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FASST: A FULLY AGE-SIZE AND SPACE-TIME STRUCTURED STATISTICAL MODEL FOR THE ASSESSMENT OF TUNA POPULATIONS

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SUMMARY

*The basic components of an age-size and space-time structured statistical stock assessment model are presented. The model could be flexible enough to capture some of the main population dynamics features observed in many tuna populations. The model could be applied to bigeye tuna (*Thunnus obesus*) data in the Atlantic Ocean.*

RÉSUMÉ

*Les éléments fondamentaux d'un modèle d'évaluation de stock structuré dans l'espace et dans le temps sont présentés ici. Le modèle pourrait être suffisamment flexible pour appréhender certains des aspects principaux de la dynamique des populations qui sont observés dans nombre de stocks de thon. Le modèle pourrait être appliqué aux données sur le thon obèse (*Thunnus obesus*) dans l'Atlantique.*

RESUMEN

*Se presentan los componentes básicos de un modelo de evaluación estadística del stock estructurado espacio-temporalmente y por edad-talla. El modelo puede ser lo suficientemente flexible para detectar algunos de los rasgos principales de dinámica de poblaciones observados en muchas poblaciones de túnidos. El modelo puede aplicarse a los datos de patudo (*Thunnus obesus*) del océano Atlántico.*

KEYWORDS

Stock assessment models; Mathematical models; Stochastic processes; Tuna fisheries

INTRODUCTION

The goal of this paper is to present a project for what a future ICCAT bigeye tuna assessment model could be. Primarily designed for representing Atlantic bigeye tuna fisheries, the proposed model is designed to be generic enough to be potentially extended to other species/regions.

Tuna populations and their associated fisheries exhibit very specific characteristics which have to be taken into account to model realistically their dynamics:

- Tuna fisheries are highly heterogeneous in space and time and such heterogeneity has a high functional importance in their functioning. The mixing rate of fish between different regions is generally not total. Then, the stock biomass located in a given fishing area interacts more or less strongly with the biomass located in other areas or with an unavailable part of the population located outside the fishing area. Important migrations and movements of fishes occurs at various scales so that the different regions interact differently: fish movements must be explicitly represented either with a continuous model (such as an advection-diffusion-reaction model) either with a bulk transfer rate compartment model;

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- Recruitment is permanent in time but highly heterogeneous in space and time (Cayre, 1986) so that no singular cohort can easily be identified: either continuous recruitment either a discretization of it such as the concept of mensual micro-cohorts (Fonteneau, 1998) must be used;
- Due to non uniform mortality over sizes (due to both size dependant natural mortality and selectivities), bias on both growth and mortality estimates may be caused by simply adding a gaussian size distribution to an age structured model (Fig. 1) (as multifan-cl or a-scala do for instance): an alternative explicit age and size structured model must be used.
- Growth is potentially variable in space (especially for skipjack) depending of the region considered (Bard, 1986) so that fishes of the same age will exhibit very different sizes depending of their various history: a spatialized approach taking explicitly into account the potential variability of growth in space should be used;
- Many different fleets with different selectivity patterns and heterogeneous and changing catchabilities (in general showing an increasing efficiency) due to technical progress or to changes in fishing strategy and tactics are present and fish the same population so that the use of fishing effort is problematic. A process error structure must be added to fishing effort/mortality relationship and catchability time series.
- The uncertainty of quantities needed for management needs to be estimated: a statistical approach must be used.

Conducting reliable stock assessments taking into account those problems requires the development of complex spatially explicit models dealing with all the fleets present in the fishery and with the movements of fish.

Such a modern stock assessment tool should profitably integrate a deterministic modelling of major processes with a statistical structure for both observation and process components. Space may be either considered using continuous representations such as advection-diffusion-reaction models (Bertignac *et al.* 1998; Sibert *et al.* 1999; Maury *et al.* 1999) either using discrete compartment models with fish transfer rates between zones (Fournier *et al.* 1998). Statistical models provide confidence intervals for the estimated parameters and infered management policies (Hilborn and Walters 1992; Fournier *et al.* 1998). Their parameter estimation may be conducted using maximum likelihood methods in a bayesian framework to easily handle the uncertainty concerning reference points useful for management (McAllister and Ianelli 1997; Punt and Hilborn 1997).

