

A MULTI STOCK TAG INTEGRATED AGE STRUCTURED ASSESSMENT MODEL FOR THE ASSESSMENT OF ATLANTIC BLUEFIN TUNA

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SUMMARY

We present a Beta version of a spatial, Multistock Age Structured Tag-integrated stock assessment model (MAST) of Atlantic bluefin tuna. MAST models two populations (East and West) of Atlantic bluefin tuna simultaneously in 4 areas, with quarterly time steps. The model estimates F_{msy} and MSY as leading parameters. Each stock has specific growth, maturity and natural mortality parameters. The western stock is assumed to spawn only in the Gulf of Mexico (GOM, ICCAT area 1) and the eastern stock in the Mediterranean (MED, ICCAT area 6). During spawning periods we assume that movement transition from all areas to the spawning area of a given stock are given by that stock's maturity-at-age ogive. Non-spawning fish during that period move according to movement transition probabilities estimated for non-spawning fish but are not permitted in spawning areas during this period. We divided each mark-recapture dataset into three groups according to whether or not the marked animal's stock of origin could be designated as western (1), eastern (2) or unknown (0). In a few cases with recently marked animals, these designations could be made using genetics but we designated the vast majority as eastern or western fish according to whether or not they had been observed in one spawning area or another.

RÉSUMÉ

Nous présentons une version bêta d'un modèle spatial d'évaluation des stocks intégrant le marquage, structuré par âge, pluri-stock (MAST) pour le thon rouge de l'Atlantique. Le MAST modélise simultanément les deux populations (Est et Ouest) de thon rouge de l'Atlantique dans quatre zones, avec des intervalles temporels trimestriels. Le modèle estime F_{PME} et la PME comme paramètres principaux. Chaque stock a des paramètres spécifiques de croissance, de maturité et de mortalité naturelle. Nous nous basons sur le postulat que le stock de l'Ouest ne fraie que dans le Golfe du Mexique (GOM, zone 1 ICCAT) et que le stock de l'Est fraie en Méditerranée (MED, zone 6 ICCAT). Pendant la période du frai, les déplacements postulés de toutes les zones vers le lieu de ponte d'un stock donné sont représentés par l'ogive de maturité par âge du stock. Les poissons ne frayant pas au cours de cette période se déplacent selon les probabilités de déplacement estimées pour les poissons ne frayant pas, mais ils ne sont pas autorisés dans les frayères durant cette période. Nous avons divisé chaque jeu de données de marquage-recapture en trois groupes, selon que le stock d'origine du spécimen marqué pouvait être, ou non, désigné comme de l'ouest (1), de l'est (2) ou inconnu (0). Dans quelques cas avec des spécimens marqués, cette désignation a pu être réalisée en utilisant la génétique mais nous avons désigné la grande majorité des poissons comme originaires de l'est ou de l'ouest, selon qu'ils aient été observés, ou non, dans un lieu de ponte ou dans un autre.

RESUMEN

En este documento se presenta una versión beta de un modelo de evaluación espacial multistock estructurado por edad y que integra el marcado (MAST) del atún rojo del Atlántico. MAST modela dos poblaciones de atún rojo (Este y Oeste) de forma simultánea en cuatro áreas, con etapas temporales trimestrales. El modelo estima F_{RMS} y RMS como parámetros principales. Cada stock tiene parámetros específicos de crecimiento, madurez y mortalidad natural. Se asumió que el stock occidental desova sólo en el Golfo de México (GOM, área 1 de ICCAT) y el stock oriental en el Mediterráneo (MED, área 6 de ICCAT). Se partió del supuesto

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de que durante los periodos de reproducción la transición de los movimientos desde todas las zonas hasta la zona de reproducción de un stock dado estaba determinada por la ojiva de madurez por edad del stock. Durante dicho periodo los ejemplares no reproductores se mueven según las probabilidades de transición de movimiento estimadas para los ejemplares no reproductores, pero no se incluyen en las zonas de reproducción durante dicho periodo. Se dividieron los conjuntos de datos de marcado-recuperación en tres grupos en función de si podía o no designarse el stock de origen del ejemplar marcado como Oeste (1), Este (2) o desconocido (0). En unos pocos casos con ejemplares recientemente marcados, estas designaciones pudieron realizarse utilizando técnicas genéticas, pero la gran mayoría fue designada como ejemplares del Este o del Oeste en función de si habían sido observados o no habían sido observados en una zona de reproducción o en otra.

KEYWORDS

Bluefin tuna, stock assessment, simulation model, tagging

1. Introduction

We fitted MAST to ICCAT's indices of abundance for each area as well as conventional mark-recapture data starting in 1950, archival and pop-off satellite tag data. Abundance indices are fit using log-normal likelihoods where the predicted vulnerable biomass (or number as applicable for each index) is given by the sum of vulnerable biomasses for each stock, area, and quarter combination. Selectivities are modeled as a function of mean length at age, given by stock-specific von Bertalanffy growth parameters. The joint likelihood function therefore consists of 10 components for CPUE data, and for each stock designation (0, 1, and 2) of each mark-recapture data type (conventional, archival or pop-off).

For a base case fit, we treat gear selectivities equal between fleets and growth as known and equal and fit the model estimating movement parameters, leading recruitment F_{msy} and MSY estimates for both stocks at their posterior mode. We explore 4 reconstruction scenarios where we fitted the model to the data with F_{msy} fixed and unfixed and another two testing the performance of the model for these scenarios but down-weighting CPUE likelihoods by 90 %. We show reconstructions for western and eastern stocks of total numbers, biomasses. We emphasize that our software is not catalogued or simulation tested and that we have no intention that the results be put forward for management advice.

2. Methods

Overview

MAST is spatially explicit, age-structured model of discreet Mediterranean (MED) and Gulf of Mexico (GOM) Atlantic bluefin tuna stocks. Fish are moved from area to area at quarterly time steps according to stock-specific movement transition probabilities that are estimated by the model. We assume that recruitment occurs in the second quarter and that it only occurs in designated spawning areas. As such, movement transitions to spawning areas are set to the maturity ogive for that stock. In addition we assume that GOM fish are MED fish do not ever use each other's spawning areas. In this way, GOM and MED fish can only overlap in areas 2 and 3 (ICCAT areas 2-5). The master prediction equation of MAST is.

$$N_{i,l',a+1,t+1} = \sum_{l=L_i(1)}^{l=L_i(3)} N_{i,l,a,t} \mu(l,l') e^{-m_i + \sum_g v_{i,a,g} F_{g,t}}$$

Equation 1. Master prediction equation of MAST where predicted numbers N_{t+1} at time t of stock i at age a are given by numbers at the previous time step $N_{i,t,a}$, the product of gear vulnerability v of stock i to gear g and fishing rate through all gears ($\sum_g v_{i,a,g} F_{g,t}$) and the movement transition matrix μ .

