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USE OF A GENERALIZED STAGE-BASED, AGE-, AND SEX-STRUCTURED MODEL FOR SHARK STOCK ASSESSMENT

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SUMMARY

An age-, and sex-structured model that simulates shark population dynamics taking into account specific characteristics of shark biology and shark fisheries is used in this paper to evaluate the status of a shark population. The model incorporates sex-specific growth and movement and allows for heterogeneity in the spatial distribution of fish. It also models the pupping process and accounts for density-dependence in pup survival and for fishery/gear-specific selectivity Because of limited information on e.g., pup survival, some parameters of the model are treated as estimated parameters. A Bayesian approach is applied to fit the model to data and estimate model parameters. For demonstration purposes, a simple version of the methodology is applied to data for blacktip sharks, Carcharhinus limbatus. Using catch and abundance information, we produce estimates for parameters such as carrying capacity, K_o and pup survival at low densities (1/a). We analyse alternative scenarios for some of the biological parameters and discuss their effect on model results. Our study illustrates the advantages of a Bayesian framework as a way to integrate different kinds of information into stock assessment and stresses the benefits of improved data as an indispensable prerequisite for better stock assessment.

RÉSUMÉ

Le présent document utilise un modèle structuré par âge et par sexe qui simule la dynamique des populations de requins en tenant compte des caractéristiques spécifiques de leur biologie et de leur pêche. Le modèle comporte la croissance spécifique du sexe et les déplacements et tient compte de l'hétérogénéité de la distribution spatiale du poisson. Il modèle également le processus juvénile et tient compte de la densité-dépendance de leur survie et de la sélectivité spécifique de la pêche/engin. Les informations étant limitées, par exemple sur la survie des juvéniles, certains paramètres du modèle sont traités en tant que paramètres estimés. Une approche bayésienne est appliquée à l'ajustement du modèle aux données et à l'estimation de ses paramètres. Aux fins de la démonstration, une version simple de la méthodologie est appliquée aux données sur le requin bordé, Carcharhinus limbatus. D'après l'information sur la capture et l'abondance, nous calculons des estimations de paramètres tels que la capacité de cale, K_0, et la survie des juvéniles à de faibles densités (1/a). Nous analysons des scénarios alternatifs pour quelques-uns des paramètres biologiques et débattons de leur incidence sur les résultats du modèle. Notre étude illustre les avantages d'une structure bayésienne comme moyen d'intégrer différentes sortes d'information dans l'évaluation de stock et met l'accent sur les avantages de données améliorées en tant qu'exigence fondamentale d'une meilleure évaluation des stocks.

RESUMEN

En este documento se utiliza un modelo estructurado por edad y sexo que simula la dinámica de poblaciones de tiburones y que incluye características especiales de la biología y la pesquería de tiburones para evaluar el estado de las poblaciones de tiburones. El modelo incorpora el desplazamiento y crecimiento específico por sexos y tiene en cuenta la heterogeneidad de la distribución espacial de los peces. También modeliza el proceso de cría y contempla la densidad-dependencia de la supervivencia de las crías y la selectividad específica

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arte/pesquería. Debido a la limitación de la información, como, por ejemplo, sobre la supervivencia de crías, algunos parámetros del modelo se tratan como parámetros estimados. Se ha aplicado un enfoque bayesiano para ajustar el modelo a los datos y estimaciones de los parámetros del modelo. A efectos de demostración, se ha aplicado una versión simplificada de la metodología a los datos de tiburón macuira, Cacharhinus limbatus. Utilizando la información sobre captura y abundancia, hemos realizado estimaciones para parámetros como capacidad de transporte, K_o y supervivencia de crías en bajas densidades (1/a). Analizamos escenarios alternativos para algunos parámetros biológicos y discutimos su efecto en los resultados del modelo. Nuestro estudio ilustra las ventajas de una estructura bayesiana como un modo de integrar diferentes tipos de información en la evaluación de los stocks y hace hincapié en los beneficios de datos mejorados como prerrequisito indispensable para una mejor evaluación de los stocks.

KEYWORDS

Sharks fisheries, Stock assessment, Age-structured model, Population dynamics, Recruitment, Bayesian methods

1. INTRODUCTION

The recent increase in shark exploitation has raised concerns about the fate of shark populations and emphasised the need for specific shark management measures (FAO 1999). In the last decade, modelling work has begun to focus on developing methodologies for the assessment of the status of shark populations (Cortés, 1998; Smith et al., 1998; McAllister et al., 2001). However, scarce biological information and lack of long time series of catch and abundance have constrained the assessment of shark stocks (FAO, 1999). For this reason, models tend to be simple (e.g. demographic analysis, surplus production models) and sometimes aggregated over species. Additionally, the models do not account, in some cases, for important processes such as recruitment or density-dependent regulation of population (Cortés, 1995; Sminkey and Musick, 1996).

