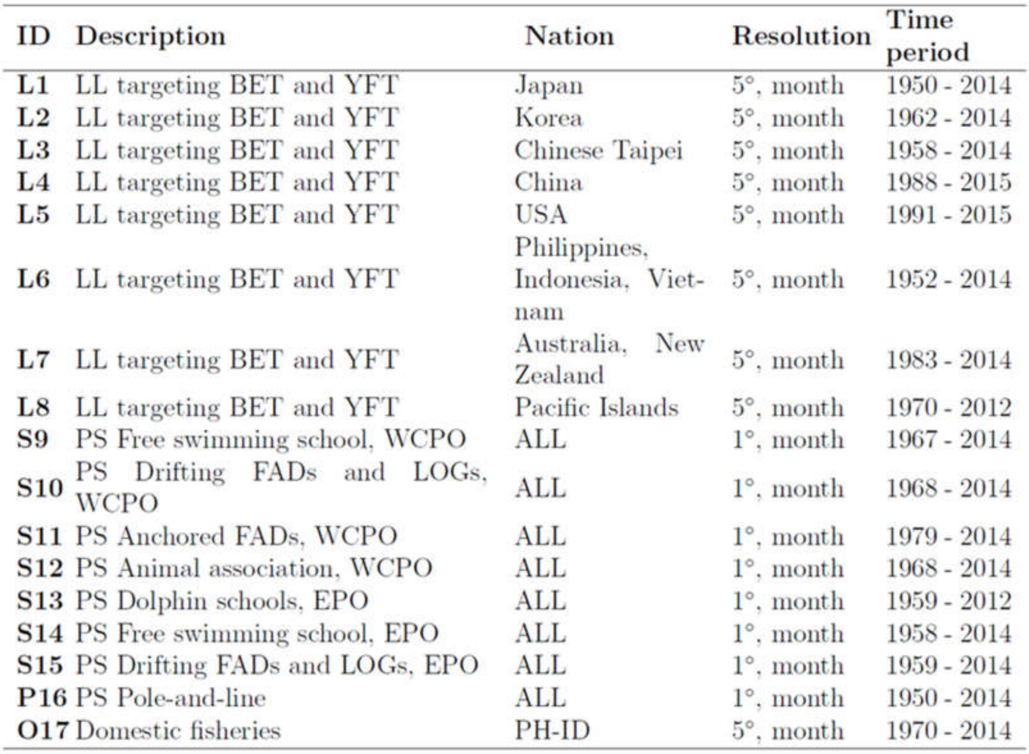
Table A2: Definition of Pacific skipjack tuna fisheries and fishing data used in basin-scale optimization experiments performed for the Pacific Ocean domain (PL: pole-and-line; PS: purse seine).



ID	Description	Nation	Resolution	Time period
P1	PL sub-tropics	Japan	1°, month	1972 - 2012
P21	PL	Japan	1°, month	1972 - 1982
P22	PL	Japan	1°, month	1982 - 1990
P23	PL	Japan	1°, month	1990 - 2012
P3	tropical PL	Pacific Islands	1°, month	1970 - 2012
S4	PS sub-tropics	Japan	1°, month	1970 - 2012
S5	PS Anchored FADs, WCPO	ALL	1°, month	1967 - 2012
S6	PS	Philippines, Indonesia	1°, month	1986 - 2010
S7	PS Free swimming school, WCPO	ALL	1°, month	1967 - 2012
L8	LL, WCPO	ALL	5°, month	1950 - 2012
L9	LL, Domestic fisheries	Philippines, Indonesia	5°, month	1970 - 2011
S10	PS Anchored and Drifting FADs, EPO	ALL	1°, month	1996 - 2013
S11	PS LOGs, EPO	ALL	1°, month	1996 - 2013
S12	PS Animal acossiations, EPO	ALL	1°, month	1996 - 2013
S13	PS Free swimming school, EPO	ALL	1°, month	1996 - 2013
S14	PS Unknown Log, EPO	ALL	1°, month	1996 - 2013
P15	PL EPO	ALL	5°, month	1972 - 2008

Table A3: Definition of Pacific yellowfin tuna fisheries and fishing data used in basin-scale optimization experiments performed for the Pacific Ocean domain.



ID	Description	Nation	Resolution	Time period
L1	LL targeting BET and YFT	Japan	5°, month	1950 - 2014
L2	LL targeting BET and YFT	Korea	5°, month	1962 - 2014
L3	LL targeting BET and YFT	Chinese Taipei	5°, month	1958 - 2014
L4	LL targeting BET and YFT	China	5°, month	1988 - 2015
L5	LL targeting BET and YFT	USA	5°, month	1991 - 2015
L6	LL targeting BET and YFT	Philippines, Indonesia, Vietnam	5°, month	1952 - 2014
L7	LL targeting BET and YFT	Australia, New Zealand	5°, month	1983 - 2014
L8	LL targeting BET and YFT	Pacific Islands	5°, month	1970 - 2012
S9	PS Free swimming school, WCPO	ALL	1°, month	1967 - 2014
S10	PS Drifting FADs and LOGs, WCPO	ALL	1°, month	1968 - 2014
S11	PS Anchored FADs, WCPO	ALL	1°, month	1979 - 2014
S12	PS Animal association, WCPO	ALL	1°, month	1968 - 2014
S13	PS Dolphin schools, EPO	ALL	1°, month	1959 - 2012
S14	PS Free swimming school, EPO	ALL	1°, month	1958 - 2014
S15	PS Drifting FADs and LOGs, EPO	ALL	1°, month	1959 - 2014
P16	PS Pole-and-line	ALL	1°, month	1950 - 2014
O17	Domestic fisheries	PH-ID	5°, month	1970 - 2014

Table A4: Definition of Pacific bigeye tuna fisheries and fishing data used in basin-scale optimization experiments performed for the Pacific Ocean domain.