Our goal is to build an age-size and time-space structured synthetic model of tuna population dynamics and to use simultaneously all the information available (catches, effort, size frequencies, tagging[3], otolith increments, length/weight relationships, ...) in a bayesian framework to estimate the posterior probability distribution of the parameters (recruitment, growth, movement, natural mortality and catchability). Such statistical approach has already proven to be very powerful (Fournier et al, 1990 and 1998) and could be an important improvement for tuna stock assessment in ICCAT.

MODEL STRUCTURE

Notations

variables

N, the fish number
C, the catches
R, the recruitment
f, the fishing effort
q, the catchability
F, the fishing mortality

[3] The reliable parameterization of such complex spatially explicit statistical models has proven to be impossible without using tagging data (Hilborn 1990; Fournier *et al.* 1998; Sibert *et al.* 1999) which bring to the model an important amount of information concerning growth and length-specific natural mortality (Hampton 2000), catchabilities and selectivities (Anganuzzi *et al.* 1994) and age-dependent movements. Such reliable parameterization should be profitably conducted by using simultaneously fishery data and tagging data and potential auxiliary information for integrating the fishing effort standardization into the stock assessment model.

γ, the growth rate
D, the dispersion parameter of size
Q, the proportion of fish in a given data set lying in a given length interval
matur indicating maturity
Θ, the percentage of females in a size class
W, the body weight

subscripts
t, the time in months
a, the age in months
l, the length in cm
j, the zone j
k, the fleet k
α, indicates the length frequency data set
g, indicates the tag group (all the fish tagged the same month)
o, concerns otolith

parameters
A, the maximal age
n, the total number of zones
T, the fish transfert rates between zones
M, the natural mortality
P, the fishing power
s, the selectivity
$L\infty$, K, a_0, X, the generalized Von Bertalanfy growth parameters
β, χ, δ, the original Von Bertalanfy growth parameters
θ, m, the parameters for the length/weight relationship
i, relates length at maturity to asymptotic length
$\underset{..}{E}$ is the total number of length-frequency samples
Ω, is the total number of otolith samples
σ, the standard errors

random variables
ε, the catchability random walk error
η, the fishing mortality/ effort error
μ, the selectivity random walk error
ω, the natural mortality random walk error

Population dynamics

A compartment model which takes deterministically into account movement between homogeneous zones, growth in length (and growth variability), natural and fishing mortality is used for population dynamics. It is based on the following equations:

(1)

$$\begin{cases}\dfrac{\partial N_{1,l,t,a}}{\partial t}+\dfrac{\partial N_{1,l,t,a}}{\partial a}=\sum_{i=2}^{n}T_{i\to 1,l,t}N_{i,l,t,a}-\left(F_{1,l,t}+M_l+\sum_{i=2}^{n}T_{1\to i,l,t}\right)N_{1,l,t,a}-\dfrac{\partial(\gamma_{1,l,t}N_{1,l,t,a})}{\partial l}+\dfrac{\partial\left(D_{1,l,t}\dfrac{\partial N_{1,l,t,a}}{\partial l}\right)}{\partial l}+R_{1,t}\\ \quad\vdots\\ \dfrac{\partial N_{j,l,t,a}}{\partial t}+\dfrac{\partial N_{j,l,t,a}}{\partial a}=\sum_{\substack{i=1\\ i\neq j}}^{n}T_{j\to i,l,t}N_{i,l,t,a}-\left(F_{j,l,t}+M_l+\sum_{\substack{i=1\\ i\neq j}}^{n}T_{j\to i,l,t}\right)N_{j,l,t,a}-\dfrac{\partial(\gamma_{j,l,t}N_{j,l,t,a})}{\partial l}+\dfrac{\partial\left(D_{j,l,t}\dfrac{\partial N_{j,l,t,a}}{\partial l}\right)}{\partial l}+R_{j,t}\\ \quad\vdots\\ \dfrac{\partial N_{n,l,t,a}}{\partial t}+\dfrac{\partial N_{n,l,t,a}}{\partial a}=\sum_{i=1}^{n-1}T_{i\to n,t}N_{i,l,t,a}-\left(F_{n,l,t}+M_l+\sum_{i=1}^{n-1}T_{n\to i,l,t}\right)N_{n,l,t,a}-\dfrac{\partial(\gamma_{n,l,t}N_{n,l,t,a})}{\partial l}+\dfrac{\partial\left(D_{n,l,t}\dfrac{\partial N_{n,l,t,a}}{\partial l}\right)}{\partial l}+R_{n,t}\end{cases}$$