The movement transition matrix μ consists of from-area rows and to-area columns. Rows must sum to 1 (fish either stay in the area they are or go to other areas). We include all symbols, for state dynamics equations in

Table 1 and variable indices in **Table 2**. Catches by gear and area are converted numerically integrating the fishing mortality until the predicted catches over the time step are within 1 ton of observed catches.

MAST is initialized in the first year with maximum sustainable yield, MSY and the fishing rate at MSY , F_{msy} as leading parameters (Forrest et al. 2008) allowing management parameters to be estimated directly from the data. We model all fleets as having the same asymptotic gear selectivity as a function mean size at age (in quarters) given by

$$v_{i,a} = \frac{1}{1 + e^{-\rho_g(\bar{L}_i - Lh)}} \quad -$$

Equation 2. Gear selectivity function for all gears where ρ is the slope of the gear selectivity function, \bar{L}_i is the mean length of stock i at age a and Lh_i is the length at which fish are 50 % vulnerable to the gear. Parameters are given in **Table 1**.

and hence the same partition of the leading MSY and F_{msy} . This is an initial simplification that can be modified later to better reflect gear and regulation changes.

The model is initialized with growth parameters set to those specified by (Parrack and Phares 1979). Set age at maturity for the western stock according (Diaz and Turner 2007) and for the eastern stock we set a_h to 8. We approximate this using a functional form as:

$$\varphi_a = \frac{1}{1 + e^{-\lambda(a - a_h)}}$$

Equation 3. Maturity φ at age a where λ is the slope of the function and age a_h is the age at 50 % maturity.

Sampling for basic life-history parameters sometimes occurs from the mixed stock pool. While currently not implemented the model can use stock composition information and likewise include the effects of sampling from the mixed stock on life-history parameters such as growth, mortality or fecundity, which may or may not have occurred in areas where the stock are mixing fitting such observations to predicted proportions using multinomial likelihoods. At each time step, we predict number and biomass at age in each area. Therefore the proportion of biomass and numbers of each stock is predicted in each area so that predicted stock composition can be fit to observations current being compiled with genetics and otolith microchemistry.

Although we describe a 4 area base case above, the model can use multiple areas and fleets. There are multiple versions, including one that has been formulated with a discreet fishing mortality occurring at each time step using a single fleet. We present the instantaneous, 4 fleet version here.

We use catch by fleet data from ICCAT's TASK1 database. To translate catches into the designated area groups we summed up the latitude longitude cell data corresponding to ICCAT areas. We converted the 6 areas into 4 by making areas 3 4 and 5 a single area so that first is ICCAT area 1, the second area ICCAT area 2, the third area being the sum of ICCAT areas 3-5 and the fourth as ICCAT area 6. For the rest of this paper we will refer to these areas 1-4 (1 GOM; 2. Western Atlantic; 3. Eastern Atlantic; and 4. MED). We fitted MAST to a combination ICCAT's 21 CPUE indices by gear and area. We fitted the indices by summing total predicted numbers at age over which months (reduced to quarters) the index applies to. We fitted the data using a log normal likelihood function using the observation error variances published for each index as the variance term. Catches by area and fleet are plotted in **Figure 1**.

Mark-recapture data

We use conventional tag data (from 1950 to present) from the ICCAT conventional tag database, archival tag, and pop-up satellite tag data for this analysis. Documentation of archival and satellite tag data is found in (Block et al. 2001, Block et al. 2003, Block et al. 2005).

We divided all mark-recapture datasets into three groups: those that could be designated western stock, eastern stock or unknown. In a few cases these designations could be based on genetics but in the vast majority of cases we made this designation based on whether or not tagged fish were observed in the GOM or in the MED, in which case they were designated as being GOM or MED fish. Thus implicit in this analysis is the assumption that fish from either stock do not use each other's particular spawning areas. We then parsed all mark-recapture observations into histories with initial time at marking, and subsequent observations o .

Mark-recapture likelihoods (Table 11)

MAST uses 9 different discreet state-space likelihoods (De Valpine and Hastings 2002) to model mark-recapture data. We will give an overview of the method here but encourage readers to consult this reference for underlying theory and details. We chose this method in order to use all location-state information for each tag time series, rather than just start and end points. Strictly speaking we model tags, not fish, through discreet states for each model time step. We discuss the designation of these states below.

Seasonal and age dependencies of movement rates are incorporated in the estimation by (1) assigning each fish of stock i an apparent age-at-first-capture based on its length based on (Parrack and Phares 1979) and then assigning fish to a particular age group whose movement parameters are assumed to be the same. Currently length-to-age conversions are applied to both stocks with the same growth parameters external to the model to reduce computational burden but it is possible to do so in the model according to estimated stock-specific growth parameters, and propagate age-assignment and growth uncertainty in this conversion forward. The data do not permit estimating movement transition matrices for each age group so we divide movement parameters into three groups corresponding to ages 1-3, 4-8 and 9+ assuming that movement is similar between those groups.

Whether tags be conventional, archival or pop-up types, we have a recapture history of the form $Y_t = \{0, 0, 0, \dots, 0, 0, \dots\}$ where for each possible sampling date an observation $y_t=0$ denotes no recapture and a $y_t=l$ denotes at least one recapture in location l . In addition to location-state events we define capture gears g for conventional and archival tags that define gear used to recover the tag.

We calculate the likelihood $P(Y_t)$ of each history using the recursive method reviewed in (De Valpine and Hastings 2002) where $P(Y_t)$ is represented as:

$$P(Y_t) = P(Y_{t-1})P(y_t/Y_{t-1}).$$

Equation 4. Probability of mark-recapture histories.

To use this representation, we note that the probability of an event k , in a recapture history $P(y_t/Y_{t-1})$ can be written as:

$$P(y_t/Y_{t-1}) = \sum_s P(s_t/Y_{t-1})P(y_t/s_t, Y_{t-1})$$

Equation 5. Probability of observation y_t given the state up until time $t-1$.

where s_t represents possible tag states ($s_t = \{ \text{on dead fish, on live fish in location 1, alive in location 2, } \dots \}$) and $P(y_t/s_t, Y_{t-1})$ is the observation probability of y_t given that the fish is in state s_t . Representation for $P(y_t/Y_{t-1})$ in terms of states s_t expresses the problem of calculating it as two simpler problems, calculation of location state probabilities $P(s_t/Y_{t-1})$ and observation probabilities $P(y_t/s_t)$.

