

SCIENTIFIC COMMITTEE SEVENTH REGULAR SESSION

9-17 August 2011 Pohnpei, Federated States of Micronesia

Prospects for effective conservation of bigeye tuna stocks in the Western Central Pacific Ocean

WCPFC-SC7-2011/MI-WP-05

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Executive Summary

The Western and Central Pacific Fisheries Commission (WCPFC) agreed to close certain highseas areas in the Western and Central Pacific Ocean to purse seine tuna fishing starting in 2010. These measures have potential economic benefits to the countries surrounding the closed areas and may also have potential stock conservation benefits for tunas. We used a spatially explicit ecosystem model of tuna population dynamics, SEAPODYM, to simulate the effects of closures on stock biomass and catch of bigeye tuna (Thunnus obesus) 1980 through 2003. The fate of the fishing effort displaced by these closures was not considered in the WCPFC conservation measures. Therefore we examine two different effort displacement scenarios: (1) complete loss of the displaced fishing effort; and (2) redistribution of effort proportional to the historical (average) distribution of catch per unit effort (CPUE). When fishing effort is redeployed, the benefits to the stock are not detectable. The beneficial effect on stock biomass is greatest when the displaced fishing effort was completely lost. However, even in this latter case, the effects of the closures on stock size are quite small (less than 4 % averaged over the simulation period). In view of the limited stock conservation benefits of the closures, we also considered other potential bigeve conservation measures. If spatial closures are extended to longline fisheries, the biomass increase becomes greater (approximately 7%). Prohibition of the use of fish aggregating devices by the purse seine fleet produces a similar biomass increase. We conclude that:

1.Closing areas to purse seine fishing without consideration of the fate of displaced fishing effort will not be effective for bigeye conservation.

2. Conservation measures that combine closing areas to purse seine fishing and proportional reduction of fishing effort may yield a small bigeye conservation benefit.

3. Restricting longline fishing in known bigeye spawning areas in combination with purse seine area closures and effort reduction offers the best option for achieving effective bigeye conservation.

4. Limitation of FADs use would have a strong positive impact on bigeye stock conservation.

5. Benefits from any bigeye conservation measure will only be detectable after 10 years and be fully realized after two decades, i.e. in the 2030s assuming timely implementation. Recovery will be modulated by both natural and anthropogenic climate-related ecosystem variability. Environmental changes induced by anthropogenic release of greenhouse gases should be clearly visible by the end of the 2030's (Lehodey et al 2010b). The status of bigeye stock at that time will depend on today's conservation and management measures.

6. The bigeye population encompasses both the WCPFC and IATTC convention areas. Though spatial measures have a strong local effect, they also have a spillover effect at the whole range of the species. Thus, the management of this stock would benefit from collaborative and coordinated actions of both international Commissions.

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Introduction

The total annual catch of the four main species of tuna in the WCPFC Convention area exceeded 2,000,000 mt every year since 2004 and reached a record high (~2,468,000 mt) in 2009 (Williams and Terawasi 2010), representing 58% of the estimated global tuna catch. Purse-seine and pole and line vessels in the surface fishery landed 77% and 7% of this catch, respectively. The subsurface longline fishery accounted for 9%. The remaining 7% was taken by troll gear and a variety of artisanal fishing methods, mostly in eastern Indonesia and the Philippines. Landings of juvenile bigeye tuna in the purse seine fishery increased during the late 1990s due to expanding use of FADs. In 2009, the purse-seine catch of skipjack was 1,790,000 mt, and the incidental bigeye catch, predominantly juveniles, was 43,600 mt. In contrast the 2009 WCPO longline catch of bigeye, mainly adults, was 66,000 mt, only 34% greater than the incidental purse-seine catch.