$$\begin{cases}\dfrac{dC_{1,k,l,t}}{dt}=q_{1,k,l,t}f_{1,k,t}N_{1,l,t}\\ \quad\vdots\\ \dfrac{dC_{j,k,l,t}}{dt}=q_{j,k,l,t}f_{j,k,t}N_{j,l,t}\\ \quad\vdots\\ \dfrac{dC_{n,k,l,t}}{dt}=q_{n,k,l,t}f_{n,k,t}N_{n,l,t}\end{cases}$$

with $N_{j,\,l,\,t,\,a}$, the number fish of age a and length l in zone j at time t, $T_{i\to j,t}$, the transfer rate from zone i to zone j at time t, q_i the catchability coefficient in zone i, M the natural mortality rate and $f_{i,t}$ the fishing effort in zone i at time t.

The system (1) is integrated analytically on a monthly time basis for the movements, mortality and catch components and numerically using a semi-implicit scheme for the growth component. A closed boundary is used for the age dimension at age $a=A$, the maximal age which accumulates old fishes (A is a "+" group).

Growth

We consider that, in a given zone, fish growth follows a generalized Von Bertalanfy curve which allows for slower growth rates for young fish as they are frequently observed for tunas, especially for yellowfin tuna (Pauly and Moreau, 1997; Gascuel et al., 1992). From a process point of view[4], this growth curve is based on a length-dependent growth rate, independent of age:

$$\gamma_{j,l,t}=\frac{\partial l}{\partial a}=anabolism-catabolism=\beta_{j,t}l^{\chi_{j,t}}-\delta_{j,t}l^{m_{j,t}}\qquad\left|\begin{array}{l}\chi\approx 2\\ m\approx 3\end{array}\right.$$

According with that formulation, fish belonging to the same cohort will have a different growth rate if they have a different size. The parameter m may be estimated externally with a length-weight relationship. With homogeneous mortality over sizes, this will cause a non-gaussian distribution of size frequencies for a given age[5].

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[4] From a processes point of view, growth results from the antagonism between anabolism proportional to a physiological surface and catabolism proportional to fish weight.

[5] If a more standard analysis based on the usual generalized Von Bertalanffy growth curve $\left(l_a=L_\infty\left(1-e^{-K\mathrm{X}(a-a_0)}\right)^{1/\mathrm{X}}\right)$ is desired, the growth rate may be assumed to be age-dependent and written as follows:

Different assumptions can be made about the dispersion rate over the length dimension. They will have implications on the standard deviations of the fish length at age distributions. The *a priori* more realistic assumption is a dispersion coefficient being linearly related to growth rate:

$$D_{j,l,a,t} = u\gamma_{j,l,a,t} + v$$

which also allows for growth-independent dispersion rate when $v=0$.

Mortality

In the model, the natural mortality M is length-dependant (Hampton, 2000). Its structure is assumed to be a random walk with respect to length:

$$M_{l+1} = M_l e^{\omega_l - \frac{\sigma_\omega^2}{2}} \quad \omega \sim N(0, \sigma_\omega)$$

The fishing mortality F is also length-dependent and defined as the sum of the fishing mortality of the n fleets k: $F^*_{j,l,t} = \sum_{k=1}^{n} F^*_{k,j,l,t}$ with $F^*_{k,j,l,t} = q_{k,j,l,t} f_{k,j,t}$ (here, the * indicates that the statistical part of the fishing mortality has not yet been introduced).

