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PROJECT 62: SEAPODYM APPLICATIONS IN WCPO – PROGRESS REPORT

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1 Introduction

SEAPODYM is a model developed for investigating spatial tuna population dynamics, under the influence of both fishing and environmental effects. The model SEAPODYM is based on advection-diffusion-reaction equations. The main features of this model are i) forcing by environmental data (temperature, currents, primary production and dissolved oxygen concentration), ii) prediction of both temporal and spatial distribution of mid-trophic (micronektonic tuna forage) functional groups, iii) prediction of both temporal and spatial distribution of age-structured predator (tuna) populations, iv) prediction of total catch and size frequency of catch by fleet when fishing data (catch and effort) are available, and v) parameter optimization based on fishing data assimilation techniques. In 2009, the fifth regular session of the Scientific Committee for the Western and Central Pacific Fisheries Commission endorsed, “Project 62: SEAPODYM simulation modeling”, to ensure continued development of the model and application to the WCPO. The following key tasks of “Project 62” are:

- Development of a Pacific swordfish application;
- Simulation experiments to improve the model calibration for tuna species, using higher resolutions of fishing data and oceanic environmental data;
- Model calibration for albacore with a basin-scale application including both north and south populations;
- Incorporation of conventional and archival tagging data in the model calibration; and
- Projection of impact of global climate change on distribution and abundance of tuna stocks

The project is expected to continue the collaboration between CLS, Space Oceanography Division and SPC-OFP. This report provides an overview of the main results achieved during the last 12 months under the following areas:

1. Model development
2. Reference fits for Pacific Tuna
3. Development of Swordfish application

2 Model development

Key model developments include a better definition of habitat indices, movements, and accessibility of tuna and tuna-like predators to different vertically migrant and non-migrant micronekton functional groups (Lehodey et al., 2008, Lehodey et al., 2010). In the current model version it is possible to configure a variable time step for the age structure to improve the estimation of the dynamics of younger cohorts using the length-frequencies data and to increase the step size for the older cohorts (characterized by slower growth) to reduce the computing time.

In addition to developments intended to improve the integration of various types of fishing data and manipulating the input-output files, the main purpose of adding new functionalities into the model was to facilitate the likelihood optimization and the selection of the best parameterization (cf. User’s manual) as well as analysis of the results. It is now possible to run a series of computer experiments for i) determining model sensitivity to variable parameters and, hence, investigate their observability, ii) to estimate observable parameters and their uncertainties, and iii) to justify the reliability of the solution found. In the following paragraphs a more detailed description of the new SEAPODYM features is shown.

Sensitivity analyses are a useful approach to reveal which parameters can be estimated from available data and which cannot. If model predictions are insensitive to some parameters, it is unlikely that they will be determined uniquely from available observations and should, therefore, be removed from the optimization (i.e., fixed arbitrarily). Two types of sensitivity analyses can be performed with the new version of SEAPODYM: “Sensitivity to parameters” and “Sensitivity to objective function”.

Identical Twin experiments consist in estimating parameters from artificial data series constructed from predictions given by the model. If optimization works well, then after perturbation of optimal parameters we should be able to retrieve them, because they determine known a-priori solution represented in the artificial data series.

Computing 2D likelihood profiles may be useful to explore the likelihood function visually, looking at different projections over the parameter space. It gives the clue what the sensitivity of a certain parameter is, whether the boundaries of the parameter should be modified, how the imposed penalty functions change the shape of the likelihood etc. Plotting the cost function over a couple of variable parameters is also a simple way to visualize the localization of the solution. For example, the likelihood function can have multiple minima and the likelihood projection plot can reveal the local minimum problem and help to navigate the minimization experiments further.

The Hessian matrix is evaluated at the minimum of the negative log-likelihood function. The diagonal elements of the inverse of the Hessian matrix provide estimates of the variance of the optimal parameters. From the variance, the standard deviation can be calculated for estimated parameters, allowing us to get the information about the uncertainty on these estimates. Correlation coefficients between pairs of estimated parameters can also be calculated from the error-covariance matrix. This is useful to identify problems in the optimization approach and eventually to define new experiments trying to estimate the correlated parameters separately.

New metrics are used to facilitate the analysis of numerous simulations produced for the parameter optimization, new metrics have been created. The overall spatial fit between predicted and observed catch (or CPUE) is provided by the standard R-squared goodness of fit. However, since in the optimization we fit thousands of spatially distributed data it can happen that two simulations result in nearly the same total likelihoods while different sets of parameters lead to different spatio-temporal solutions. It is then important to have a criterion that would allow choosing between two models relying on their spatial likelihoods. As such criterion we use generalized coefficient of determination.

Other technical developments of the code are being continuously implemented, among them are the development of the new NetCDF format for input-output files that include the definition of dimensions, attributes and the grouping of variables in the files, R routines to visualize, analyze the simulation results and to compare them with Multifan-CL regional predictions, GMB software updates to read and write land mask files in NetCDF format.

Model documentation has been updated with a new User’s Manual presented as an information paper during the scientific meeting of WCPFC in 2009, and a technical documentation of the code of the model generated using a source code documentation generator tool (DOxygen).

3 Reference fits for Pacific tuna

Reference fits were achieved for the 4 main tuna species skipjack, bigeye, yellowfin and south Pacific albacore, by running and analyzing a large number of optimization experiments based on available recent fishing data. Since SEAPODYM is an explicit spatial model the oceanic environmental variables and the fishing data (catch, effort and size frequencies) are spatially-disaggregated, typically at monthly, 1 to 5 degree square resolution for catch and effort, and quarterly, 5 to 20 degree square resolution or more for size frequency data.

To evaluate the capacity of the model to capture the essential features of the dynamic of the tuna species, we carried out hindcast simulations back to the early 1960s, i.e., the beginning of the industrial fishing, with the fixed “best-parameterization” achieved from optimization experiments and compared predicted catches conditioned on the observed fishing effort and observed catches. Predicted biomass trends are also compared to the estimates from the stock assessment model MULTIFAN-CL used for the tuna stock assessment carried out by the WCPFC.

The “optimal parameterization” obtained strongly depends on the amount and quality of fishing data as well as of the oceanic environment forcing fields. In both cases, we have been facing important difficulties. Though coupled physical-biogeochemical models predict relatively good basin scale variability of the environment, they only approximate the exact oceanic conditions, and each model configuration has its own strong and weak points. Fishing data have been provided by SPC, but there are confidential restrictions imposed by the fishing nations and we were not able to obtain a better resolution than 5 deg x 5 deg x month for longline and pole-and-line fishing data. Fisheries definition has been revised several times (and thus optimization experiments restarted) to adjust with emerging data issues.

3.1 Model configurations

For skipjack, yellowfin and bigeye, the model domain covers the entire Pacific basin at a spatial resolution of 2 deg x 2deg and a monthly time resolution. For south Pacific albacore a sub-domain was extracted to represent the south Pacific basin between 5°N and 55°S.

In addition to previous environmental forcing used for optimization experiments (here and after referred as ESSIC), two other configurations were used for this work. They are the predictions of the same physical (NEMO OGCM) and biogeochemical (PISCES) models, which used two different atmospheric reanalyses: NCEP and ERA40. The first NCEP-based reanalysis (Aumont et al. 2003, Gorgues et al. 2005, Bopp et al. 2005; Aumont and Bopp, 2006, visit also http://www.nemo-ocean.eu) provides 50-year record of global oceanographic variables: meridional and zonal velocities, temperatures, primary productivity and dissolved oxygen. The ERA40-based reanalysis (Uppala et al., 2005, visit http://www.ecmwf.int/research/era/do/get/era-40) covers the period from mid-1957 to 2001.

Both PISCES reanalyses predicted almost the same primary production in the sub-tropical to temperate regions (Fig. 1). However, in the equatorial region, though the variability is very similar, there is a discrepancy between the two simulations, ERA40-PISCES predicting higher primary production but with a decreasing trend over time. Conversely, there is a positive trend over time in the equatorial region for the ESSIC reanalysis, but here again the variability, essentially dominated by the El Niño Southern Oscillation (ENSO) is comparable.

All physical variables and dissolved oxygen were integrated over three vertical layers, defined through euphotic depth: epipelagic layer between 0 and one euphotic depth (Zeu), mesopelagic layer between 1 and 3Zeu and bathypelagic layer between 3Zeu and 1000m. Temperature fields showed a surprising large difference in the mesopelagic layer between ERA40 and NCEP forced reanalyses (Fig. 2), while the temperature distribution is very similar in the surface and deep layers. This difference is due to the predicted intensity of equatorial upwelling and thus the depth of the euphotic zone used to define the boundaries of vertical layers.

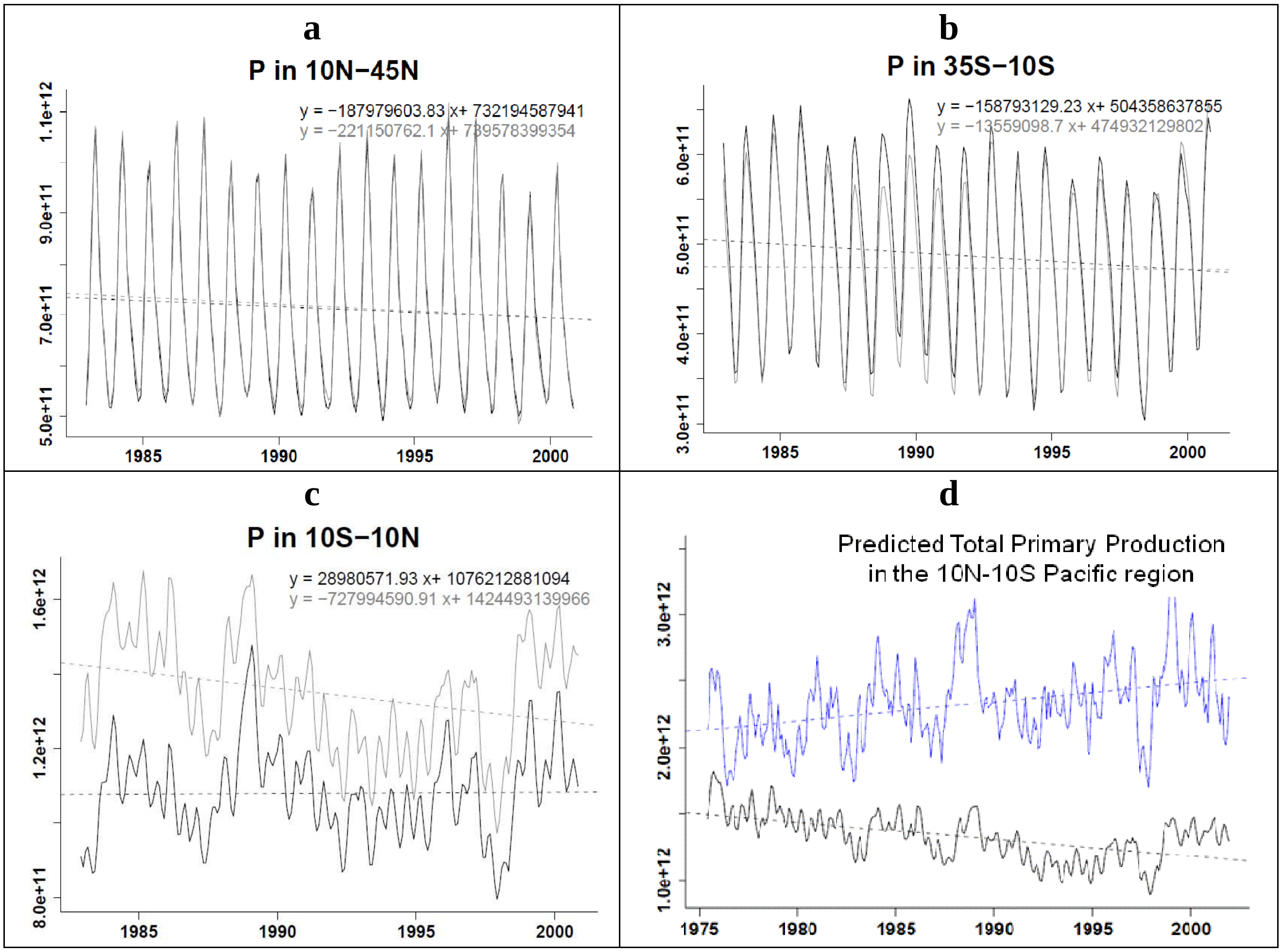
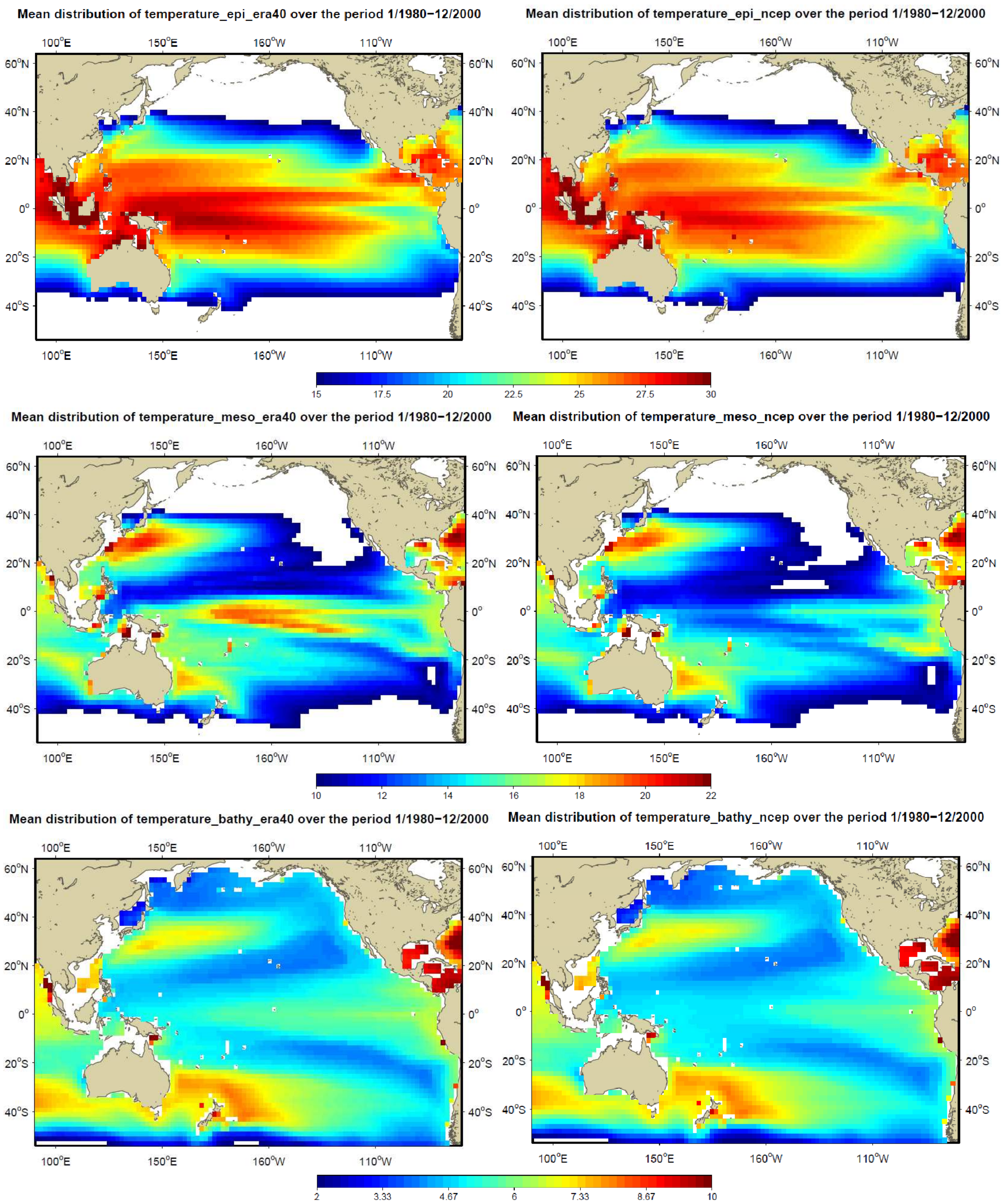


Figure 1. Total primary production predicted in the reanalyses with different model configurations. **a**) from NCEP-PISCES and ERA40 PISCES in the 10°N-45°N geographical area; **b**) from NCEP-PISCES and ERA40 PISCES in the 10°S-25°S geographical area; **c**) from NCEP-PISCES and ERA40 PISCES in the 10°N-10°S geographical area; **d**) from NCEP-PISCES and ESSIC (in blue) in the 10°N-10°S geographical area.