To reduce biases from such simplifications, scientists have recently developed age-structured models which account for the biological characteristics of individual species (Bonfil, 1996; Powers, 1998; Punt and Walker, 1998). However, the limited understanding of important processes that govern shark dynamics, such as stock-recruitment relationships, continues to impair shark assessment. Realistic models which account for processes in shark population dynamics and the uncertainty that characterises our knowledge about them could increase our understanding of shark dynamics and lead to the adoption of less risk-prone sustainable fisheries management systems.

In this study, a sex- and age- structured model is used to simulate shark population dynamics taking into account specific characteristics of shark biology and shark fisheries. The model is capable of taking into account density-dependent processes in population regulation, non-uniform spatial distributions of fish (specific nursery or pupping grounds etc.) and the effects of different fisheries for sharks (different gears and/or selectivity, effort etc.). It also explicitly models the pupping and recruitment processes. Because of limited information on e.g., pup survival and population distribution under virgin conditions, some parameters of the model are treated as estimated parameters. A Bayesian approach is applied to fit the model to data and estimate model parameters (Punt and Walker, 1998; McAllister et al., 1999). This approach allows for incorporation of a diversity of prior knowledge for some of the parameters of the model into the estimation process.

In order to illustrate the implementation of the model we loosely apply the methodology to data for blacktip sharks, *Carcharhinus limbatus* from the US east coast and Gulf of Mexico. We use catch and catch rate data for the period 1981-1998 presented in the 1998 SEW (Shark Evaluation Workshop; NMFS, 1998) for the calculations (Figure 1 and Table1).

The model assesses the current status of the shark population based on available data. It could also be used to assess the effectiveness of existing and alternative fisheries management measures and make predictions about the status of the population in the future under different management scenarios. In this study we use a simple version of the model to evaluate the effects of key parameters and assumptions on the outcome of the model. Different ways to handle relative abundance indices are used and the results in each case are discussed.

2. SHARK POPULATION DYNAMICS MODEL

Fish are separated into different age and sex groups and can be separated by spatial areas if appropriate. If the number of fish from each group that are caught or die from natural reasons in a period of time is known then the number of fish surviving to the next period can be computed. The number of fish of age *a* and sex *g* in area *r* and time *t*, $N_{g,t,a,r}$, will be:

$$(1) \quad N_{g,t,a,r} = \begin{cases} f_g \cdot R_{t,r} & a = 1 \\ \left[N_{g,t-1,a-1,r} \cdot S_{a-1}^{1/2} - C_{g,t-1,a-1,r}\right] \cdot S_{a-1}^{1/2} & 1 < a < a_{\max} - 1 \\ \left[N_{g,t-1,a_{\max}-1,r} \cdot S_{a_{\max}-1}^{1/2} - C_{g,t-1,a_{\max}-1,r}\right] \cdot S_{a_{\max-1}}^{1/2} + & \\ + \left[N_{g,t-1,a_{\max},r} \cdot S_{a_{\max}}^{1/2} - C_{g,t-1,a_{\max},r}\right] \cdot S_{a_{\max}}^{1/2} & a = a_{\max} \end{cases}$$

where S_a is survival at age *a* from natural cause of death, $C_{g,t,a,r}$ is the number of fish of sex *g* and age *a* that were caught in year *t* and area *r* , $R_{t,r}$ is the number of fish of age 1 year old in area *r* in time *t* and f_g is the fraction of pups of sex *g*. We assume that females give birth at the beginning of the year and that the number of fish in each year is also calculated at the same time. Following the assumptions used by Punt and Walker (1998) we have assumed that the catch is taken in a pulse in the middle of the year, *t*. In the above expression it has been assumed that fish less than one year old are not vulnerable to any gear. However if our catch data include fish of age less than one year old then an extra factor should be included in the formula for the calculation of one-year–old fish to account for the increase in mortality of 0+ group.

The number of pups, $P_{t,r}$, in year *t* and at area *r* is calculated as follows:

$$(2) \quad P_{t,r} = \sum_{a=t_g}^{a_{\max}} \Phi_{a-t_{gest}} \cdot \overline{\Phi}_{a-t_{gest},t-t_{gest}} \cdot N_{f,t-t_{gest},a-t_{gest},r} \cdot \overline{\overline{\Phi}}_{a-t_{gest}}$$

where Φ_a is the proportion of female fish at age *a* that are mature, $\overline{\Phi}_{a,t}$ is the proportion of mature female fish at age *a* that mate in year *t*, $\overline{\overline{\Phi}}_a$ is the number of pups per pregnant female of age *a* and t_{gest} is equal to the gestation period.