ID	Description	Nation	Resolution	Time period
L1	LL traditional BET, YFT target	Japan, Korea, Chinese Taipei (DWFN)	5°, month	1950-2014
L2	LL shallow night	China, Chinese, Taipei	5°, month	1958-2014
L3	LL targeting albacore	Chinese Taipei, Vanuatu (DWFN), Korea, Japan	5°, month	1958-2014
L4	LL Pac. Is.	US (Am.Sam) Fiji, Samoa, Tonga, NC, FP, Vanuatu (dom.); PNG, Solomon	5°, month	1988-2015
L5	LL Hawaii	US Hawaii)	5°, month	1991-2015
L6	LL targeting BET & YFT	Indonesia, Vietnam	5°, month	1969-2014
L7	LL targeting BET & YFT	Australia, New Zealand	5°, month	1984-2015
L8	LL targeting BET & YFT	All	1°, month	1982-2015
S9	PS WCPO, free school	All	1°, month	1967-2014
S10	PS WCPO, FAD & LOG	All	1°, month	1968-2014
S11	PS WCPO anchored FADs	All	1°, month	1979-2014
S12	PS WCPO associated	All	1°, month	1968-2014
S13	PS EPO schools	All	1°, month	1959-2012
S14	PS EPO FAD	All	1°, month	1968-2012
P15	Pole-and-Line	All	1°, month	1950-2014
O16	Domestic fisheries	PH-ID	5°, month	1970-2014

Table A5: Definition of South Pacific albacore fisheries and fishing data used in basin-scale optimization experiments performed for the South Pacific Ocean domain.

ID	Description	Nation	Resolution	Time period
L1	LL distant-water. 140°E-210°E; 20°S-65°S	Japan	5°, month	1952-2012
L2	LL distant-water. 140°E-250°E; 0°S-65°S	Korea	5°, month	1962-2012
L3	LL distant-water. 140°E-250°E; 0°S-65°S	Ch. Taipei	5°, month	1964-2012
L4	LL domestic fleet	Australia	5°, month	1985-2015
L5	LL domestic fleet	New Caledonia	5°, month	1984-2015
L6	LL targeting Alb	ALL	5°, month	1955-2012
L7	LL targeting Alb	New Zealand	5°, month	1989-2015
T8	Troll	New Zealand, United States	5°, month	1986-2014
G9	Driftnet	Japan, Chinese Taipei	5°, month	1983-1991
L10	LL 200°E-290°E; 10°S-20°S LL 210°E-290°E; 20°S-65°S	Japan	5°, month	1957-2012
L11	LL domestic fleet	American Samoa, Samoa	5°, month	1998-2015
L12	LL tropical distant water: 140°E-160°W; 0-10°S	Japan	5°, month	1952-2012
L13	LL targeting Alb	Fiji, Korea, Vanuatu, Cook Australia, New Zealand	5°, month	1990-2015
L14	LL domestic fleet targeting Alb	French Polynesia	5°, month	1993-2015
L15	LL China Taipei	Fiji, Tonga, Taipei	5°, month	1983-2014
L16	Offshore domestic LL: 140°E-110°W; 0°-65°S	Fiji, China, Taipei	5°, month	1997-2015

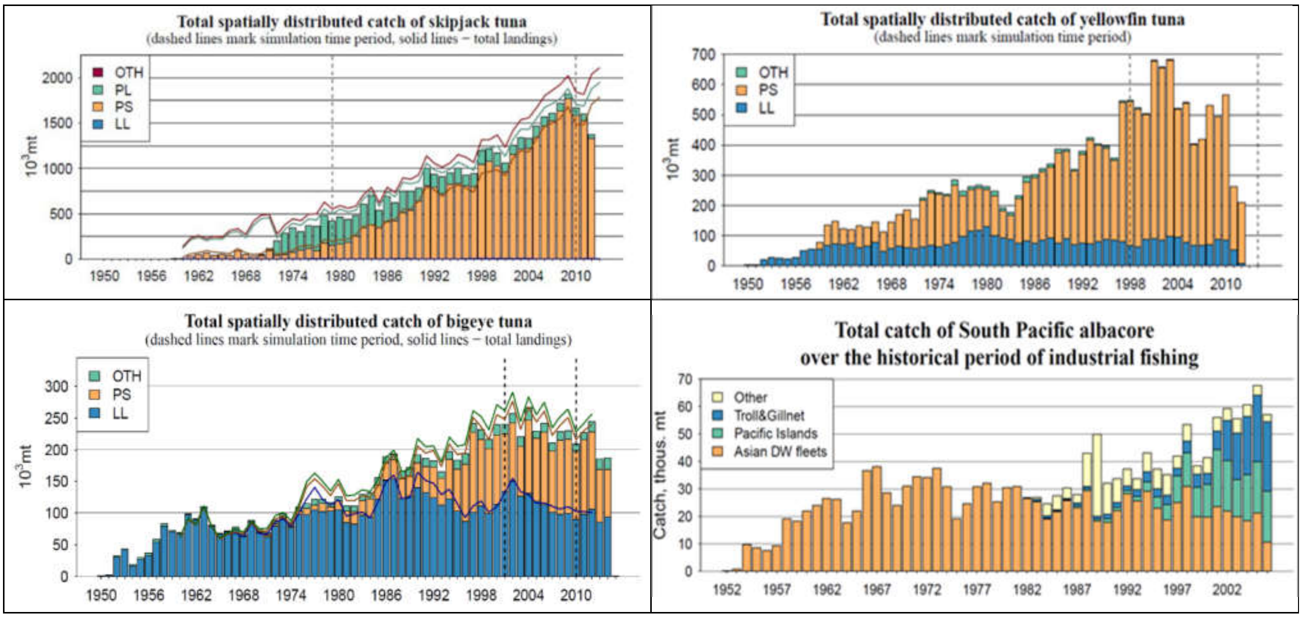


Figure A1: Comparison of total annual catches from spatial fishing datasets used in this study for model optimization and fishing mortality estimates with total nominal catch declared from port landings.