Mean distribution of temperature_epi_era40 over the period 1/1980−12/2000

Mean distribution of temperature_epi_ncep over the period 1/1980−12/2000

Mean distribution of temperature_meso_era40 over the period 1/1980−12/2000

Mean distribution of temperature_meso_ncep over the period 1/1980−12/2000

Mean distribution of temperature_bathy_era40 over the period 1/1980−12/2000

Mean distribution of temperature_bathy_ncep over the period 1/1980−12/2000

Figure 2: Average temperature predicted in reanalyses forced by ERA40 (left) and NCEP (right) in the three layers defined in SEAPODYM; epipelagic, mesopelagic, and bathypelagic.

These differences have consequences on the tuna simulations either directly -- e.g., thermal habitat is a key component of both feeding and spawning habitats, and the spawning index uses primary production as a proxy for the prey of tuna larvae – or indirectly, through the simulation of micronekton functional groups and thus the feeding habitat, movement and natural mortality of tuna. Nevertheless, it should be noted that as far as possible we have introduced relative mechanisms in the model to avoid absolute parameterization which is extremely difficult or even impossible in some cases. Thus, the impact due to the differences observed between the model configurations can be partly compensated, especially since the reanalyses present very close variability.

It should be noted that due to the coarse resolution, these simulations do not reproduce mesoscale activity and underestimate the intensity of oceanic circulation in the most dynamical oceanic areas, e.g., Kuroshio, East equatorial Pacific.

3.2 Fishing data

The definition of fisheries has been revised several times. Here we present the results with the latest definition and the best available fishing data set provided by SPC and IATTC for the Eastern Pacific Ocean (see Appendix 1). The total amount of fishing data used for the model calibration is very high (Table 1), but the optimization experiments have shown a strong sensitivity to limited but obviously aberrant fishing data. The lack of convergence in the optimization process frequently allowed quick identification of problems in the fishing dataset, e.g., obvious mistakes in latitude or longitude, switch between catch and effort, aberrant effort or catch, catch with zero effort… etc. It has also been necessary to exclude from the optimization procedure some fisheries, either because of their lack of accuracy (e.g., Philippine and Indonesia fisheries) or because of gradual change in the fishing strategy and target species (e.g., Japanese longline in the case of albacore). However, the catch is always taken into account for the calculation of the fishing mortality.

Table 1 – Ocean model configurations used for optimization experiments with four Pacific tuna species in the final experiments

	SKJ	YFT	BET	SP Alb.
Periods used for optimization	1980-2004 1981-2001	1983-2004	1984-2001	(1) 1981-2001
Fishing events used in optimization (catch-effort / size frequencies)	174,221 / 1,571 61,926 / 16/135	352,160 / 9,534	362,424 / 1,492	(1) 23,751 / 4,291 (2) 39,601 / 3,475
Hindcast and validation	1970-2004		1978-2004	1971-2003
Nb fisheries (cf. appendix 2)	WCPO: 4 EPO: 2 PS	WCPO: 15 EPO: 3 PS & 2 LL (MFCL)	26 (MFCL)	12 LL

3.3 Skipjack

3.3.1 New optimization experiments

Optimization experiments with NCEP and ERA40 forcing allowed substantial improvement in the SEAPODYM fit to observed fisheries data in the Eastern Pacific Ocean and sub-tropical regions. This is due to: 1) enhanced definition of vertical layers using euphotic depth; 2) a better fishing dataset for this region, including fine-resolution length-frequencies data. The model has still some problems to fit the CPUE in the equatorial eastern Pacific, the Kuroshio region and to a less extend in the western equatorial fishing ground of Bismarck Sea and Solomon Sea (Fig. 3). Skipjack is not the target species of the purse seine fisheries in the eastern Pacific; this may lead to a biased relationship between abundance and catch rates in this region and explain the lack of fit between predicted and observed CPUE. A too coarse resolution and underestimated primary production is likely the reason for the poor CPUE fit in the other listed regions.

The model simulations confirmed previous results on the strong influence of ENSO events. There is a clear enhancement of spawning and larvae survival conditions during El Niño periods all over the equatorial Pacific (Fig. 4). Conversely during la Niña events, only the western central pacific is favorable. The result is a higher recruitment in the following cohorts that is propagated until in the oldest (4 years) adult cohorts. The propagation of higher recruitment due to the major El Niño events in 1982-83, 1986-87, 1991-92 and 1997-98 is visible on the estimated biomass time series (Fig. 5).

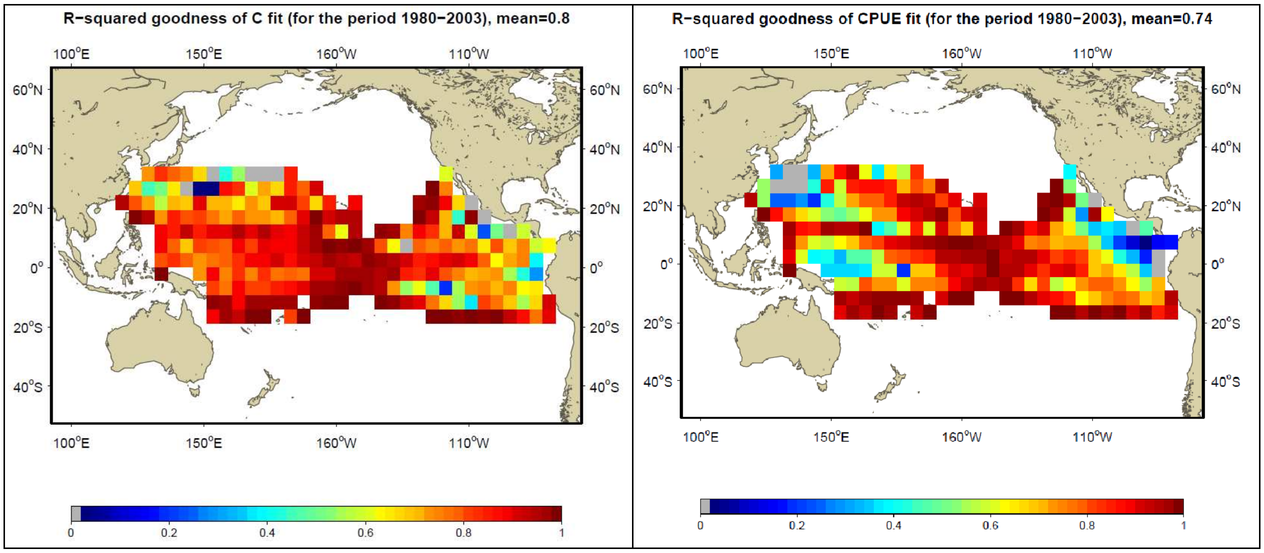
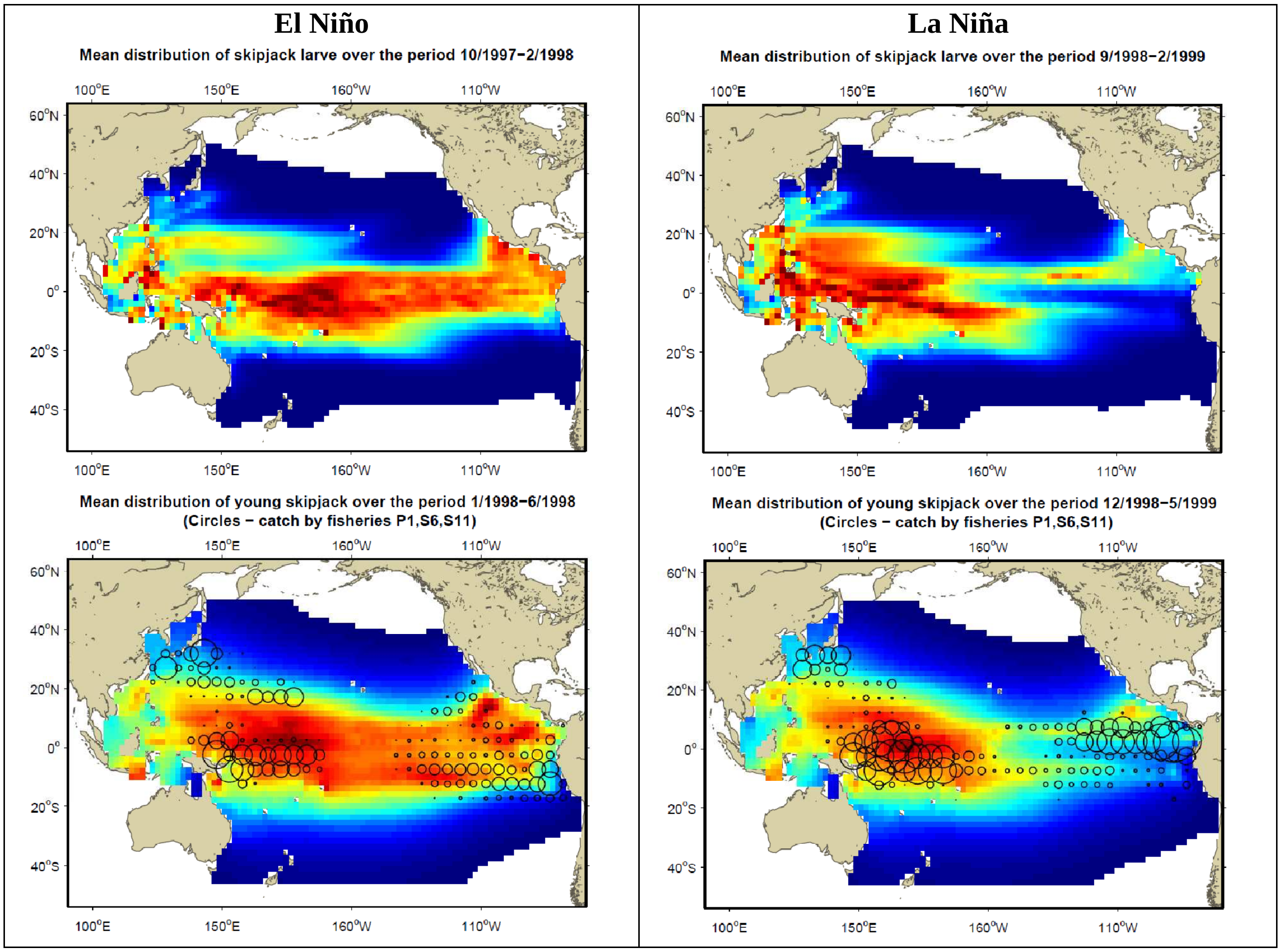


Figure 3. Spatial fit to observed catch (left) and cpue (right) of skipjack with the NCEP-ORCA2-PISCES configuration for all fisheries over the entire time series used for optimization.



El Niño

Mean distribution of skipjack larve over the period 10/1997−2/1998

Mean distribution of young skipjack over the period 1/1998−6/1998 (Circles − catch by fisheries P1,S6,S11)

La Niña

Mean distribution of skipjack larve over the period 9/1998−2/1999

Mean distribution of young skipjack over the period 12/1998−5/1999 (Circles − catch by fisheries P1,S6,S11)

Figure 4. Impact of ENSO on Pacific skipjack. Predicted distribution of larvae density during El Niño and La Niña phases and following recruitment in the young cohorts with observed catch superimposed.

3.3.2 Comparison with MULTIFAN-CL

The range of variability associated to ENSO is lower than the variability predicted by MULTIFAN-CL (Fig. 5). There are at least two potential explanations:

- Environmental reanalyses from coupled physical- biogeochemical model at coarse resolution are usually underestimating the variability. SEAPODYM simulations at coarse resolution tend to reinforce this effect by smoothing the distribution of fish to increase the fit with fishing data.
- Alternatively, MULTIFAN-CL may overestimate recruitment variability, especially because the structure of the model cannot account for interannual variability in the transfer of biomass between the large regions used, particularly regions 5 and 6.

Biomass estimates are also higher with SEAPODYM than with MULTIFAN-CL (Fig. 5). Here also there are two possible reasons:

- The coarse resolution of both the SEAPODYM model configuration and the fishing dataset is potentially leading to overestimated biomass as the model tend to increase diffusion and biomass to fit the catch data, while in reality, catch can be highly concentrated due to mesoscale activity, not represented in these simulations.

- However, it is also possible that MULTIFAN-CL underestimates biomass. Because the estimation is based on catch and effort aggregated by large regions, if the effort data covers only a fraction of these region it may not provide sufficient information for a good estimate over all the area. Thus the estimate would be representative of such fraction of the region only and thus potentially underestimated.

