



**SCIENTIFIC COMMITTEE
SIXTEENTH REGULAR SESSION**

ELECTRONIC MEETING
11-20 August 2020

SEAPODYM: revisiting bigeye reference model with conventional tagging data

WCPFC-SC16-2020/EB-IP-05

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1 Executive Summary

1.1 Scope of work

This paper describes the progress in developing the "next generation" SEAPODYM reference model for Pacific bigeye tuna. "Next generation" SEAPODYM models apply robust methods to integrate both fisheries and tagging data to inform model parameters.

1.2 Current progress in bigeye reference model

The bigeye stock reconstructed by SEAPODYM with parameter estimation based on catch and length (CL) data, is around 2Mt in 2010 starting from much larger stock, around 3Mt, in the early eighties, distributed spatially across Pacific Ocean and shared between EPO and WCPO with roughly the same levels of biomass (Fig. 1). Here we revisit this reference model with two types of analyses: a global sensitivity analysis and a parameter estimation from conventional tagging data only.

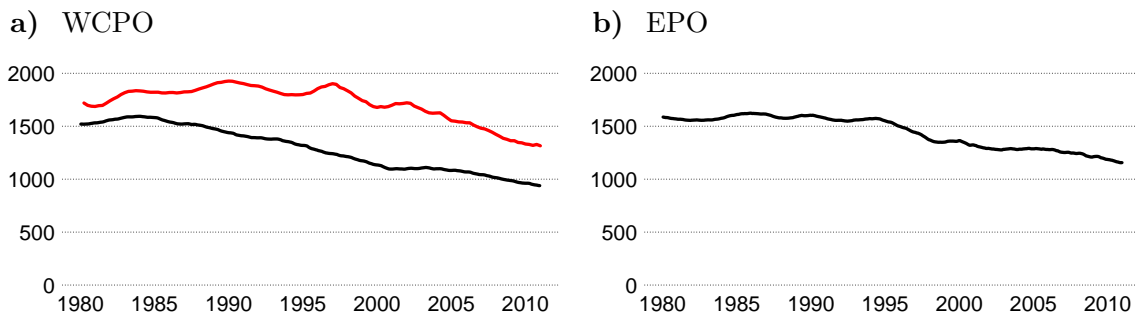


Figure 1: Biomass of bigeye (in thousand metric tons) including immature and mature individuals predicted by SEAPODYM (black) and estimated in WCPO by Multifan-CL (red).

A global sensitivity analysis (SA) based on variance methods (Saltelli et al. 2008) was performed for each type of data that can be used in the parameter estimation: catch, length frequency and tag recaptures. This analysis allows evaluating the model response to each parameter given the information contained in corresponding data and the type of likelihood function, hence provides essential information on parameter observability and on capacity of the minimization method to provide an unbiased estimate.

The results of SA showed that catch and effort fishing data mostly inform the model on reproduction and mortality processes, while length frequency data control principally the recruitment. Model parameters controlling movement rates are also observable from the fisheries data. However, likelihood profiles confirm previously known [Senina *et al.*, 2020] tendency of fisheries data to increase diffusivity and reduce directed movement rates, both contributing to non-zero biomass everywhere in the model domain and low patchiness.

Integration of tagging data in the likelihood enhances observability of movement parameters while modifying the shape of the likelihood hyper-surface with optimal values

towards lower diffusions and non-zero advection rates. Model sensitivity to the temperature preferred by oldest tunas, T_K , is rather low, although significant compared to being totally unobserved by fisheries data as shown by sensitivity analysis. This lower sensitivity of tag likelihood to the parameter controlling movements of largest tuna might be due to the fact that tagging data observe mostly young bigeye captured by purse-seine gear.

An optimization study of the model of tagged tunas confirms the results of the sensitivity analysis, with movement rates being very different from those estimated from fisheries data alone. The validation of habitat and movement parameters with tagging data show that 1) the CL reference model fails to simulate observed movements of tags and 2) the model of tag movement with parameters estimated from 2008-2013 conventional tagging dataset can reproduce the movement of tags during 2000-2007.

1.3 Future work and key milestones

The future work will focus on the following:

1. The full population model for bigeye tuna will be revised with the inclusion of fisheries and tagging data in the likelihood function.
2. The bigeye reference model will be downscaled and adapted to operational model forcing at $1/4^\circ$ x week.
3. The complete software, reference manual, and tools developed to facilitate the use of SEAPODYM and the analyses of simulations will be provided to SPC to enable the use of quantitative models and further analyses. This includes:
 - command-line simulation tools to compute SEAPODYM habitats and exchange rates between assessment regions;
 - the R-tools to facilitate extractions of model outputs and derived information for use in complementary analyses (fisheries scenarios, spatial closures);
 - the forcing data sets;
 - the parameter files for all tuna reference models.

1.4 Acknowledgments

We thank Beatriz Calmettes from CLS for preparing INTERIM and FREE-GLORYS model forcing data. We are thankful to Sylvain Caillot for providing consolidated tagging dataset including information from various SPC tagging campaigns. We are especially grateful to Peter Williams from the Oceanic Fisheries Programme of the Pacific Community for providing and continuously updating the complete geo-referenced fisheries dataset for the Pacific Ocean bigeye tuna. The Inter American Tropical Tuna Commission has provided access to non-public domain data for the purposes of progressing the work programme of the WCPFC-SC. This work is supported by Pacific Community under a contract agreement between CLS and SPC.

2 Introduction

SEAPODYM is a numerical model developed for investigating population dynamics of tunas under the influence of environment and fishing. The underlying continuous equations of SEAPODYM are classical advection-diffusion-reaction equations with ageing term, describing the population dynamics in time, age and two-dimensional space. The quantitative modelling of tuna population dynamics with SEAPODYM has been continuously improving, including development of reference models that integrate fisheries catch and length data for Pacific Ocean populations of skipjack, yellowfin, bigeye and South Pacific albacore.

The ‘next-generation’ of SEAPODYM reference models include integration of tagging data in the likelihood estimation approach, implementation of robust statistical methods for sensitivity analysis of model parameters and cost function profiling, enhanced algorithm of the fisheries data use within likelihood function and complete validation on independent data sets. This leads to better estimates of both stock size and stock spatial structure (Senina et al. 2020). Next generation reference model have been completed for the Pacific Ocean populations of skipjack and South Pacific albacore.

This Information Paper reports on the progress towards a “next-generation” Pacific bigeye reference model. The current reference model constrained by fisheries data only is presented in Senina et al. (2018). However focusing on climate change application this paper did not provide detailed description of the MLE solution. Here we report the main results from this reference model in terms of the estimation of model parameters in order to demonstrate how integrating tagging dataset can influence and improve them. Next, we present the results of comprehensive sensitivity analysis based on an ensemble of $\approx 0.5 \cdot 10^6$ simulations preformed with 1) the reference model configuration evaluating separately catch and length-frequency likelihoods and 2) the model of tag dynamics with conventional tagging data in the likelihood. Then, we present the results of the optimization study performed with the model of tag dynamics in order to establish the tagging data sub-set allowing unbiased MLE parameters. Finally, using independent data, we validate three optimal solutions of: 1) the current CL reference model, 2) the model of tag movement integrating 3 years of tag recaptures and 3) the model of tag movement integrating 6 years of tag recaptures. The results of of this study are discussed with their consequences on the next steps needed to develop the new reference model.

3 Data

3.1 Bigeye tuna fisheries

The definition of SEAPODYM fisheries for bigeye tuna is provided in Table 1. A fishery is defined by the homogeneous fishing catchability and selectivity, unique fishing gear, having the same target species and fishing strategy. All longline catch and effort fishing data are at a resolution of $5^\circ \times 5^\circ \times$ month while for surface gears (purse seine and pole-and-line) the resolution is $1^\circ \times 1^\circ \times$ month, excepted for Philippine and Indonesia fisheries. Size frequency data are at a resolution of $5^\circ \times 5^\circ$ (WCPO purse seine) $10^\circ \times 20^\circ$, or aggregated over a bigger region. A major revision of fisheries definition has been realized since the last optimization experiment, with careful data screening procedure to

i) remove outliers using a method based on the computation of CPUE variance and 2) convert the fishing effort of EPO purse seine fisheries in fishing days when only total effort in days and number of sets by fishery was available. See Fig. 3) for overview of fishing data being used in this work. Finally, we checked that the geo-referenced catch dataset for the Pacific fisheries matches closely the total landings declared by countries (Fig. 2).

3.2 Conventional tagging data

Conventional tagging data are integrated into the optimization method in SEAPODYM essentially to improve the estimates of habitat and movement parameters that are critical to control the overall population dynamics. Therefore, the approach considers only fish that have been recaptured, as these are the only data that contain information about potential movement (for details, see Senina et al., 2020). Tags are aggregated into groups by their common time (month, quarter) of recapture. The groups of tags were defined using compiled tagging datasets provided by SPC and IATTC from different tuna tagging programs between 1967 and 2015, which contains 18350 records on released and recaptured bigeye. Note that 99% of all records in this dataset occur between 2000 and 2013, with only 23 released bigeye before 2000 and 59 after 2013. For more details on tagging programs see [SPC-OFP]. The tagging data temporal coverage and the distribution in terms of mean length and time at liberty are illustrated in Fig. 4. Two characteristic periods with massive tagging of bigeye can be selected within 2000-2013 time range, clearly distinguished by the length of released tunas, the positions of release and the distributions of recaptures. During the first one, from early 2000 to mid-2007, the mean length of bigeye at release was 77 cm, they were mostly tagged at three release position around equator at 95°W longitude and a few dozens of tunas were tagged and recaptured in the warm pool area. During the second period, from mid-2007 to the end of 2013, much smaller bigeye, 56 cm on average, were tagged extending the area of release towards central Pacific Ocean. The maps and the data statistics are depicted in Fig. 4, the red and blue lines corresponding to the first and the second tagging periods respectively.

Unfortunately, neither sub-set of conventional data represents the whole population, but essentially the juveniles and immature adult part adult fish that are associated to surface schools and caught with surface gears. First, juvenile and immature bigeye tunas were tagged and released primarily in six positions along the equator, three in the western and central equatorial region and three in the EPO. Multiple minor releases were done all over the warm pool area. Second, 89% of all tagged tunas are recaptured before one year of liberty at sea, 10% between one and two years and only 1% more than two years. In consequence, with size at 50% maturity being 115 cm, majority (93%) of recaptures are still immature tunas. As a consequence, observing only part of population may present difficulties for estimating model parameters, in particular those responsible for dynamics of an unobserved fraction of a population.

For the purposes of reducing computational costs and integrating maximum information to inform dynamics processes through all model dimensions, the second sub-set of recaptures (2008-2013) constituting 50% of the dataset was used in the present work in order to estimate model parameters, while the first one was left for validation.

3.3 Environmental forcing

SEAPODYM uses ocean physical (temperature and horizontal currents) and biogeochemical (primary production, euphotic depth and dissolved oxygen concentration) variables. Physical variables are provided by ocean general circulation models (OGCM), either from hindcast simulations or reanalyses. They both provide the same outputs but in the first case the ocean model is forced by atmospheric variables only. In reanalyses, the simulation assimilates observations of oceanic variables (e.g. Argo profilers, satellite sea surface temperature and altimetry) to produce more realistic circulation patterns, especially at mesoscale resolution. Primary production and euphotic depth can be simulated by a biogeochemical model coupled to the physical model or estimated from satellite ocean colour, solar radiation and sea surface temperature data (Behrenfeld and Falkowski 1997). The euphotic depth is used for averaging the physical data and the dissolved oxygen concentration data over three vertical layers representing i) the epipelagic layer, between the surface and 1.5 the euphotic depth; ii) the upper mesopelagic layer, between 1.5 and 4.5 the euphotic depth; and iii) the lower mesopelagic layer, between 4.5 and $\max[1000\text{m}; 7.5 \text{ euphotic depth}]$. Dissolved oxygen concentration is provided by most biogeochemical models. A monthly climatology compiling all available observations can be also used, but in that case, it cannot represent the interannual variability (e.g. ENSO). SEAPODYM tuna habitats rely of the biomass distributions of micronekton functional groups, which need to be computed with the SEAPODYM-LMTL (Low and Mid Trophic Levels) model. There are 6 micronekton groups inhabiting the epipelagic, upper and lower mesopelagic layers.

In this study we use two different ocean environmental forcing datasets to cover past and recent periods. We have started the work with the longest hindcast that has been used for all current reference models (Senina et al., 2018). However, integration of tagging data required using forcing covering more recent years, to coincide with the tagging of bigeye tuna between 2009-2013.

3.3.1 INTERIM

This forcing dataset covers the period 1979-2010. It is obtained from a coupled NEMO-PISCES model: NEMO ocean circulation model was coupled to the biogeochemical model PISCES (Pelagic Interaction Scheme for Carbon and Ecosystem Studies, Aumont and Bopp, 2006), ran at a coarse horizontal resolution of ORCA2 grid (2° in longitude and high latitudes with a refined resolution of 0.5° in the equatorial band), see [Nicol et al., 2014]. This coupled model is driven by the atmospheric ERA-INTERIM reanalysis, which has been corrected using satellite data (Dussin et al., 2013). Salinity, temperature and biogeochemical tracer concentrations were initialized from the World Ocean Atlas climatology (WOA09, Garcia et al., 2009), and from model climatologies for iron and dissolved organic carbon. Hereafter, this forcing is named INTERIM.

3.3.2 GLORYS-free

The second forcing dataset covers the period 1998-2019. The physical variables are those from the ocean hindcast simulated with the Mercator-Ocean global eddy-permitting NEMO OGCM in the ORCA025 configuration under project GLORYS. This simulation

was also forced by the atmospheric reanalysis ERA-INTERIM and did not have data assimilation. To distinguish it from GLORYS reanalysis with data assimilation hereafter this dataset is called GLORYS-free. To these physical variables are associated the primary production derived from satellite data and the WOA climatology for dissolved oxygen concentration (see Table 2).

All forcing variables were interpolated to a regular 2° grid and degraded to monthly time step. See Table 2 for details on the original NEMO-PISCES-INTERIM outputs and Figures A1 - A4 showing the mean state of key environmental variables of each forcing data set.

4 The model configuration

The model PDE equations [Senina *et al.*, 2020] are numerically solved on a 2° regular grid on the spatial domain covering the Pacific Ocean domain $\Omega = \{x \in (88.5^\circ E, 68.5^\circ W), y \in (54.5^\circ S, 65.5^\circ N)\}$ and monthly time step. The age is discretized between 0 and $\text{age}_{max} = 14$ (years) into monthly cohorts resulting for bigeye in 85 cohorts, so that the first seven years are split into 84 monthly age classes and the oldest individuals are aggregated into a single A+ cohort.

4.1 Static model parameters

The estimates of length-at-age, weight-at-age and maturity-at-age relationships were taken from the 2014 MULTIFAN-CL assessment report [Harley *et al.*, 2014] and interpolated to model age structure.

The maximal predation mortality at age 0 is usually hard to estimate due to weak observability of early life stage dynamics and correlations with other parameters of mortality functions. It was set to constant 0.6 yr^{-1} in the current configuration. Also, bigeye is assumed to be an opportunistic spawner with a spawning success proportional to the spawning habitat index.

4.2 Model parameters estimated from fisheries data

MLE parameters estimated with catch and length data are listed in Table 3 (see column CL-I) and resulting functional relationships for reproduction, mortality, habitat and movement processes are shown in Fig. 5.

The estimation of the mortality function parameters resulted in decreasing mortality rates between 0 and 1 year of age and constant mortality rate at 0.24 yr^{-1} for older tunas. Overall, MLE for demographic parameters provide the estimation of bigeye stock around 2Mt in 2010 (end of INTERIM forcing), with WCPO stock below Multifan-CL estimations mostly due to predicting lower immature stock (see Figs. 1, 7 and A6). This led to an estimated fishery impact of 57% on adult stock and 42% on immature stock by 2010 with local impacts raising to 80% on both life stages in assessment region 7 (see Fig 7 and 8). Comparison between exploited and virgin biomass distributions (Fig. 6) shows that western stock of immature bigeye is much more depleted by fisheries than eastern one.