According with the separability assumption, the catchability for each fleet is split into a length component (varying slowly over time), the selectivity s, and two time-varying components, the fleet fishing power p and the fish disponibility (availability) d for a given fleet:

$$F^*_{k,j,l,t} = \sum_k q_{k,j,l,t} f_{k,j,t} = \sum_k s_{k,l,t} p_{k,t} d_{k,j,t} f_{k,j,t}$$

To take into account a potential seasonality due to fish behavior (reproductive concentrations, …), the disponibility d may be allowed to have a sinusoidal structure :

$$d_{k,j,t} = d^r_{k,j} + d^*_{k,j}\left(\varsigma_{k,j} + \sin\left(\frac{2\pi}{\tau_{k,j}} + \phi_{d,k,j}\right)\right)^+ \quad \left|\begin{array}{l}\left(d^r_{k,j}, d^*_{k,j}\right) \in R^{+2} \\ \varsigma \in [-1;1]\end{array}\right. \quad \left|\begin{array}{l}\tau \in [0;12] \\ \phi \in [0;2\pi]\end{array}\right.$$

with the positive part of a real number noted $()^+$.

Catchability may also be related to external factors such as environmental factors (thermocline depth, ...) with a deterministic function.

Stochasticity is added to the deterministic F^* parameterization to take into account time variability of the key parameters due to non-explicit external processes. A random walk structure is assumed for selectivity with respect to length:

$$s_{k,l+1,t} = s_{k,l,t} e^{\mu_{k,l,t} - \frac{\sigma_\mu^2}{2}} \quad \mu \sim N(0, \sigma_\mu)$$

Selectivities by size may be allowed to vary in time on a slow time basis (*e.g.* every 5 years) for each fleet.

To account for potential fluctuations of fishing power, we assume a random walk structure for the annual fishing power time series for each fleet. Such trends in fishing power may be due to changes in targeting or due to technological progress for instance. The random walk structure for $log(p_t)$ allows

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$$\gamma_{j,a,t} = \frac{\partial l}{\partial a} = L_{\infty,j,t} K_{j,t} e^{-K_{j,t}\mathrm{X}(a-a_0)} \left(1 - e^{-K_{j,t}\mathrm{X}(a-a_0)}\right)^{\frac{1-\mathrm{X}}{\mathrm{X}}}$$

With homogeneous mortality over sizes, this will cause a Gaussian distribution of size frequencies for a given age.

the catchability to vary slowly over time without *a priori* assumption on its trend (increase or decrease) (Fournier *et al.*, 1998). For that purpose, we assume that the yearly variability of p has the following structure :

$$p_{k,t+1} = p_{k,t} e^{\varepsilon_{k,t} - \frac{\sigma_\varepsilon^2}{2}} \qquad \varepsilon \sim N(0, \sigma_\varepsilon)$$

To address high-frequency variability of the catchability coefficient, a lognormal process-error structure is assumed for the fishing mortality. Then, the fishing mortality of fleet k at time t is written $F_{k,j,l,t} = F^*_{k,j,l,t}.e^{\eta_{k,j,t} - \frac{\sigma_\eta^2}{2}}$ where the $\eta_{k,j,t}$ are robustified normally-distributed random variables with mean 0 (Fournier *et al.*, 1998).

Spatial structure of the model

The geographical structure of the model is based on the heterogeneity of the fishery and the data available. Considering fleets to be zone-specific enables the model equations to be fully nested if zones are grouped. Then, different level of resolution (from a model with no spatial structure to a model with a fully detailed spatial structure) will be compared by using usual statistical tests (AIC, PBF, likelihood ratios) to select the resolution according to the amount of information contained into the data.

Fish movement rates are restricted to occur only between spatially adjacent zones. They are supposed to have two components. A diffusive one which does not vary in time for a given adjacent pair of zones and an advective one which has a truncated sinusoidal structure which enables for seasonal advective movements. To account for length-dependent variation of fish speed, movement rates are supposed to be proportional to a power of fish length:

$$\begin{cases} T_{i\to j,l,t} = \left(T^r_{i\to j,l} + T^*_{i\to j,l}\left(\Upsilon_{i\to j,l} + \sin\left(\frac{2\pi}{\Lambda} + \phi_{T,i\to j,l} \right)\right)\right)^+ l^y \\ T_{j\to i,l,t} = \left(T^r_{j\to i,l} + T^*_{j\to i,l}\left(\Upsilon_{i\to j,l} + \sin\left(\frac{2\pi}{\Lambda} + \phi_{T,i\to j,l} \right)\right)\right)^- l^y \end{cases} \quad \left| \begin{array}{l} \left(T^r_{i\to j,l}, T^*_{i\to j,l}\right) \in R^{+2} \\ \Upsilon \in [-1;1] \end{array} \right. \quad \left| \begin{array}{l} \Lambda \in [0;12] \\ \phi \in [0;2\pi] \end{array} \right.$$