To test this latter hypothesis, we have extracted biomass predicted with SEAPODYM in each MULTIFAN-CL sub-region, but not accounting for biomass in cells where the number of fishing events (i.e., biomass sampling) was very low. Practically, we built up a spatial mask using a minimum threshold value of "representative" fishing events (Fig. 6). This threshold was set to 5% of the total number of time steps in the time series used for optimization. In other terms, to be accounted for, a cell in the domain needs to have been fished at least 5% of the historical fishing data time series used in MULTIFAN-CL application.

As a result, the new estimates are much closer in absolute values to the MULTIFAN-CL estimates, and indeed they are now lower (Fig. 7). However, the range of variability is still much larger in MULTIFAN-CL estimate.

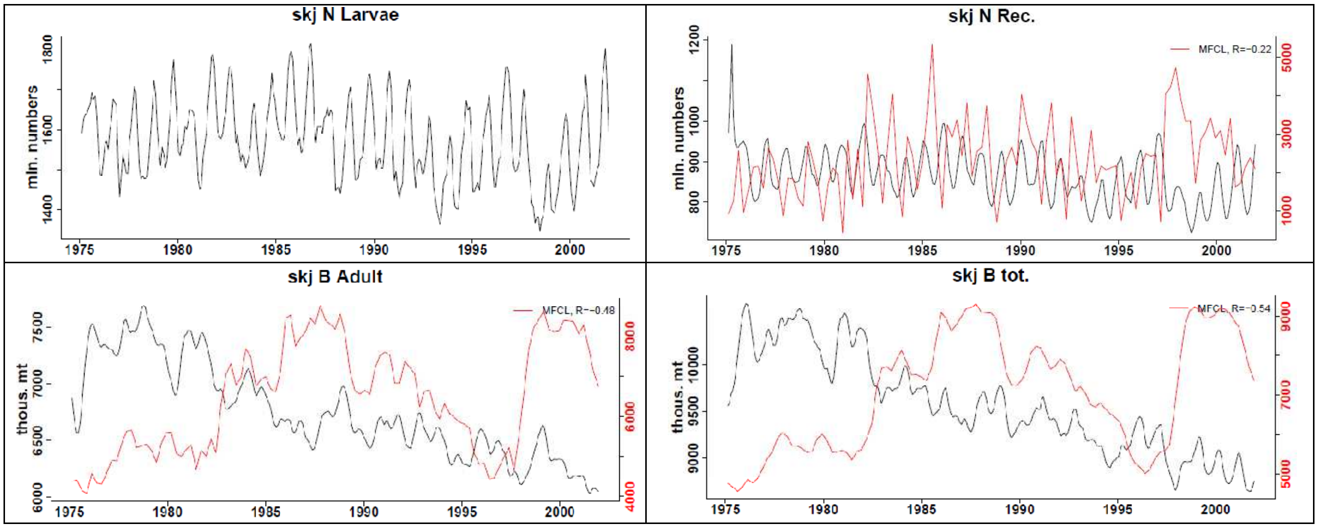


Figure 5. Comparison between SEAPODYM (black; NCEP configuration) and MULTIFAN-CL (red) estimates of recruitment, adult and total biomass in the WCPO (MFCL regions 1 to 6).

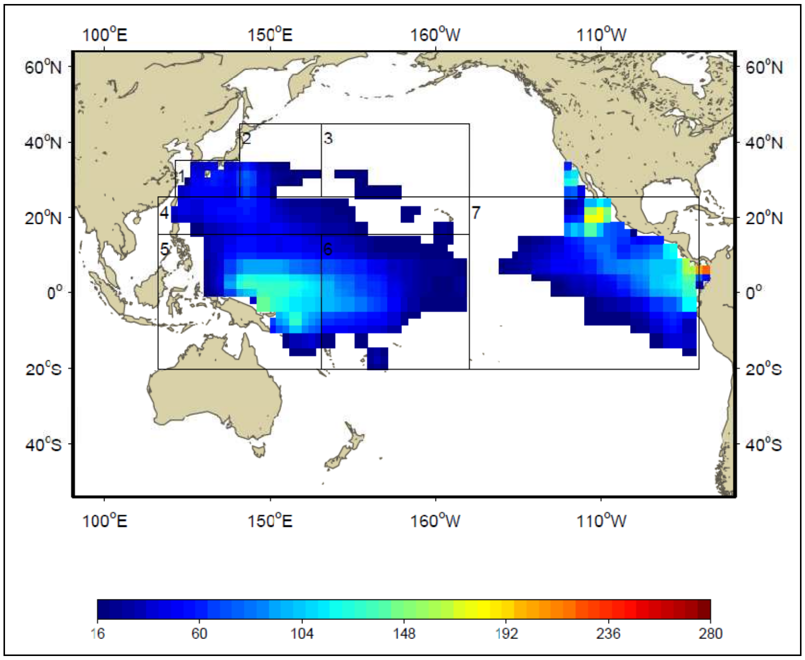


Figure 6. Distribution of total effort for all skipjack fisheries and large geographical regions used by MULTIFAN-CL.

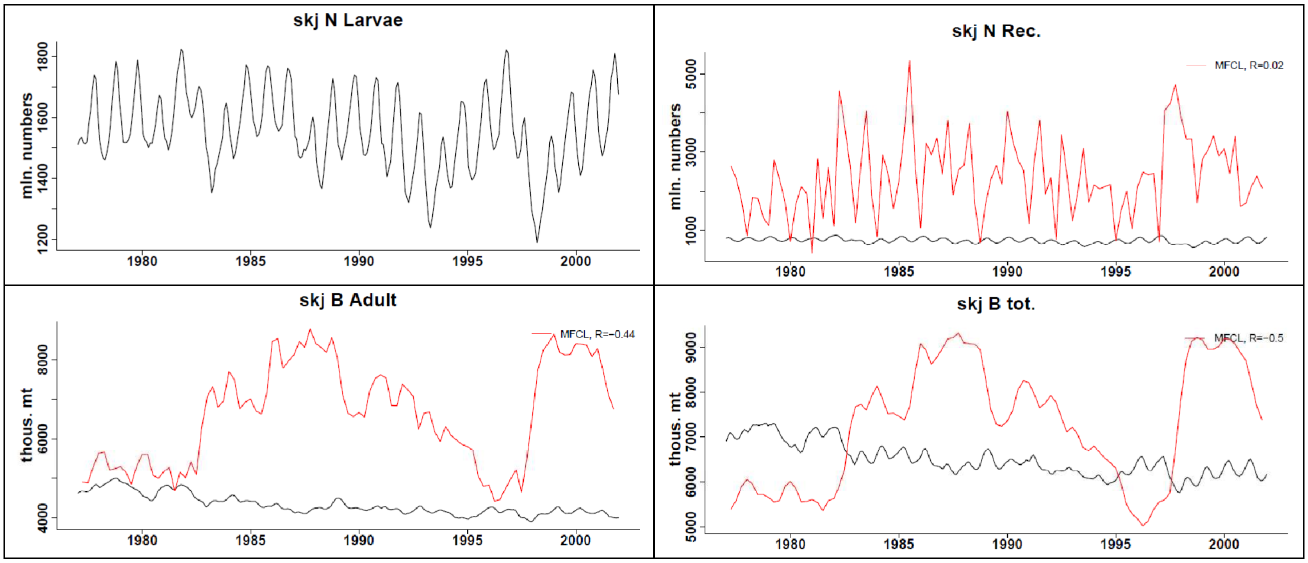


Figure 7. Comparison between SEAPODYM (black; NCEP configuration) and MULTIFAN-CL (red) estimates of recruitment, adult and total biomass in the WCPO (regions 1 to 6) as in Fig 5, but using data mask to extract seapodym biomass.

3.4 Bigeye

3.4.1 New optimization experiments

Optimization experiments with NCEP and ERA40 forcing gave similar general spatial distribution of biomass but it differs from previous ESSIC spatio-temporal solution by strongly increasing the contrast between high level of biomass in the equatorial region and the subtropical region (Fig. 8).

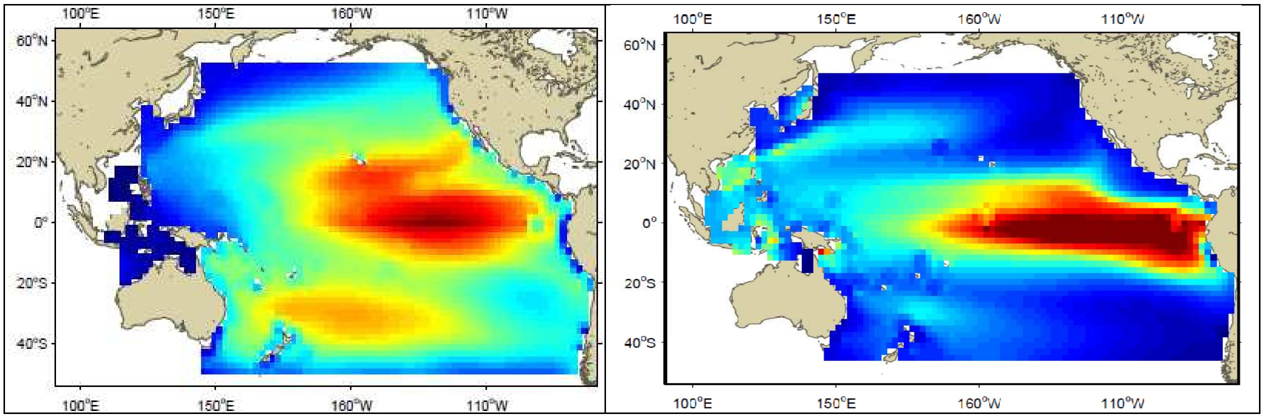


Fig. 8. Mean distribution of bigeye for the optimization period 01/1984-12/2003 predicted under ESSIC (left) and ERA40 (right) physical-biogeochemical forcing.

Biomass levels and trends predicted with NCEP and ERA40 experiments are very similar (Fig. 9), with a slightly lower adult biomass predicted by the NCEP configuration due to higher estimated natural mortality. However they are both largely higher than the first estimates based on ESSIC configuration and show quite different trends over the 20-year period used for optimization (1980-2000). It should be noted that between these two series of experiments the fishing dataset also has changed including more fishing data and an enhanced definition of fisheries in the last experiments.

The biomass is higher also in the eastern equatorial region with NCEP-ERA40 configuration, likely due to the enhanced definition of vertical layers using euphotic depth and the use of prognostic dissolved oxygen fields instead of a climatology used with ESSIC.

The overall fit to fishing data is good and improved compared to the previous ESSIC-based experiment (Fig. 10). There is a small advantage in term of likelihood for the NCEP experiment compared to ERA40. This latter configuration gave a better fit to the fishing data in the eastern Pacific but conversely NCEP experiment was better in the WCPO. A slight linear increase in catchability was allowed for purse seine fisheries, allowing a good match between predicted and observed catch series without trend over time in the residuals. While this linear trend was not used for longline fisheries, the residuals suggest that it would be necessary to include one for the fishery L2, i.e., the Chinese-Taiwanese "shallow-night setting" longline fishery.

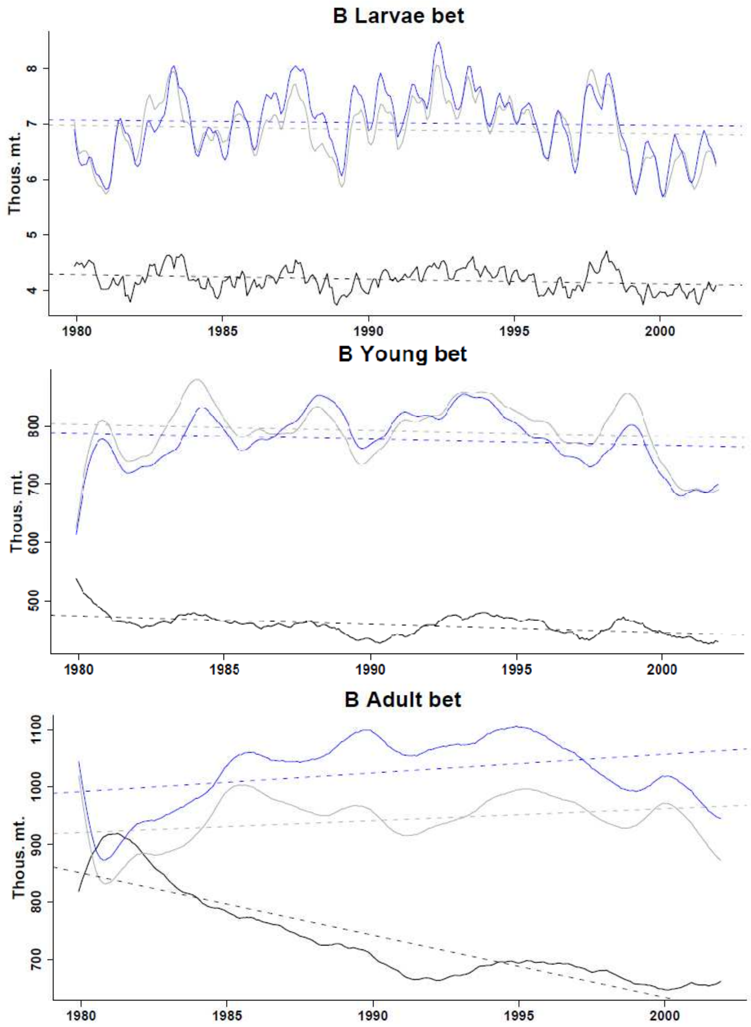


Figure 9. Biomass of juvenile, young immature and adult bigeye predicted by the model under three physical forcings: ESSIC (black curve), NCEP (grey curve) and ERA40 (grey curve) over the optimization period 1980-2002.

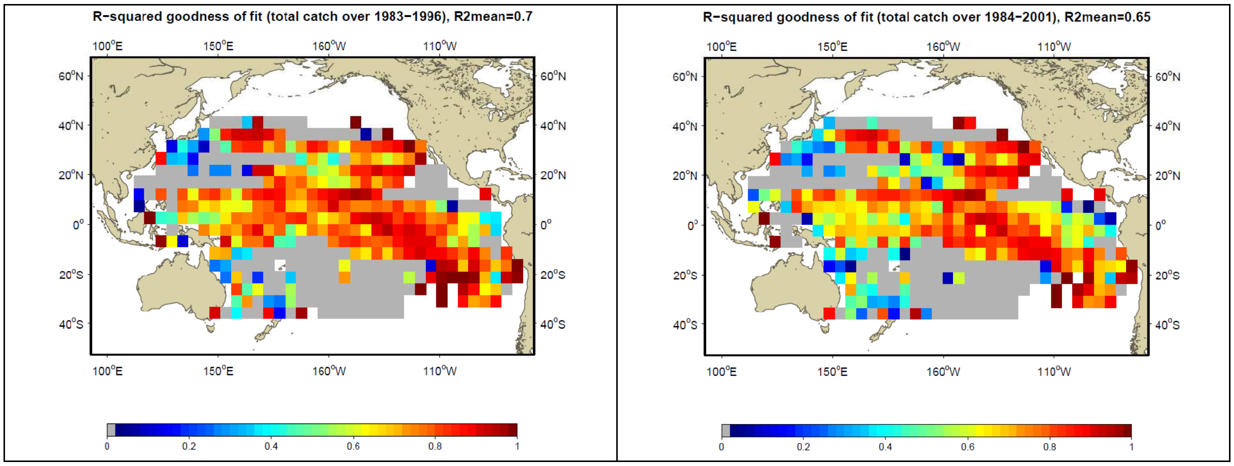


Figure 10. Spatial fit to observed catch of bigeye with the NCEP (left) and ERA40 (right) configuration for all fisheries over the entire time series used for optimization.