For different combinations of stock-designation and tag type, possible states and observation probabilities are modeled differently. We describe these differences in some detail below. In general however, tag states are assumed to be: attached to living fish in permitted stock areas (i.e. on GOM fish in areas 1-3 or on a MED fish in areas 2-4); attached to a recently captured fish on the deck of a fishing vessel in areas; shed or dead.

Archival tag state-space likelihood for fish having stock designations

In those cases where fish stock of origin is assumed known, tags states are assumed to be either on a living fish of stock i in stock areas, captured in fishing gear, shed, or attached to a dead fish. Given a matrix L_i of permitted

areas ($L_i(1,2,3)$ for the GOM stock and $L_i(2,3,4)$ for the MED stock) we define 8 states, the observation probabilities given these states ($p(y_i/s_i)$) and the state probabilities given all observation up until t , $P(s_i/Y_{t-1})$ and summarize how these values are computed in tables **Table 3** for $p(y_i/s_i)$ and **Table 5**.

Observation probabilities given the state $p(y_i/s_i)$ can be easily defined when there is an observation ($o>0$) in a capture history. If the tag is 'observed' in areas 1-3 ($s=1$ to 3), it remains implanted in the fish, with the tag still recording geositions. In this case, the observation probabilities are given by the (possibly time or area-dependent) probability of getting a geosition γ . If the fish is observed captured ($s=4-6$) in areas $L_i(1,2,3)$, then $p(y_i/s_i)$ is the reporting rate R for fleet g . Observation probabilities for shed or dead state are typically set zero. Since each event is mutually exclusive (i.e. tags cannot be on a living swimming fish and also on the deck of a fishing boat or dead or shed), when an observation is made the probabilities of all other $p(y_i/s_i)$ are null. When no observations are made, $p(y_i/s_i)$ for states 1-3 are set to the compliment of the capture probabilities ($1-\gamma$), the compliment of the possible time and fleet varying reporting rate ($1-R$) for states 4-6 and to 1.0 for states 7-8.

Computation of $P(s/Y_{t-1})$ for each s are more complex. The sequence of fates for each fish is assumed to be movement, shedding, natural mortality then fishing mortality. Since in this case stock designation is assumed known, the probability that the tag is on a fish from stock i in the release area is 1. At the next time step we calculate $P(s_{t+1}|Y_t)$ (which is $P(s_t|Y_{t-1})$ for the next time step) according the equations listed in **Table 3**. The computations can be understood using the following example. In order for a tag to be on a fish in area s' , the fish may have been alive in other areas (given by $P(s_i/Y_{t-1})$), then moved from area l to area l' according to the estimated movement transition matrix for that fish $\mu_{l,l'}$, survived natural mortality and fishing

($e^{-m_{t-1} + \sum_g v_{g,t-1} F_{g,i,t-1}}$) and finally did not shed its tag ($1-D_{t-1}$). The probability of the state is given by

Equation 5 by summing across all transitions from s to s' . The parameter μ is the estimated movement transition matrix consisting of from-area rows, and to-area columns. Diagonals of μ are the probability that the fish states where it is. Mathematically this is example is represented by the first row in **Table 5** with all other model states in subsequent rows. Note that MAST does not permit fish to spontaneously return from dead or shed states to living states - so transitions from dead to dead states are set to 1. Similarly transition probabilities from shed or dead states to $s=1-3$ are set to zero. The log-likelihood then simply the sums of the log of the probability of the entire capture history given by equation 1.

Conventional tags with stock designations

Modeling state transitions for conventional tags is identical to archival except with shedding rates D corresponding to the tag type k . However modeling $p(y_i/s_i)$ is modeled differently for obvious reasons if the tag is still on the fish in areas L_i then the probability of observing it is zero. A few conventional tags were re-released alive, or with a new tag, in which case $P(s_{t+1}/Y_t)$ is set to 1 for the area released. With conventional tags, $p(y_i/s_i)$ is simply 1 in the area that it was observed (with all observation probabilities set to zero). We show how $p(y_i/s_i)$ is designated in

Table 4.

PSAT tag state-space likelihood for fish having stock designations

Computation of the likelihoods for pop-off tags having stock designations is the same except that we add an additional state for the tag popping π and where D in this case is a combined shedding/malfunction probability instead of a shedding rate for archival tags. Computation of $p(y_i/s_i)$ is listed in

Table 7 and of the state probabilities in **Table 8**. Note here that γ and D refer to the specific tag type. We created and addition type of observation type when a pop-off event occurred ($k=10$). The probability such an event is the probability that the fish survived fishing and natural mortality, and tag failure and that the tag popped off. We model the probability the tag popped off given the programmed pop-off date π as being normally distributed with mean programmed pop-off date μ_π and the estimated pop-off date standard deviation σ_π .

$$\pi_t \sim N(\mu_\pi, \sigma_\pi)$$

Equation 6. Probability of a pop-off event.

We model states just as we did for archival tags but with the addition of the popped-off state **Table 8**.

Archival tag state-space likelihood for fish without stock designations

Modeling movement trajectories for fish of unknown stock of origin is more complex. Recall that when the stock of origin is known, the probability of the state at the first time step is trivial (tag is on a fish of stock i in the area where it was marked). However if the stock of origin is unknown, then the tag could be on a GOM fish or on a MED fish. Therefore for each state transition we must model whether or not the tag is on a GOM or a MED fish, moving and dying according to stock-specific-natural mortality, fishing mortality (due to possible differences in size at age) and movement transitions. We include these model equations in **Table 9** for archival and conventional tags and in for PSAT tags in **Table 10**.

CPUE index and parameter fitting scenarios (Table 13)

We fitted the model to available indices listed in **Table 15** and to all available mark-recapture data. We ran two scenarios where we allowed F_{msy} and MSY to be estimated freely with no likelihood re-weighting. For the second set, we down-weighted CPUE likelihoods by 90%. We summarize runs conducted and parameter estimates in **Table 14**.

Likelihood

We use prior densities for all estimated parameters listed in **Table 12**. The joint posterior then consists of 16 log-normal likelihood for CPUE data, 3 multinomial likelihoods for each stock designation of archival tags, 3 multinomial likelihoods for each stock designation of PSAT tags, and 3 multinomial likelihood likelihoods for conventional tag data. Priors are listed in **Table 12**. Fitting was done using conjugant gradient fitting algorithm provided by AD model builder, which is a C++ library that does automatic differentiation. AD model builder is proprietary software used under license by the Fisheries Center at the University of British Columbia. Full documentation of it and trial versions can be obtained at <http://otter-rsch.com/admodel.htm>.