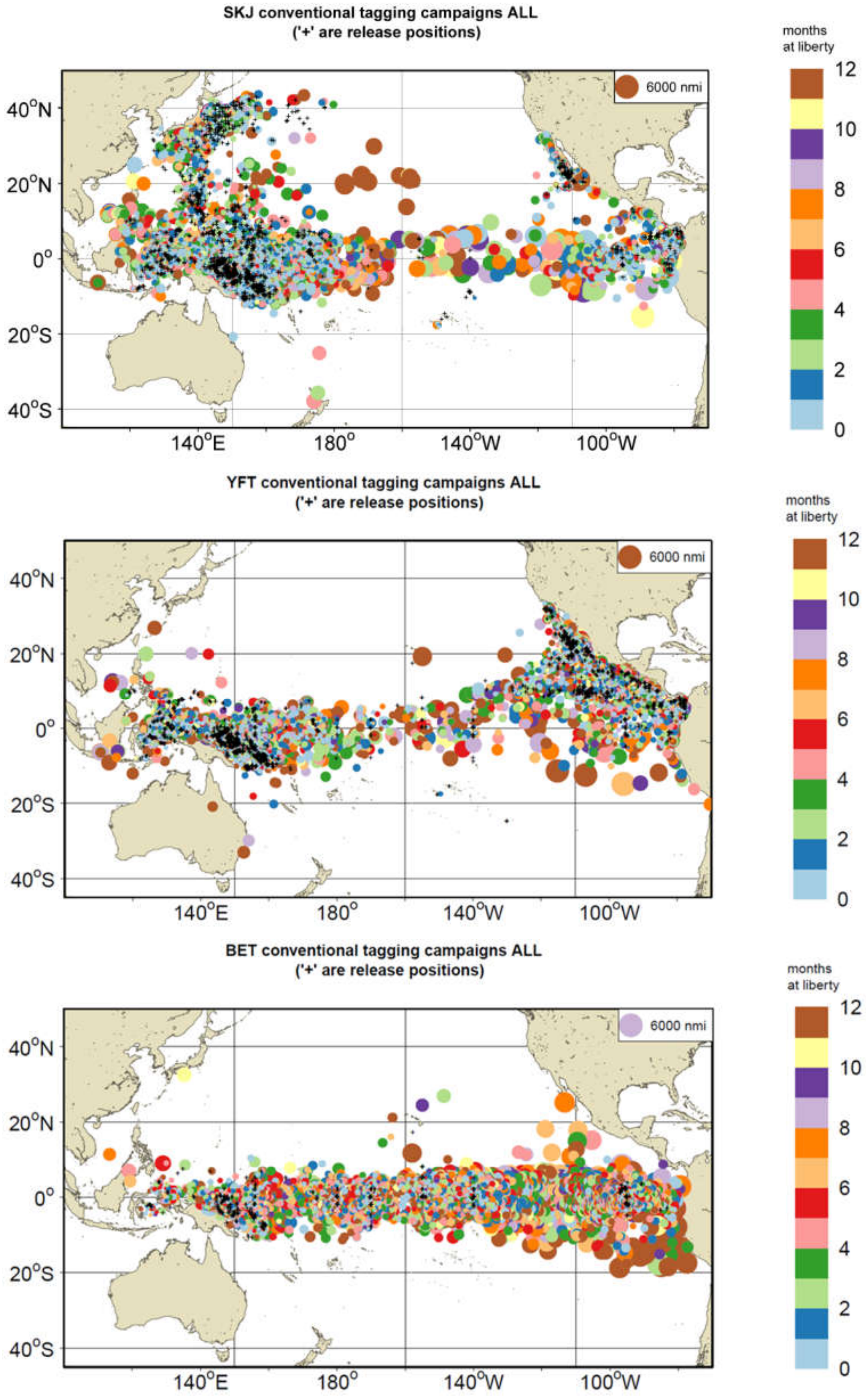


Figure A2: Release-recapture tagging data used in model optimisation (from top to bottom: skipjack tuna, yellowfin tuna and bigeye tuna).

B. Model parameterization

Table B1: Population structure based on independent information, for skipjack, yellowfin and bigeye tuna and albacore (McKechnie et al. 2016; 2017; Tremblay-Boyer et al., 2017; Harley et al. 2014, 2015).

Description	SKJ	YFT	BET	ALB
Maturity				
Age at 1st maturity (mo)	11	20	36*	54
Age structure (number of monthly cohorts)				
Larvae	1	1	1	1
Juvenile	2	2	2	2
Immature	8	17	33	51
Adults	25	38	46	94
Last cohort	36+	58+	82+	148+