As in previous simulation with ESSIC forcing, these new experiments predicted a strong impact of ENSO events on the larvae recruitment of the species. There is higher recruitment during El Niño events with an extension of the spawning grounds through all the equatorial Pacific and much favourable zones in the eastern equatorial Pacific. Alternatively during La Niña events, the spawning ground is shifted in the western central equatorial Pacific. The impact is propagated in the older cohorts during the following months (Fig. 11). Given the relatively long life span (>12 yr) of the species, the population can integrate several ENSO events and thus the signal becomes less clear in the adult population.

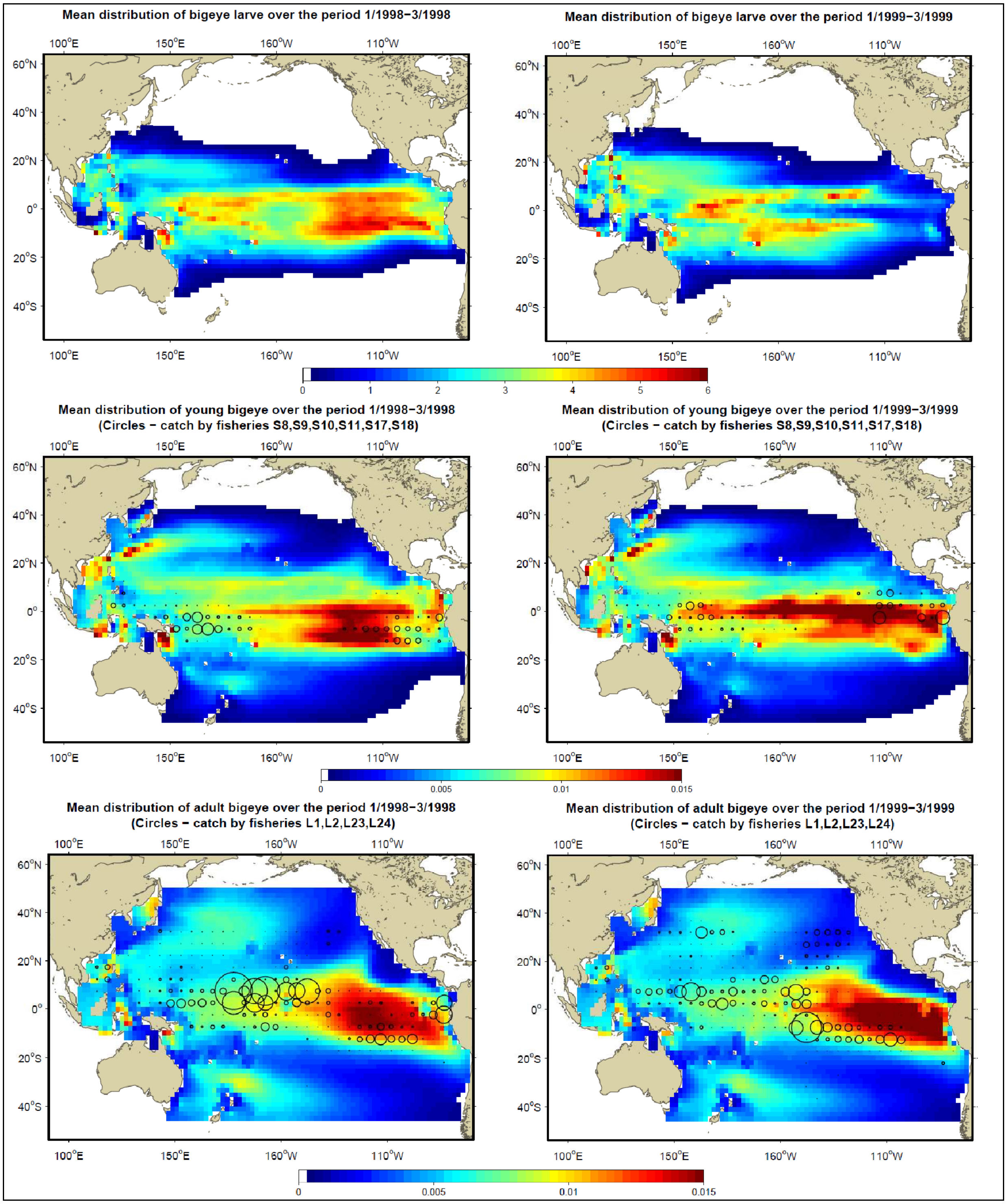


Fig 11. Biomass distribution of bigeye tuna by life stage during El Niño (left) and La Niña (right). From top to bottom: mean distributions of larvae; mean biomass distributions of young stage (4 to 26 months) with observed purse seine catch proportional to the size of circles; mean biomass distributions of adult stage (older than 26 months) with observed longline catch proportional to the size of circles.

3.4.2 Comparison with MULTIFAN-CL

Skipping the first five years of the simulations that are strongly influenced by the initial conditions, we compared the new biomass estimates with MULTIFAN-CL results for the whole Pacific basin (regions 1 to 9). During this period of time the biomass estimated with SEAPODYM is predicted to be 40-70% higher than the MULTIFAN-CL estimate (Fig. 12).

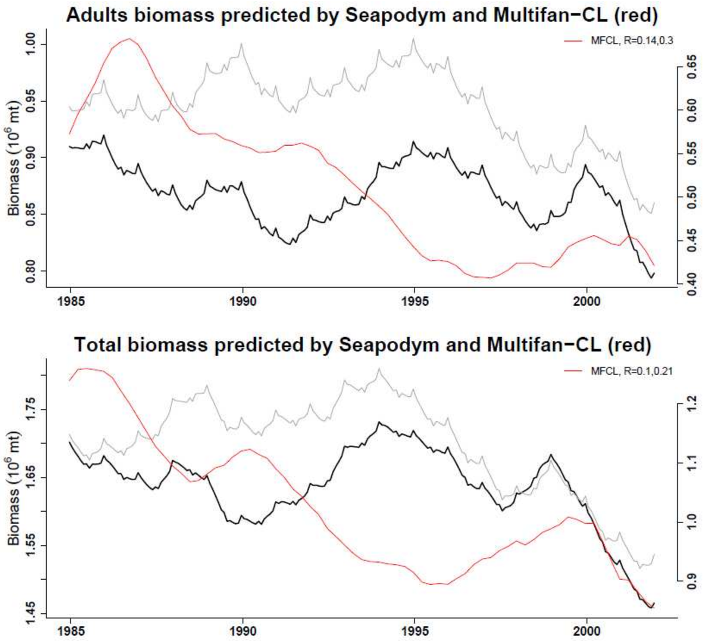


Figure 12. Comparison of predicted biomass for adult and total biomass of bigeye tuna between SEAPODYM (NCEP and ERA40) and MULTIFAN-CL for the optimization period (1985-2004).

3.5 Yellowfin

The first optimization experiments have shown high sensitivity to the oceanic environment predicted by coupled physical-biogeochemical models (Lehodey and Senina, 2009). We conducted a new series of experiments after a revision of the fishing data set including an enhanced fishing dataset in the EPO with the size frequency data that are essential to estimate the selectivity functions. Nevertheless, the results remain unsatisfactory as shown by a relatively low fit to fishing data (Fig. 14) and inconsistency in several parameter estimates between the different configurations.

With ERA40 forcing, it was not possible to obtain convergence during the optimization. With NCEP forcing (Fig. 15), the model was able to converge when the estimation was carried out by phases. In the first phase the biological parameters were constant (best guess values) and only the catchability and selectivity parameters were estimated. In a second phase, the temperature and oxygen parameters were released and the model converged but we obtained two quite different solutions. One gave optimal temperature of 26.76°C for spawning and 13.15°C for oldest cohort habitat, the other 28.97°C and 10°C (i.e. the parameter lower boundary). In both case it was not possible to estimate movement parameters: the diffusion rate tend to increase and directed velocity always stuck on the lower boundary leading to the spatial distributions of the cohorts defined mainly by the environmental conditions and recruitment.

Parameterization experiments still need to be continued with a careful check of fishing data but also by testing other environmental forcing data sets and particularly those that are based on data assimilation and consequently predicting more realistic environment. The use of tagging data, both conventional and electronic should also help to estimate most plausible habitat and movement parameters. Ideally they should be included directly in the data assimilation framework.

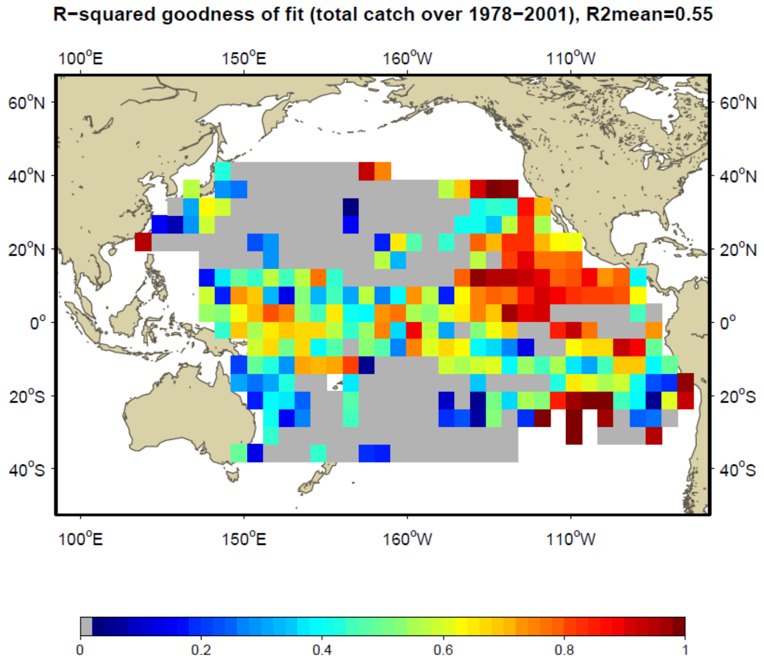
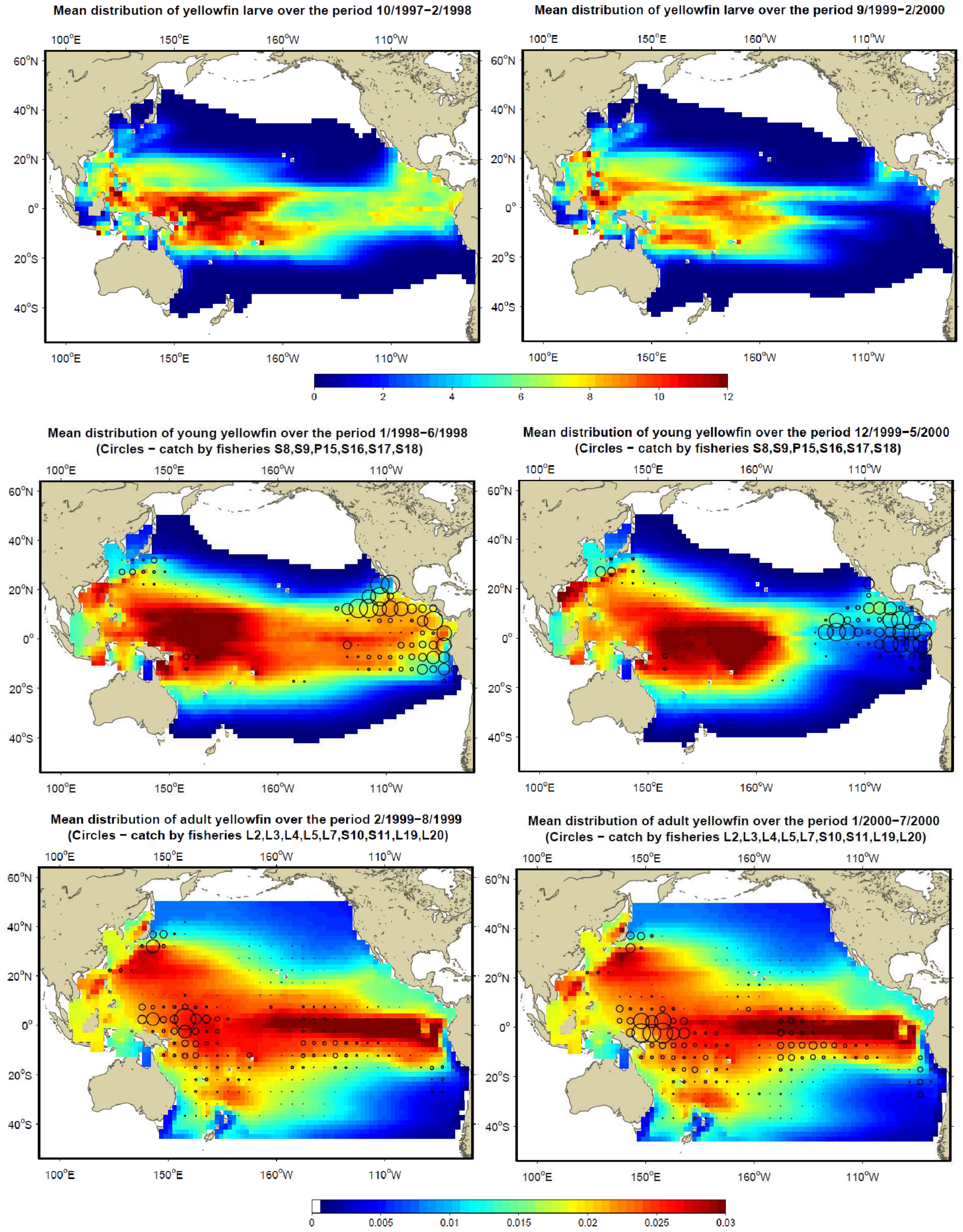


Figure 14. Spatial fit to observed catch of yellowfin with the NCEP configuration for all fisheries over the entire time series used for optimization.