3. Results and discussion

Having two stocks moving presents statistical catch-at-age models such as MAST with many possible ways of explaining the data and the relative weighting of different data sources has big effects on MAST's predictions. The major explanation for this is that there are very few data that can be used to describe stock-specific movement trajectories since the vast majority of mark-recapture observations consist of fish that have undesignated stocks of origin (see **Table 16**). As a result, the model can move fish around in order to best fit CPUE indices with little penalty for producing unreasonable GOM or MED stock sizes. One desperately needed item is to assign stock of origin for tagged fish, to the extent possible and to sample historical and current catch samples for relative stock numbers. This information can be readily included in MAST as a set of multinomial observations. Additional iterative re-weighting schemes should be employed to further test the model's sensitivity to such likelihood weighting of various kinds. It would also be useful to have longer time CPUE series for times before the 1970's VPA assessment start point. While the VPA cannot use them, it should prove hugely useful to fit them with this model to help properly characterize the population dynamics earlier in the time series.

In spite of some of the existing drawbacks, modeling Atlantic bluefin population dynamics at finer scale offers several advantages over traditional one or even two boxes. In particular, our principle aim in stock assessment modeling is to present the possible consequences of different policy actions. With MAST it will be possible to examine the effects of smaller scale temporal and spatial closures.

While finer spatial dynamics are possible with MAST, the existing model stretches the limit of conventional 32 bit operating systems since a lot of memory is required to store derivative information needed in order to calculate Hessian and covariance matrices. The memory footprint is about 1.1 gigabytes. In addition to the memory burden, the model is slow - the current four area model requires at least an hour to converge.

While we have been critical of the problems associated with CPUE indices here our own analysis of mark-recapture data begs a thorough examination of potential biases by mark-recapture programs used to date. Indeed some of the same criticisms applied to how CPUE data does not representatively sample the potential fish distribution apply to mark-recapture data also. To a large extent, tags of all types have been put on fish only over a very limited distribution. Given that the stocks are distributed over much of the Atlantic Ocean over a tiny sample of the possible sampling universe. In addition, we have only sampled those fish having movement trajectories that allowed them to be captured and marked, and subsequently recaptured making our sample one only of those fish whose movement trajectories resulted in their getting captured in fishing gear. A related matter to examine here is how time and area-dependent reporting rate will affect our interpretation of stock movement. These are matters that still require considerable examination in the form of simulation testing.

Including additional analysis of tag-reporting rates, and better characterizing gear-selectivity, and how it has changed over the course of the fishery are the next most important matters to attend to in the development of MAST. While we recognized it to be an issue from the very beginning that simplification of gears into a single gear type with an asymptotic shape was not representative of the current state of affairs this simplification was necessary to get the model off the ground. To deal with the latter, it would be hugely useful to build this model conditioned on effort, rather than on catches. In this way, dynamics producing CPUE hyperstability could be modeled and tested. We initially explored the use of the TASK-II dataset for this purpose but it was incomplete. Modeling the dynamics conditioned on effort would help deal with changes in effort distribution as well as smaller spatial scale dynamics.

It bears repeating that we in no way intend our results to be used for management purposes until this model has been properly vetted. These results are intended to be a description of what the model is capable of doing and some preliminary explorations of the sensitivities of different data types. Much work remains to be done in properly scaling stock reconstructions and simulation testing.

References

- Block, B.A., Boustany, A., Teo, S., Walli, A., Farwell, C.J., Williams, T., Prince, E., Stokesbury, M., Dewar, H., Seitz, A. and Weng, K., 2003. Distribution of western tagged Atlantic bluefin tuna determined from archival and pop-up satellite tags. *Collect. Vol. Sci. Pap. ICCAT*, 55(3): 1127-1139.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L. H., Seitz, A., Walli, A., and Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293: 1310-1314.
- Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J., Weng, K. C., Dewar, H. and Williams, T. D., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434:1121-1127.
- De Valpine, P. and Hastings, A., 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs* 72:57-76.
- Diaz, G. and Turner, S. C., 2007. Size-frequency distribution analysis, age-composition and maturity of western bluefin tuna in the Gulf of Mexico from the U.S. (1981-2005) and Japanese longline fleets. *Collect. Vol. Sci. Pap. ICCAT*, 60(4): 1160-1170.
- Forrest, R.E., Martell, S.J. D., Melnychuk, M.C. and Walters, C.J., 2008. An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 286-296.
- Parrack, M.L. and Phares, P.L., 1979. Aspects of growth of Atlantic bluefin tuna determined from mark-recapture data. *Collect. Vol. Sci. Pap. ICCAT*, 8(2): 356-366.

Table 1. Model variables and symbols.

<i>Parameter Name</i>	<i>Symbol</i>	<i>Value stock 1 (GOM)</i>	<i>Value stock 2 (MED)</i>
Asymptotic size	L_{∞}	313cm	313cm
von Bertalanffy growth parameter	K	0.09	0.09
Age at theoretic zero length	t_0	0.96 years	0.96 years
Gear selectivity length at half selectivity (all gears)	L_h	{50,50,50,50} cm	{50,50,50,50} cm
Gear selectivity slope (all gear)	ρ	{0.1 0.1 0.1 0.1}	{0.1 0.1 0.1 0.1}
Maturity at age	ϕ	-	-
Age at half maturity	a_h	11	8
Slope of the maturity ogive	λ	2	2
Length-weight conversion coefficient	α	36.285	36.285
Length-weight conversion exponent	b	0.3381	0.3381
Length-weight conversion equation	$L=\alpha W^b$	-	-
Natural mortality	M	0.13	0.13

Table 2. Table of indices for population dynamics equations.

<i>Indices</i>	<i>Symbol</i>
Stock	i
Year	y
Age	a
Gear	g
Quarter	qa
Time	t
State	s
Area	l
Tag type	k

Table 3. Probability of observations given the state $p(y_t/s_t)$, by state index for archival tags.

State Index	Tag State s_t	Observation Probabilities $p(y_t/s_t)$ where	Observation Probabilities $p(y_t/s_t)$ where
1-3	On fish area i	γ	$1-\gamma$
4-6	Captured in fishing gear g in area l	R	$1-R$
7	Shed	0	1
8	Dead	0	1

Table 4. $p(y_t/s_t)$ for conventional tags.

State Index	Tag State s_t	Observation Probabilities $p(y_t/s_t)$ where $k>0$	Observation Probabilities $p(y_t/s_t)$ where $k>0$
1-3	On fish in areas L_i	0	0
4-6	Captured in fishing gear g in area l	R	$1-R$
7	Shed	0	1
8	Dead	0	1

Table 5. Probability of the state given the data $P(s_{t+1}|Y_t)$ until time t-1 for archival tags in fish of known stock origin.