*Age at y=0.5 from the maturity ogive

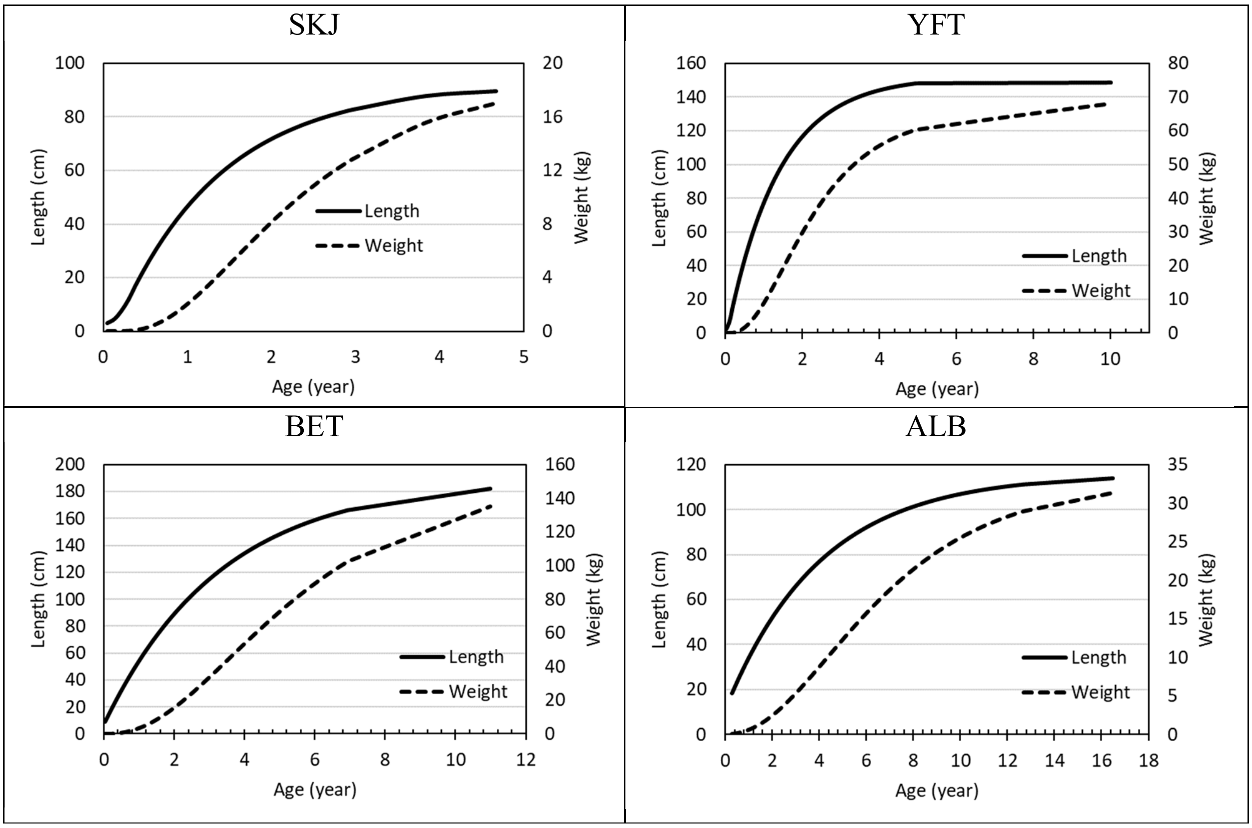
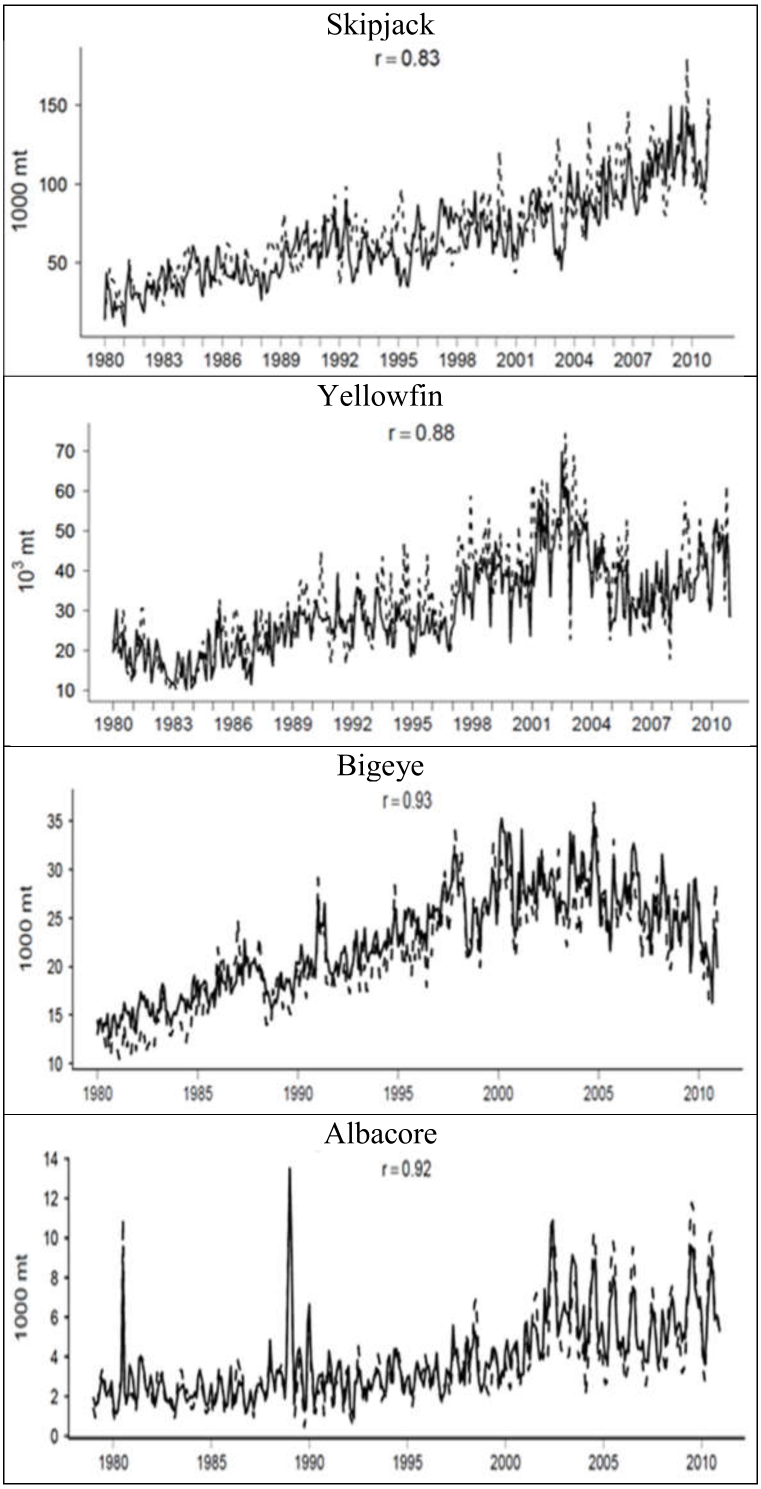


Figure B1: Growth functions (size and weight by age) for skipjack, yellowfin and bigeye tuna and albacore (McKechnie et al. 2016, 2017; Tremblay-Boyer et al. 2017; Harley et al. 2014, 2015).

Table B2: Parameter estimates for the four Pacific tuna species skipjack (SKJ), yellowfin (YFT), bigeye (BET) and South Pacific albacore (ALB). Parameter with "[" or "]" were estimated at their lower or upper boundary correspondingly. The dash indicates that the parameter is not effective and could not be estimated.