The latest assessments for bigeye tuna (Harley et al. 2010) estimate the current biomass to be only slightly above the biomass capable of producing maximum sustainable yield (MSY), but the estimated fishing mortality rates are far greater than the fishing mortality at MSY. The bigeye stock is approaching or may already be overfished, and current exploitation rates will inevitably reduce bigeye stock sizes to levels less than those capable of producing MSY. The fate of the bigeye stock is inextricably mixed with the purse seine fishery targeting skipjack and yellowfin tuna. Skipjack stocks are usually considered to be moderately exploited, but the most recent assessment (Hoyle et al. 2010) raises the possibility that overfishing may be occurring. Nevertheless, the skipjack stock is safely above the level of producing maximum sustainable yield (MSY) and not overfished, and high juvenile mortality of bigeye stocks will continue as long as the skipjack fishery operates in its current mode.

The WCPFC has implemented conservation and management measures (CMMs) with the objective of reducing fishing mortality on bigeye tuna (WCPFC 2008). These measures include closure of two high-seas enclaves in the WCPFC Convention Area bounded by 10°N and 20°S to purse seine tuna fishing (area I in Figure 1). A second closure would extend spatial closures to all high seas waters of the convention areas west of 150°W and between 15°N and 20°S (area II in Figure 1). These closures are equivalent to closing 6% of total convention area, i.e., 12% of its tropical waters (~20°N-20°S), and the catches in these areas comprise a substantial proportion of the total catch in the Convention Areas (Table 1, Figure 2).

We apply an ecosystem-based model of tuna population dynamics and fisheries to investigate the potential utility of spatial fishery management measures. This model was selected because it includes a fully explicit description of spatial population dynamics over all life stages from larvae to adult (Lehodey et al. 2008) and a statistically rigorous approach for its parameterization (Senina et al 2008). Specifically we examine the efficacy of closed areas as a means to reduce incidental mortality of bigeye tuna in the purse seine fishery for skipjack. In addition, we explore possible complementary strategies to area closures that might be more effective in conserving bigeye tuna stocks.

Methods

We analyze area closures by simulating the growth of the WCPO tuna fishery from 1980 to 2003 using the spatially explicit ecosystem model, SEAPODYM (Spatial Ecosystem And population Dynamics Model; Lehodey et al 2008; Senina et al 2008; Lehodey et al. 2010a; Lehodey et al 2010b). The main features of this model are: i) forcing by environmental data (temperature, currents, primary production, euphotic depth and dissolved oxygen concentration); ii) prediction of both temporal and spatial distribution in three vertical layers of functional groups at the mid-trophic level, i.e., tuna forage

iii) prediction of both temporal and spatial distribution of stage-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 maximum likelihood using commercial fishing data. The simulation period, 1980-2003, was selected because changes in longline fishing practice and expansion of the purse seine fishery began to occur around 1980, and because at the time of the study, the availability of oceanographic forcing available to SEAPODYM ended in 2003. Applications of SEAPODYM to tropical tuna populations are described in the previously cited references. For the simulations reported here, the optimization has been updated with the new environmental forcing and revised fishing data. See Supplementary Material for details of the model configuration and SEAPODYM references presented in previous WCPFC SC meetings.

We define nine alternative conservation and management scenarios emphasizing closures of high-seas zones in the WCPO (Table 2). Closure of area II to longline fishing was included in the scenarios because it is an area of substantial LL catches of bigeye and relatively low PS catches of both skipjack and bigeye. Area II also includes part of the known bigeye spawning area (Schaefer et al 2005).

We apply three different metrics to evaluate each scenario. Let B_{ati} be the total biomass of tunas of age group *a* in the population at time *t* under scenario *i*.

1. The change in biomass age group *a* of the population at time *t* under scenario *i* is given by $\Delta B_{ati} = B_{ati} - B_{at0}$ for i > 0.