As a result of estimation of thermal preferences for spawning between 28°C and 30°C, during the larval stage bigeye are predicted to occupy the tropical area of the central Pacific ocean with year round presence in the warm pool and exhibiting marked seasonality in the eastern Pacific ocean (see Fig. A5). However, the preferred temperature decreases rapidly with age. The mean distribution of young bigeye indicates that at this stage bigeye prefer tropical waters with mean surface temperatures above 24°C, where they can access the upper mesopelagic layer for foraging. The estimated steep slope of the thermal habitat function with age and preference for 10°C water temperature is likely biased as it results in high densities of adult bigeye in the temperature zones that are not supported by catches. Although the high tolerance to the oxygen content is well estimated from catch distributions, which are characterized by zero catches in the areas with oxygen levels below 1 ml/l in upper mesopelagic layers. The mean speed of bigeye density around 3 nmi/day (Fig. 3, panel *Movement rates*) indicates rather active than resident behaviour (population density should not be confused with an individual bigeye). For comparison, the integration of tagging data provided the estimation of the mean speed of skipjack between 3-6 nmi/day at ages of 1 and 3 years respectively [Senina *et al.*, 2020]. However due to very high diffusivity estimated for bigeye by CL model, the random movement process becomes dominant over directed movement. This can be seen in the very smooth edges of density distributions of both young and mature adult tunas (Fig. 6). Also, it is likely that high densities of adult bigeye in the temperature zones that are not supported by catches, are due to weak estimation of movement and biases in thermal habitat parameters.

5 Methods

5.1 The global sensitivity analysis

We perform a global quantitative SA based on variance methods to evaluate model sensitivity to its parameters [Saltelli et al., 2008, Pianosi et al., 2016]. For this we compute the first-order ("main effect") indices measuring the direct contribution from each parameter to the output variance and the total-order ("total effect") indices measuring the overall contribution from a parameter including its interactions with other parameters. These indices are computed as follows:

$$S_i^F = \frac{\mathbf{V}_{\theta_i}[\mathbf{E}_{\theta_{\sim i}}(L^-|\theta_i)]}{\mathbf{V}(L^-)}; \quad S_i^T = \frac{\mathbf{E}_{\theta_{\sim i}}[\mathbf{V}_{\theta_i}(L^-|\theta_{\sim i})]}{\mathbf{V}(L^-)} \quad (1)$$

where \mathbf{E} denotes expected value and \mathbf{V} denotes variance, $\theta_{\sim i}$ means varying all parameters but i -th. The main and total effect indices are useful to rank and to exclude the non-influential parameters respectively. The S_i^F measures the relative contribution of each parameter to the total output variance, $\sum_i S_i^F \leq 1$ for non-linear non-additive models. In other words, computing first order sensitivity indices we measure direct and independent from other parameters contribution of each parameter to the output variance. The parameter θ_i is not influential if and only if the index $S_i^T = 0$. Having $S_i^T > S_i^F$ indicates existing correlation with other parameters. Hence, total-order sensitivity indices

measure overall contribution from each parameter to the output variance, thus including interactions between correlated parameters.

According to 1 the indices S_i^F can be computed in so called All-At-a-Time (AAT) SA experiments, i.e. randomly sampling all parameters at every model run. The evaluation of S_i^T requires One-At-a-Time (OAT) SA experiments, where only one parameter is randomly varied in a series (here 25) of model runs while others are fixed. In order to evaluate model sensitivity to its parameters given the information contained in each type of data, we set-up SA simulation study with three model configurations integrating either catch, length frequency or tag recaptures. First 10000 AAT simulations were done for each data type. Second, the set of parameters providing the lowest likelihood values in AAT SA simulations was selected to conduct OAT SA simulations. This allowed exploring within OAT SA simulations only those likelihood profiles that are close to the optimum. Also, after each series of 25 runs in OAT simulations, the parameter was fixed at value providing lowest likelihood found. Overall, 65,000 OAT (25 parameters x 25 sampled values of parameter x 104 parameter files with lowest AAT likelihood values) simulations were run to compute catch and length likelihood respectively and 105,000 (14 parameters x 25 sampled values of parameter x 300 runs) OAT simulations with tagging data exploring two tagging datasets (2008-2010 and 2008-2013) and model forcings (INTERIM and GLORYS-free, see Table 2 for details). In total, 475,000 simulations were conducted within this SA study.

5.2 Maximum likelihood estimation

The MLE approach used in SEAPODYM as well as the method for integrating tagging data in SEAPODYM has been detailed and used for skipjack tuna in (Senina et al. 2020). Here we use only the model of tag movement with the focus on estimating the optimal model parameters from tagging data only. The model of tags movement is driven by the same advection-diffusion equations with ageing term and the same parameters defining habitats at age and movement rates at age as the full population dynamics model in SEAPODYM. In the model of tags we use only the tagged fish that were recaptured and reported, hence omitting the mortality process and the use of fishing effort, fisheries parameters and reporting rates. Tags are aggregated into groups by their time of recapture. Using such an approach allows accounting precisely for the time at liberty of all tags and hence adapting the integration of release-recapture data into the Eulerian model, which, by definition, does not permit tracing the density.

In the optimization study we used either 2008-2010 or 2008-2013 conventional tagging dataset. Further validation of the MLE models based on the independent dataset provides insight into the minimal size of tagging data that is needed to obtain an unbiased estimate of model parameters. Also, two types of tag likelihood, normal, as described in (Senina et al., 2020), and log-normal, as well as the use of weights depending on time at liberty were revised within the optimization study. For each type of likelihood function the series of optimization runs (50 on average) with different starting points were performed with and without weighting by time at liberty.

6 Results

6.1 Model sensitivity to parameters

As seen from Fig. 9, which represents the quantitative results of global sensitivity analysis, integrating catch and length frequency data into the likelihood increases model sensitivity to those parameters that influence the reproduction and mortality processes (m_p , β_p , m_s , β_s and α_p , β_F , R respectively, see the description of these parameters in Table 3). Besides, the length frequency data principally controls the estimation of recruitment, especially parameters of the spawning habitat index, α_p and β_F , that drive the seasonality of spatial distribution of recruits. Diffusion and advection rates are also among the most sensitive parameters, informed by all three types of data. Habitat indices parameters, σ_1 , T_1 , σ_K , T_K , and all micronekton multipliers produce almost no change in the model output with fisheries data. One exception is dissolved oxygen threshold \hat{O} . Its estimation should be well constrained by geo-referenced catch data showing strong gradients in spatial distribution of catches around zones with low oxygen content in the upper mesopelagic layer.

On the contrary, it seems that both, oxygen tolerance and parameters of bigeye thermal preferences directly controlling the habitat quality and extension for young tunas (σ_1 and T_1) can be well informed by tagging data. One more habitat parameter, the allometric coefficient b_T , modifying the shape of the thermal preferences at age function, has remarkably higher sensitivity for tagging data compared to fisheries data. Sensitivity to the preferred temperature by oldest tunas, T_K , is rather low, although significant compared to being totally unobserved by fisheries data. This lower sensitivity of tag likelihood to the parameter controlling movements of largest tuna might be due to the fact that tagging data observe mostly young bigeye captured by purse-seine gear.

Likelihood profiles, obtained with help of OAT simulations are shown in Figs. 10 - 12. It is interesting to note the remarkably well-shaped profiles for one of the spawning habitat index parameters, responsible for seasonal dynamics of recruitment linked to seasonal dynamics of micronekton. Parameter β_F allows selecting the areas with low but non-zero densities of surface micronekton playing the role of prey for adults and the predator for larvae. Not surprisingly that MLE estimate of $\beta_F = 1.054g/m^2$ in the current reference model belongs to the interval of lowest catch and length likelihood values. There is also a clear signal for estimation of prey encounter rate, α_P , from a Holling type III functional response, although sensitivity is high only for low values of prey densities and there seem to be two types of profiles, obviously due to correlation with other parameters, which is shown also by total effect sensitivity index.

Length data provides better observability of spawning thermal habitat parameters (σ_0 and T_0) than catch data. The corresponding OAT profiles are well and consistently shaped for the length likelihood, while most of the catch likelihood profiles do not form the unified structure and the mean values across these parameters space form a flat surface. In further work it is worth testing the use of higher weights for the length frequency data likelihood component to better inform temperature of spawning.

For mortality-at-age only the parameters of senescence mortality, \bar{m}_s and β_s , seem to be well observed from both catch and length data. The mortality rate at age 0, \bar{m}_p as well as the slope of predation mortality of tunas at early life stages, β_p , have mostly flat

profiles with lowest likelihood values. However, neither of estimated parameters in the current reference model, $\bar{m}_s = 0.02$ and $\beta_s = 0$ (Table 3) are consistent with the results of OAT simulations, which might have been caused by starting too far from these values and finding local minimum. This result requires revision. The absence of shape and flatness of profiles for variability of species mortality with the quality of habitat index, suggests that this parameter is not informed by fisheries data.

The profiles obtained for habitat parameters (Fig. 12), governing thermal accessibility to prey species and hence the habitat quality, illustrate clearly that most of these parameters cannot be well estimated from fisheries data alone. As mentioned above, bigeye tagging data inform better the thermal preferences of young tunas, i.e. parameters σ_1 , T_1 and b_T . The standard deviation of the temperature function for oldest age σ_K remains unobserved even by tagging data. Among fisheries data, only the catch likelihood responds strongly to the parameter measuring tolerance to low oxygen content, \hat{O} , suggesting that optimal value is located between 0.5 and 1.5 ml/l. Note that the values within (1,1.5) ml/l interval are not optimal for tagging data.

Profiles for movement rates confirm previously known tendency of fisheries data to increase diffusivity and reduce directed movement rates, both contributing to non-zero biomass everywhere in the model domain and low patchiness. However, cutting-off a few profiles with highest likelihood values (not shown) shows that there is a slight decrease of length frequency likelihood with increasing velocity at maximal habitat gradient from 0 to 0.5 m/s . Integration of tagging data to the bigeye model enhances observability of movement parameters while modifying the shape of the likelihood hyper-surface with minimal values towards lower diffusions and small but non-zero advection rates. Note that since the advection parameter plays the role of the proportionality coefficient for the habitat gradient, it is correlated with those habitat parameters, which control the magnitude of the habitat gradient, namely with parameters eF_n (not shown).

6.2 Parameter estimates from tagging data

Optimization study with the model of tagged tunas confirm the results of sensitivity analysis with less than half (5 out of 13) of parameters being estimated between their fixed boundaries (see Table 3, columns TAGS-I and TAGS-G). Drastic differences between the estimation of habitat and movement rates from fisheries and tagging data, suggests that the full likelihood MLE might be a trade-off between deteriorated quality of the fit to catch data and valid parameterization of the movement model. In particular, almost zero contributions of micronekton groups into species habitat in the CL reference model means very low quality habitats and small habitat gradients and hence increased diffusion and decreased advection rates. On the contrary, the integration of tagging data tends to decrease the diffusion and increase advection, usually by increasing the habitat quality and enhancing habitat gradients defining the direction and magnitude of the tuna velocity field.

The weak observability of thermal habitat parameters for older ages of tunas was also revealed by sensitivity analysis. As a consequence, they were stuck to their boundaries in optimization. Some additional work is required to explore how different fixed parameter values influence the optimization and validation with an independent dataset. Optimization with a smaller sub-set provided a biased estimation of thermal preference at first

autonomous age (3 months in this configuration). The use of 2008-2010 tagging sub-set leads to a very low preferred temperature $T_1 = 21^\circ\text{C}$ for juvenile bigeye. As a result, this model suggests that bigeye feeds mostly on lower mesopelagic micronekton (at depths below 400m on average) during the day, estimating highest contribution, eF_{32} for the migrant lower mesopelagic functional group. This biased estimation is likely attributed to 1) the low observability of thermal habitat parameters shown by the sensitivity analysis and 2) too small size of the individual data that is insufficient to allow approximation of the observed movements by a Eulerian model. The model constrained by 2008-2013 sub-set provides more plausible estimation of thermal preference of youngest bigeye at 24.5°C and the predominant prey species being resident upper mesopelagic forage (with highest contribution, eF_{22}) inhabiting higher mesopelagic layer (between 150-400m on average).

Previously established method with normal tag likelihood and weights depending on time at liberty of tags [Senina *et al.*, 2020] was confirmed to be essential in order to estimate such parameters that have advection prevailing over diffusion and pass the validation test (see below). Although skewed and heavy-tailed distribution of tags cannot be considered normal, the normal likelihood tends to fit better higher densities of recaptures, thus bringing essential signal within the Eulerian model by integrating the movement that is shown by large number of tags and not by an individual. Log-normal function, on the opposite, fitting well the lower tag densities, leads to highly diffusive model solution and fails the validation with independent dataset. The higher weights on tag recaptures with longer time at liberty means that the short-living tags which are usually recaptured within the first month at liberty being still very close to the release site and so not showing any movement, are downweighted, so that the tags recaptured after longer time at liberty drive function minimization, hence forcing the model to find such solution that actually explains movement.

6.3 Validation

The fit to the catch and length data provided by the MLE solution of the CL reference model can be seen in Appendix, section A.3 *Fit to the catch and LF data*. Here we compare the skills of the model with three optimal parametrizations in describing the movement of tagged tunas: 1) reference model with only fisheries data in the likelihood, 2) tag dynamics model INTERIM forcing and optimal parameters estimated on the sub-set 2008-2010 and 3) tag dynamics model with GLORYS-free forcing and optimal parameters estimated on the longer sub-set 2008-2013. The validation of optimal solutions was performed on the independent dataset, i.e. releases and recaptures data from 2000 to 2007, which were not used in parameter estimation in either of three models. Note that in the current sensitivity analysis and optimization runs, the resolution used to compute the likelihood term for the tagging data was 6° in longitude, 6° in latitude and a 3-month time step. However, the validation of the optimization results was undertaken on the model's spatio-temporal resolution, i.e. 2° and 1 month. First, the MLE parameters of each model were used to run tag simulations for the 2000-2007 period. The likelihood values for validation runs with the reference MLE model, the model obtained with 2008-2010 and 2008-2013 tagging data sub-set are 2906, 2791 and 2206 respectively. Besides, the reference MLE parametrization was also used to simulate the tag dynamics of 2007-2010, then the fit was evaluated.

Neither sub-set of data can be described by the MLE solution obtained with fisheries data only (see Fig. 13 and A10). The distributions of tags is driven by diffusion, hence the spatial structure has a significant south-eastern bias, showing the displacements of tagged tunas around three release positions with noticeable drift by equatorial countercurrent and the tag density distortion by the Peru current pushing the density patch from south-east. Also, spatial distributions for both time periods are characterised by excessive density extension in latitudinal direction.

The spatial distribution shown by the MLE model obtained from 2008-2010 recaptures sub-set was also not satisfactory (Fig. 13). Although the likelihood has improved, the structure is much less diffused and the overall spatial extension is more coherent with the observed one, too many recaptures are predicted to the south and the east of observed recapture positions. The majority of recaptures are actually predicted to the east and not to the west of release positions, the latitudinal distribution has secondary, unobserved peak. The third optimal solution achieved with the largest 2008-2013 tagging data sub-set, presents significant improvement in simulating the observed dynamics of tags released and recaptured before 2008. Although still presenting some eastern bias, more that two third of tags released at 95°W moved towards central Pacific. The latitudinal extension is well reproduced with more bigeye moving to the southern hemisphere both from eastern and western positions of release.

7 Conclusion

In the present study we used conventional tagging data integrated into the optimization method in SEAPODYM to improve the estimates of model habitat and movement parameters. Only the recapture data are used to inform model parameters. The release-recapture data starting in 2008 were used in the parameter estimation and the rest of the dataset was used to validate the model solutions. The MLE model informed by the 6-years tagging dataset can describe the movement of tags from independent dataset. The addition of archival tagging data into the likelihood may be beneficial to estimation of parameters describing habitats of older tunas not observed by conventional tagging data.

Results of the sensitivity analysis will be further used to estimate parameters of the full population dynamics model maximizing the likelihood that includes fisheries and tagging data. Being very computationally demanding, the function minimization in spatial dynamics models with age structure will benefit from this study, which provided essential information on the observability of model parameters from three types of data. First, the efficient technique of independent AAT and OAT sensitivity simulations allowed comprehensive exploration of likelihood super-surface and selection of the best set of parameters as initial conditions for the function minimizer. Second, setting only sensitive parameters as control ones and fixing unobserved parameters will improve convergence of minimization method and facilitate the process of searching for global minimum.

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8 Tables

Table 1: Bigeye Fishing Dataset. Definition of SEAPODYM fisheries in Pacific Ocean. The time period shows the range with available forcing fields and full-year dataset.