Parameters estimated by the model		**Unit**	**SKJ**	**YFT**	**BET**	**ALB**
Reproduction						
σ_0*	*Std. dev. in temperature Gaussian function at age 0 based on SST*	*°C*	1.49	1.85	2.99]	3.170
T_0*	*Optimal SST for larvae*	*°C*	[28.50	28.94	26.5*	27.985
α_P	*Prey encounter rate in Holling (type III) function*	day^{-1}	0.0006	0.78	0.10075	0.00025
α_F	*Gaussian mean parameter predator-dependent function*	$g\ m^{-2}$	2.31	0.21	[0.075	1.00087
β_F	*Gaussian shape parameter in predator-dependent function*	$^{-}$	1.53	0.91	1.159	2.178
R	*Reproduction rate in the Beverton-Holt function*	mo^{-1}	0.04	0.051	0.00403	0.00318
b	*Slope value in the Beverton-Holt function*	$nb\ km^{-2}$	0.16	10*	16.05	1.5
Natural mortality						
$\bar{m}_p$	*predation mortality rate at age 0*	mo^{-1}	0.25*	0.1*	0.05*	0.05*
β_p	*slope coefficient in predation mortality*	mo^{-1}	0.07	0.18	0.299]	0.01083
$\bar{m}_s$	*senescence mortality at age 0*	-	0.005	0.00026	0.03893	0.0004
β_s	*slope coefficient in senescence mortality*	-	1.14	1.15	[-0.249	0.8000
ε	*Coefficient of variability of mortality rate with habitat index*	-	[0	2.07	0.1499]	1.7491
Feeding habitat						
T_0	*Optimal temperature (if Gaussian function), or temperature range for the first young cohort*	*°C*	31.1]	32.0	29.99]	23.50
σ_0	*Std. Err. Of the temperature function for the* 1^{st} *young cohort*	*°C*	1.50	[1.50	5.499]	1.99]
T_K	*Optimal temperature (if Gaussian function), or temperature range for the oldest adult cohort*	*°C*	26.0]	13.3	[10.0	11.862
σ_a	*Std. Err. of the adult temperature function at maximum age*	*°C*	1.948		6.499]	5.206
γ	*Slope coefficient in sigmoid oxygen function*	-	0.0001	0.00015	0.000112	[1.0e-05
$\hat{O}$	*Threshold value in sigmoid oxygen function*	$mL\cdot L^{-1}$	3.76	0.41	0.504	3.427
eF_1	*contribution of epipelagic micronekton*	-	4]	0.37	4.94e-15	2.999]
eF_2	*contribution of upper mesopelagic micronekton*	-	0.05*	0.35	0.6487	3.591
eF_3	*contribution of upper migrant mesopelagic micronekton*	-	0.897	0.351	0.05*	2.87e-05
eF_4	*contribution of lower mesopelagic micronekton*	-	0.0*	0.0*	0.398	0
eF_5	*contribution of lower migrant mesopelagic micronekton*	-	0.0*	0.0*	0.05*	0
eF_6	*contribution of lower highly migrant mesopelagic micronekton*	-	4]	0.35	0.3467	4.05e-15
Seasonal migration						
J_m	*Spawning season peak*	*Julian d*	-	-	-	125
ρ_{cr}	*day to night threshold ratio to mark spawning season*	*d*	-	-	-	1.0521
Movement						
V_{max}	*Maximal sustainable speed*	$B.L.\ s^{-1}$	0.5	[0.7	[0.35	0.952
a_V	*Slope coefficient in allometric function for maximal speed*	-	0.43	[0.85	0.750	0.45*
σ	*Weighting coefficient of maximal theoretical diffusion rate*	-	4.8	0.03	1.367	5.49]
c	*Slope coefficient of the diffusion-habitat function*	-	0.93	0.3*	0.5*	1.2006
Fisheries						
q_f	*Catchability coefficient of fishery f*	-	3 or 4 parameters by fishery			
s_f	*Minimal target (if sigmoid) or mean fish length (if Gaussian function) of fishery f*	*Cm*				
d_f	*Selectivity slope coefficient (if sigmoid function) or width (if Gaussian function) of fishery f*	-				
h_f	*Selectivity for the last age class ((if asymmetric Gaussian function)*	-				