State Index	Tag State s_t	State Probabilities $p(s_t Y_{t-1})$
1-3	On fish areas L_i	$P(s_{t+1} Y_t) = \sum_{l=L_t(s=1)}^{L_t(s=3)} \mu(l, l') P(s_t Y_{t-1}) e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1} F_{g,i,t-1})} (1 - D_{t-1})$
4-6	Captured in fishing gear g in area l	$P(s_{t+1} Y_t) = \sum_{l=L_t(1)}^{L_t(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}}) (1 - D_{t-1}) + \sum_{s=4}^6 P(s_t Y_{t-1})$
7	Shed	$P(s_{t+1} Y_t) = \sum_{l=L_t(1)}^{L_t(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}}) D_{t-1} + P(s_t = 7 Y_{t-1})$
8	Dead	$P(s_{t+1} Y_t) = \sum_{l=L_t(1)}^{L_t(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}} (1 - e^{-m_{i,t-1}}) (1 - D_{t-1}) + P(s_t = 8 Y_{t-1})$

Table 6 . Probability of the state given the data $P(s_{t+1}|Y_t)$ until time t-1 for PSAT tags in fish of known stock origin.

State Index	Tag State s_t	State Probabilities $p(s_t Y_{t-1})$
1-3	On fish areas L_i	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1 - \pi)\mu(l, l') P(s_t Y_{t-1}) e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1} F_{g,l,t-1})} (1 - D_{t-1})$
4-6	Captured in fishing gear g in area l	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1 - \pi)\mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,l,t-1}}) (1 - D_{t-1}) + \sum_{s=4}^6 P(s_t Y_{t-1})$
7	Popped off	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \pi\mu(l, l') P(s_t Y_{t-1}) e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1} F_{g,l,t-1})} (1 - D_{t-1})$
8	Shed	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1 - \pi)\mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{g,t-1} F_{g,i,t-1}}) D_{t-1} + P(s_t = 8 Y_{t-1})$
9	Dead	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1 - \pi)\mu(l, l') P(s_t Y_{t-1}) e^{-\sum_g v_{g,t-1} F_{g,i,t-1}} (1 - e^{-m_{i,t}}) (1 - D_{t-1}) + P(s_t = 9 Y_{t-1})$

Table 7 . $p(y_t/s_t)$ for PSAT tags.

State Index	Tag State s_t	Observation Probabilities $p(y_t/s_t)$ where	Observation Probabilities $p(y_t/s_t)$ where
1-3	On fish areas L_i	γ	$1 - \gamma$
4-6	Captured in fishing gear g in area i	1	$1 - R$
7	Shed	0	1
8	Pop off	1	0
9	Dead	0	1

Table 8 . Probability of the state given the data $P(s_{t+1}|Y_t)$ until time t-1 for PSAT tags in fish of known stock origin.

Table 9. Model of archival tag states put on fish of unknown origin.

State Index	Tag State s_t	State Probabilities $p(s_t Y_{t-1})$
1-3	On GOM fish areas $l=L_i$	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1} F_{g,i,t-1})} (1 - D_{t-1})$
4-6	On MED fish areas $l=L_i$	$P(s_{t+1} Y_t) = \sum_{l=L_2(1)}^{L_2(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1} F_{g,i,t-1})} (1 - D_{t-1})$
7-9	On GOM (i=1) Fish Captured in fishing gear g	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}}) (1 - D_{t-1}) + \sum_{s=7}^9 P(s_t Y_{t-1})$
10-12	On MED (i=2) fish Capture in fishing gear g	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}}) (1 - D_{t-1}) + \sum_{s=10}^{12} P(s_t Y_{t-1})$
13	Shed on GOM (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}}) D_{t-1} + P(s_t = 7 Y_{t-1})$
14	Shed on MED (i=2)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-m_{i,t-1}} (1 - e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}}) D_{t-1} + P(s_t = 7 Y_{t-1})$
15	Dead GOM (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}} (1 - e^{-m_{i,t}}) (1 - D_{t-1}) + P(s_t = 9 Y_{t-1})$
16	Dead on MED (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \mu(l, l') P(s_t Y_{t-1}) e^{-\sum_g v_{i,g,t-1} F_{g,i,t-1}} (1 - e^{-m_{i,t}}) (1 - D_{t-1}) + P(s_t = 9 Y_{t-1})$

Table 10. Table of modeled tag state for PSAT tags attached to fish of unknown origin.

State Index	Tag State s_t	State Probabilities $p(s_t Y_{t-1})$
1-3	On GOM fish areas $l=L_i$	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1}F_{g,i,t-1})} (1-D_{t-1})$
4-6	On MED fish areas $l=L_i$	$P(s_{t+1} Y_t) = \sum_{l=L_2(1)}^{L_2(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1}F_{g,i,t-1})} (1-D_{t-1})$
7-9	On GOM (i=1) Fish Captured in fishing gear g	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-m_{i,t-1}}(1 - e^{-\sum_g v_{i,g,t-1}F_{g,i,t-1}})(1-D_{t-1}) + \sum_{s=7}^9 P(s_t Y_{t-1})$
10-12	On MED (i=2) fish Capture in fishing gear g	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-m_{i,t-1}}(1 - e^{-\sum_g v_{i,g,t-1}F_{g,i,t-1}})(1-D_{t-1}) + \sum_{s=10}^{12} P(s_t Y_{t-1})$
13	Popped off on GOM (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \pi\mu(l,l')P(s_t Y_{t-1})e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1}F_{g,i,t-1})} (1-D_{t-1})$
14	Popped off on MED (i=2)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} \pi\mu(l,l')P(s_t Y_{t-1})e^{-(m_{i,t-1} + \sum_g v_{i,g,t-1}F_{g,i,t-1})} (1-D_{t-1})$
15	Shed on GOM (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-m_{i,t-1}}(1 - e^{-\sum_g v_{i,g,t-1}F_{g,i,t-1}})D_{t-1} + P(s_t = 7 Y_{t-1})$
16	Shed on MED (i=2)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-m_{i,t-1}}(1 - e^{-\sum_g v_{i,g,t-1}F_{g,i,t-1}})D_{t-1} + P(s_t = 7 Y_{t-1})$
17	Dead GOM (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-\sum_g v_{i,g,t-1}F_{g,i,t-1}}(1 - e^{-m_{i,t-1}})(1-D_{t-1}) + P(s_t = 9 Y_{t-1})$
18	Dead on MED (i=1)	$P(s_{t+1} Y_t) = \sum_{l=L_i(1)}^{L_i(3)} (1-\pi)\mu(l,l')P(s_t Y_{t-1})e^{-\sum_g v_{i,g,t-1}F_{g,i,t-1}}(1 - e^{-m_{i,t-1}})(1-D_{t-1}) + P(s_t = 9 Y_{t-1})$

Table 11. Table of symbols for mark-recapture likelihoods.