ID	Description	Nation	Resolution	Time period
L1	LL traditional BET, YFT target	Japan	5°, month	1979 - 2013
L2	LL targeting BET and YFT	Korea	5°, month	1979 - 2013
L3	LL targeting BET and YFT	Taiwan	5°, month	1979 - 2013
L4	Distant-water longline	China	5°, month	1979 - 2014
L5	Longline swordfish target	ALL	5°, month	1979 - 2014
L6	LL targeting BET and YFT	Vietnam, Philip- pines, Indonesia	5°, month	1990 - 2010
L7	Mixed-target longline	New Zealand, Australia	5°, month	1979 - 2014
L8	Longline	PICs	5°, month	1979 - 2014
S9	PS free schools, WCPO	ALL	1°, month	1979 - 2013
S10	PS drifting logs and FADs, WCPO	ALL	1°, month	1979 - 2013
S11	PS anchored FADS, WCPO	ALL	1°, month	1980 - 2014
S12	PS marine mammals, WCPO	ALL	1°, month	1979 - 2013
S13	PS free schools, EPO	ALL	1°, month	1979 - 2012
S14	PS free schools, EPO	ALL	1°, month	1979 - 2012
P15	Pole-end-line, WCPO	ALL	5°, month	1979 - 2012
O16	Domestic fisheries, multiple gears	Philippines, In- donesia	5°, month	1997 - 2014

Table 2: Forcing variables used in current SEAPODYM application. Note that table shows original resolutions, all variables were then interpolated onto SEAPODYM spatial and temporal resolutions 2° , 30 days.

Variable	Description	Resolution	Time period
<i>INTERIM forcing</i>			
T, u, v	NEMO OGCM hindcast simulation with ERA-interim atmospheric forcing	ORCA2	
P, Z, O_2	Coupled NEMO-PISCES model with ERA-INTERIM atmospheric forcing	ORCA2	1/1979 -12/2010
F	SEAPODYM-LMTL simulated six micronekton groups*	2° , 30 days	
<i>GLORYS-free forcing</i>			
T, u, v	Global ocean reanalyses without data assimilation, NEMO OGCM forced by atmospheric ECMWF reanalyses	ORCA025	
P, Z	EPPLEY-VGPM primary production and euphotic depth computed with Morel model from satellite-derived Chl-a	$1/4^\circ$, 7 days	1/1998 -12/2019
F	SEAPODYM-LMTL simulated six micronekton groups**	$1/4^\circ$, 7 days	
O_2	WOA monthly climatology	$1/4^\circ$, 30 days	clim. year

*Lehodey et al., 2010; **QUID 2019

Table 3: Parameter estimates for the following model configurations: CL-I - population model with INTERIM forcing and likelihood with Catch and Length data only, TAGS-I - tag density dynamics model with INTERIM environmental forcing and 2008-2010 tagging dataset in the likelihood, TAGS-G - tag density dynamics model with GLORYS-free environmental forcing and 2008-2013 tagging dataset in the likelihood. Parameters marked by asterisks were fixed in optimization run. Parameter with [or] were estimated at their lower or upper boundary respectively.

θ	Description	CL-I	TAGS-I	TAGS-G
<i>Reproduction</i>				
σ_0	standard deviation in temperature Gaussian function at age 0, $^{\circ}C$	3]		
T_0^*	optimal surface temperature for larvae, $^{\circ}C$	28.9		
α_P	prey encounter rate in Holling (type III) function, day^{-1}	0.073		
α_F	Log-normal mean parameter predator-dependent function, g/m^2	[0.05		
β_F	Log-normal shape parameter in predator-dependent function, g/m^2	1.054		
R	reproduction rate in Beverton-Holt function, mo^{-1}	0.0038		
b	slope parameter in Beverton-Holt function, nb/km^2	16.05*		
<i>Mortality</i>				
\bar{m}_p	predation mortality rate age age 0, mo^{-1}	0.05*		
β_p	slope coefficient in predation mortality	0.434		
\bar{m}_s	senescence mortality rate at age 0, $mo^{-1-\beta_s}$	0.02		
β_s	slope coefficient in senescence mortality	[0		
ϵ	variability of mortality rate with habitat index $M_H \in (\frac{M}{1+\epsilon}, M(1+\epsilon))$	0.5]		
<i>Habitats</i>				
σ_1	standard deviation in temperature Gaussian function at first young age, $^{\circ}C$	5.5]	1.98	4]
T_1	optimal temperature (if Gaussian function), or temperature range for the first young cohort, $^{\circ}C$	[25	[21	24.5
σ_K	standard deviation in temperature Gaussian function at age K, $^{\circ}C$	6.5]	[1	[1
T_K	optimal temperature (if Gaussian function), or temperature range for the oldest adult cohort, $^{\circ}C$	[10	15]	15]
b_T	allometric power coefficient for thermal preferences at age	[1	2.58	2.51
\hat{O}	threshold value of dissolved oxygen, ml/l	0.758	2.5]	[1.0
eF_{11}	contribution of epipelagic forage to the habitat	[0	[0.5	[0.5
eF_{22}	contribution of upper mesopelagic forage to the habitat	[0.1	1.12	3]
eF_{21}	contribution of migrant upper mesopelagic forage	0.05*	[0	0.34
eF_{33}	contribution of lower mesopelagic forage to the habitat	0.005	0*	0*
eF_{32}	contribution of migrant lower mesopelagic forage	0.05*	2]	2]
eF_{31}	contribution of highly migrant lower mesopelagic forage	0.079	[0	[0
<i>Movement</i>				
V	velocity at maximal habitat gradient and $A = 1$, BL/s	1.7895	2.02	0.13
A	slope coefficient in allometric function for tuna velocity	0.75*	0.73*	0.73*
σ	multiplier for the maximal diffusion rate	1.4091	0.22	1e-4
c	coefficient of diffusion variability with habitat index	0.5*	0.93*	0.93*

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9 Figures

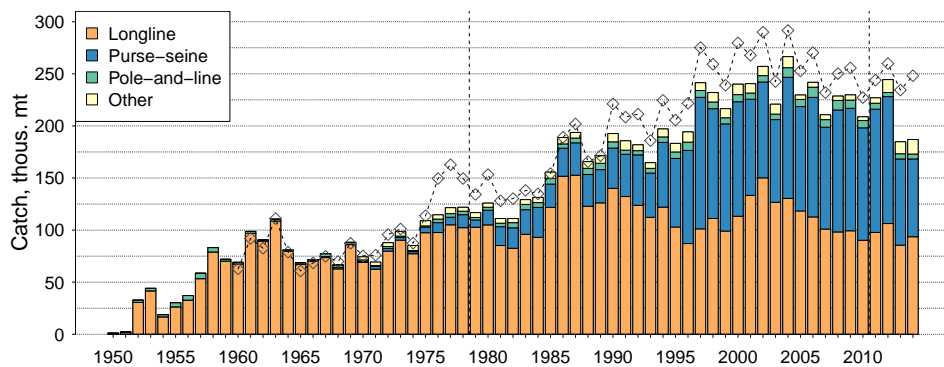


Figure 2: Total annual bigeye catch aggregated from geo-referenced catch (Pacific-wide) used in SEAPODYM analyses. Dashed line corresponds to total landings of bigeye (SPC Year Book, 2016).

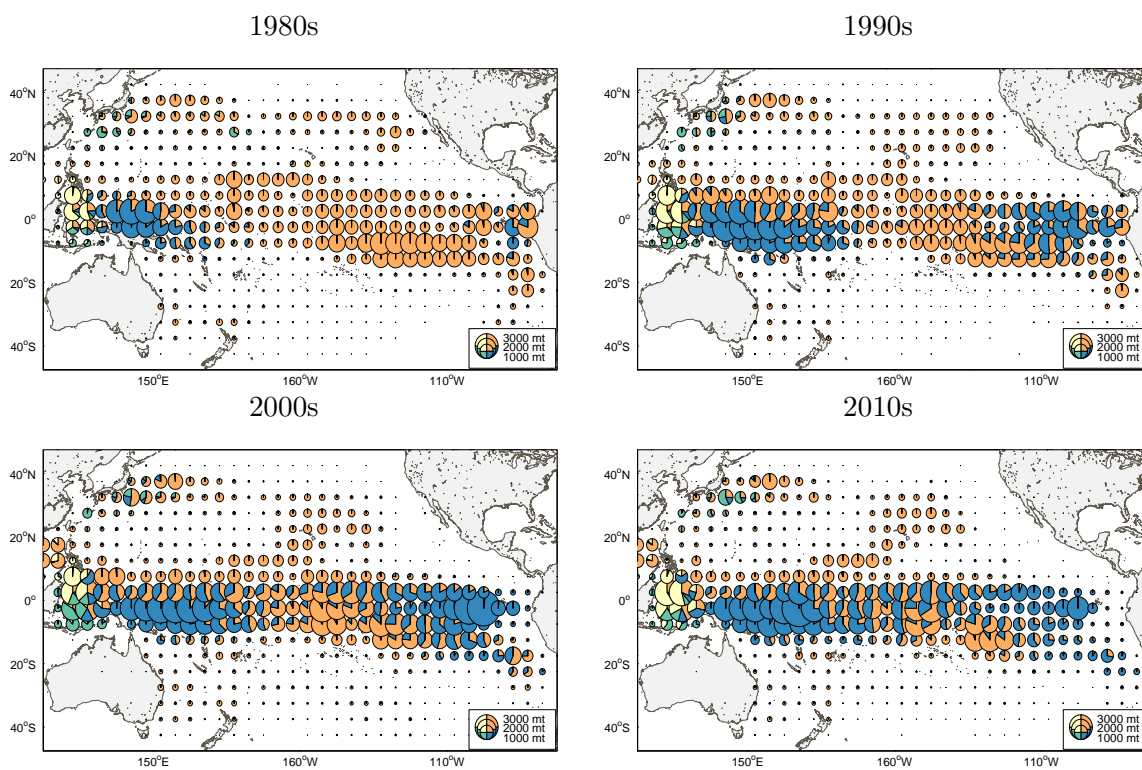


Figure 3: Spatial distributions of catches by decade and by gear: longline (orange), purse-seine (blue), pole-and-line (green), and others (yellow).

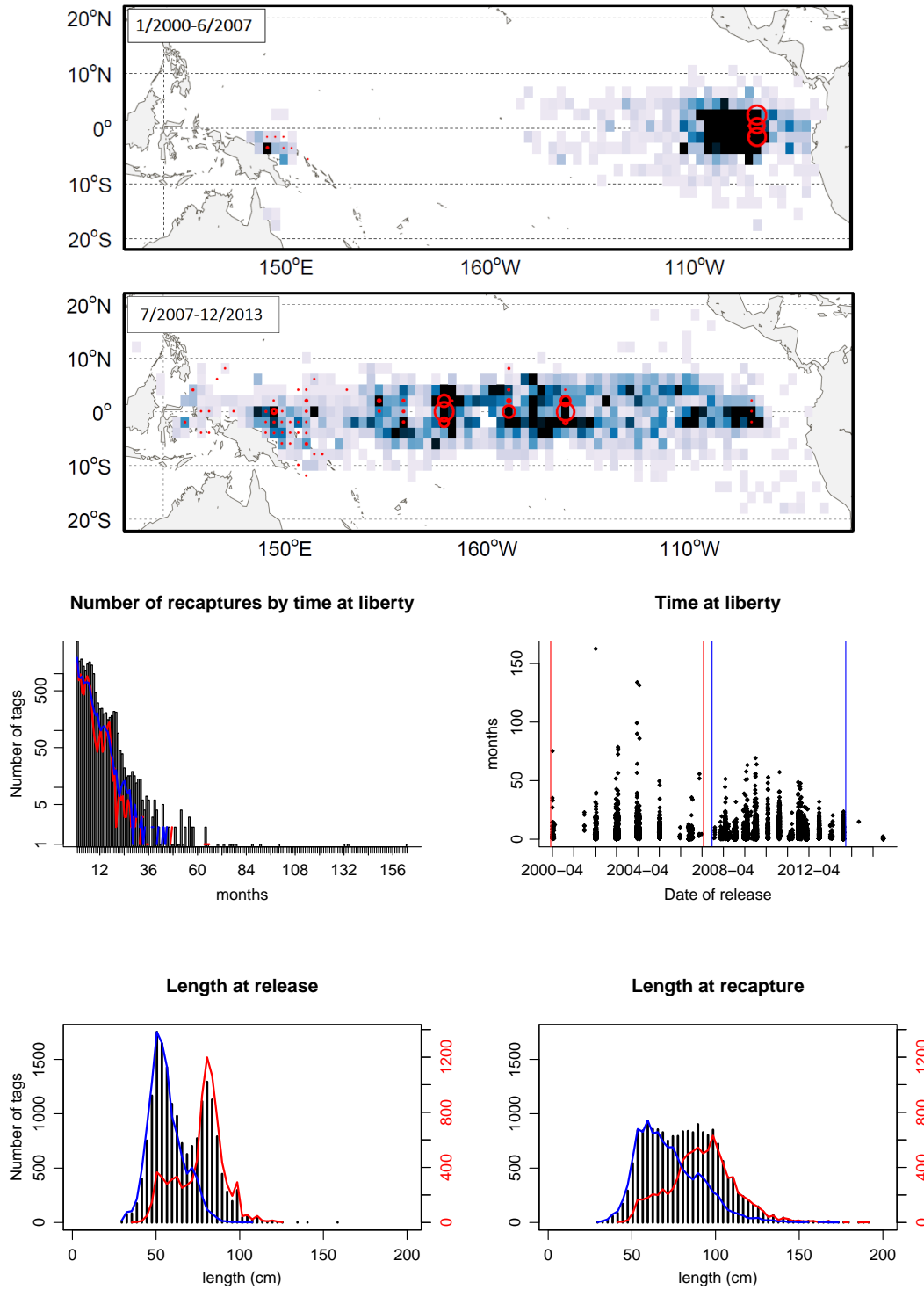


Figure 4: Top panel: number of bigeye tuna recaptured between June 2008 and September 2013 tagged during conventional tagging campaigns (using linear color bar from white to blue indicating 0 to 40 and more tag returns respectively). These data are used to inform SEAPODYM model parameters. Bottom panel: available conventional tagging (black bars and dots) and the data being used in optimization (red lines): (top) time at liberty histogram and time at liberty of the tags depending on their date of release; (bottom) size distribution at release and recapture.

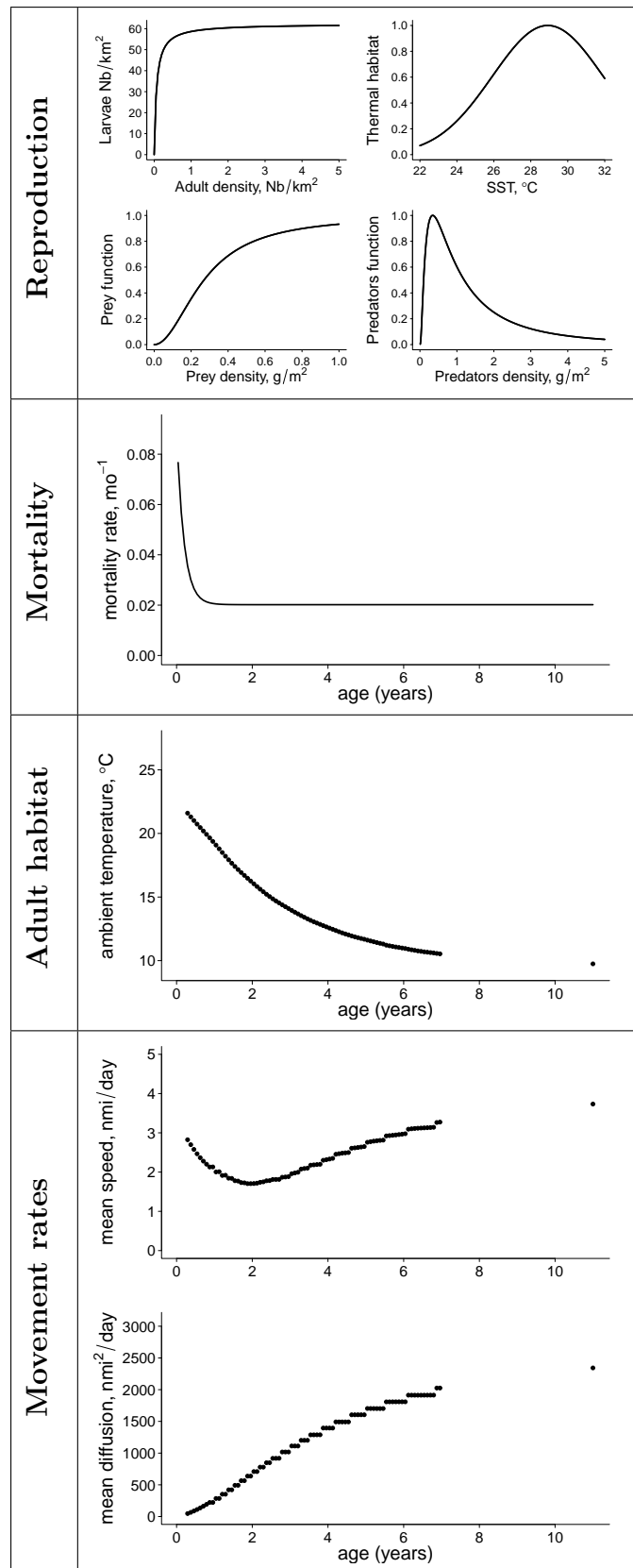


Figure 5: Estimated functional relationships in main dynamical processes (reproduction, natural mortality and movement) of reference MLE model constrained by fisheries data only. Habitat temperature and movement rates are computed as weighted spatio-temporal average with weights being the population density at age.