2. The average percentage increase in the population in relation to the base case, scenario 0, over the simulation period is $100 \frac{\Sigma_t \Delta B_{ati}}{\Sigma_t B_{at0}}$ for i > 0

3. Fishery impact is the ratio of the biomass under some fishery management scenario to the biomass that the population might have attained in the absence of fishing (Sibert et al 2006),

 $100\left(1-\frac{\bar{B}_{ayi}}{\bar{B}_{ayr}}\right)$, where \bar{B}_{ayi} is the average biomass of age *a* bigeye in final year *y* of the simulation

under scenario *i* and \overline{B}_{ayr} is the average biomass of age *a* bigeye in year *y* of the simulation when fishing mortality is set to zero. Fishery impact is a measure of the effect of the fishery on the stock biomass. It is a non-parametric reference point that is easy to compute, makes fewer assumptions than reference points based on maximum sustainable yield, and compensates for environmental change. A fishery managed to produce maximum sustainable yield would reduce the adult biomass of the stock to approximately 40% of that which might occur in the absence of fishing, and the fishery impact would be approximately 60%

Results

The current SEAPODYM model configuration and parameterization substantially improved the agreement between predicted and observed catch and catch per unit of effort (CPUE) described in our earlier optimization experiments (Senina et al 2008; Lehodey et al. 2010b). The overall mean spatial correlation of the bigeye catch and CPUE is high (See Supplementary Material, Figure S1) and the set of optimized biological parameters are consistent with existing knowledge of the biology of the species. In particular, estimated optimal spawning temperature ($26.6^{\circ}C \pm 2.2^{\circ}C$) is within the range of temperatures observed when mature and spawning bigeye tuna are encountered (e.g., Schaeffer 2005).

The trends in total adult biomass predicted by SEAPODYM are somewhat higher than the MFCL estimates even when started in 1980 from the initial biomass estimated by MFCL (Figure S2). However, the overall trends from the two models are similar, particularly with respect to timing of the maximum biomass and the trend in the final years of the simulation.

The model predicts a long slow rebuilding of bigeye biomass from 1980 to 1995 in the absence of fishing (Figure 3, F=0). The rebuilding begins immediately after the cessation of fishing on the already depleted bigeye stock. The biomass continues to increase until environmental factors become limiting in the mid 1990s and subsequently begins to decrease. The recovery period is approximately 15 years, slightly longer than the lifespan of bigeye tuna. Similar but less pronounced increasing and decreasing trends are visible under all fishing scenarios with smaller increases until the mid 1990s and more rapid subsequent decreases (Figure 3). The effects of fishing are to dampen the environmentally driven increase and accelerate the subsequent decrease. The accelerated rate of biomass decrease in the fishing scenarios begins in the late 1990s when the use of FADs in the purse seine fishery became prevalent.

The absolute differences in biomass between fishery scenarios (Figure 3) appear small, but relative changes in biomass relative to scenario 0 (no change from the observed fishing pattern) are more apparent (Figure 4). Scenario C, closure with reallocation of displaced effort, has negligible effect on adult bigeye biomass. Reducing total effort over the model domain in proportion to the potential effort lost in the closed areas, scenario E, appears to be slightly more effective, and almost equivalent to area closure combined with loss of displaced effort, scenario CE. FAD prohibition with redistributed effort to free school sets (F2S) has equivalent impact to scenario CEL with both area I and II closed to purse seiners, loss of PS fishing effort from these areas, and closure of area II to longline fishing. Addition of the same FAD prohibition scenario to the closure of area II to longliners (F2SL) would double the percent change in adult bigeye biomass in the WCPFC convention area to reach >25% increase after 25 years of regulation.

The relative change in adult bigeye biomass varies spatially over the entire model domain as well as temporally over the time course of the simulation. Figure 5 shows the spatial differences in adult bigeye biomass at the end of the simulation period in 2003 for four scenarios. The first two have area closures either for purse seine only or for purse seine and longline. In both cases, the effect is largest in the closed areas and immediately adjacent waters (Figure 5, CE and CEL), but a substantial 10-25% spillover effect is visible over the entire range of the species. The longline area closure has a large effect that, combined with the purse seine area closure, locally increases the adult biomass to more than 25% in the EEZs adjacent to area II.

The third scenario, F2S, in Figure 5 has no spatial closure but represents the impact of prohibiting FADs use, while allowing an increment of purse seine fishing effort (in fishing days) on free schools equivalent to the lost effort on FAD sets, ("FAD to free school" scenario). The result is a substantial increase of adult biomass mainly in the western Pacific and Indonesian waters where there is a long tradition of intense FAD usage. Finally, adding longline closure in area II to the "FAD to free school" scenario produces the maximum impact in the WCPO, with adult biomass increases of more than 40% in the core region (Fig. 6, F2SL). The "spillover" effect is even larger in the temperate regions of the North Pacific and in the EPO.