<i>Parameter Description</i>	<i>Units</i>	<i>Symbol</i>
Maximum sustainable yield	yr ⁻¹	<i>MSY</i>
Fishing rate to achieve MSY	yr ⁻¹	<i>F_{msy}</i>
Fishing mortality	yr ⁻¹	<i>F</i>
Natural mortality	yr ⁻¹	<i>M</i>
Movement transitions	yr/4 ⁻¹	<i>μ</i>
Recapture History	-	<i>Y</i>
Recapture Observation	-	<i>y</i>
State	-	<i>s</i>
Probability of observation given the state and all data until t-1	-	<i>P(y_t/s_t, Y_{t-1})</i>
Probability of the state given all data up until time t-1	-	<i>P(s_t/Y_{t-1})</i>

Table 12. Prior densities used for base-case model fitting.

<i>Parameter</i>	<i>Symbol</i>	<i>Prior</i>
Maximum sustainable yield (<i>kt</i> {stock1, stock 2})	<i>MSY</i>	{N~(5,10), N~(25, 50)}
Fishing rate to yield msy (/yr) {stock1, stock 2}	<i>Fmsy</i>	{ N~(5,10), N~(25, 50)}
Movement parameters	<i>μ</i>	Beta(2,2)
Probability of a geolocation	<i>γ_g</i>	Beta(2,2)
Standard Deviation of pop-off quarter given programmed pop-off	<i>σ_π</i>	N~(1,5)

Table 13. Fitting scenarios used for preliminary fitting.

<i>Scenario Number</i>	<i>F_{msy} estimation</i>	<i>CPUE likelihood weighting</i>
1	Free	0.5
2	Fixed at {0.6,0.6}	0.5
3	Free	0.1
4	Fixed at {0.6,0.6}	0.1

Table 14. Estimated parameters and corresponding values for each scenario run.

Parameter Name	Symbol	Value				Fit		or		Fixed	
		Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 1	Scenario 2	Scenario 3	Scenario 4		
Fishing mortality producing MSY (/yr)	F_{msy}	GOM=0.120 MED=0.122	GOM=0.06 MED=0.06		GOM=0.06 MED=0.06	Fit	Fixed	Fit	Fixed		
Maximum sustainable yield (kilotonnes)	MSY	GOM=6.63 MED=23.34				Fit	Fit	Fit	Fit		
Archival and PSAT probability of geoposition	γ_g	0.65				Fit	Fit	Fit	Fit		
Reporting R conventional tag	Rc	0.12	0.12	0.12	0.12	Fixed	Fixed	Fixed	Fixed		
Reporting Rate Archival and PSAT	Ra	0.20	0.20	0.20	0.20	Fixed	Fixed	Fixed	Fixed		
Conventional Tag shedding rate /yr	Dc	0.12	0.12	0.12	0.12	Fixed	Fixed	Fixed	Fixed		
Archival Tag shedding Rate /yr	Da	0.12	0.12	0.12	0.12	Fixed	Fixed	Fixed	Fixed		
Standard deviation of pop-off date (quarters)	σ_π	0.65				Fit	Fit	Fit	Fit		
Mean pop-off date given predicted popoff date (quarter)	μ_π	0	0	0	0	Fixed	Fixed	Fixed	Fixed		

Table 15. Table of CPUE indices fitted with for base run.

<i>CPUE Index</i>
CAN GLS
CAN SWNS
US RR >195
JLL Area 2
JLL GOM
GOM Larval Zero Inflated
US PLL GOM
SP BB1
SP BB2
SP BB3
SP BB4
SP BB5
SP BB 7-15
SP BB 15-25
SPBB All
SP Trap

Table 16. Summary of mark-recapture data used.

<i>Mark-recapture data type</i>	<i>Number of modeled tags</i>
GOM Archival Tags	10
MED Archival Tags	13
Undesignated Archival Tags	29
GOM PSAT Tags	17
MED PSAT Tags	14
Undesignated PSAT Tags	114
GOM Conventional	1965
MED Conventional	92
Undesignated Conventional	43791