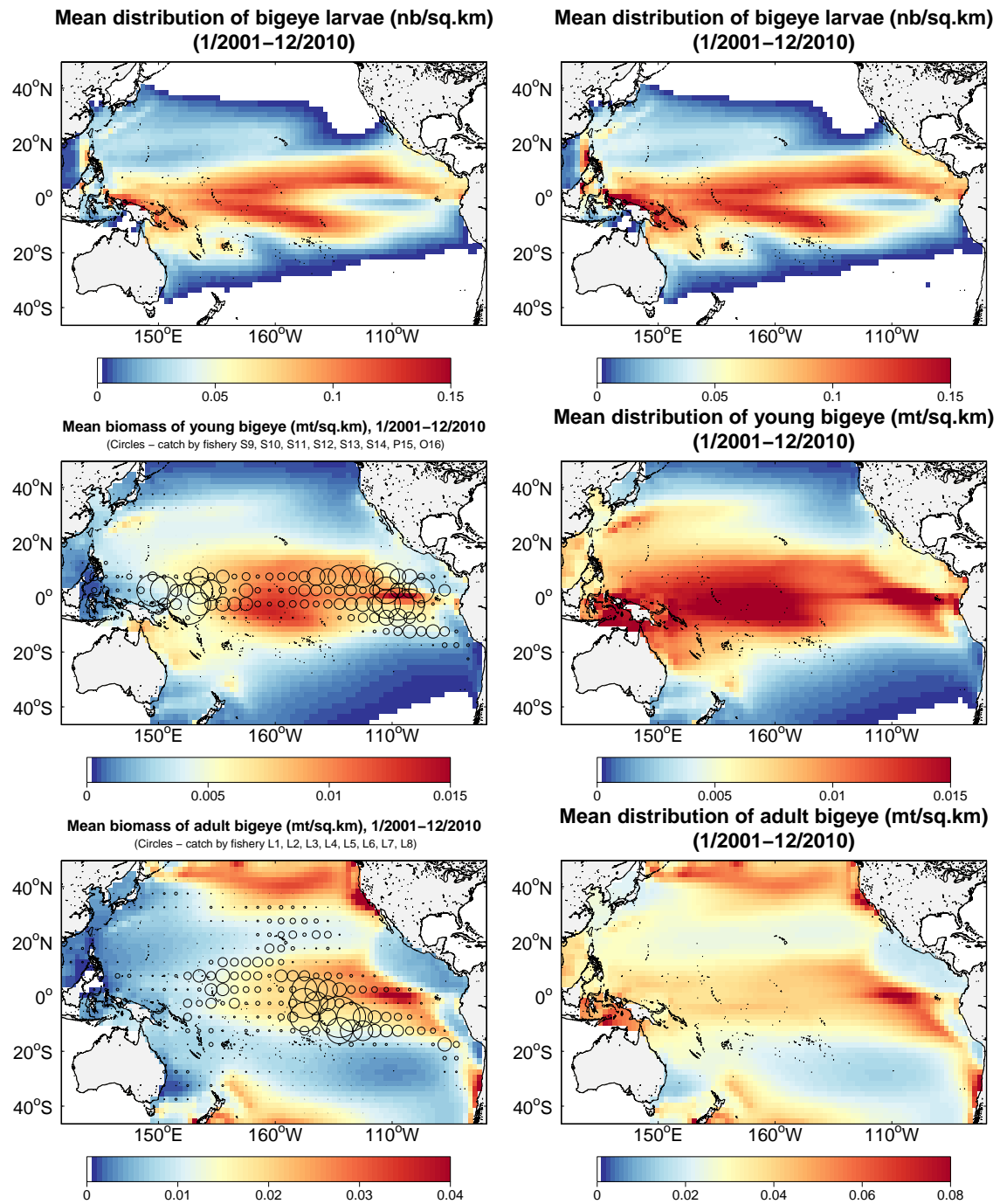
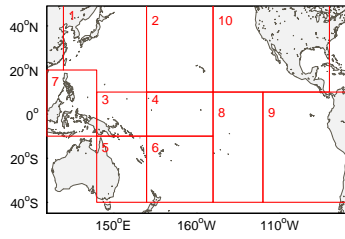
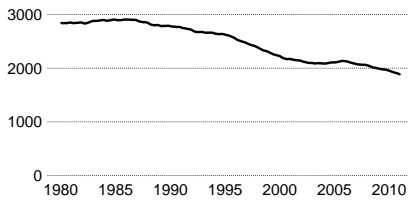


Figure 6: Average density of larvae in Nb/km² (top) and young (middle) and adult in mt/km² (bottom) bigeye predicted with (left) and without fishing (right). Note different range of values of adult density shown for exploited and virgin stock.

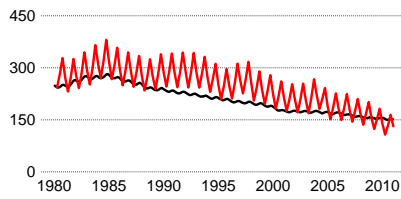
a) Bigeye stock assessment regions



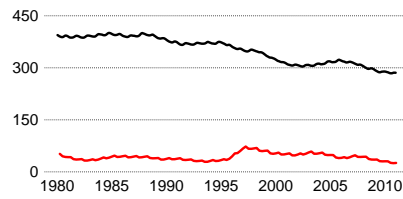
b) Overall



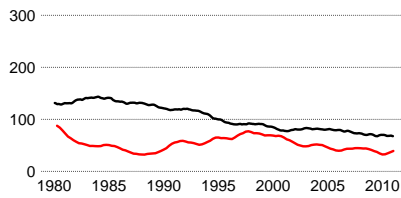
c) Region 1



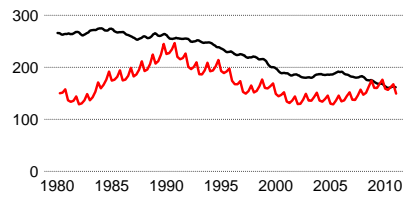
d) Region 2



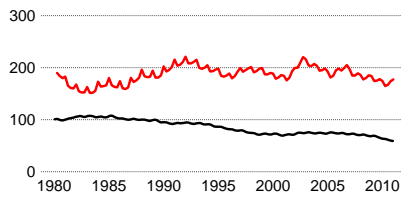
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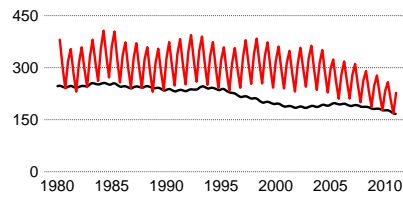
f) Region 4



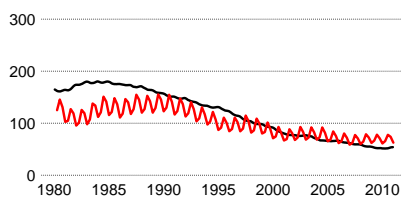
g) Region 5



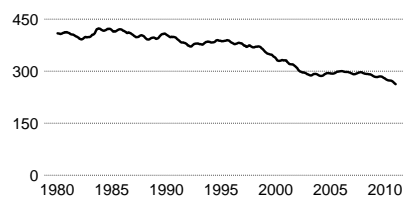
h) Region 6



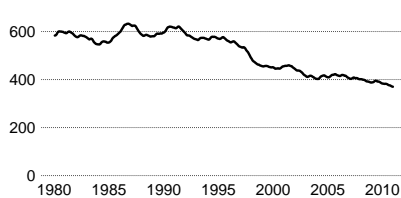
i) Region 7



j) Region 8



k) Region 9



l) Region 10

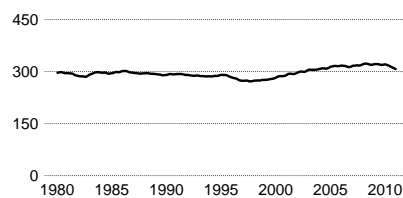


Figure 7: Comparison between SEAPODYM (black) and Multifan-CL (red) stock assessment model predictions for the Western and Central Pacific stock of mature adult bigeye (in thousand metric tons).

Fishery impact on bigeye tuna population

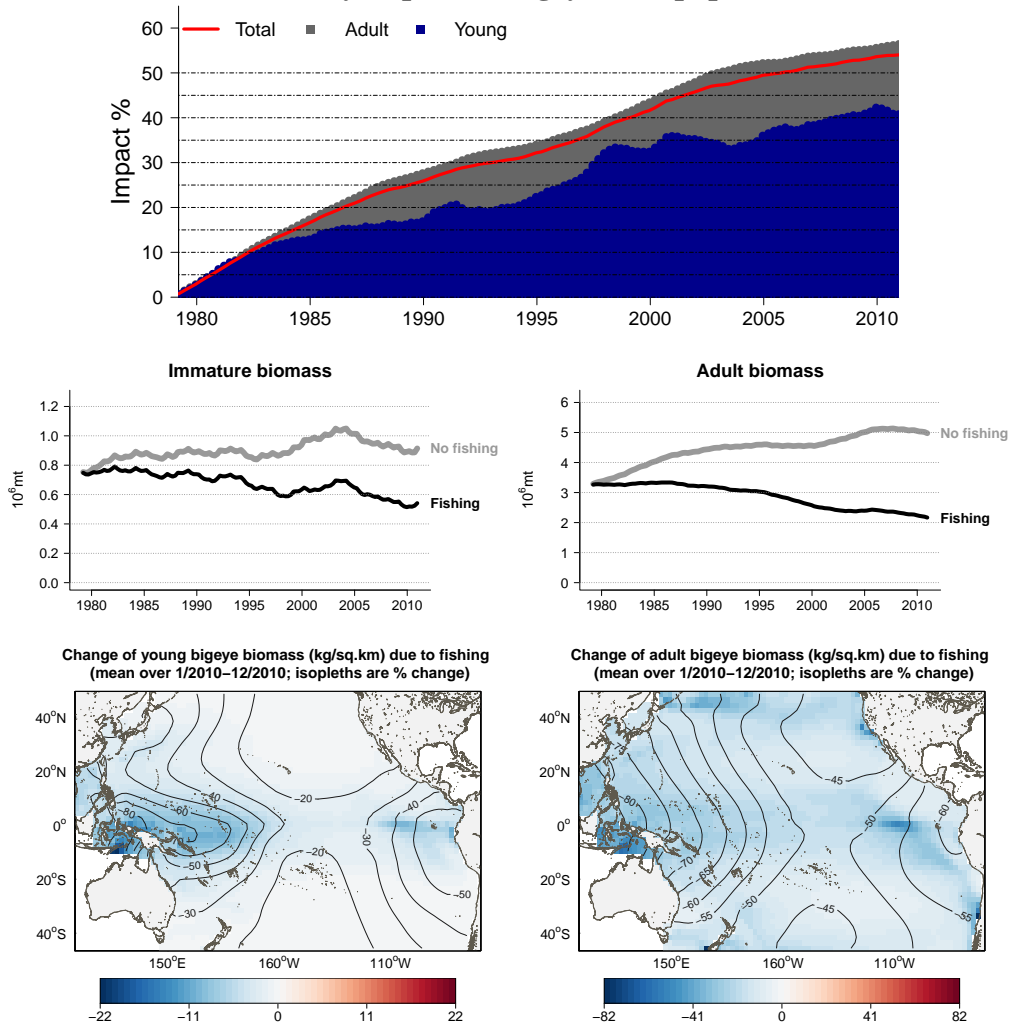


Figure 8: Spatial fishing impact on young and adult population stages of bigeye. Contour lines show the index $\frac{B_{F0} - B_{ref}}{B_{F0}}$ and colour shows the average biomass reduction due to fishing.

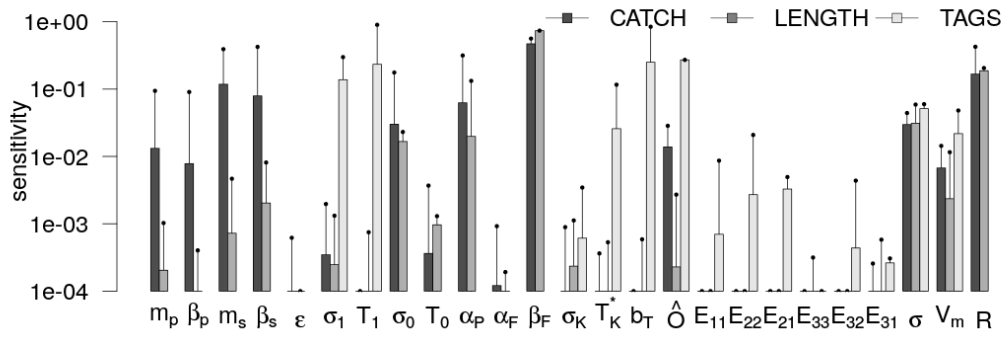


Figure 9: Sensitivity indices computed for three likelihood terms depending on catch, length and tagging data respectively. Bars correspond to first-order sensitivity showing direct contribution of a parameter to the model output variance and vertical lines correspond to total effect sensitivity, including correlations between model parameters (vertical lines)

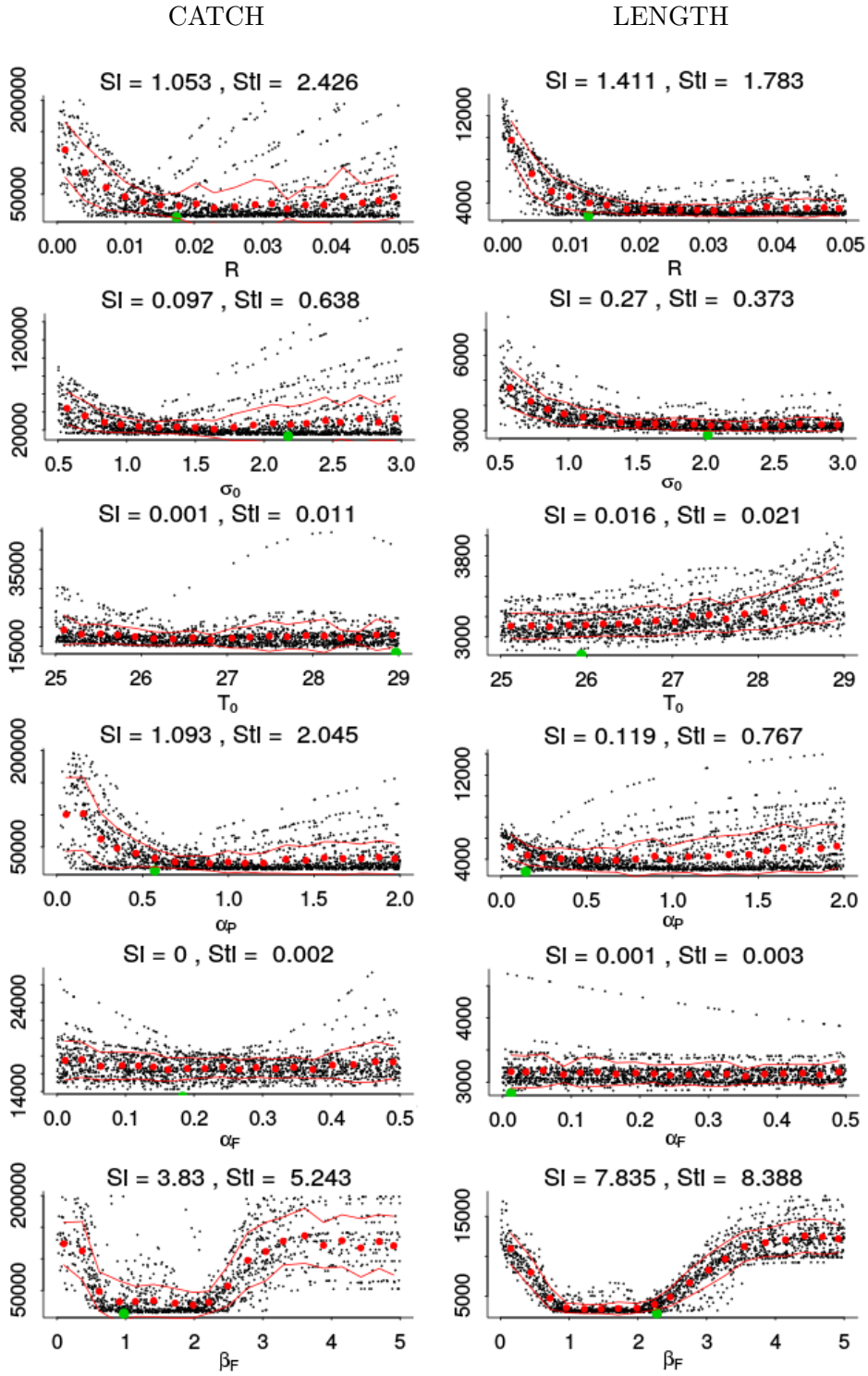


Figure 10: OAT profiles of reproduction parameters computed for catch data likelihood (left) and length-frequency likelihood (right). Green dots correspond to the best parameters providing minimal likelihood value as a result of OAT SA simulations.