SEAPODYM estimates the impact of the fishery on the adult bigeye population to be 57% in 2003 under the observed distribution of fishing effort, scenario 0 in Figure 6. The most optimistic conservation scenario, shifting PS effort from fads to schools and closure of longline fishery in area II

(F2SL), reduces the impact at 46%.

Discussion

Our model results do not constitute a forecast of the future development of the fishery. Rather we attempt to reconstruct its historical development. Forecasts for use in fishery management would require seasonal and inter-annual projections of environmental forcing and some means of forecasting the spatial distribution and nature of future fishing effort. Several models are available for projecting oceanographic forcing variables (Lehodey et al 2010b) but there are no suitable models for forecasting fishing effort. Such forecasts may be possible over a very short time period by simply extrapolating current fishing conditions one to three years into the future, but longer term forecasts would require a realistic, quantitative theory of commercial fishing fleet dynamics. We have attempted to make this simulation as realistic as possible, using the best available oceanographic and biogeochemical models and fishing data over the period that the fishery experienced its greatest historical expansion. To the extent it is an accurate description of what actually happened in the past, it may also be a general guide for planning effective conservation measures for tropical tunas in the future.

The updated oceanographic forcing applied to SEAPODYM and more complete fishing data have improved the accuracy of model catch predictions (Figure S1), but the the overall biomass estimates by SEAPODYM are generally higher than the MFCL estimates (Figure S2). Preliminary experiments at higher resolution indicated that the biomass estimated with SEAPODYM decreases when using more realistic environmental forcing, especially including resolution of mesoscale features such as eddies and fronts to create more patchy concentrations of prey and fish that enables predicting very high catch. At the low resolution used here, in the absence of mesoscale features, the optimization process increases biomass and diffusion to improve the fit to high catch events. The result may artificially overestimate biomass density in $2^{\circ}x2^{\circ}$ cells when, in fact, sporadic large catch events, e.g. from capture of unusually large surface tuna schools, can occur in isolated spots surrounded by extended areas empty of tuna. Schooling behavior in bigeye is less prevalent after the juvenile phase, and unresolved mesoscale oceanographic features in the model likely do not necessarily produce strong biases in predicting longline catch of more diffuse adult biomass.

Hampton et al (2004) estimate the fishery impact on the adult bigeye stock in 1980 to be approximately 30% and to nearly 60% in 2003. Our estimate of the fishery impact on the adult bigye stock in 2003 at 57% is consistent with the impacts estimated from the MFCL stock assessment. More recent assessments, Harley et al (2010), estimate the current fishery impact to be approximately 80%. Reducing the impact to 46% would be a substantial conservation benefit and is consistent with a stock producing maximum sustainable yield.

The purse seine fishing ground was concentrated mainly in the western equatorial Pacific (Figure 2) over the historical fishing period. Closure of area II for purse seine fishing in the WCPFC helps to compensate for the profound effect of the El Niño-Southern Oscillation (ENSO) on the distribution of tropical tunas (Lehodey et al 1997). The extension of the warmer water preferred by skipjack tuna to the east during El Niño episodes results in high purse seine catches of skipjack, and presumably high incidental catches of bigeye, in the central region. SEAPODYM skipjack simulation results (Figure S4) reproduce the observed large ENSO-related zonal displacements of tuna between regions I and II at different stages of the ENSO cycle. There is evidence that ENSO influences the recruitment of tuna. SEAPODYM simulations predict favorable spawning and larval habitat in the equatorial region in agreement with observation (Nishikawa et al 1985), but with a strong variability

associated to the dynamics of ENSO (Figure S4). The result is a high correlation at basin scale between the biomass of skipjack recruited to the stock and the Southern Oscillation Index eight months earlier (Lehodey 2001, Senina et al. 2008). The predicted larval recruitment zone largely overlaps the closure areas I and II.