Mean distribution of yellowfin larve over the period 10/1997−2/1998

Mean distribution of yellowfin larve over the period 9/1999−2/2000

Mean distribution of young yellowfin over the period 1/1998−6/1998
(Circles − catch by fisheries S8,S9,P15,S16,S17,S18)

Mean distribution of young yellowfin over the period 12/1999−5/2000
(Circles − catch by fisheries S8,S9,P15,S16,S17,S18)

Mean distribution of adult yellowfin over the period 2/1999−8/1999
(Circles − catch by fisheries L2,L3,L4,L5,L7,S10,S11,L19,L20)

Mean distribution of adult yellowfin over the period 1/2000−7/2000
(Circles − catch by fisheries L2,L3,L4,L5,L7,S10,S11,L19,L20)

Figure 15. Distributions of yellowfin biomass by life stage (larvae, young, adult) predicted under NCEP physical-biogeochemical forcing.

3.6 South Pacific Albacore

3.6.1 Optimization experiment with ERA40 and NCEP configurations

Due to the long lifespan of albacore and the relatively short time series used, as well as limited information (fishing data) for juvenile fish, the model calibration for this species is particularly sensitive to initial conditions. We therefore conducted a preliminary optimization experiment for the period 1958-1978 to define initial condition used to run the 1980-2001 experiment. In both configurations the model can converge with a reasonable fit to fishing data. The redefinition of Japanese longline fishery in the ERA40 configuration allowed a substantial improvement in the likelihood and the fit to both catch and size frequency, as albacore catch in the tropical region (L12) is characterized by a larger size than in the temperate fishery (L1).

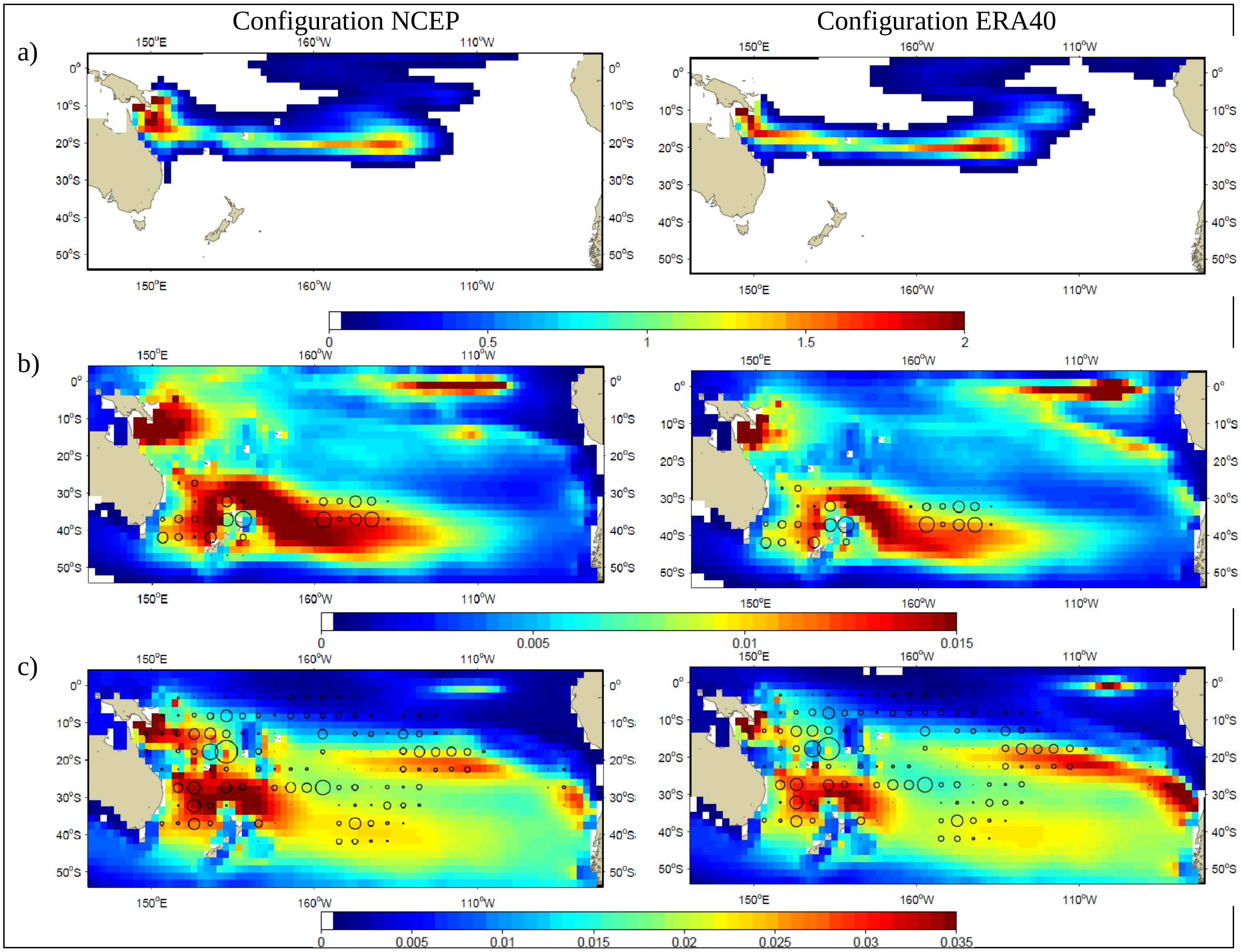


Figure 16. Predicted biomass distributions of albacore tuna: a) mean biomass of albacore larvae over 09/1999 – 02/2000; b) mean biomass of young (immature) tunas during months 12/1999−05/2000; c) mean biomass of adult albacore over the period 01/2000-07/2000.

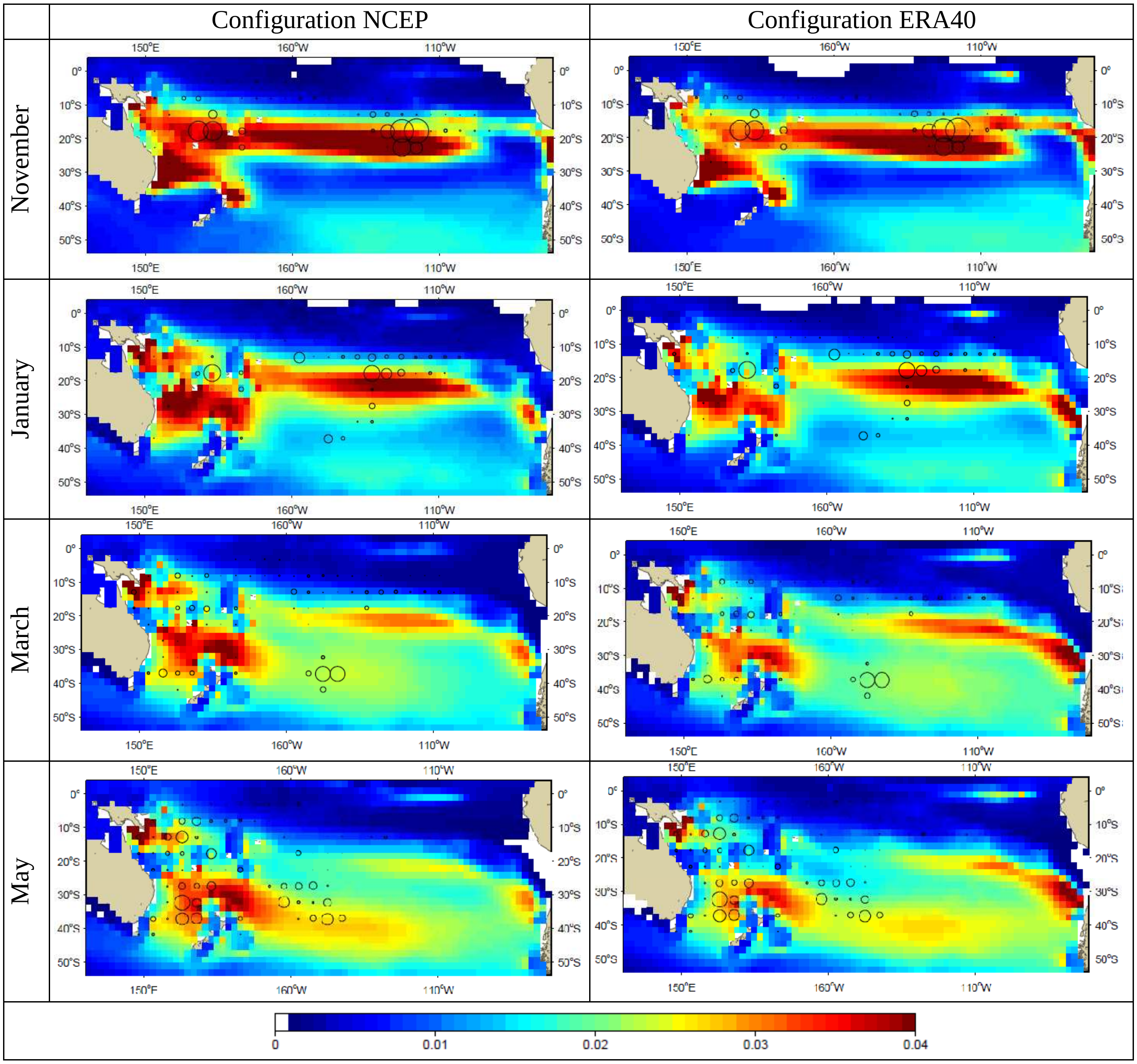


Figure 17. Characteristic seasonal migrations of adult albacore predicted with NCEP-ORCA2-PISCES and ERA40-ORCA2-PISCES configurations. Maps show adult biomass (in g m-2) of albacore in 1999, i.e., the last year taken for the optimization experiments, with superimposed observed catch proportional to circles.

To test the impact of initial conditions, we ran a new series of optimization experiments with initial conditions forced to be at the same level of biomass estimated by MULTIFAN-CL. In that case the results of both models are very close both considering the range of biomass and its temporal trend (Fig. 18).

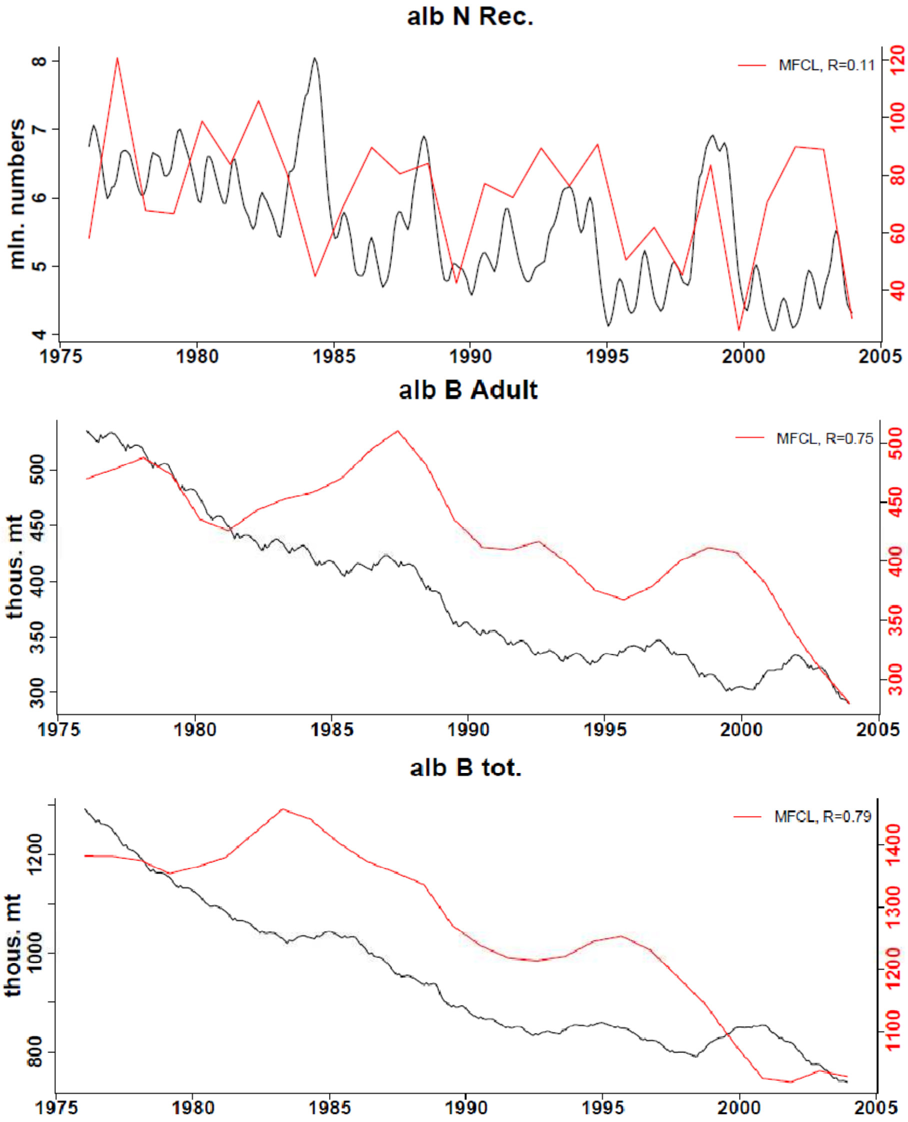


Figure 18. Comparison between estimates from SEAPODYM with NCEP (black) model and MULTIFAN-CL (red) for adult and total biomass of albacore (in metric tonnes).

3.6.2 Results with SODA and Satellite-derived primary production

As a first step to move to a more realistic spatial prediction of albacore population dynamics, we produced a new environmental forcing data set using the physical fields of temperature and currents provided by the SODA (Simple Ocean Data Assimilation) reanalysis (Carton et al., 2000) and primary production derived from satellite data. The resolution was degraded at 1° x month for optimization. Satellite ocean color data are available only since end of 1997, thus the time series used was relatively short (Jan 1998- Dec 2007) and even not covering a life span of the species. In this case the influence of initial conditions is of primordial importance. We constructed the initial conditions of the albacore population from the results obtained with the ERA40/NCEP simulations and used the corresponding parameterization as initial guess values of the parameters.

The model converged with a good fit to the fishing data (Fig. 19) but with optimal temperature for spawning reaching the fixed lower boundary (24.5°C). However at the difference of the previous simulation, it was possible to get an estimate of the optimal habitat temperature for the oldest cohort (7.9°C). The movement parameters were also estimated with relatively high advection values compared to other species. This latter result appears reasonable given that this species seems to have the most marked seasonal migration between feeding grounds in the subtropical convergence zone in the south and spawning ground in the sub-equatorial region. The biomass estimates with SEAPODYM and this new configuration were in the same range than biomass estimates from MULTIFAN-CL (Fig. 20).