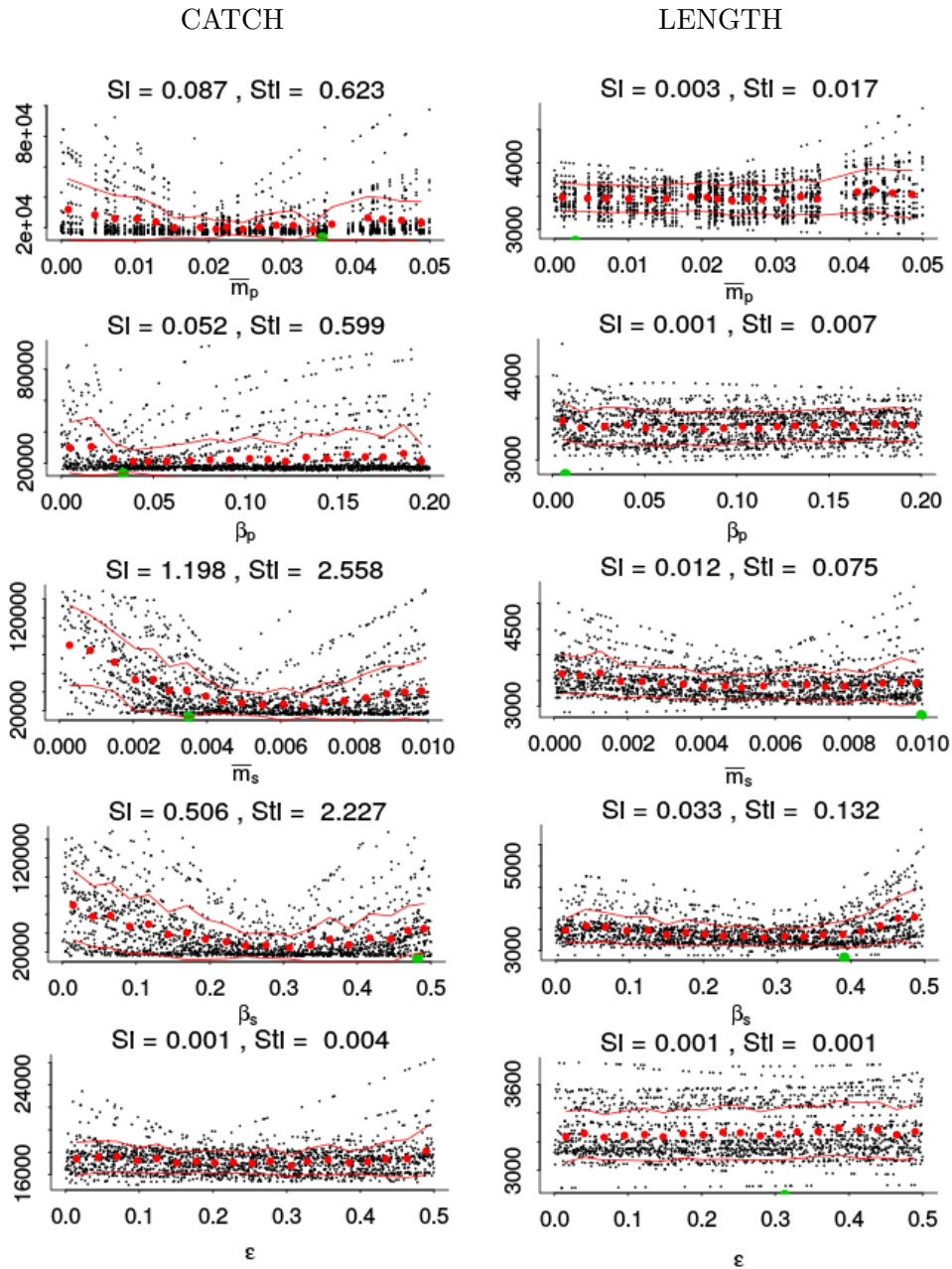


Figure 11: OAT profiles of mortality parameters computed for catch data likelihood (left) and length-frequency likelihood (right). Green dots correspond to the best parameters providing minimal likelihood value as a result of OAT SA simulations.

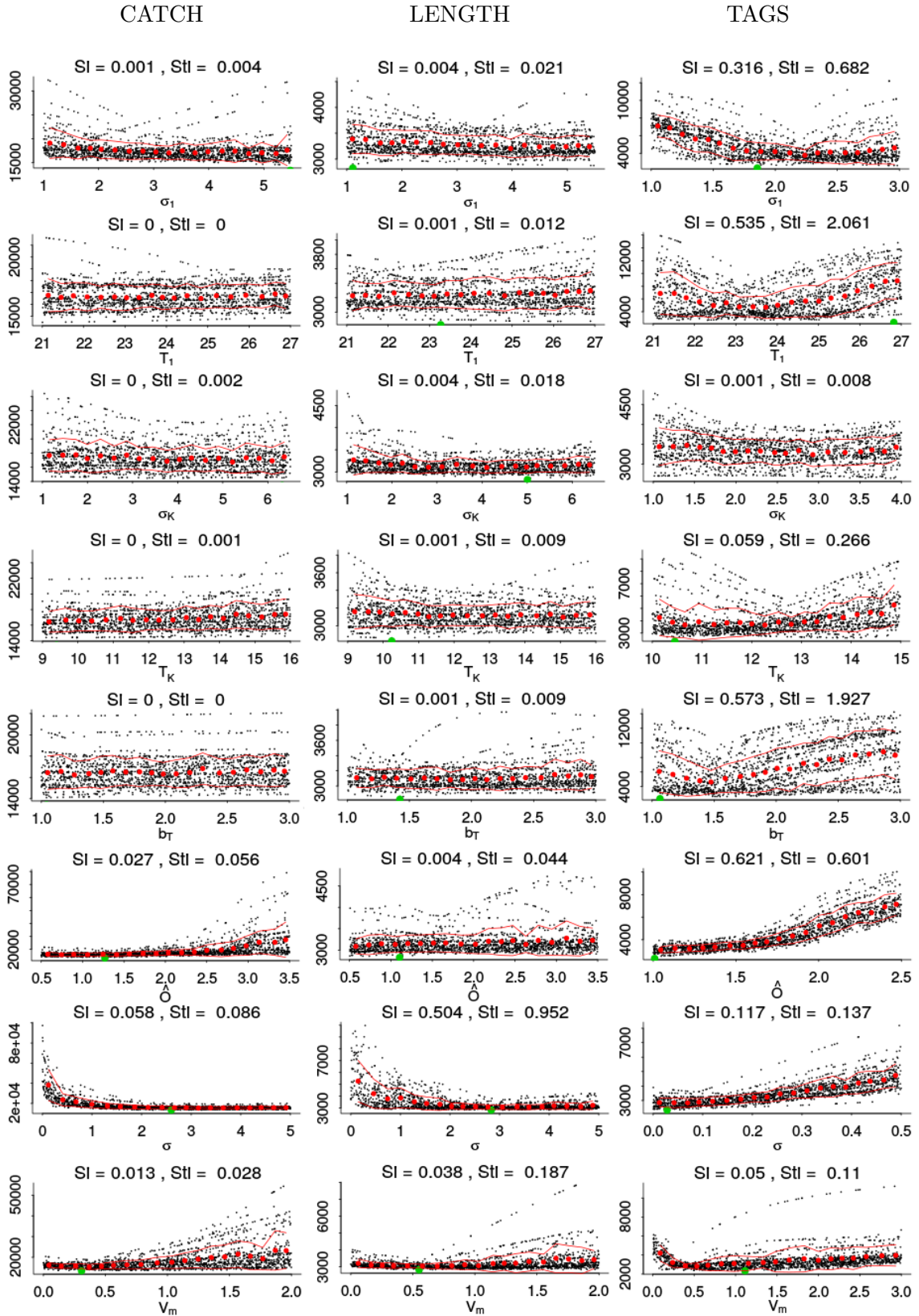


Figure 12: OAT profiles of habitat and movement parameters computed for catch data likelihood (left), length-frequency likelihood (middle) and tagging data likelihood (right). Green dots correspond to the best parameters providing minimal likelihood value as a result of OAT SA simulations.

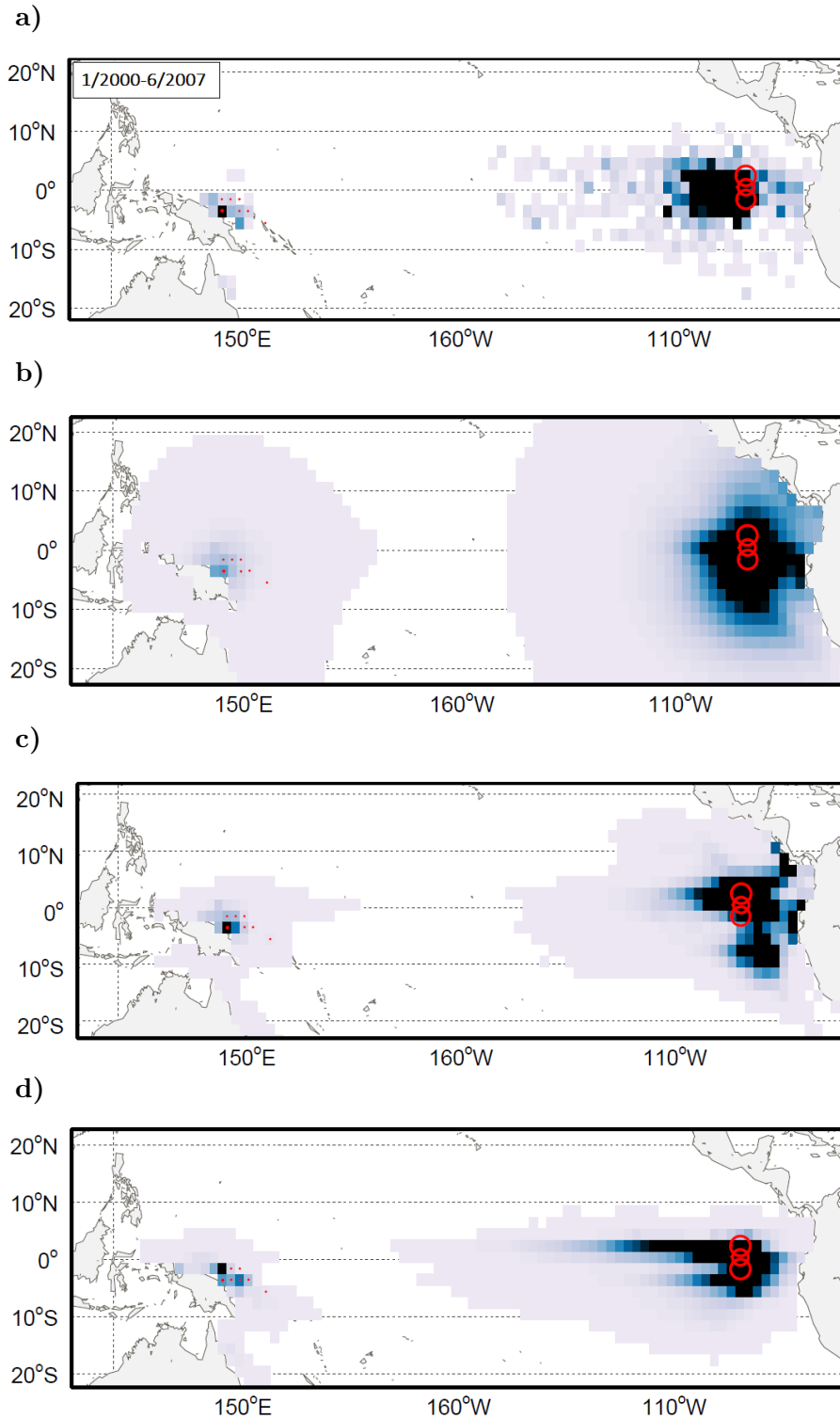
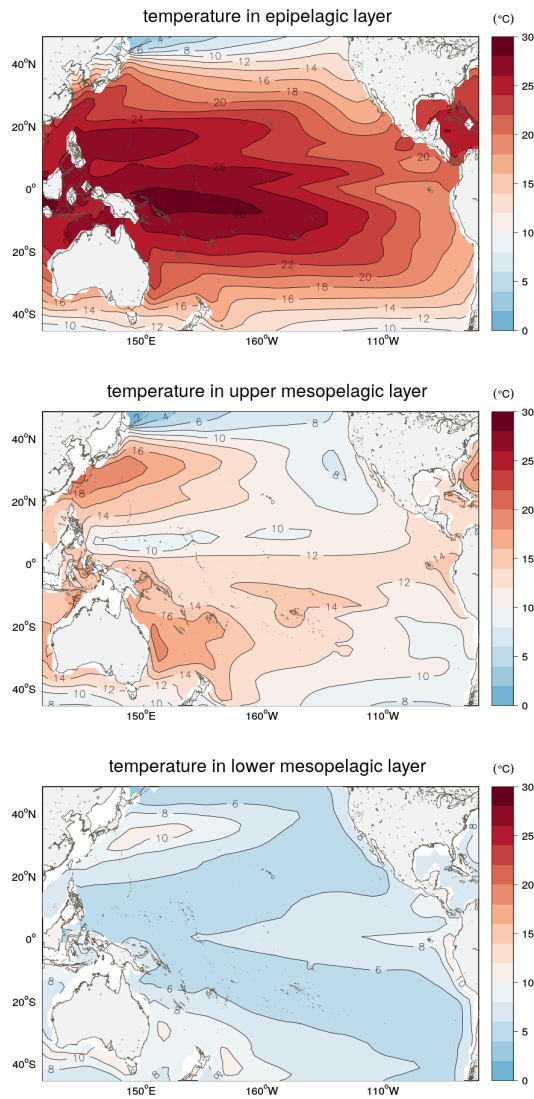


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A Appendices

A.1 Model forcing

a) INTERIM



b) GLORYS-free

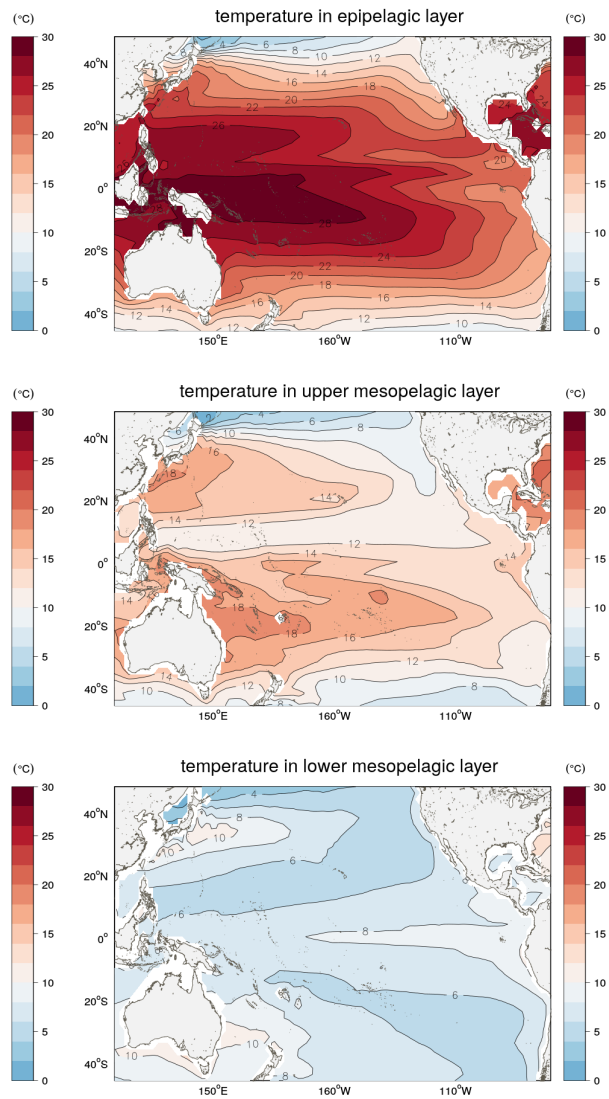


Figure A1: Water temperature from INTERIM and GLORYS-free forcing of SEAPODYM, integrated over three pelagic layers, epipelagic, upper and lower mesopelagic layers. These variables control accessibility to prey species inhabiting respective pelagic layer. Maps show the mean variable over decade 2001-2010.