Therefore, implementing the area closures in region II in combination with the closure in region I would ameliorate the effects of ENSO on the efficacy of the area closures as conservation measures, and mitigate the long-term variability, both by reducing catch of juveniles and protecting part of the spawning grounds whatever the ENSO phase. If future changes projected under IPCC scenarios predicting more frequent central ("Modoki-type") El Niño events are correct, a spatial shift of the core habitat of skipjack and bigeye tunas toward the central Pacific will occur (Lehodey et al 2010b; Lehodey et al, in press). Therefore, closure area II should be effective for management of these fisheries as the climate warms.

Simply closing areas to purse-seine fishing, however, produces only very small increases in bigeye biomass. Area closures could even be counter-productive in some cases if fishing effort is simply displaced and the closure is used as a justification to increase fishing effort outside of the closed areas. Provisional analysis of the 2010 PS closure of area I alone shows that the closure was fairly well respected by the PS fleets, but total PS effort increased by 10% and was deployed in the EEZs surrounding area I. This outcome suggests that the response of the PS fleets to the closures was not only to deploy effort in areas adjacent to the closed areas but also to increase effort in these areas. This "redeployment" of fishing effort is more extreme than the redeployment scheme assumed by our scenario C, that gives almost no effect on the bigeye adult stock with decrease of biomass in some regions (not shown). Given the negligible benefit to bigeye attributable to scenario 1, the 2010 situation almost certainly increased fishing mortality of juvenile bigeye.

Even if the displaced effort from the purse seine fishery is permanently deleted, the average increase in bigeye biomass is 1% or less at the population level and reaches 5-6% locally, i.e., in and near the closed-areas. Nevertheless, this area closure scenario, coupled with effort reduction, allows the spawning stock to grow slightly under historical oceanographic conditions instead of continuing to decline and also maintains the fishery impact near that estimated for 1980. Significant increase in bigeye spawning biomass (7.2%) appears when area II is closed to longline fishing in conjunction with closure and elimination of PS effort in areas I and II. The effects of closing area II to longline fishing are not only more substantial than PS closures, they are widespread throughout the Pacific Ocean (Figure 6). Area II is the western part of a known bigeye spawning area that begins in the EPO, and the size at 50% maturity of female bigeye is near the size caught by longliners (Schaefer et al 2005). The longline fishery targets sexually mature adult fish, and the effect of the growth of juvenile bigeye bycatch in the purse seine fishery is effectively to extend the fishing mortality to the entire life history of the bigeye stock. It is not surprising, therefore, that removal of longline fishing in area II would have a beneficial effect on the bigeye population in conjunction with reduction of juvenile mortality.

Our analysis confirms previous results (Martell et al 2005; Hampton and Harley 2009 and 2010) that spatial measures alone are not sufficient to achieve management objectives for heavily exploited stocks. On the other hand, our results show that area closures, provided that the displaced fishing effort is regulated, have both a strong local impact and a spillover effect through the whole entire range of the species. This conclusion supports the conclusion by Sibert and Hampton (2003) that management measures for highly migratory species taken on the scale of EEZs and the high-seas pockets can be useful fishery management tools. Predicted biomass increase is non-uniform over the model domain, and the predictions enable countries to estimate the efficacy of conservation measures based on spatial

closures in terms of economic impact on own domestic fisheries operating in their EEZs. Jensen et al (2010) also document an example of the successful use of area closures to improve management for fisheries for striped marlin (*Kajikia audax*) near the coast of Baja California.

Spatial fishery conservation measures need to be rigorously evaluated prior to implementation. Spatial measures also must be carefully monitored to determine the fate of displaced fishing effort as well as to determine the spatial extent of the results. Spatially-explicit models of population dynamics such as SEAPODYM combining environmental and fishing effects and a rigorous optimization approach seems particularly well adapted to such a task. We have explored potential fishery management measures, based on area closures combined with gear restrictions. We have certainly not exhausted the potential range of area-based conservation measures, but our results and discussions suggest approaches for developing of ecosystem-based ocean zoning resource management. Our results alos establish the SEAPODYM model as a suitable tool for evaluating area-based fishery management policies. Further research is required to explore other policies and to evaluate the costs of alternative policies. Simulations are available for skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*T. albacares*) and will be used to evaluate the magnitude of the foregone catches of these two species under different management scenarios.