Because movement patterns are likely to be different for adults which may experience reproductive migration and stay more in equatorial reproductive waters than juveniles which exhibit home range movements, two sets of movement parameters will be estimated and tested: a set for juveniles whose length is smaller than the length at first maturity l_{matur} and a set for adults whose length is greater. Length at first maturity is defined as being equals to a fixed fraction of the asymptotic length L_∞:

$$l_{matur} = iL_\infty = i\left(\frac{\delta}{\beta}\right)^{\frac{1}{x-m}} \qquad i \in [0;1[$$

Recruitment

In the model, recruitment level is allowed to vary each month in each zone. Bigeye are assumed to be recruited when their fork length reach 30cm. Between age 0 and the age corresponding to the recruitment, the growth process is applied without mortality and movement in order to obtain a realistic distribution of size at age when the micro-cohorts enter the fishery.

A Beverton and Holt type stock-recruitment relationship will be used in each zone with a large lognormal process error added on it to allow for large random fluctuations of recruitment around its mean:

$$R_{j,t} = \frac{\Psi SSB_{j,t}}{\Theta_j + SSB_{j,t}} e^{\upsilon_{j,t} - \frac{\sigma_\upsilon}{2}} \text{ with } SSB_{j,t} \propto \int_{l_{matur}}^{l_{\max}} \Theta_l W_l N_{j,l,t} dl$$

Tagging

Tagged fish are modeled by using exactly the same population dynamics equations and parameters that for non tagged fish. Additional mortality, tag shedding and tag reporting rates can be added if some information is available about it.

Fitting the model in a bayesian context

To estimate the parameters in a Bayesian context, we will use the method of the maximum of posterior distribution (Bard, 1974) by maximizing the sum of the log-likelihood of the data plus the log of the prior density function. Then, given the data, the Bayesian posterior distribution function for the model parameters has 8 components (one for the log-likelihood of the catch by fleet estimates L_C, one for the length frequency distributions of catches L_l, one for the age-length relationship from otolith reading L_o, one for the catchability statistical structure L_q, one for the recruitment deviations L_R,one for the tag recovery estimates L_{tag}, one for the natural mortality random walk over length L_M, and one for priors and penalties L_{penal}).

Then, the posterior distribution is equal to L :

$$L = L_C \times L_l \times L_o \times L_q \times L_M \times L_R \times L_{tag} \times L_{penal}$$

The parameters of the model will be estimated by finding the values of the parameters which minimize the negative log of this posterior distribution function. This minimization will be performed with a quasi-Newton numerical function minimizer using exact derivatives with respect to the model parameters with the AD model builder software (ADMB © 1993-1996 by Otter Research Ltd). ADMB calculates the exact derivatives with a technique named automatic differentiation (Griewank and Corliss, 1991).

Catches component

We assume that the log of the predicted catches are the expected values of a random variable with a normal distribution:

$$L_C = \prod_{j=1}^{n} \prod_{k=1}^{m} \prod_{l=0}^{l_{\max}} \prod_{t=0}^{t_{\max}} \left[\frac{1}{C_{j,k,l,t} \sigma_{Ck} \sqrt{2\pi}} e^{-\frac{\left(\log\left(C_{j,k,l,t}\right) - \log\left(\hat{C}_{j,k,l,t}\right)\right)^2}{2\sigma_{C_k}^2}} \right]$$

with $\hat{C}$, the observed catches and C, the predicted catches. Important additional information may be provided by fixing the variances σ by fleet which fix the weights of the corresponding likelihood components.

Length-frequencies component

The robust normal likelihood of Fournier et al. (1990 and 1998) modified by Maunder and Watters (2000) is used for the contribution of the length frequency distribution to the likelihood:

$$L_l = \prod_{\alpha=1}^{E}\prod_{l=0}^{l_{\max}}\left[\frac{1}{\tau_\alpha\sqrt{2\pi\left(\xi_{\alpha,l}+\frac{1}{N_I}\right)}}\left(e^{-\frac{\left(Q_{\alpha,l}^{obs}-Q_{\alpha,l}^{pred}\right)^2}{2\left(\xi_{\alpha,l}+\frac{1}{N_I}\right)\tau_\alpha^2}}+0.01\right)\right]$$

with $\xi_{\alpha,l} = Q_{\alpha,l}^{obs}\left(1-Q_{\alpha,l}^{obs}\right)$ and $\tau_\alpha^2 = \frac{\delta}{\min\left(S_\alpha,1000\right)}$ with $S_{\square}$ the sample size. N_I is the number of length intervals in the sample.