a) INTERIM

b) GLORYS-free

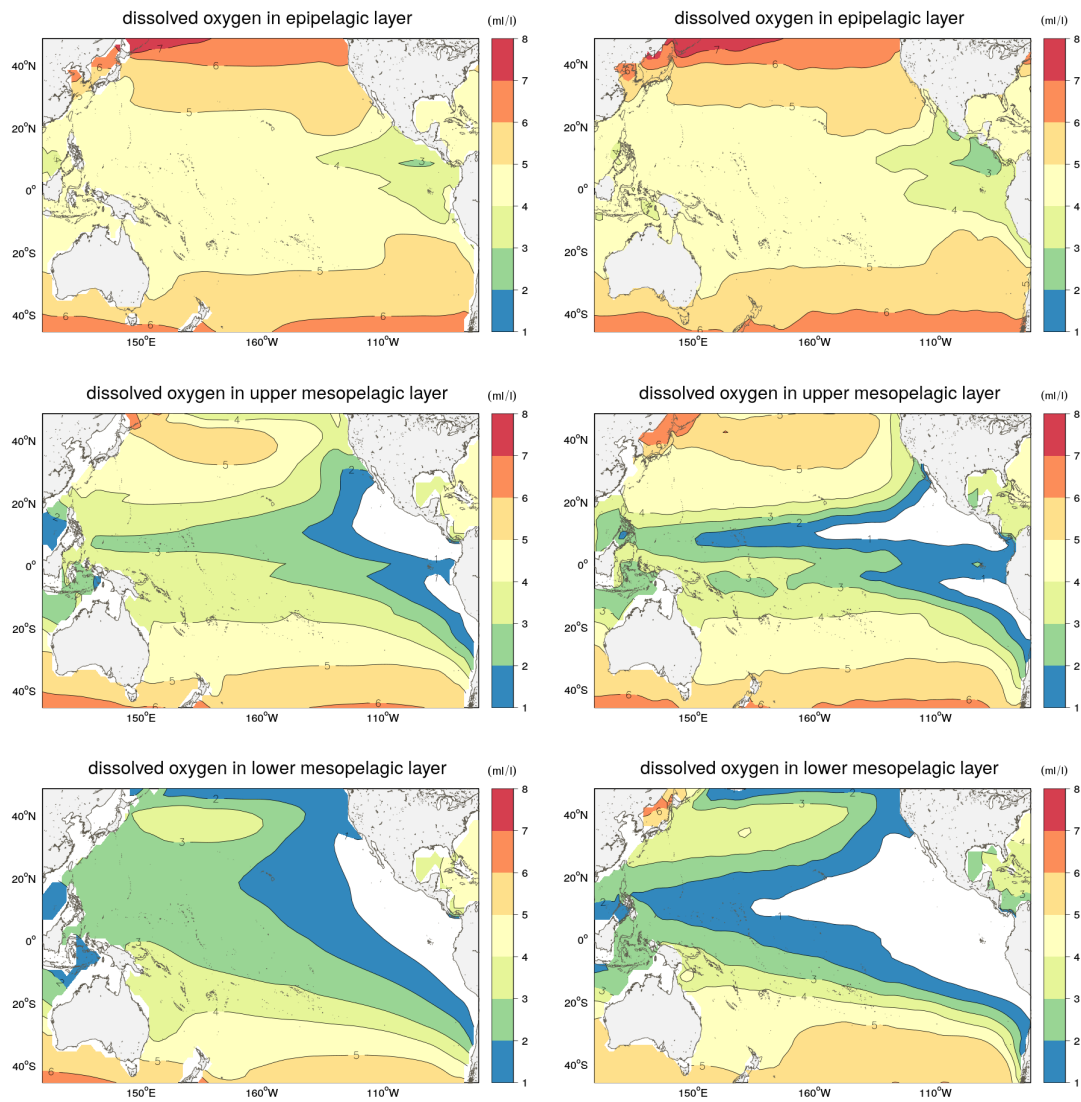
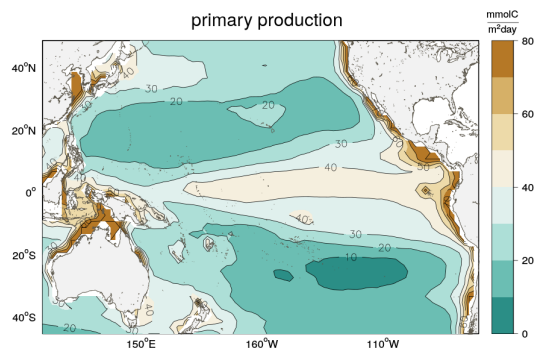


Figure A2: Dissolved oxygen from INTERIM and GLORYS-free forcing of SEAPODYM, integrated over three pelagic layers, epipelagic, upper and lower mesopelagic layers. Note that oxygen in Glorys-free dataset is WOA climatology. Given the species tolerance to dissolved oxygen, it controls its accessibility to prey species inhabiting pelagic layers. Maps show the mean variable over decade 2001-2010 for INTERIM and climatological year for GLORYS-free.

a) INTERIM



b) GLORYS-free

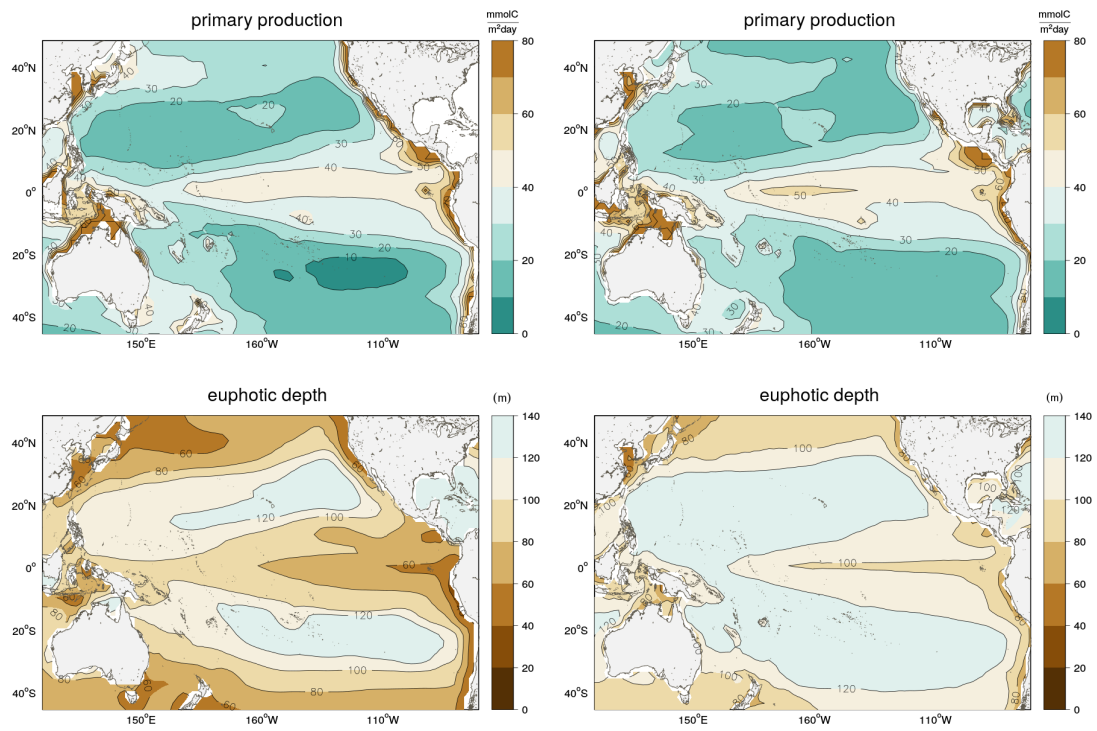


Figure A3: Primary production and euphotic depth from INTERIM and GLORYS-free forcing of SEAPODYM. Maps show the mean variable over decade 2001-2010.

a) INTERIM

b) GLORYS-free

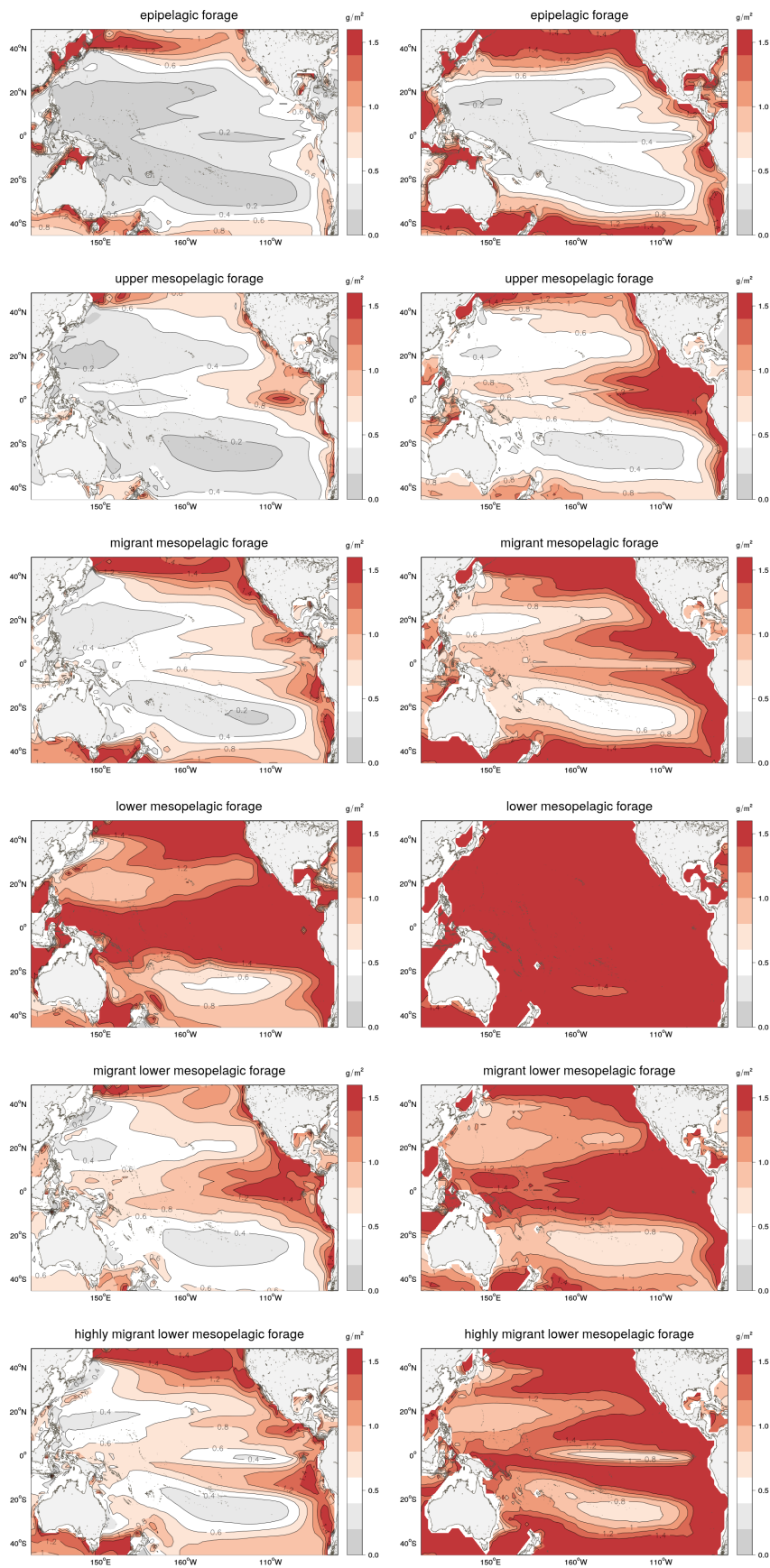


Figure A4: Six functional groups of micronekton, either resident in indicated pelagic layer or migrating to above (migrant) or to sub-surface (highly migrant) pelagic layers at night, simulated by SEAPODYM-LMTL model with INTERIM and GLORYS-free forcing.

A.2 Biomass estimations

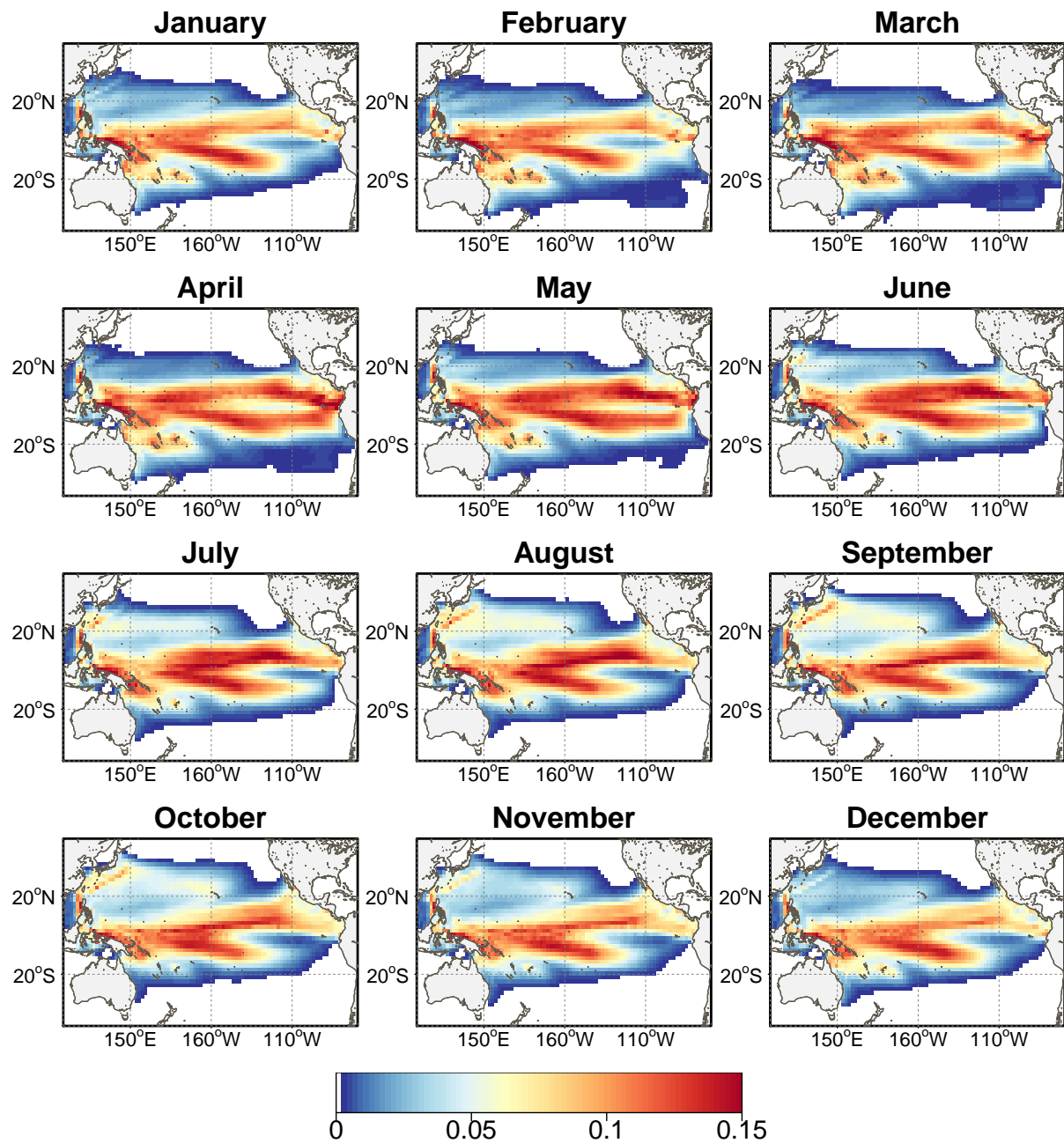
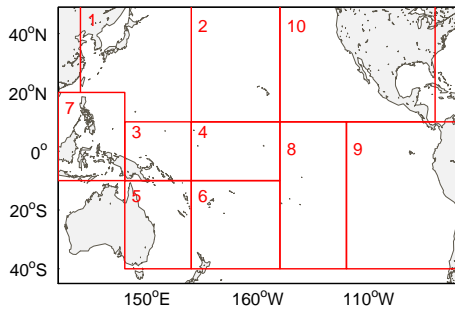
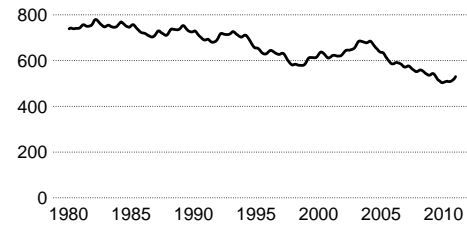


Figure A5: Mean monthly distributions of density of bigeye larvae (2001-2010 average).