Conclusions:

1.Closing areas to purse seine fishing without consideration of the fate of displaced fishing effort will not be effective for bigeye conservation.

2. Conservation measures that combine closing areas to purse seine fishing and proportional reduction of fishing effort may yield a small bigeye conservation benefit.

3. Restricting longline fishing in known bigeye spawning areas in combination with purse seine area closures and effort reduction offers the best option for achieving effective bigeye conservation.

4. Limitation of FADs use would have a strong positive impact on bigeye stock conservation

5. Benefits from any bigeye conservation measure will only be detectable after 10 years and be fully realized after two decades, i.e. in the 2030s assuming timely implementation. Recovery will be modulated by both natural and anthropogenic climate-related ecosystem variability. Environmental changes induced by anthropogenic release of greenhouse gases should be clearly visible by the end of the 2030's (Lehodey et al 2010b). The status of bigeye stock at that time will depend on today's conservation and management measures.

6. The bigeye population encompasses both the WCPFC and IATTC convention areas. Though spatial measures have a strong local effect, they also have a spillover effect at the whole range of the species. Thus, the management of this stock would benefit from collaborative and coordinated actions of both international Commissions.

Acknowledgments

We thank Laurence Cordonnery for her early contributions to the work described in this report and John Hampton of the Secretariat of the Pacific Community (SPC) for comments on previous drafts of this paper. We also thank Michael Hinton of the Inter-American Tropical Tuna Commission and Peter Williams of SPC for supplying critical fishing data from the EPO and the WCPO respectively. This work was funded by the EU-SPC SCIFISH project, CLS, France and Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA). Views expressed in the paper do not necessarily represent the views of these agencies, their sub-agencies, or their member countries.

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Table 1. Percentages of the Pacific Ocean and the WCPFC Convention Area comprised by areas I and II, and percentages of the purse seine and longline total catches (1980-2003) of bigeye and skipjack from these areas.

			PS (I)		PS (II)		PS FADs		LL (I+II)	
	Area I	Area II	SKJ	BET	SKJ	BET	SKJ	BET	SKJ	BET
WCPFC	2.0	4.0	16.6	2.4	2.8	0.97	43.6	12.8	0	14.75
Pacific	1.2	2.3	14.2	0.6	2.4	0.25	37.1	3.3	0	3.8

Table 2. Definition of fishery management scenarios used in the simulation.

Abbreviation	Description
0	No change from the observed fishing pattern.
С	Close all areas in Figure 1 to purse-seine fishing; redistribute the displaced effort in proportion to the distribution of catch per unit of effort (CPUE) outside of the closed areas.
Е	No closed areas; purse-seine fishing effort reduced by the amount that would have been lost under scenario C.
CE	Close all areas in Figure 1 to purse-seine fishing; eliminate displaced fishing effort.
CL	Scenario C plus close area II to longline fishing.
EL	Scenario E plus close area II to longline fishing.
CEL	Scenario CE plus close area II to longline fishing.
F2S	No closed areas; Prohibit use of FADs in all convention area and shift FAD purse- seine effort to "free" schools.
F2SL	Scenario F2S plus close area II to longline fishing.
F=0	Fishing mortality set to zero; no fishing in the model domain.



Figure 1. Map of the WCPO³ showing the WCPFC Convention Area (red) with Exclusive Economic Zones (EEZs) and areas closed to fishing. The high-seas pockets, Area I wholly enclosed by EEZs between 10°N and 10°S and closed from January 2010, are shown in black. The closure area proposed under PNA agreement, Area II, is shown in green and includes all high seas areas between 10°N and 20°S and 170°E-150°W.

³ This map displays indicative maritime boundaries only. It is presented without prejudice to any past, current or future claims by any State. EEZs do not include areas of territorial seas and archipelagic waters. CMM2008-01 does not apply to such areas, although paragraph 5 notes that "The Commission encourages CCMs to ensure that the effectiveness of these measures is not undermined by a transfer of effort into archipelagic waters and territorial seas".