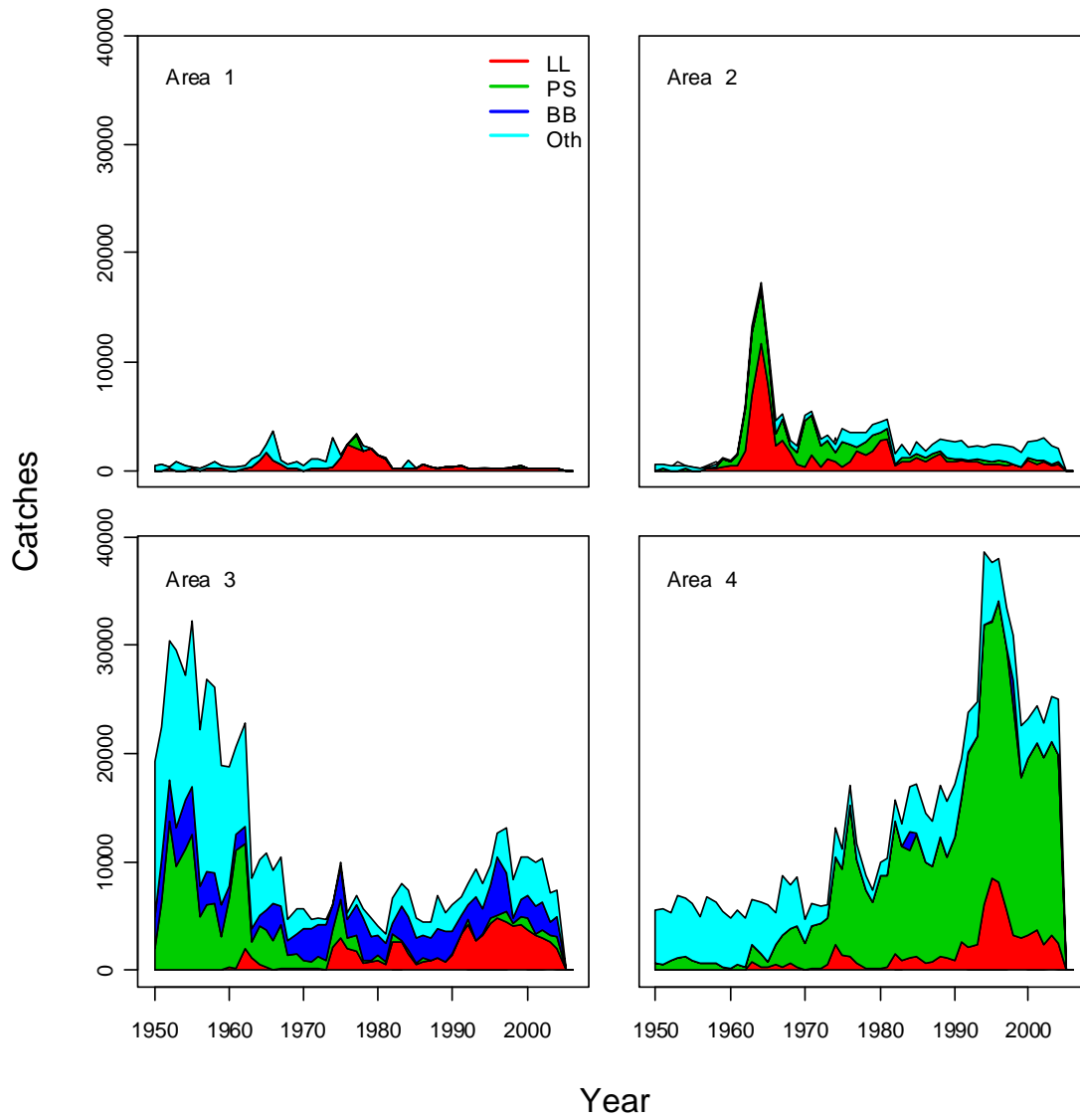


Figure 1. Catches by fleet and area.

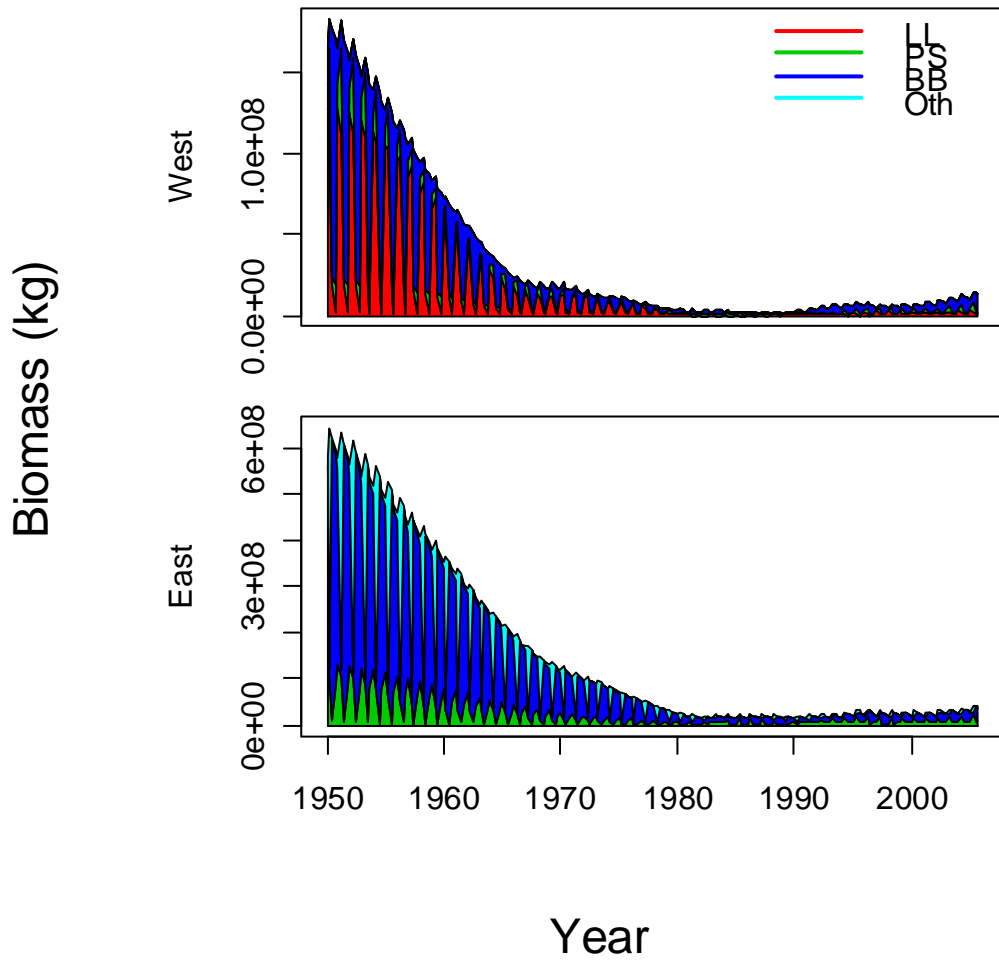


Figure 2. Reconstructed total biomasses for Western (top) and Eastern (bottom) stocks based on fits with F_{msy} free and CPUE likelihoods down-weighted by 90 %.