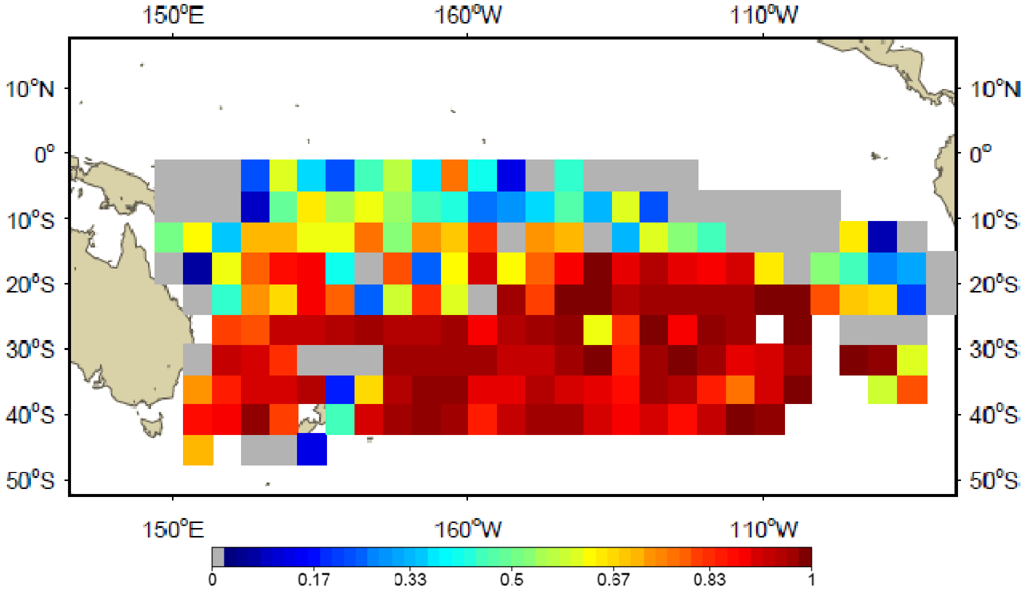


Figure 19. Spatial fit to observed catch of albacore catch for all data 1998-2007 using SEAPODYM with SODA configuration.

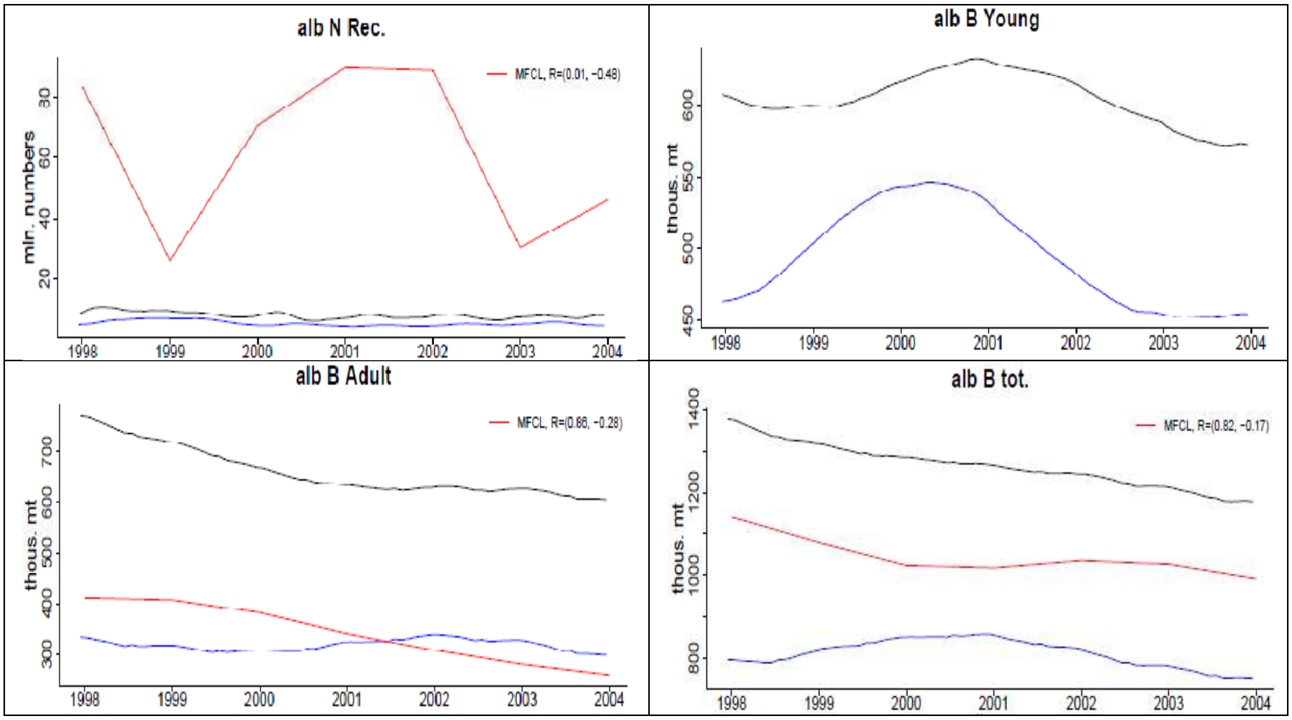


Figure 20. Comparison between estimates from SEAPODYM with SODA (black) and NCEP (blue) model configurations and MULTIFAN-CL (red) for recruits, young, adult and total biomass of albacore (in metric tonnes).

4 Development of Swordfish application

An application of the model SEAPODYM to the Pacific swordfish population(s) has commenced with a focus on the north Pacific stock exploited by the Hawaiian longline fishery. The model is tested and optimized with swordfish catch and effort. Two environmental configurations were tested for the swordfish model: NCEP-ESSIC and NCEP-ORCA2-PISCES. The NCEP-ESSIC configuration was abandoned due to known biases in subtropical and temperate areas which constitute important habitat for swordfish. The second configuration was also preferred because it included an explicit representation of dissolved oxygen concentration, a critical parameter for swordfish, whereas the first one was only using the Levitus climatology.

The NCEP-ORCA2-PISCES configuration used covers the Pacific Ocean at a spatial resolution of 2 deg x 2deg and a monthly time resolution. First guess parameters of habitat and movements were estimated using 28 tracks computed from satellite pop-up tags released in the Pacific (Figure 21) from 2002 to 2009 (paper in prep), and from literature. They will be compared to the values achieved using the optimization process based on fishing data. High-resolution fishing data, i.e., exact fishing position and date, was provided by NMFS for the Hawaii-based longline fishery, and coarse resolution (5°x5°x1 month) data for worldwide longline fisheries was provided by the WCPFC. Only longline data are being incorporated as other types of fishing (driftnet, harpoon) represent much smaller volumes of catch.

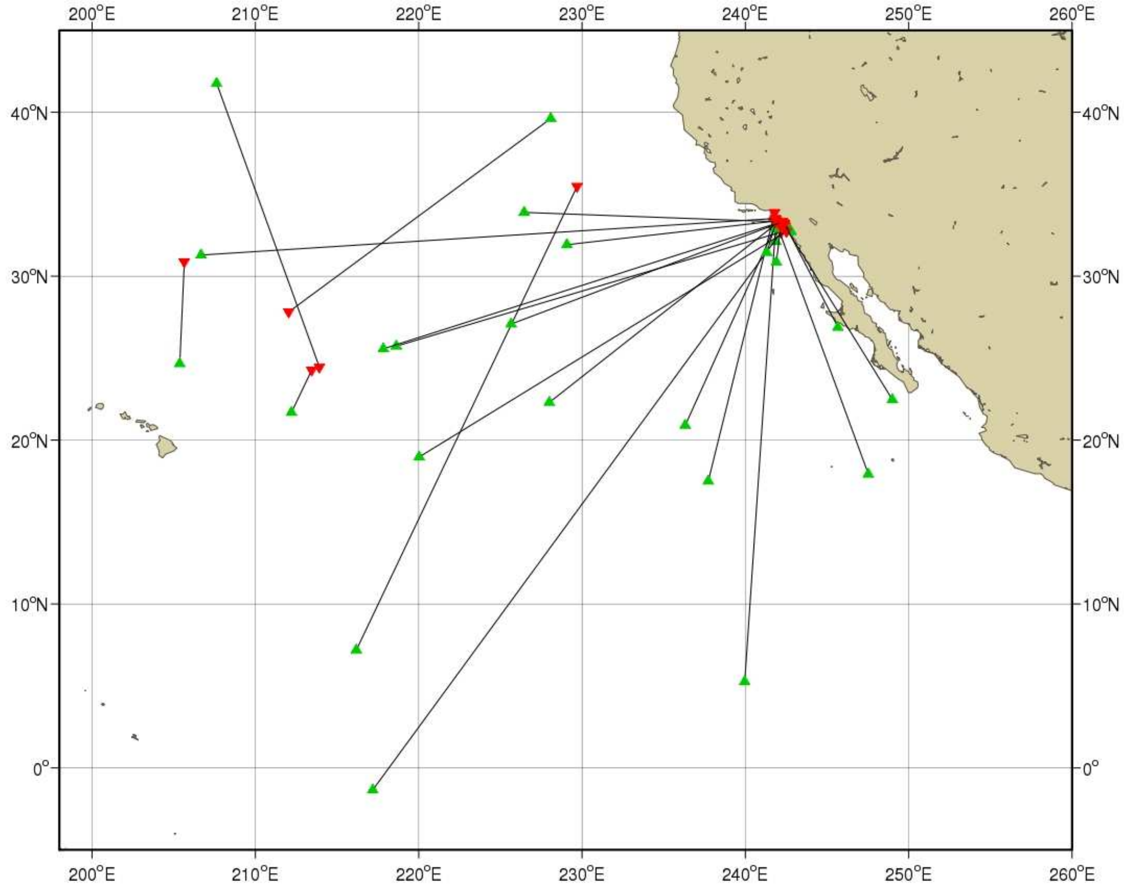


Figure 21. Tag data used to estimate first-guess habitat and movement parameters

We ran into considerable problems trying to build homogeneous fisheries (i.e., separating a fishery into two if there was some change of gear or grouping fisheries together when there are fewer data). As swordfish CPUE vary drastically between longline shallow sets and deep sets (sometimes by as much as a factor 100 in the HI longline fisheries), the gear configuration (usually not available) is of critical importance for the definition of fisheries. It would be extremely useful to have the data separated in shallow and deep sets. We haven't been able to obtain a successful optimization experiment using coarse resolution fishing data yet, since the only separation available is the separation by flag.

Hence, several experiments have been run using only the HI fine-resolution data (Figure 22). For this data, the type of each set (shallow, mixed or deep, as well as the target species: tuna or swordfish) was know. Despite its limitation in space and time this detailed dataset allowed to achieve model convergence (Gmax =0.027), but a number of parameters were stuck at the bounds. Overall, the distributions obtained are reasonable and consistent with the general distribution of catch (Figure 23). The model was able to fit the time series of catch data (Figure 24) and cpue (Figure 25). The fit to deep sets catch data is not as good as for shallow and mixed sets, which is probably due to the fact that swordfish is not the target species of deep sets. Also, the fit to cpue was not as good as the fit to catch, as catch was used in the likelihood function in this experiment.

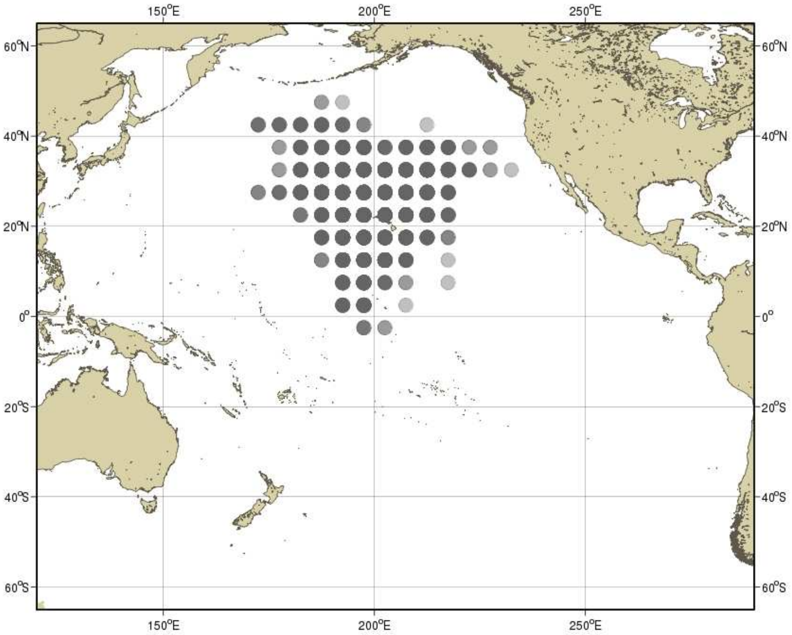


Figure 22. Distribution of effort for the Hawaii-based longline fisheries

Following this preliminary set of simulations, the next experiments will include detailed high-resolution length-frequency data for the Hawaiian fishery, and sensitivity analyses for mortality habitat parameters.

It was particularly encouraging to see that the detailed high resolution of Hawaiian fishing data allowed a first realistic parametrization for the basin scale distribution of the species, despite the lack of information coming from other Pacific fisheries. It is critical however to include these latter fisheries, at least to account for the fishing mortality, and if possible with enough details (i.e., shallow vs deep sets, target or bycatch species) to help in the optimization of model parameters. Any additional reliable and detailed fishing dataset, even limited to a small area, would thus bring valuable information in the optimization of the model.