Figure 2. Distribution of skipjack and bigeye catch between 1980 and 2003 in relation to the closed areas (shaded dark gray).



Figure 3. Adult bigeye biomass in the WCPFC convention area predicted with SEAPODYM for nine different scenarios (cf. table 2). The differences between biomass trends for some scenarios are very small, and the plotted curves overlap. The line with the highest biomass in 2003 in each overlapping group. Initial biomass in 1980 was scaled to the MFCL results (see model description in Supplementary Material).



Figure 4. Percent change, $100 \frac{\Sigma_t \Delta B_{ati}}{\Sigma_t B_{at0}}$, in adult bigeye biomass in the WCPFC convention area for eight different scenarios over the simulation period (cf. table 2).



Figure 5. Changes in the distribution of adult bigeye density in the Pacific Ocean under different scenarios at the end of the simulation 1980-2003. **CE**: areas closed to purse seiners and loss of fishing effort; **CEL**: areas closed to purse seiners and loss of fishing effort; **CEL**: areas closed to purse seiners and loss of fishing effort displaced to free schools; **F2SL**: 'F2S' but with additional closure of area II to longline fishing. The color background gives the density in kg km⁻² and the isopleths are the percentage change in biomass relative to the reference simulation with actual fishing effort, scenario '0'.



Supplementary Material

Model description and configuration

SEAPODYM simulates age-structured tuna populations using multiple different life stage cohorts: larvae, juveniles, immature adults, and mature adults. Larval and juvenile stages are transported from the spawning grounds by oceanic currents. Post-juvenile movement is the sum of autonomous movement (linked to body-size and habitat) and physical transport. Fish are considered mature after the age at first maturity. Mature fish contribute to the spawning biomass following a stock-recruitment relationship at the spatial resolution of the model, and their migration movement is controlled by a seasonal switch, function of the latitude, between feeding and spawning habitat. The last age class is a "plus class" where all oldest individuals accumulate. All temporal dynamics are computed at one month time steps in this analysis.

The model domain covers the Pacific basin at a 2° x 2° spatial resolution and monthly time resolution. Two classes of data are used by SEAPODYM. The environmental variables used to regulate the movement and population dynamics in SEAPODYM simulations are temperature, currents, primary production, euphotic depth and dissolved oxygen concentration. Physical variables are provided by the ocean circulation model OPA 9.0 (http://www.nemo-ocean.eu/) in its standard configuration ORCA2, forced by the atmospheric reanalysis NCEP (http://www.cgd.ucar.edu/cas/guide/Data/ncep-ncar_reanalysis.html). This model has been extensively validated and simulates the large scale dynamical and thermodynamical features successfully (Lengaigne et al., 2003). However, it does not resolve mesoscale features as well as coastal upwelling regions. It was coupled to the model PISCES (Aumont and Bopp, 2006) that provided biogeochemical variables. PISCES simulates the marine biogeochemical cycles of carbon and of the main nutrients (N, P, Si and Fe) which limit phytoplankton growth. Description of the model behavior and validation to observations are found in Gorgues et al. (2005), Bopp et al. (2005) and Aumont and Bopp (2006).

Although we are investigating management measures in the WCPO, the stocks we consider occupy the entire Pacific Ocean basin, and the SEAPODYM model domain therefore includes the entire Pacific Ocean basin. Extensive simulation tests have shown that SEAPODYM applications to long living species like bigeye (> 12 yrs) are sensitive to initial conditions. Also, the MFCL stock assessment carried out for the WCPFC begins in 1950, i.e., at the early development of industrial fisheries, and predicts that the bigeye biomass was substantially reduced by 1980 when the SEAPODYM simulations begin. Therefore, initial conditions for SEAPODYM bigeye simulations are scaled to the MFCL results for the year 1980 in the WCPFC convention area, where our summary analysis focuses (Figure 1).