Age-length relationship from otoliths component

A robustified normal distribution is assumed for the error between predicted Von Bertalanffy length at age and length at age derived from otolith increments counting (preliminary trials indicate that this robust function gives the same results that a likelihood assuming normal error for age estimations).

$$L_o = \prod_{o=1}^{\Omega}\frac{1}{\sigma_o\sqrt{2\pi}}\left(e^{\frac{(l-l_o)^2}{2\sigma_o^2}}+0.01\right)$$

Catchability structure components

This component combines the log-normal structured random walks for selectivities and fishing power trends for each fleets and the effort/fishing mortality process error which has a robustified normal structure. This robustified normal distribution assumes a probability p for unlikely events (events which are more than e times the variance from the mean) and $1-p$ for the standard normal distribution (Fournier *et al.*, 1996):

$$L_q = \prod_{k=1}^{nfleet}\prod_{t=0}^{t_{\max}}\left[\frac{1}{\sigma_{\varepsilon_k}\sqrt{2\pi}}e^{-\frac{\varepsilon_{k,t}^2}{2\sigma_{\varepsilon_k}^2}}\right]\times\prod_{k=1}^{nfleet}\prod_{t=0}^{t_{\max}}\prod_{l=0}^{l_{\max}}\left[\frac{1}{\sigma_{\mu_k}\sqrt{2\pi}}e^{-\frac{\mu_{k,t,l}^2}{2\sigma_{\mu_k}^2}}\right]$$
$$\times\prod_{k=1}^{nfleet}\prod_{t=0}^{t_{\max}}\left[(1-p)\left(\frac{1}{\sigma_{\eta_k}\sqrt{2\pi}}e^{-\frac{\eta_{k,t}^2}{2\sigma_{\eta_k}^2}}\right)+p\left(\frac{\sqrt{2}}{\pi\sigma_{\eta_k}e\left(1+\frac{\eta_{k,t}^4}{\left(\sigma_{\eta_k}e\right)^4}\right)}\right)\right]$$

Natural mortality random walk component

This component corresponds to the log-normal structured random walks for natural mortality over lengths:

$$L_M = \prod_{l=0}^{l_{\max}}\left[\frac{1}{\sigma_\omega\sqrt{2\pi}}e^{-\frac{\omega_l^2}{2\sigma_\omega^2}}\right]$$

Recruitment deviations components

This component assumes a log-normal recruitment deviation from its mean in each zone and time strata:

$$L_R = \prod_{j=1}^{n} \prod_{t=0}^{t_{\max}} \left[\frac{1}{\sigma_\upsilon \sqrt{2\pi}} e^{-\frac{\upsilon_{j,t}^2}{2\sigma_\upsilon^2}} \right]$$

Tagging data component

Observed numbers of tag returns are related to predicted numbers of tag returns by a Poisson likelihood function (Sibert *et al.*, 1999):

$$L_{tag} = \prod_{g=1}^{G} \prod_{l=1}^{l_{\max}} \prod_{j=1}^{n} \prod_{t=1}^{t_{\max}} \left(\frac{\hat{C}_{g,j,t}^{TC_{g,j,l,t}} . e^{-\hat{C}_{g,j,l,t}^{TC_{g,l,j,t}}}}{C_{g,j,j,t}^{TC_{g,j,l,t}}!} \right)$$

Priors and penalties

Priors are added to the likelihood to take into account potential external information. A prior assumption based on the literature (*e.g.* Hampton, 2000) will be made for the parameters M_l. Another based on fishbase (Froese and Pauly, 1997) data will be developed for the parameter i relating length at first maturity to asymptotic length.

$$L_{penal} = \prod_{l=1}^{l_{\max}} \left[\frac{1}{\sigma_M \sqrt{2\pi}} e^{-\frac{\left(\log\left(\frac{M_l}{V_{M_l}}\right)\right)^2}{2\sigma_M^2}} \right] + \frac{1}{\sigma_i \sqrt{2\pi}} e^{-\frac{\left(\log\left(\frac{i}{V_i}\right)\right)^2}{2\sigma_i^2}}$$

Penalties on fishing mortality (cf. multifan-cl and A-scala) may be added (at least during the first phases of the estimation process) to keep results in a realistic range.