C. Fit to fishing data for the four tuna species



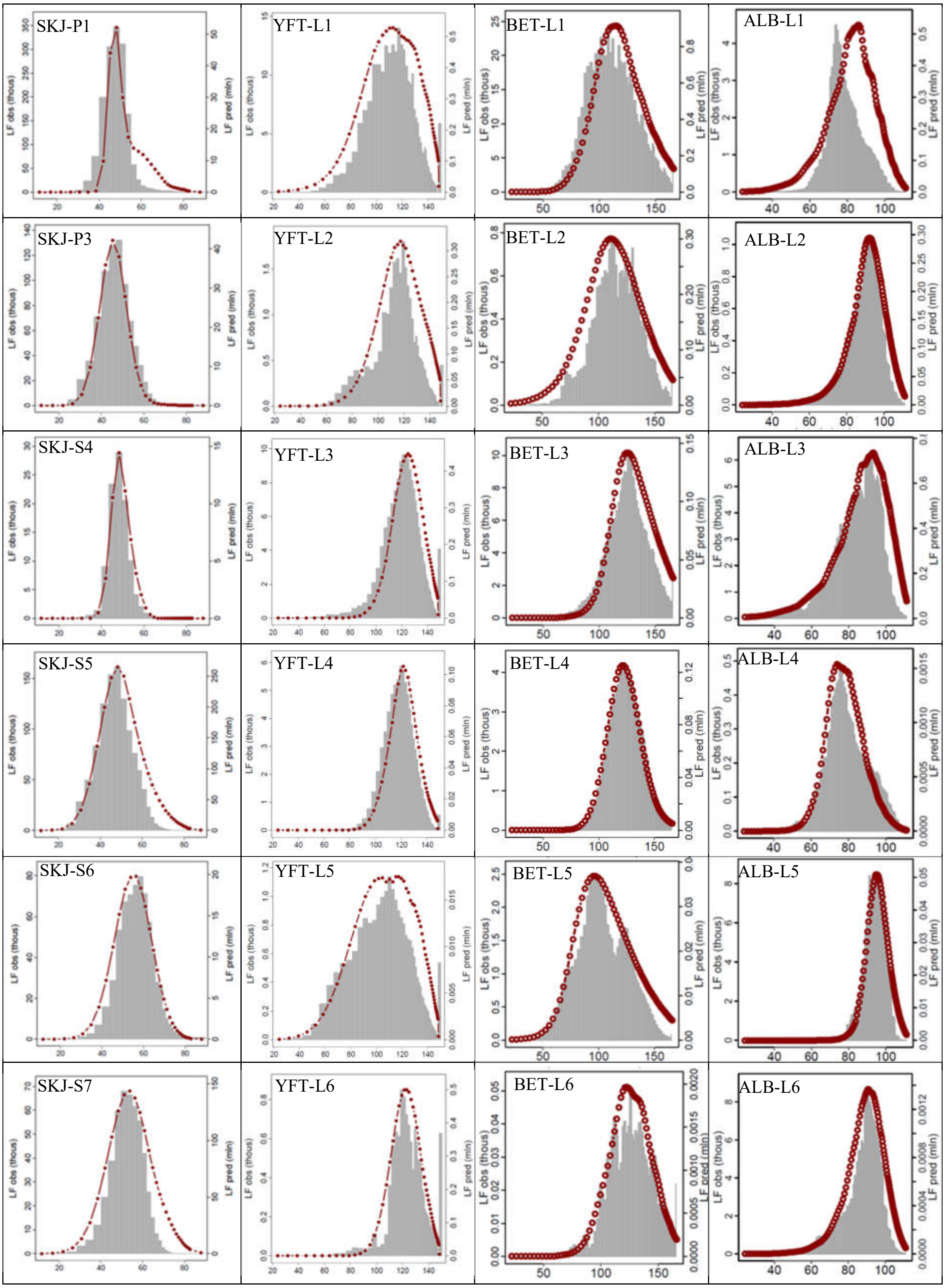
Skipjack

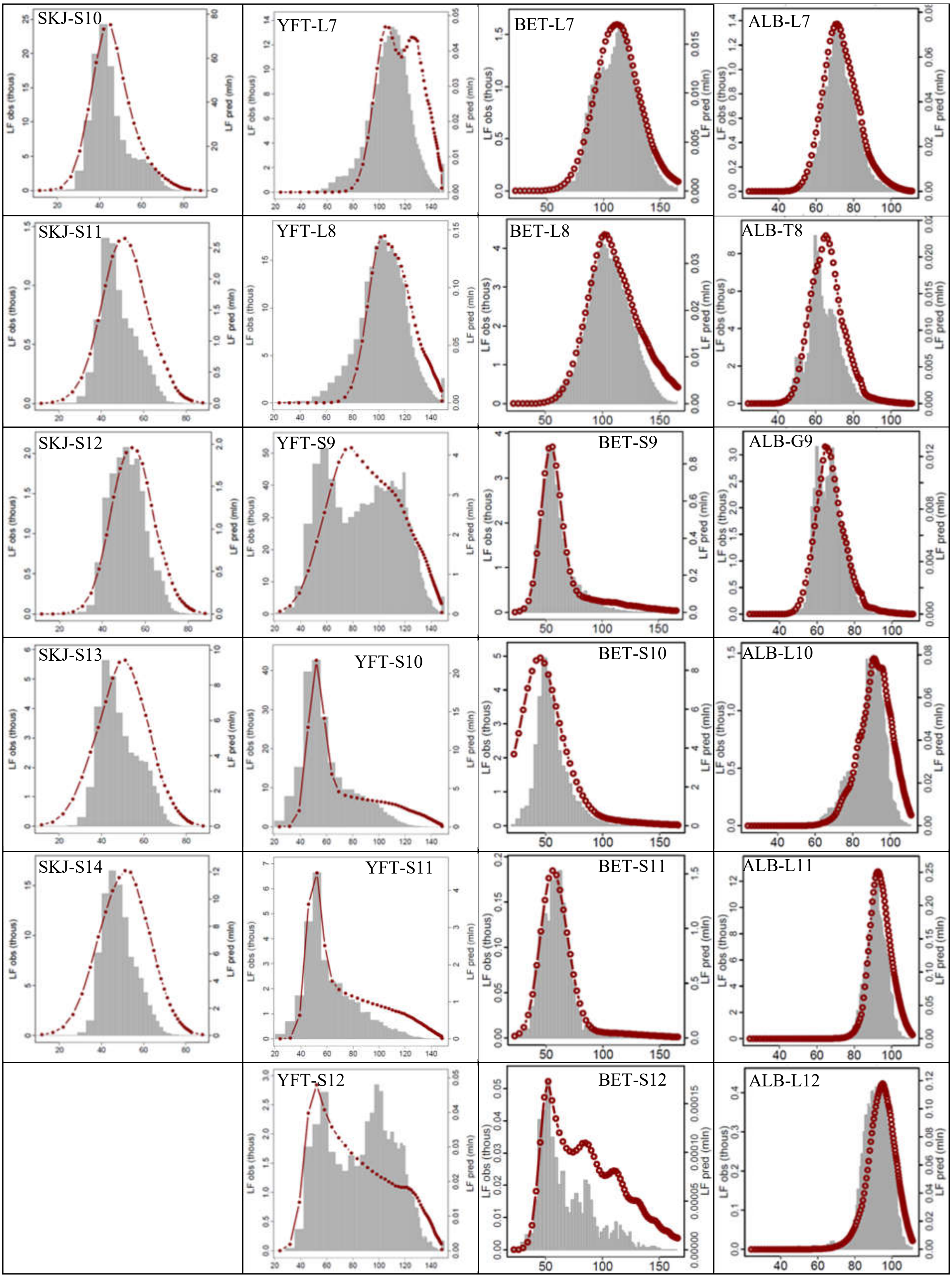
Yellowfin

Bigeye

Albacore

Figure C1: Time series of predicted (continuous line) vs observed (dashed line) total monthly catch.


SKJ-P1
YFT-L1
BET-L1
ALB-L1
SKJ-P3
YFT-L2
BET-L2
ALB-L2
SKJ-S4
YFT-L3
BET-L3
ALB-L3
SKJ-S5
YFT-L4
BET-L4
ALB-L4
SKJ-S6
YFT-L5
BET-L5
ALB-L5
SKJ-S7
YFT-L6
BET-L6
ALB-L6
LF obs (thous)
LF pred (mln)


SKJ-S10
YFT-L7
BET-L7
ALB-L7
SKJ-S11
YFT-L8
BET-L8
ALB-T8
SKJ-S12
YFT-S9
BET-S9
ALB-G9
SKJ-S13
YFT-S10
BET-S10
ALB-L10
SKJ-S14
YFT-S11
BET-S11
ALB-L11
YFT-S12
BET-S12
ALB-L12
LF obs (thous)
LF pred (mln)