Commercial fishing data (catch, effort and fish size) are used by SEAPODYM to estimate the fundamental model parameters by maximum likelihood techniques (Senina et al., 2008). The likelihood function includes contributions from both total catch and catch by size by all major fleets fishing for tunas and tuna-like species in the WCPO. The estimation procedure is implemented using adjoint techniques coupled to the AUTODIF library (www.admb-project.org) to achieve an efficient at cost-effect estimation procedure. Fishing data from the Secretariat of the Pacific Community (SPC) for the WCPO and from the Inter-American Tropical Tuna Commission (IATTC) for the Eastern Pacific Ocean (EPO, were used in this analysis. These fisheries data are briefly summarized in Table S1.

Table S1. Ocean model configurations used for optimization experiments and areas closure simulations

Seventeen fisheries in the EPO and WCPO were used in all model runs.

Run	Time period	Fishing events used in optimization (catch-effort / size frequencies)		
Optimization	1984 - 2001	313,277 / 8,520		
Hindcast and validation	1978-2003	448,689 / 11,011		
Area closure scenarios	1980-2003	421,074 / 10,716		

Optimization results

The overall spatial fit between prediction and observation is provided by the standard R-squared goodness of fit, with X the catch per unit of effort (CPUE) of fleet f in cell i,j at time step t:

$$R_{ij}^{2} = 1 - \frac{\sum_{tf} \left(X_{ijtf}^{obs} - X_{ijtf}^{pred} \right)^{2}}{\sum_{tf} \left(X_{ijtf}^{obs} - \overline{X}_{ijtf}^{pred} \right)^{2}}$$

The new model configuration and parameterization substantially improved the agreement between predicted and observed catch for both species, Figure S1. The maximum overall mean spatial correlation of the Catch Per Unit of Effort indices of all fisheries is 0.74 for skipjack and 0.66 for bigeye.



Figure S1. Spatial fit to observed CPUE (left) of bigeye for all fisheries over the optimization period (see details on optimization period in Table S1) and catch (left) for all the simulation. Area of circles is proportional to total observed catch. Note that the R-squared goodness of fit is negative in cells where there is nearly zero catch or very frequent null catch events.



Figure S2. Estimates of total Pacific biomass of bigeye by MFCL (red curve) and SEAPODYM (black curve).

Relative changes in bigeye biomass

The trends in relative biomass may exaggerate the benefits of each scenario. Averages over the 25 year simulation period are lower but may be more realistic and useful from a long term management point of view. The average increase in different bigeye biomass by age class is given it Table S3. The average increase in adult bigeye biomass is shown graphically in Figure S3. The fate of the effort displaced from the closed areas has a large effect on the resulting change in biomass. If the displaced effort is simply allowed to redistribute proportionally to existing effort patterns the benefit to the stock biomass averages only about 0.1%. Complete removal of effort without closures increases the benefit to the stock to about 0.7%, and complete removal of effort combined with closures increases the benefit to 0.9%. In all scenarios, closure of Area II to longline fishing results in the largest relative increase in adult bigeye biomass, 7.2% for scenario CEL. Restrictions on the use of FADs also produce an increase in adult bigeve biomass.

Stage	1	2	3	1L	2 L	3 L	FDs	F2S	FDsL	F2SL
Young	0.1	0.7	0.8	0.8	4.6	5.5	3.6	2.8	8.4	7.8
Adult	0.1	0.7	0.9	1.0	6.1	7.2	3.8	2.9	10.3	9.6
Total	0.1	0.7	0.9	0.9	5.4	6.4	3.7	2.9	9.4	8.8

Table S3. Average percentage changes in bigeye biomass by SEAPODYM age class under different management scenarios from 1980 to 2003.



Figure S3. Average percentage increase in adult bigeye biomass the period of the simulation 1980-2003 for eight scenarios.



ENSO Effects





Figure S4. Impact of ENSO on Pacific skipjack and bigeye population dynamics. Predicted distribution of larvae density during El Niño (a: 10/1997-02/1998) and la Niña (c: 10/1998-02/1999) events, and subsequent recruitment in young cohorts in the following months (c: 6/1998-12/1998 and d: 6/1999-12-1999) with superimposed observed total purse seine catch (proportional to circle areas).