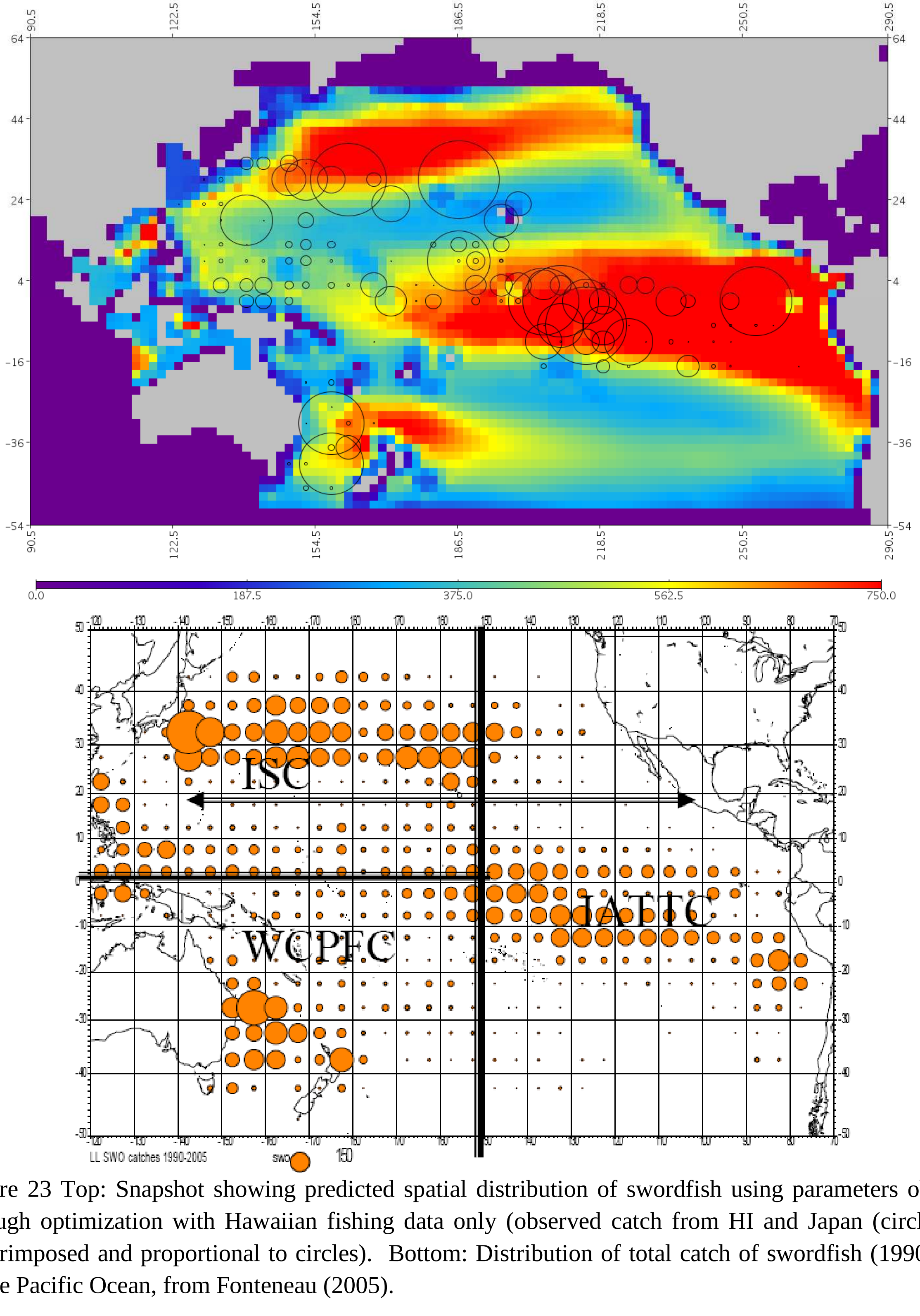


Figure 23 Top: Snapshot showing predicted spatial distribution of swordfish using parameters obtained through optimization with Hawaiian fishing data only (observed catch from HI and Japan (circles) are superimposed and proportional to circles). Bottom: Distribution of total catch of swordfish (1990-2005) in the Pacific Ocean, from Fonteneau (2005).

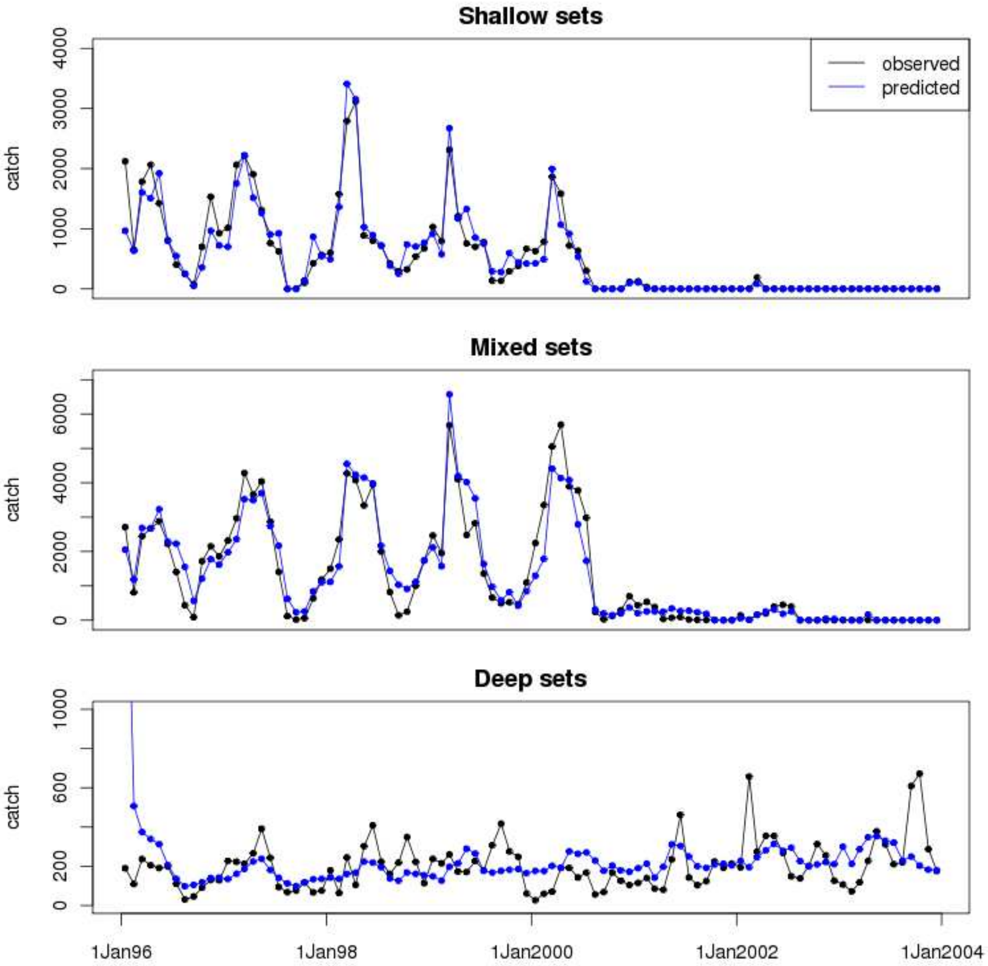


Figure 24. Fit to Hawaii longline catch data

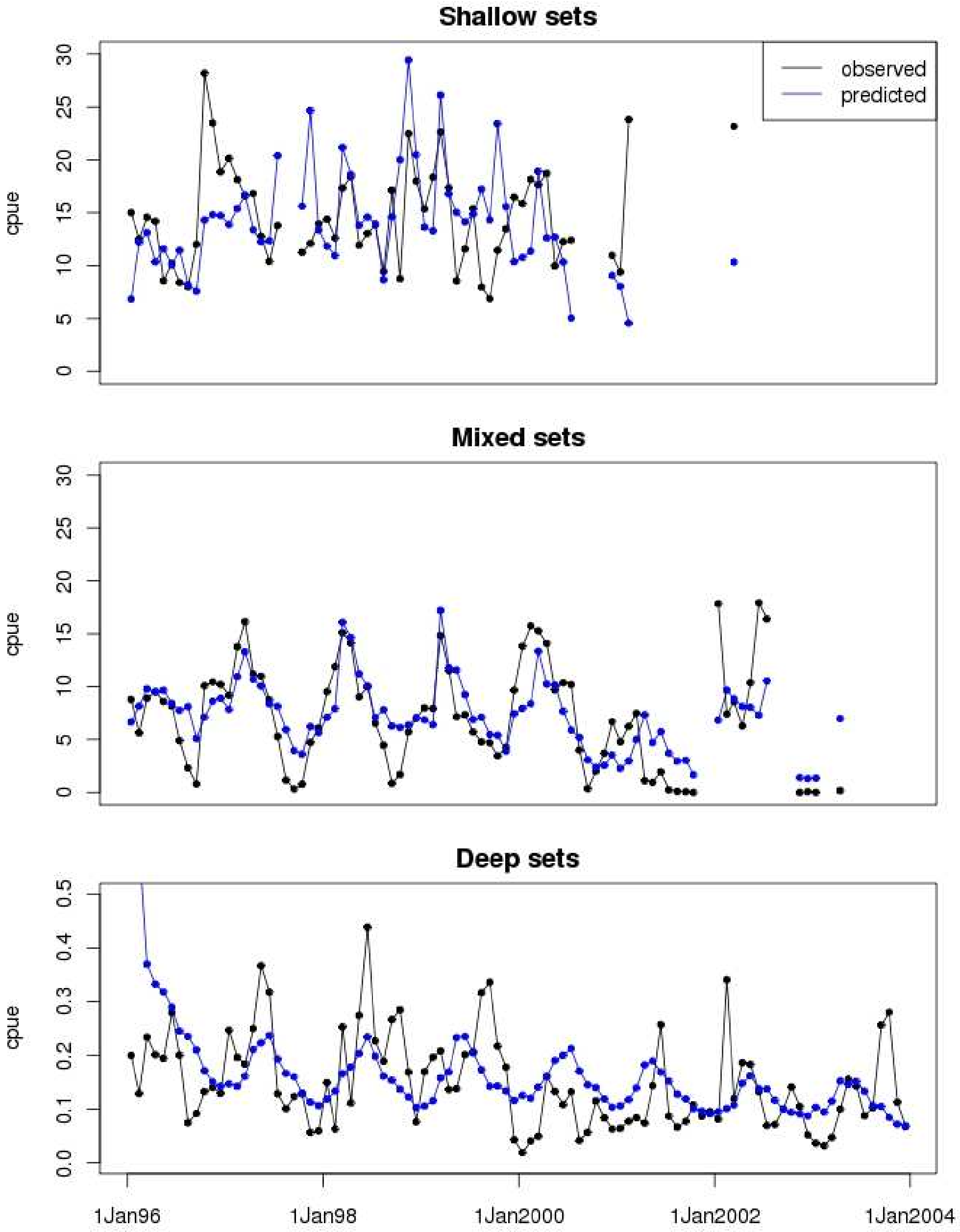


Figure 25. Fit to Hawaii longline cpue (catch per 1000 hooks) data

5 Conclusion

The new version of the model SEAPODYM now includes a general framework to use catch and size composition data from the fisheries to achieve optimization of parameters for each species. This development is a key step to gain confidence in the model estimates. While there is a small number of parameter to calibrate, achieving a plausible set of biological parameters remains a difficult task requiring a large number of simulations. Several tools for assisting in the optimization experiments and analyses of results have been developed. The qualities of fishing and environmental forcing data are the two main issues to achieve convergence and obtain plausible results. Satisfactory model configurations with optimal parameterization for each tuna species have been completed, except for yellowfin tuna. This allows the development of various applications for fisheries management. In particular we will revise the preliminary work that has been conducted to investigate the impact of High Sea Pockets closure. There is also a strong interest from WCPFC members to assess the biomass of tuna inside their EEZ allowing a better management at local scale and providing key information to establish the level of fishing effort and catch that can be allocated to domestic and distant-water fisheries. Using the model configuration and optimal parameterization achieved for the reference fit above, and higher resolution and more realistic environmental forcing datasets in the future, it is possible to extract model variables in any given EEZ using specified EEZ mask.

Acknowledgements
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6 References

Aumont, O., L. Bopp, 2006. Globalizing results from ocean in situ iron fertilization studies, Global Biogeochemical Cycles, 20.

Aumont, O.; Maier-Reimer, E.; Blain, S.; Monfray, P. (2003). An ecosystem model of the global ocean including Fe, Si, P colimitations. Global Biogeochemical Cycles, 17(2), DOI 10.1029/2001GB001745

Bopp L, Aumont O, Cadule P, S. Alvain and M. Gehlen (2005). Response of diatoms distribution to global warming and potential implications: A global model study, Geophysical Research Letters, 32 (19).

Gorgues, T., C. Menkes, O. Aumont, J. Vialard, Y. Dandonneau, and L. Bopp (2005), Biogeochemical impact of tropical instability waves in the equatorial Pacific, Geophys. Res. Lett., 32, L24615, doi:10.1029/2005GL024110.

Hampton, J., Langley, A., & Kleiber, P. (2006). Stock assessment of bigeye tuna in the western and central Pacific Ocean, including an analysis of management options. 2nd Meeting of the Scientific

Committee of the Western and Central Pacific Fisheries Commission. Manila, Philippines, 7-18 August 2006, WCPFC-SC2-SA WP-2, 103 pp

Hoyle,S., A. Langley,and J. Hampton (2008). Stock assessment of Albacore tuna in the south Pacific Ocean. 4th Meeting of the Scientific Committee of the Western and Central Pacific Fisheries Commission. Port Moresby, Papua New Guinea, 11-22 August 2008, WCPFC-SC4-2008/SA-WP-8, 126 pp

Langley, A., Hampton, J., Kleiber, P., Hoyle S. (2007). Stock assessment of yellowfin tuna in the western and central Pacific Ocean, including an analysis of management options. 3rd regular session of the Scientific Committee of the Western Central Pacific Fisheries Commission, 13-24 August 2007 Honolulu, United States of AmericaWCPFC–SC3 SA WP–1: 120 pp.

Lehodey P., Senina I., & Murtugudde R. (2008). A Spatial Ecosystem And Populations Dynamics Model (SEAPODYM) - Modelling of tuna and tuna-like populations. *Progress in Oceanography*, **78**: 304-318.

Lehodey P., Senina I., (2009). An update of recent developments and applications of the SEAPODYM model. Fifth regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission, 10–21 August 2009, Port Vila, Vanuatu, WCPFC-SC5-2009/EB-WP-10, 44 pp. http://www.wcpfc.int/meetings/2009/5th-regular-session-scientific-committee

Lehodey P., Senina I., (2009). A user manual for SEAPODYM version 2.0: application with data assimilation. Fifth regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission, 10–21 August 2009, Port Vila, Vanuatu, WCPFC-SC5-2009/ EB-IP-13, 82 pp. http://www.wcpfc.int/meetings/2009/5th-regular-session-scientific-committee

Lehodey P., Murtugudde R., Senina I. (2010). Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. *Progress in Oceanography*.

Senina I., Sibert J., & Lehodey P. (2008). Parameter estimation for basin-scale ecosystem-linked population models of large pelagic predators: application to skipjack tuna. *Progress in Oceanography*, **78**: 319-335.