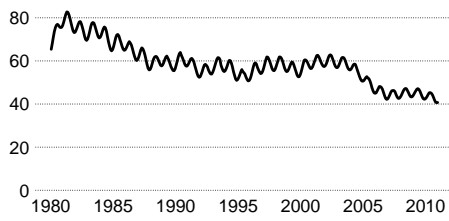
a) Bigeye stock assessment regions



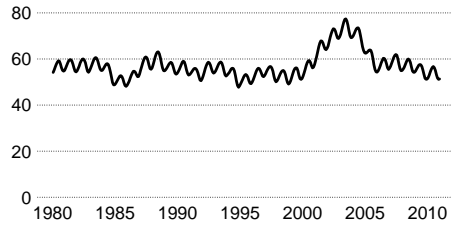
b) Overall



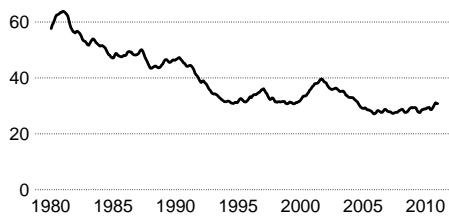
c) Region 1



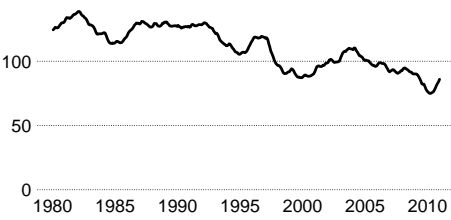
d) Region 2



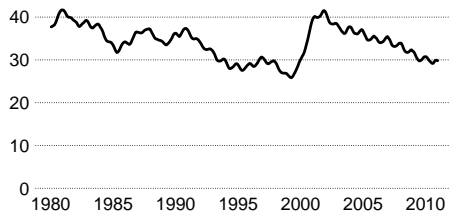
e) Region 3



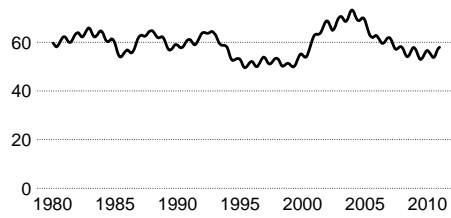
f) Region 4



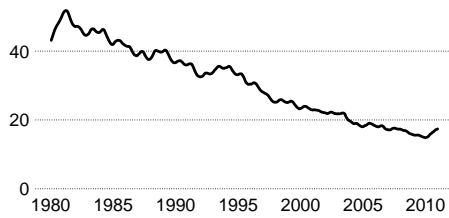
g) Region 5



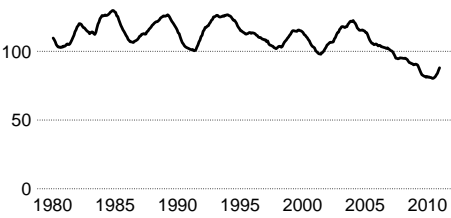
h) Region 6



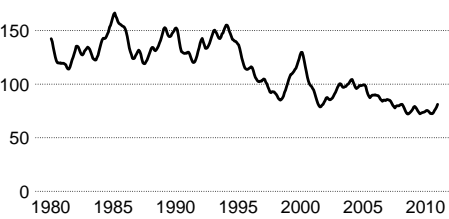
i) Region 7



j) Region 8



k) Region 9



l) Region 10

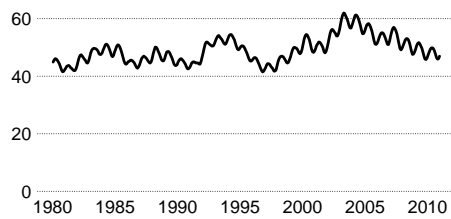


Figure A6: SEAPODYM model predictions for immature adult bigeye (in thousand metric tons) over the stock assessment regions.

A.3 Fit to the catch and LF data

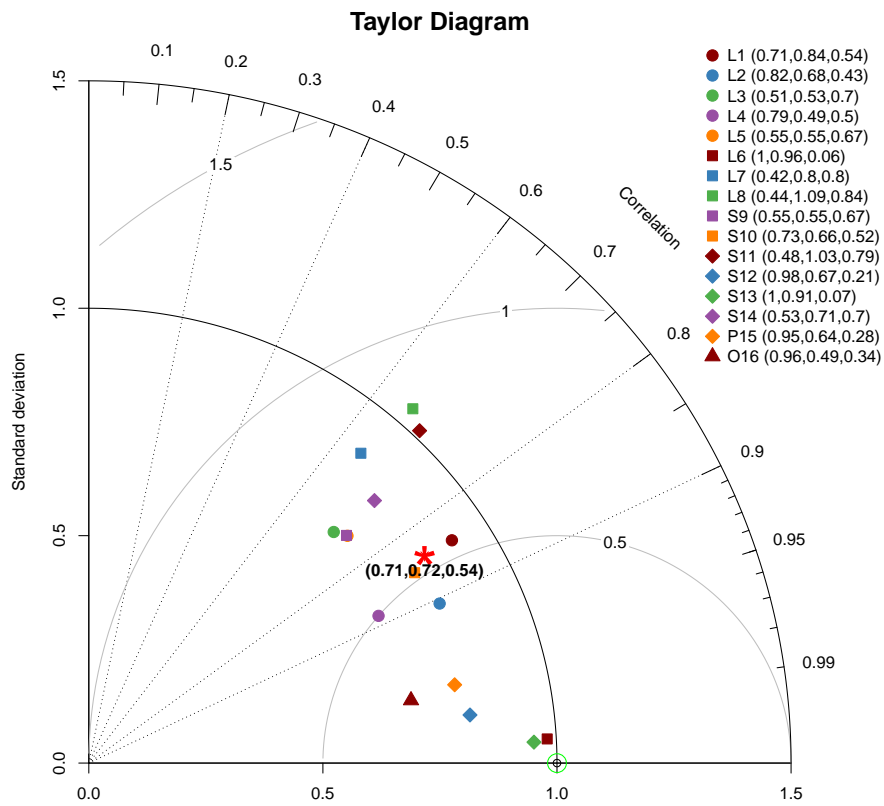


Figure A7: Taylor diagram, providing three aggregated metrics of model fit to the data: correlation (angular coordinates) between predictions and observations, standard deviation ratio (distance from (0,0) point depicts the ratio between model and data standard deviation) and normalized mean squared error (concentric circles with the green bullet being the center). Each point on the graph shows three metrics of the fit to the catch data by each fisheries (Table 1).

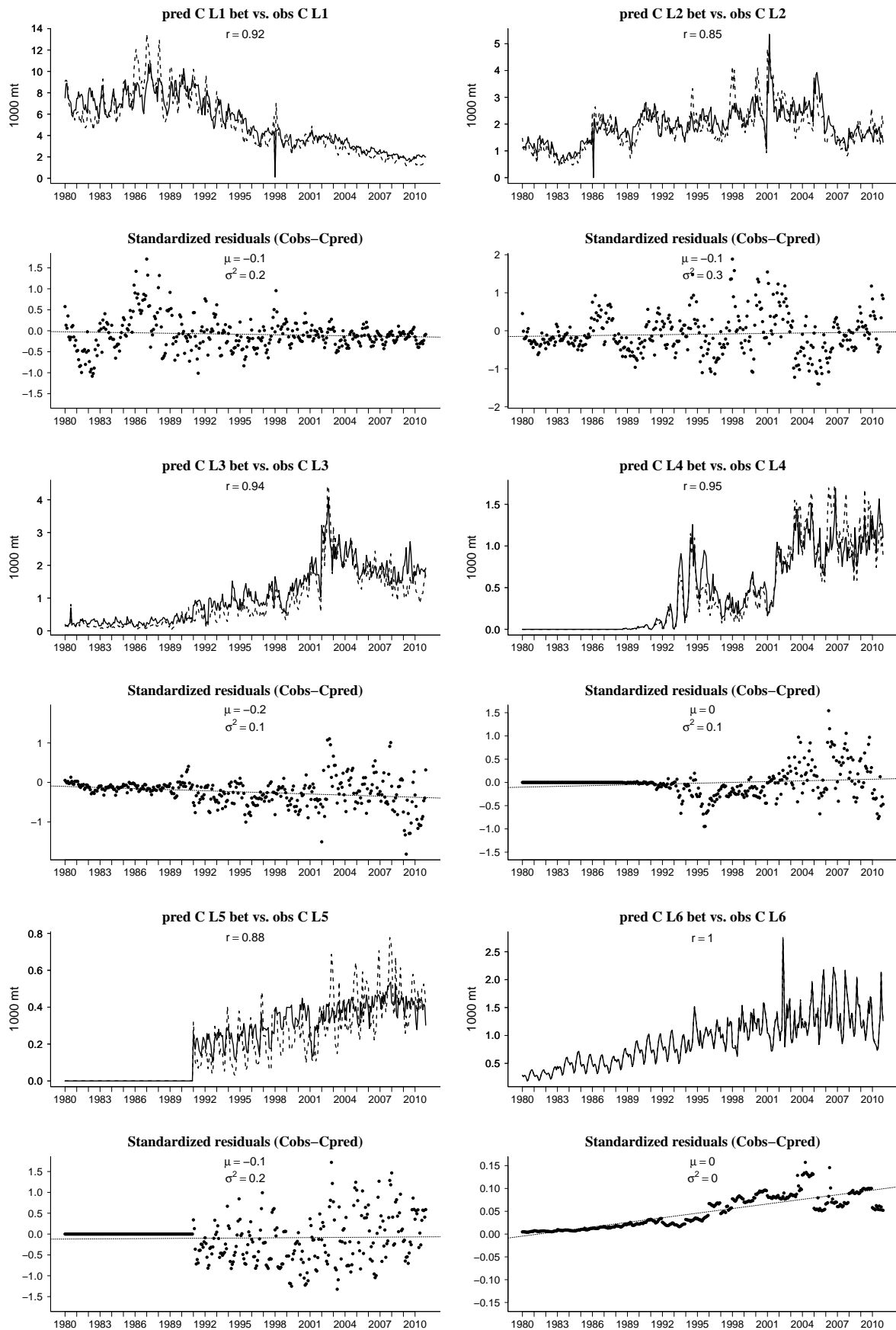


Figure A8: Monthly time series of observed (dashed) vs. predicted (solid) catch by fishery and standardized residuals. Three statistical scores shown on the plots are Pearson correlation coefficient (r) between predicted and observed catches, mean (μ) and variance (σ^2) of standardized residuals).

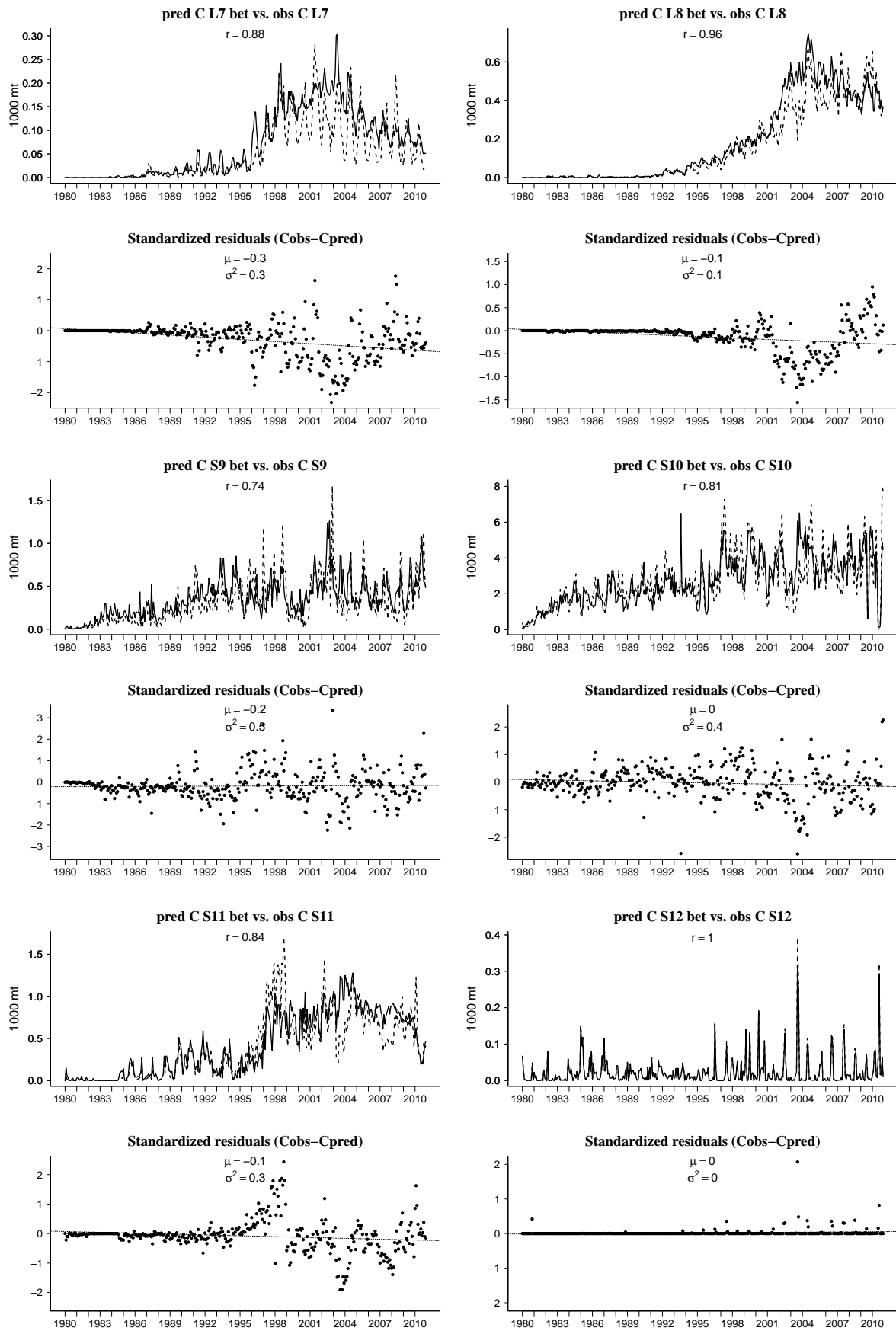


Figure A8: Monthly time series of observed and predicted catch by fishery (Continued)