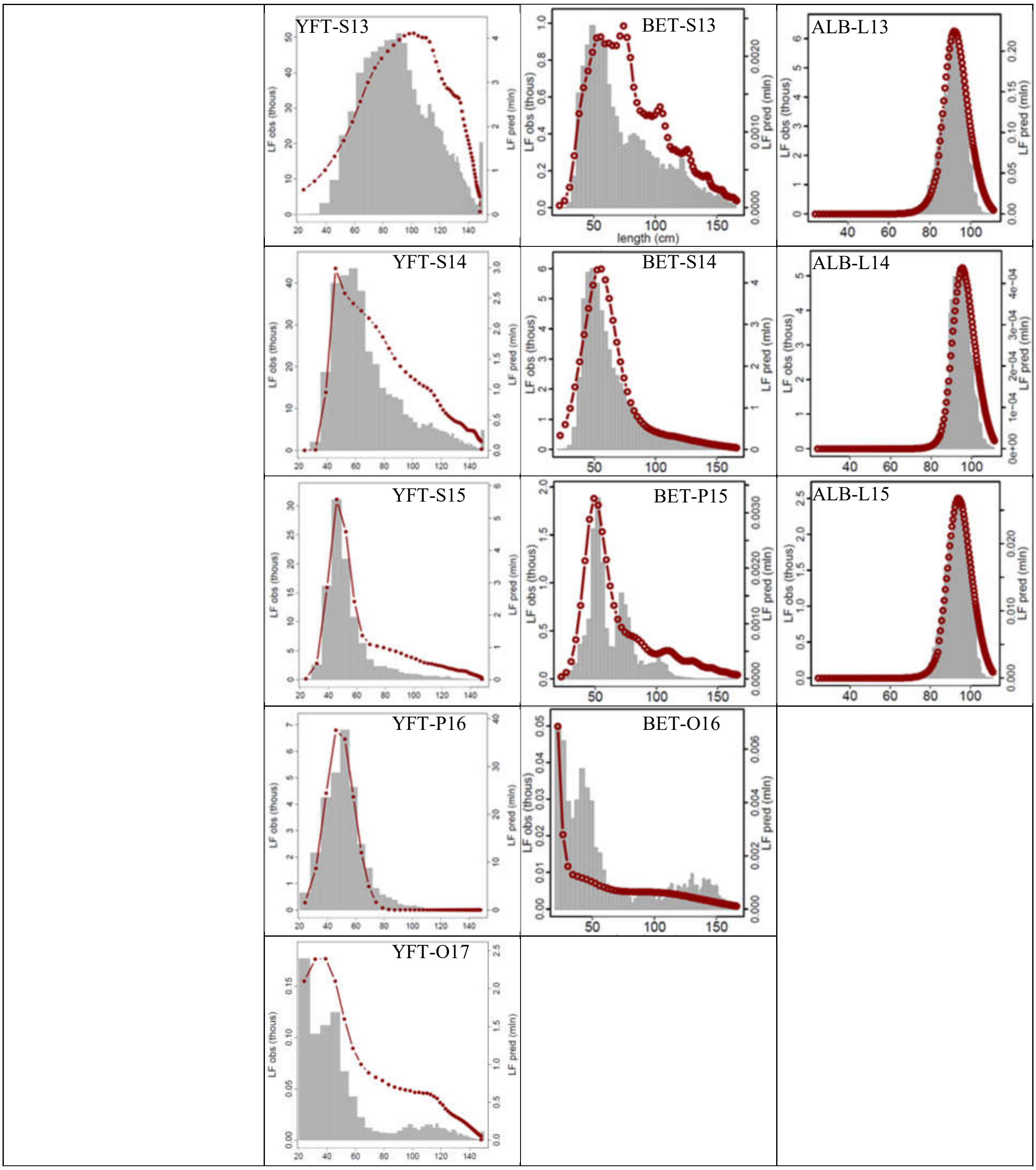


Figure C2: Composite (all time periods combined) observed (histograms) and predicted (line) catch at length for all fisheries with samples for the four Pacific tuna species (SKJ: skipjack; YFT: yellowfin; BET: bigeye; ALB: albacore). See Tables A2-A5 for fisheries definitions.

D. Ocean acidification effect on juvenile yellowfin tuna

Impact of ocean acidification on the life history of tuna was incorporated to the natural mortality curve. The parameterisation of the functional response to pH level is based on the experimental study described in Frommel et al. (2016). The decrease in pH level was found to significantly reduce larval survival by 64% and 70% at pH 7.3 and 6.9, respectively, during the first 7 days. For higher pH levels, there are statistically insignificant results with a mean reduction of survival at pH = 7.6 by 27% (mean reduction of 27% with a range of 6% increase to 49% decrease). It is therefore assumed that additional mortality due to pH is effectively null when pH is above this value. According to these findings, the monthly mortality rates of larvae in SEAPODYM were increased with decreasing pH. It is assumed that the survival rates observed after 7 days in laboratory experiments under different pH conditions are constant over the 1st month of development, i.e., during the SEAPODYM larval stage. This seems to be a conservative assumption because the impact can be expected to decrease with size/age. Then, an additional monthly mortality coefficient related to pH is derived from the observed reduction in survival rate due to pH conditions. For instance, a 70% decrease in larval survival at pH 6.9 results in an additional monthly mortality coefficient of 1.2.

Three scenarios are tested with different shapes of the functional relationship to consider the uncertainty of acidification impact at higher pH levels. The scenarios are based on the mortality rates estimated at three different pH values by Frommel et al. (2016), considering that at pH 7.6 the result is statistically insignificant:

- S1 (solid line in Fig. D1) – the mean scenario based on the three mean values of mortality observed in the experimental study;
- S2 (dashed curve on Fig. D1) – a high sensitivity scenario to ocean acidification, also implying that pH could have already have an impact in the Eastern Pacific equatorial zone where pH values below 8.0 are regularly observed (Bromhead et al., 2015); and
- S3 (dotted line on Fig. D1) – a low sensitivity scenario to ocean acidification with the lowest reduction at pH 7.6.