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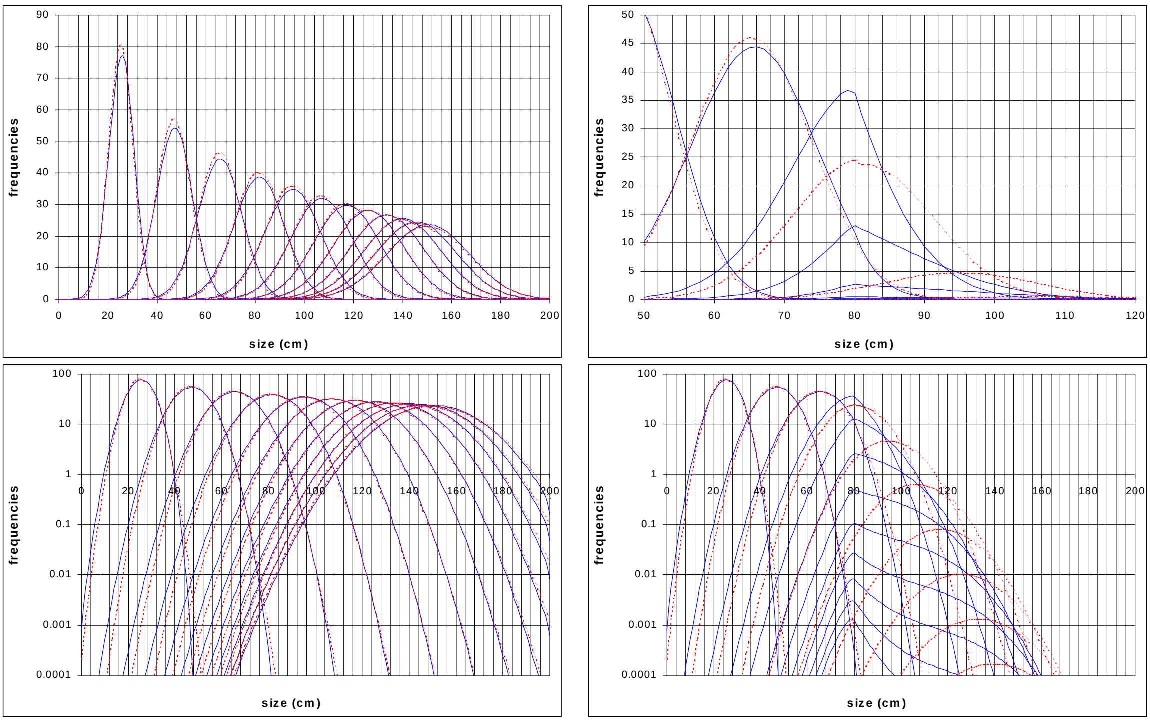

Figure 1. Simulated size frequencies obtained by using a gaussian size structure added to an age structured model (dashed line) or by using a fully size and age structured model such the one presented here (continuous line). First column, no fishing, homogeneous natural mortality over sizes. Second column, no fishing for sizes smaller than 80cm and strong fishing for longer sizes, homogeneous natural mortality over sizes. First line, absolute scale; second line, log scale. When the mortality is not homogeneously distributed over sizes (second column), it appears that simply adding a normal size structure on the age structured model may cause strong biases on abundance, position of the mode and shape of the size distribution for each cohort.

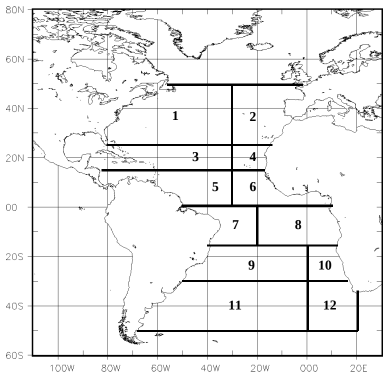

Figure 2. Detailed geographical structure of the model.