Uppala, S.M., Kållberg, P.W., Simmons, A.J., Andrae, U., da Costa Bechtold, V., Fiorino, M., Gibson, J.K., Haseler, J., Hernandez, A., Kelly, G.A., Li, X., Onogi, K., Saarinen, S., Sokka, N., Allan, R.P., Andersson, E., Arpe, K., Balmaseda, M.A., Beljaars, A.C.M., van de Berg, L., Bidlot, J., Bormann, N., Caires, S., Chevallier, F., Dethof, A., Dragosavac, M., Fisher, M., Fuentes, M., Hagemann, S., Hólm, E., Hoskins, B.J., Isaksen, L., Janssen, P.A.E.M., Jenne, R., McNally, A.P., Mahfouf, J.-F., Morcrette, J.-J., Rayner, N.A., Saunders, R.W., Simon, P., Sterl, A., Trenberth, K.E., Untch, A., Vasiljevic, D., Viterbo, P., and Woollen, J. 2005: The ERA-40 re-analysis. *Quart. J. R. Meteorol. Soc.*, 131, 2961-3012.doi:10.1256/qj.04.176

7 Appendix 1: Definition of fisheries

Id	Gear	Region	Description	Nationality	C/E data month/year	Reso-lution	Size data qtr/year	Reso-lution
SKIPJACK available data*								
P1	PL	15N-45N; 115E-150W	PL West Pac	Japan	1/1972 - 12/2007	5x5	1/1964 - 1/2004	5x5
P2	PL	25N-45N; 165E-150W	PL Central Pac	Japan	6/1972 - 11/2007**	5x5	2/1972 - 3/2003**	5x5
P3	PL	15S-0; 140E-160E	Pole and line	Papua New Guinea	3/1970 - 4/1985	5x5	3/1984 - 4/1985	5x5, 10x20
P3	PL	15S-0; 150E-165E	Pole and line	Solomon Islands	6/1971 - 10/2005	5x5	3/1971 - 3/2003	5x5

Id	**Gear**	**Region**	**Description**	**Nationality**	**C/E data month/year**	**Reso-lution**	**Size data qtr/year**	**Reso-lution**
3	PS	25N-45N; 140E-165E	PS subtropical fishery	Japan	7/1970 - 9/2007	5x5	2/1974 - 4/2003	5x5
7	PS	20S-15N; 130E-150W	PS on LOG	All	11/1970 - 4/2008 No Effort	5x5	2/1988 - 1/2007	5x5, 10x20
8	PS	20S-15N; 130E-150W	PS on FAD	All	2/1973 - 4/2008 No Effort	5x5	3/1988 - 3/2007	5x5, 10x20
9	PS	20S-15N; 130E-150W	PS on free school	All	12/1967 - 4/2008 No Effort	5x5	4/1987 - 3/2007	5x5, 10x20
L8	LL	20S-25N; 115E-150W	LL exploratory fishery	Japan	6/1950 - 11/2007	5x5	1/1970 - 3/2006	5x5
S10	PS	EPO	PS on Dolphin schools	NA (public data)	10/1959-8/2007	1x1	1/1961 – 4/2005	EPO
S11	PS	EPO	PS on Floating objects	NA (public data)	7/1959 – 8/2007	1x1	1/1961 - 4/2005	EPO
S12	PS	EPO	PS on free school	NA (public data)	3/1959-8/2007	1x1	1/1961 - 4/2005	EPO
P13	PL	20S-5N; 175E-185E	Pole and Line	Fiji	1/1976 - 11/1998	5x5	4/1991 - 4/1999	5x5, 10x20
D13	DOM	0-15N; 115E-130E	mixed set types	Philippines	1/1970 - 12/2007	5x5	-	-
D14	DOM	10S-10N; 120E-130E	mixed set types	Indonesia	1/1970 - 12/2007	5x5	-	-

* The current data for WCPO (MFCL 24-regional structure) are available on 5x5degree cells. It would be useful to have data with original (1x1 for most of PL and PS fisheries) resolution.

** Note, that Japan distant water data are available only for a given region while for MFCL regions 1,2,4 data are missing.

N	Gear	Region	Description	Nationality	C/E data month/year	Reso-lution	Size data qtr/year	Reso-lution
YFT and BET available data								
L1	LL	WCPO	Traditional LL fishery targeting BET & YFT	Japan, Korea, Chinese Taipei (DWFN)	6/1950 - 12/2007	5x5	2/1948 – 1/2007	10x20
L2	LL	10S-45N; 110E-140W	Shallow night LL fishery	China, Chinese Taipei	1/1958 - 11/2007	5x5	2/1991 – 2/2007	10x20
L3	LL	40S-10S; 140E-140W	LL fishery targeting South Pac. Albacore	Chinese Taipei, Vanuatu (DWFN), Korea, Japan	7/1952 - 12/2007	5x5	2/1951 – 4/2006	10x20
L4	LL	40S-10S; 145E-140W	Pac. Islands LL targeting South Pac. Albacore	US (Am. Sam), Fiji, Samoa, Tonga, NC, FP, Vanuatu (local)	2/1982 - 12/2007	5x5	3/1991 – 4/2007	10x20
5	LL	20S-15N; 140E-175E	Pac. Islands LL targeting BET & YFT	PNG, Solomons	10/1981 - 5/2007	5x5	2/1996 – 4/2006	10x20
6	LL	40S-10S; 140E-175E	LL Australia East Coast	Australia	10/1985 - 3/2007	5x5	3/1992 – 4/2006	10x20
7	LL	10S-50N; 130E-140W	Hawaii LL	US (Hawaii)	1/1991 - 12/2006	5x5	4/1992 – 3/2006	10x20
8	PS	40S-20N; 114E-140W	PS on drifting FAD & log	All	12/1967 - 2/2008	1x1	2/1988 – 3/2007	5x5
9	PS	40S-20N; 115E-140W	PS on anchored FAD	All	7/1979 - 1/2008	1x1	2/1984 – 2/2007	5x5
10	PS	40S-20N; 114E-140W	PS on free school	All	12/1967 - 1/2008	1x1	3/1984 – 3/2007	5x5
11	PS	10N-50N; 120E-180E	Sub-tropical PS fishery	Japan	7/1970 - 8/2007	1x1	-	-
12	Misc.	10S-15N; 115E-180E	Various domestic fisheries	Philippines	1/1970 - 9/2007	5x5	4/1980 – 4/2007	10x20
13	HL	0N-15N; 115E-130E	Handline fishery	Philippines	1/1970 - 12/2006 Effort missing before 1997	5x5	1993-2007	10x20
14	Misc	10S-10N; 120E-180E	Various domestic fisheries	Indonesia	1/1970 - 1/2007 yes/partially missing	5x5	yft – no data bet - 2006	10x20
15	PL	40S-48N; 115E-140W	Pole-and-line	Japan, Solomon Islands, PNG, Fiji	3/1970 - 12/2006	1x1	yft 4/1977-3/2005 bet 2/1965 – 1/2005	10x20
16	PS	EPO	PS targeting YFT, on Dolphin schools	NA (public data)	1/1959 – 8/2007	1x1	1/1961 – 4/2004	EPO
17	PS	EPO	PS targeting YFT,	NA (public	2/1959 –	1x1	1/1961 –	EPO

N	Gear	Region	Description	Nationality	C/E data month/year	Reso-lution	Size data qtr/year	Reso-lution
			on Floating objects	data)	8/2007		4/2004	
18	PS	EPO	PS targeting YFT, Not associated	NA (public data)	1/1959 – 8/2007	1x1	1/1961 – 4/2004	EPO
19	LL	10N-50N; 150W-90W	Traditional LL targeting BET & YFT	Japan, Korea, Chinese Taipei	11/1954 – 6/2006	5x5	1/1965 – 4/2003	= reg
20	LL	40S-10N; 150W-70W	Traditional LL targeting BET & YFT	Japan, Korea, Chinese Taipei	10/1954 – 7/2006	5x5	4/1954 – 4/2003	= reg

N NCEP ERA40	**Gear**	**Region**	**Description**	**Nationality**	**C/E data month/year**	**Reso-lution**	**Size data qtr/year**	**Reso-lution**
ALBACORE available data								
L1 L1	LL	50S-25S; 140E-110W	JP, JPDW	Japan high latitude	1/1952-12/2006	5x5	3/1964-3/2005	10x20
L1 L12	LL	25S-0; 140E-110W	JP, JPDW	Japan low latitude	1/1952-12/2006	5x5	3/1964-3/2005	10x20
L2 L2	LL	50S-0; 140E-110W		Korea	3/1962-12/2008	5x5	1/1966-2/2006	5x5
L3 L3	LL	50S-0; 140E-110W	Distant-water fleet	Chinese Taipei	7/1964-12/2008	5x5	3/1964-2/2007	5x5; 10x20
L4	LL	50S-10S; 140E-175E	LL targeting Alb	Australia	3/1985-12/2007	5x5	2/2002-2/2007	5x5; 10x20
L5 L5	LL	25S-0; 150E-180E	LL targeting Alb	New Caledonia	11/1983-12/2007	5x5	1/1993-4/2007	5x5; 10x20
L6 L6	LL	50S-0; 140E-180W	LL targeting Alb	Other	11/1957-12/2008	5x5	3/1963-3/2005	5x5; 10x20
L7	LL	50S-25S; 145E-180E	LL targeting Alb	New Zealand	8/1989-12/2007	5x5	2/1992-4/2006	5x5; 10x20
L5	LL	25S-0; 150E-180E	LL targeting Alb	Fiji	8/1989-12/2007	5x5	3/1992-3/2007	5x5; 10x20
L5 L11	LL	25S-0; 180E-155W	LL targeting Alb	American Samoa, Samoa	1/1993-5/2008	5x5	1/1998-3/2007	5x5; 10x20
L5	LL	25S-5S; 180E-140W	LL targeting Alb	Tonga	2/1982-3/2008	5x5	3/1995-242006	5x5; 10x20
L5	LL	25S-0; 180E-110W	LL targeting Alb	French Polynesia	1/1992-5/2007	5x5	2/1991-4/2007	5x5; 10x20
T8	T	50S-25S; 140E-110W	Troll	New Zealand, United States	1/1967-12/2007	5x5	4/1986-2/2006	5x5; 5x10; 10x20
G9	D	45S-25S; 140E-125W	Driftnet	Japan, Chinese Taipei	11/1983-1/1991	5x5	4/1988-1/1990	5x5; 10x20
L10	LL	50S-0; 180-70W	LL targeting Alb	Other	11/1957-12/2008	5x5	3/1963-3/2005	5x5; 10x20

8 Appendix 2: SEAPODYM parameters

Parameters estimated from the data			Unit	SKJ			BET			YFT		ALB	
				ESSIC	ERA40	NCEP	ESSIC	ERA40	NCEP	NCEP	ERA40	NCEP	ERA40
		Habitats											
1	T_s	Optimum of the spawning temperature function	^{o}C	30.5	27.8	29.8	26.2	26.99]	26.6	28.97	26.53	28.9	25.56
2	σ_s	Std. Err. of the spawning temperature function	^{o}C	3.5*	2.5]	2.05	0.82	2.56	2.19	1.89]	3.49]	2.09	0.75*
3	α	Larvae food-predator trade-off coefficient	-	3.67	0.38	2]	0.63	7.5e-6	1.9e-5	2.33	7.15	5*	5*
4	T_a	Optimum of the adult temperature function at maximum age	^{o}C	26*	21.1	23.4	13	[5.00	[5.00	[10	17	17.47	5.65
5	σ_a	Std. Err. of the adult temperature function at maximum age	^{o}C	1.62	1.14	3.5]	2.16	3.99]	3.99]	[1.9	3.99]	2.23	3.84
6	Ô	Oxygen value at Ψ_O =0.5	ml · l^{-1}	3.86	0.93	1.5	0.46	0.81	0.74	0.4*	0.677	3.93	2.98
7	□	Curvature coefficient of the oxygen function	-	7.3e-5	0.001*	0.001*	0.001*	0.001*	0.001*	0.001*	0.001	0.002*	0.016
		Movements											
8	V_M	Maximum sustainable speed	B.L.·s^{-1}	1.3	0.96	1.13	0.32	1.19	0.97	[0.2	0.85*	1.65*	1.61
9	c	coefficient of diffusion habitat dependence	-	0.4	0.3	0.3	0.22	0.999]	0.996]	0.073	3]	0.382	1.9
		Larvae recruitment											
11	R_s	Coefficient of larvae recruitment (Beverton-Holt function)	-	0.5*	0.12*	0.15	0.0045	0.025	1.0	0.06	0.01	0.347	0.002
		Mortality											
12	M_{Pmax}	maximal mortality rate due to predation	mo^{-1}	0.15*	0.025*	0.025*	0.25	0.155*	0.155*	0.1*	0.125*	0.15*	0.2*
13	M_{Smax}	maximal mortality rate due to senescence	mo^{-1}	0.5*	0.195	[0.1	0.259	0.203	0.164	0.436	0.185	0.0084	0.0095
14	β_P	slope coefficient in predation mortality	-	0.296	0.043	0.01	0.073	0.0769	0.0685	0.158	0.059	0.024	0.121
15	β_S	slope coefficient in senescence mortality	-	-0.044	-0.114	-0.103	-0.097	-0.016	-0.016	-[0.15	-0.147	-0.01*	-0.5
16	$A_{0.5}$	age at which ½ M_{Smax} occurs	mo	31*	38*	38*	80.6	95.9	76.1	46	40	96*	58

*Fixed; [val = value close to mimimum boundary value; val] = value close to maximum boundary value

Pre-defined parameters		unit	SKJ	YFT	BET	SP alb.
	Population structure					
	Number of larvae cohorts (month)		1	1	1	1
	Number of juvenile cohorts (month)		2	2	2	2
	Age at 1st autonomous displacement	month	4	4	4	4
	Number of young cohorts (3 mo; 6 mo; 12 mo)		2 (3 mo)	2 (6 mo)	4 (6 mo)	9 (6 mo)
	Age at 1st maturity	month	9	15	27	57
	Number of adult cohorts (3 mo; 6 mo; 12 mo)		12 (3 mo)	12 (6 mo)	16 (6 mo)	11 (12 mo)
	Growth					
l_a	Predator' size of cohort *a*	cm	*	*	*	*
w_a	Predator' weight of cohort *a*	kg	*	*	*	*
	Food requirement (*optional*)					
r	Daily ration (relative to weight at age)	-	0.10	0.06	0.06	0.05
ρ	Coefficient of the Food requirement index function	-	0.02			
	Habitats					
κ	curvature parameter in the function to switch continuously from feeding to spawning habitat	-	1000	1000	1000	1000
$\hat{G}_d$	Threshold in the gradient of day length at which the switch occurs between spawning and feeding habitat	$h.d^{-1}$	0.015	0.010	0.025	0.008

* from independent studies (Langley et al., 2005; Hampton et al., 2006; Langley et al. 2007; Hoyle et al. 2008)