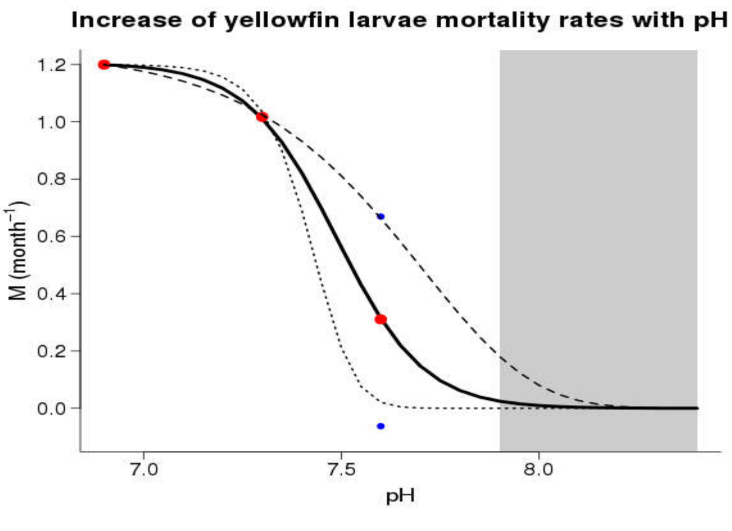


Figure D1: Change in additional monthly mortality rates of yellowfin larvae deduced from experimental results (Frommel et al., 2016) corresponding to 70%, 64% and 27% (red points) decrease in larvae survival during first 7 days of life at pH value of 6.9, 7.3, 7.6 respectively. The solid line shows the analytical function implemented in SEAPODYM based on these three mean values (scenario S1). Two other curves (dashed, S2 and dotted, S3) are high and low sensitivity scenarios. The shaded area corresponds to the historical pH values in the ocean.

The predicted additional impact of ocean acidification during the 21st Century is minor (Fig. D2). There is no impact at all when considering the low sensitivity scenario (S3). A very small effect appears by the end of the century in the eastern equatorial Pacific Ocean with the intermediate scenario S1. The high sensitivity scenario (S2) shows a stronger negative impact on larval recruitment in the same area, with anomalies reaching locally -10% in 2050 and -15% in 2100. Interestingly, it also shows a visible but small impact for the end of the historical period.

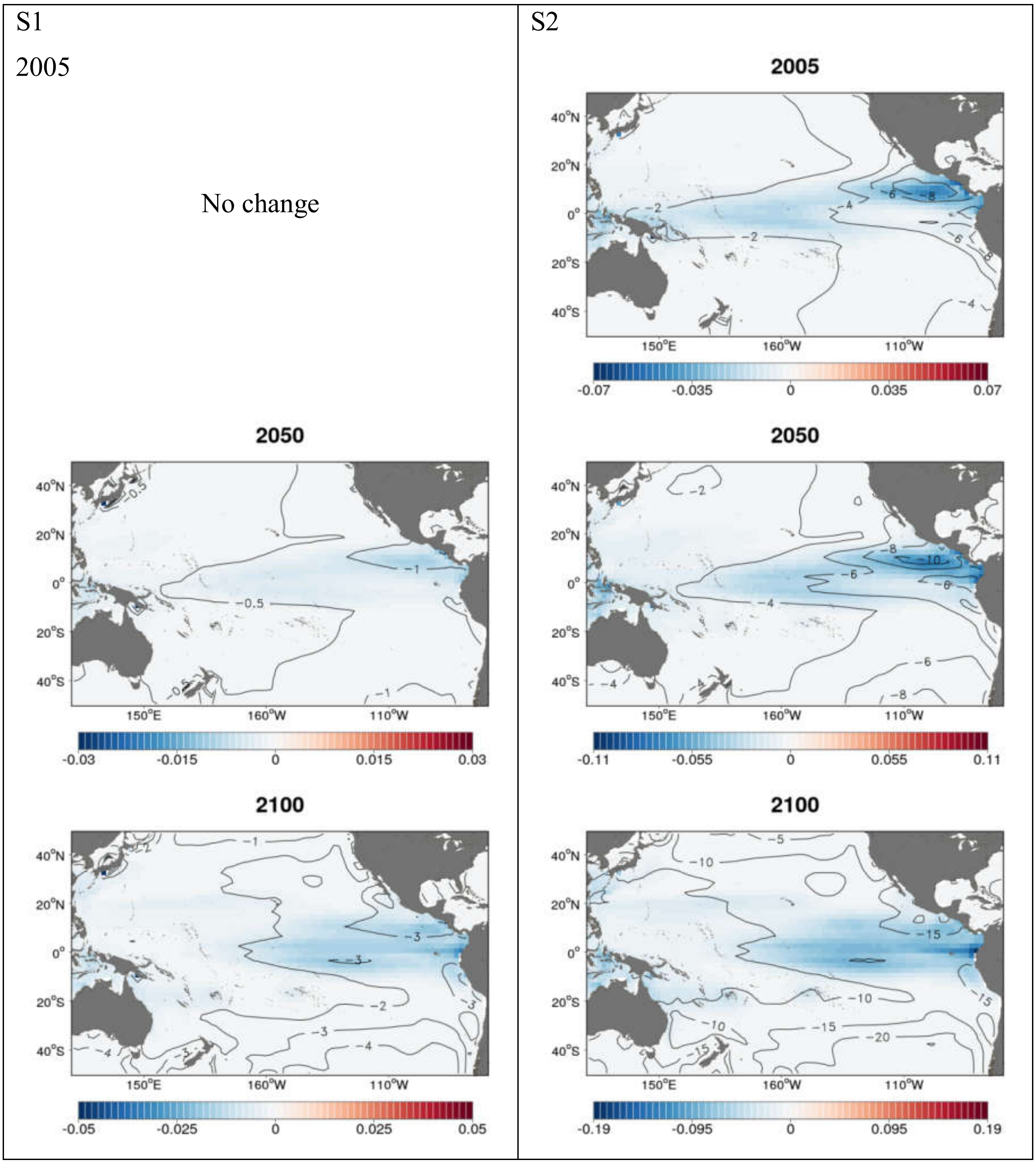


Figure D2: Change in yellowfin tuna larval density due to ocean acidification effects included in SEAPODYM, in 2050 (average 2046-2055) and 2100 (average 2090-2099) for intermediate scenario S1 and high sensitivity scenario S2. There is no change for scenario S3. The colour maps show the average biomass change since 2005 projected to occur under a high emissions scenario (RCP8.5) with 5 different atmospheric forcings generated by Earth Climate models. Isopleths gives the relative percentage change in biomass with respect to 2005, i.e. 100*(B_{year} – B_{REF})/B_{REF}.