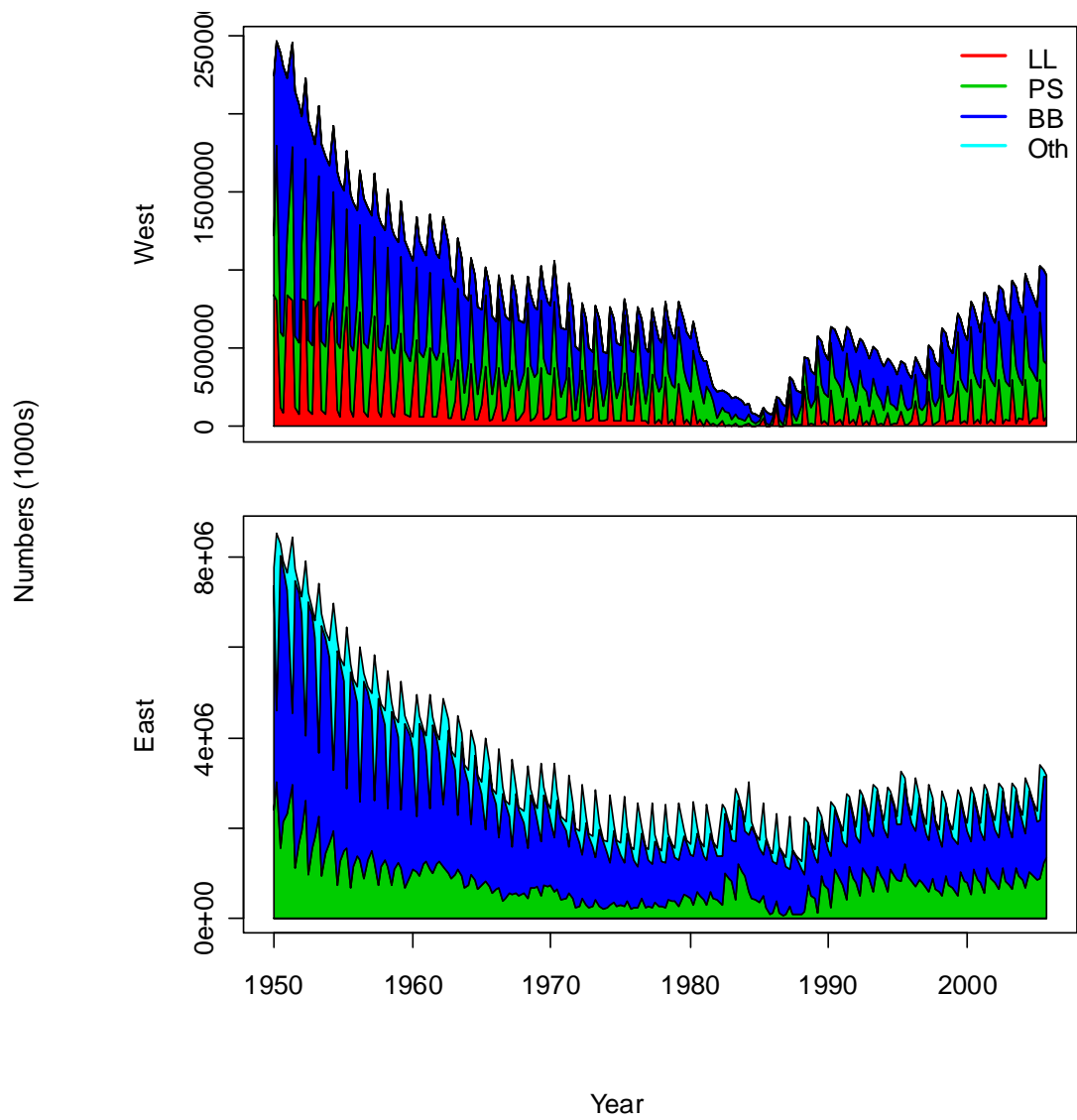


Figure 3. Reconstructed total numbers (1000s) for Western (top) and Eastern (bottom) stocks based on fits with F_{msy} free and CPUE likelihoods down-weighted by 90 %.

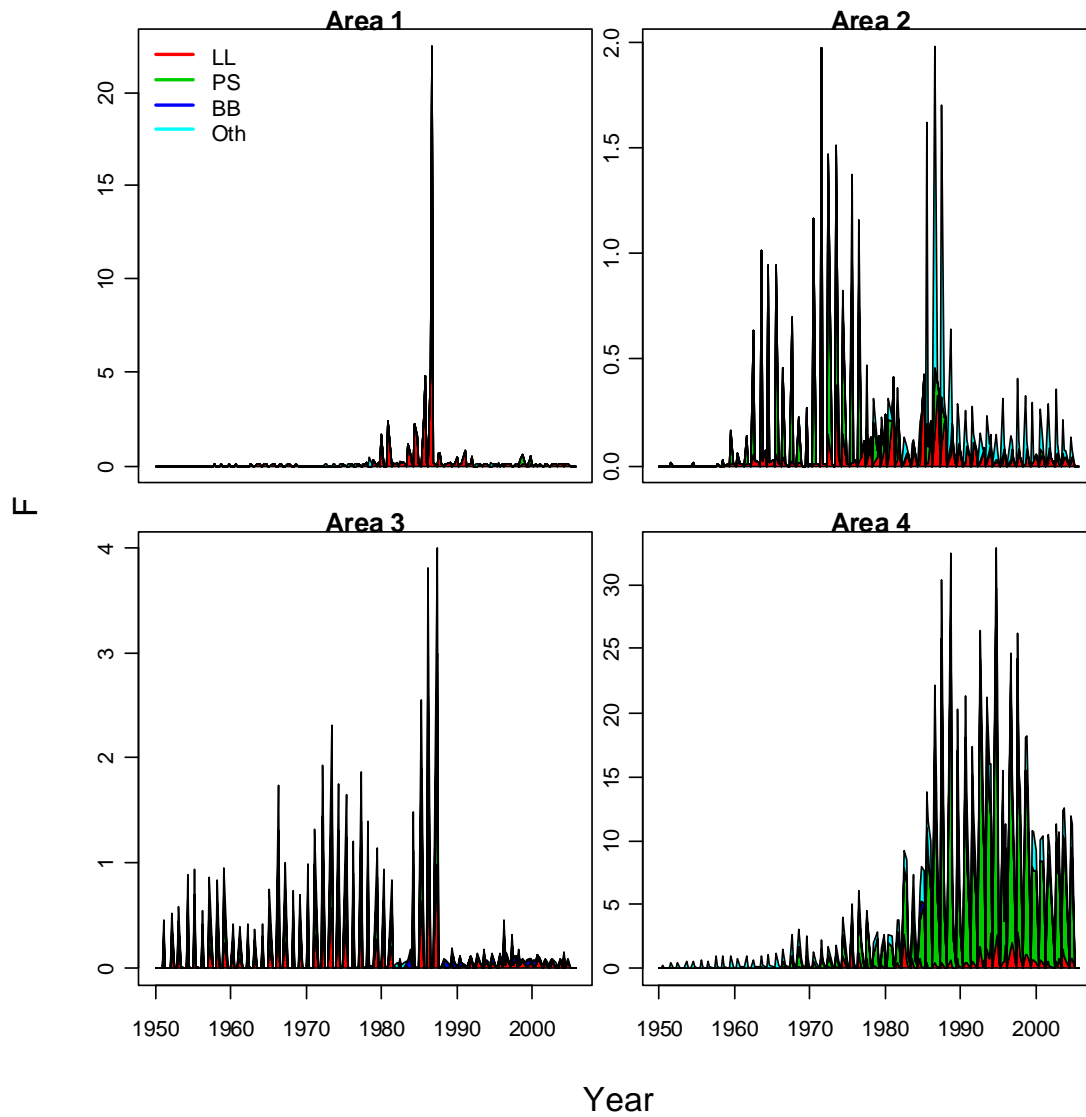


Figure 4. Estimated F mortality (yr^{-1}) by area and fleet for scenario 2 (F free and CPUE likelihoods downweighted).