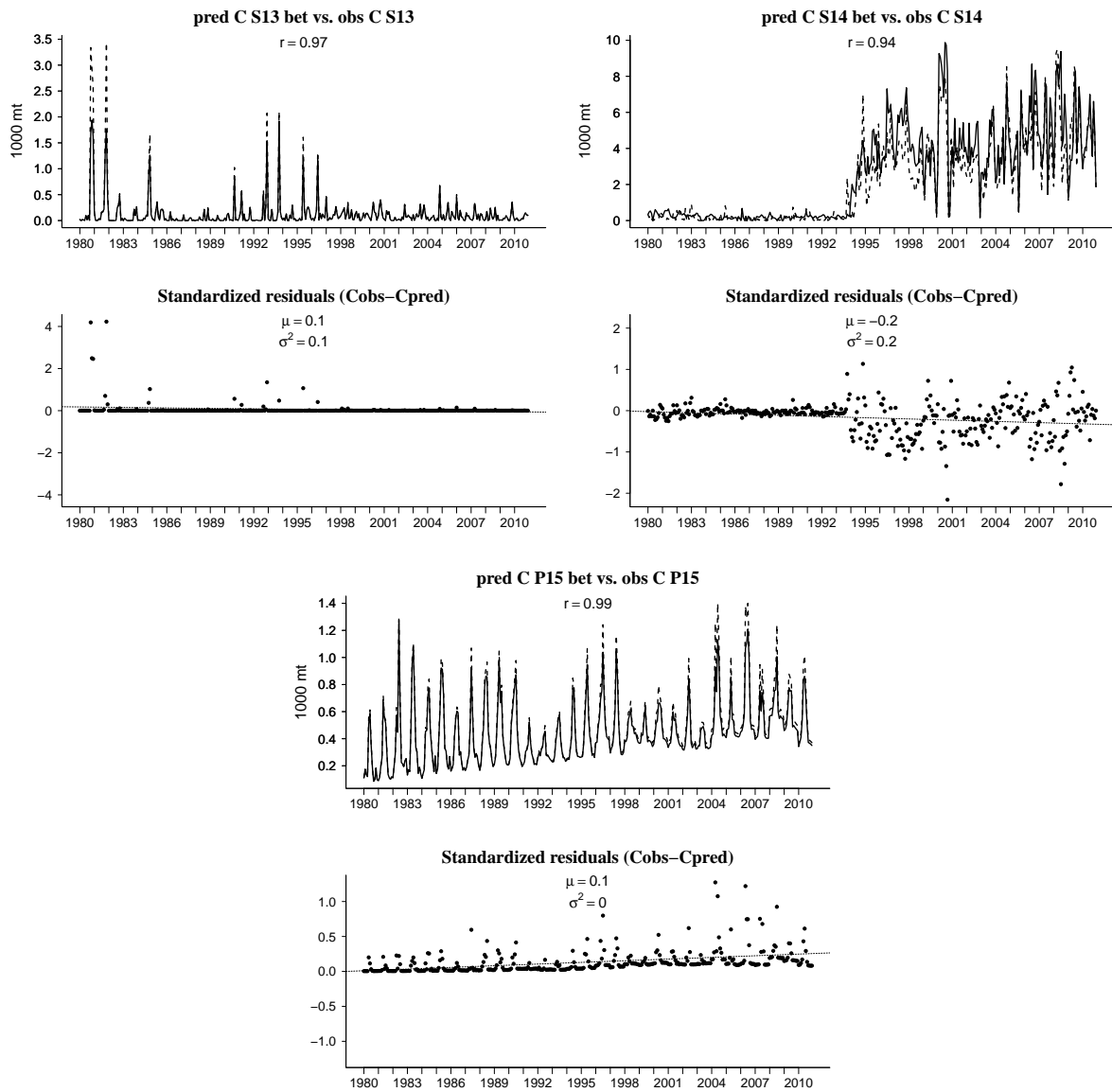


Figure A8: Monthly time series of observed and predicted catch by fishery (Continued)

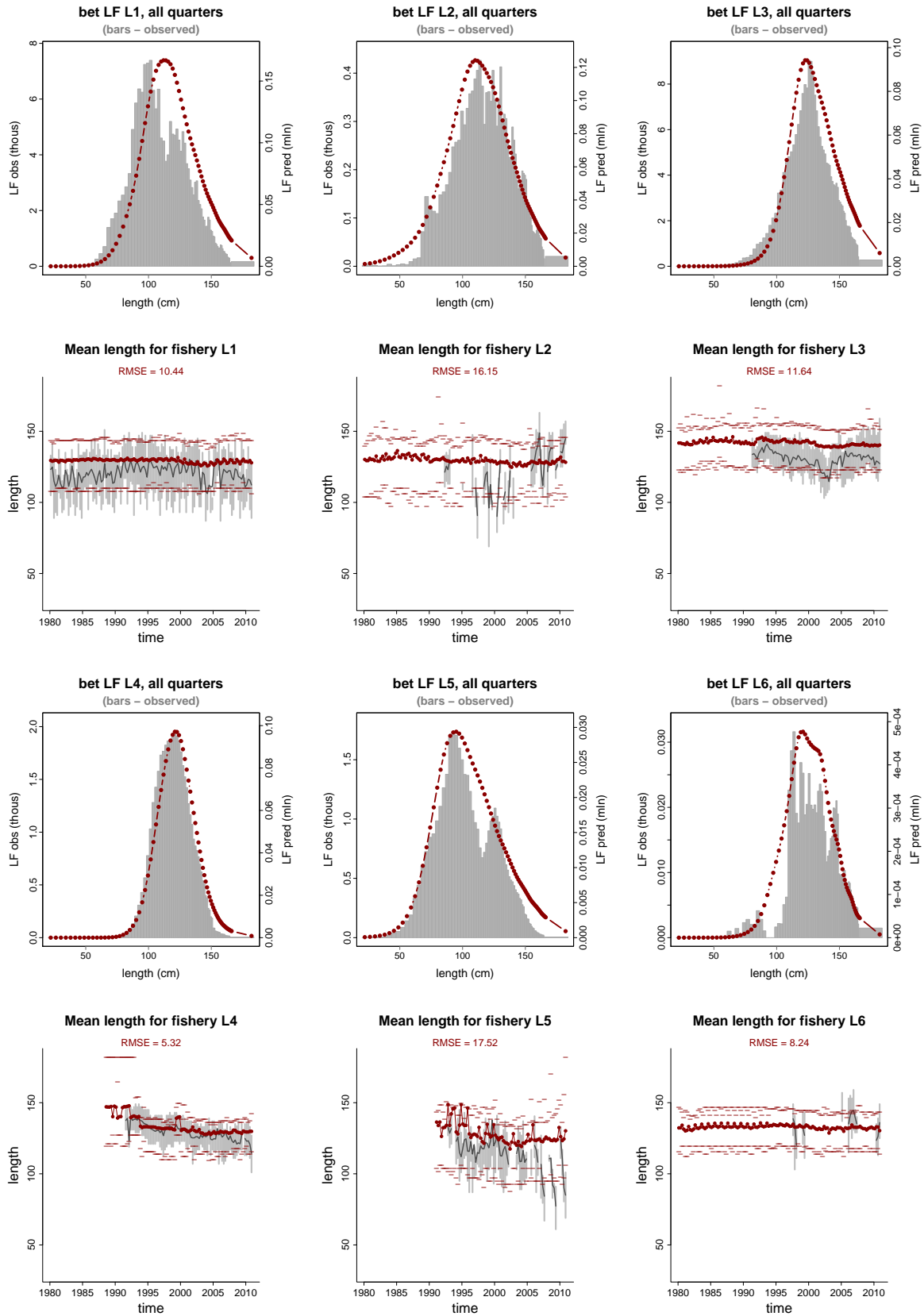


Figure A9: Observed (grey) and predicted (red) length frequencies distribution and mean length in catches.

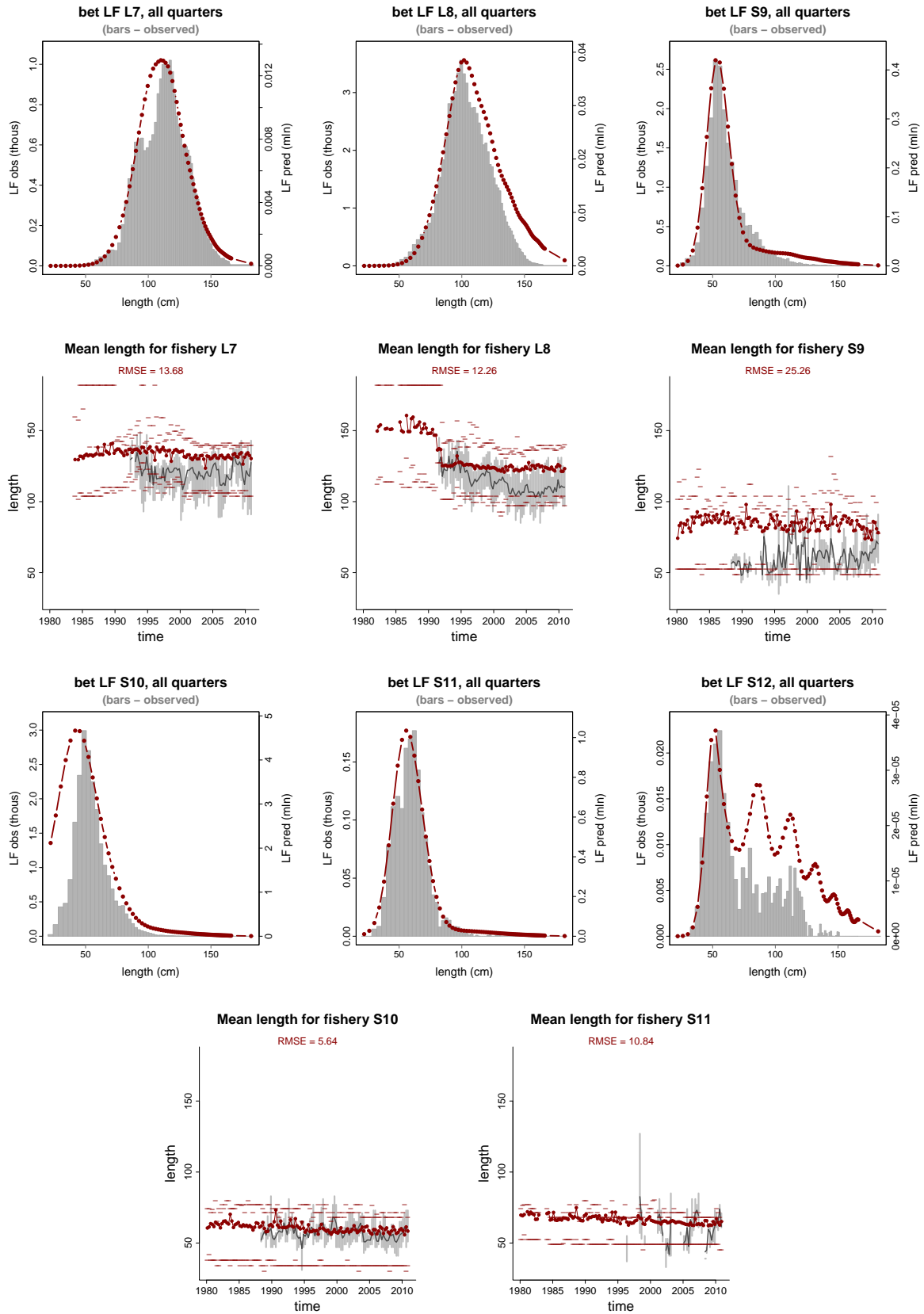


Figure A9: Fit for the length frequencies data. Continued.

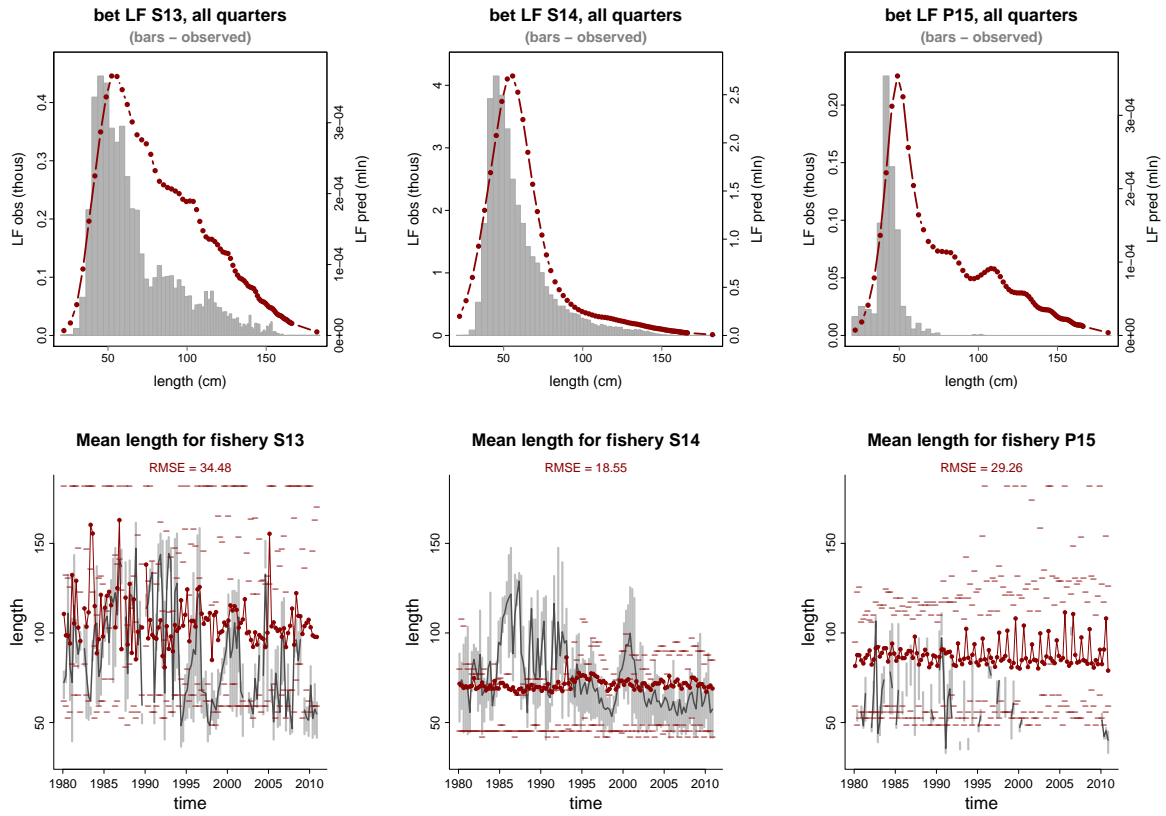


Figure A9: Fit for the length frequencies data. Continued.

A.4 Fit to the tagging data

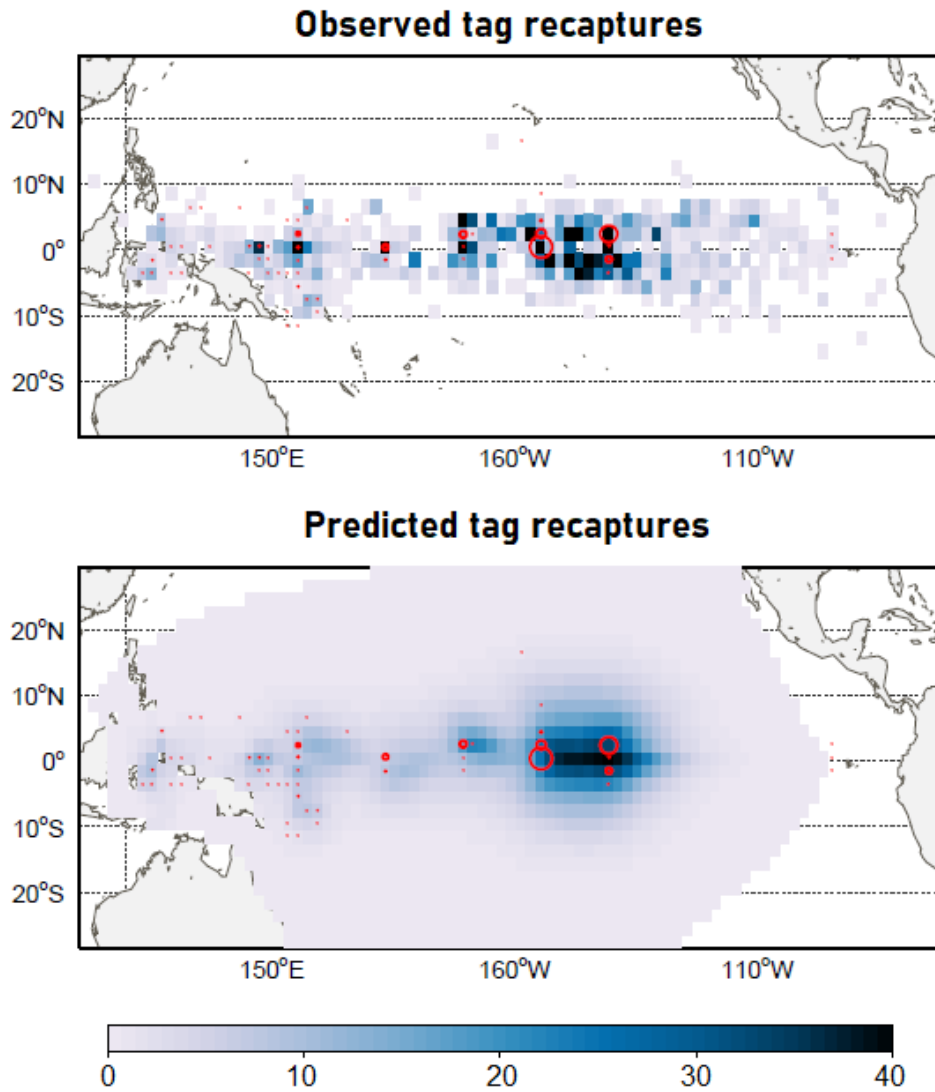


Figure A10: Number of bigeye tuna recaptured between July 2007 to December 2010 (top). Distribution of tag recaptures predicted for the same time period by current reference model with MLE parameters, estimated from fisheries data only (bottom).