The number of fish of age 1 year old is related to the number of pups produced using the Beverton-Holt stock-recruit formula (Beverton and Holt, 1957):

(3) $$R_t = \frac{P_{t-1}}{a_1 + b_1 \cdot P_{t-1}}$$

where the a and b are calculated from the following expressions (Francis, 1992):

(4a) $$a_1 = P_o \cdot \frac{(1-h)}{4 \cdot h \cdot R_o}$$

(4b) $$b_1 = \frac{(5 \cdot h - 1)}{4 \cdot h \cdot R_o}$$

where h is the steepness of the stock-recruit relationship and is equal to the fraction of the recruits under virgin conditions, R_o (the recruitment corresponding to P_o), that are expected when the number of pups is reduced to 20% of P_o.

Two other stock recruitment relationships were also used to investigate how the results are affected by a change in the assumptions regarding pup survival; the generalised hockey stick model and the Ricker stock recruitment function. According to the generalised hockey stick model, pup survival remains constant at low stock sizes, increases at intermediate stock sizes and reaches an asymptote when the stock size approaches or is greater than the virgin stock size. The survival of pups is calculated as follows (Barrowman and Myers, 2000):

(5) $$S_o = \begin{cases} A & P \le \cdot\overline{P} \cdot (1-d) \\ A \cdot \left(1 - \frac{\left[P - \overline{P} \cdot (1-d)\right]^2}{4d \cdot P \cdot \overline{P}}\right) & \overline{P} \cdot (1-d) \le P \le \overline{P} \cdot (1+d) \\ A \cdot \frac{\overline{P}}{P} & P \ge \overline{P} \cdot (1+d) \end{cases}$$

where A is a constant that is equal to pups survival at low fish densities, $\overline{P}$ is equal to the mean of the number of pups produced under virgin conditions (carrying capacity) and the minimum number of pups at which density dependent survival occurs. d is a constant that determines the range of values of P, below carrying capacity, at which density dependent survival occurs.

The Ricker stock recruitment model (Ricker, 1954) assumes that recruitment initially increases with the number of pups, reaches a maximum and then decreases as the number of pups gets large according to the formula:

(6) $$R = a_2 \cdot P \cdot e^{-b_2 \cdot P}$$

where a_2 and $ß_2$ are constants that give the slope of the curve at the origin and the level of density dependence, respectively.

If either the number of fish caught by area each year, $C_{t,j,r}$, or the total weight of fish caught by area, year, $\tilde{C}_{t,j,r}$, is available for each of the fisheries of interest (recreational, commercial etc.) and the selectivity, $V_{g,j,a}$, of the gears used is known then catch at age per fishery/gear, j, sex and area, $C_{g,t,a,j,r}$, can be calculated (Punt and Walker, 1998):

(7) $$C_{g,t,a,j,r} = H_{t,j,r} \cdot V_{g,j,a+0.5} \cdot (N_{g,t,a,r} \cdot S_a^{1/2} - \sum_{i=1}^{j-1} C_{g,t,a,i,r})$$

where $H_{t,j,r}$ denotes exploitation rate by fishery/gear, *j*, and area, *r*, in year *t*, calculated as:

(8a) $$H_{t,j,r} = \frac{C_{t,j,r}}{\sum_g \sum_{a=1}^{a_{\max}} V_{g,j,a+0.5} \cdot \left[N_{g,t,a,r} \cdot S_a^{1/2} - \sum_{i=1}^{j-1} C_{g,t,a,i,r} \right]}$$

when catch is available in numbers, and as:

(8b) $$H_{t,j,r} = \frac{\tilde{C}_{t,j,r}}{\sum_g \sum_{a=1}^{a_{\max}} w_{g,a+0.5} \cdot V_{g,j,a+0.5} \cdot \left[N_{g,t,a,r} \cdot S_a^{1/2} - \sum_{i=1}^{j-1} C_{g,t,a,i,r} \right]}$$

when catch is available in weight. $w_{g,a}$ is fish weight at age *a* and of sex *g*. The above two formulas will be different if fishing does not take place in the middle of the year only, or if the pattern of exploitation by some fisheries is not the one that corresponds to these formulas. Fish weight at age *a*, $w_{g,a}$, is expressed as a function of fish length, $L_{g,a}$:

(9) $$w_{g,a} = d_g (L_{g,a})^{b_g}$$

where d_g and b_g are constants and fish length at age is described by the von Bertalanffy growth equation (VBGE):

(10) $$L_{g,a} = L_{\infty,g} \cdot (1 - e^{-k_g (a - t_{o,g})})$$

where $L_{\infty,g}$ is the theoretical maximum asymptotic length of fish of sex *g*, and k_g , $t_{o,g}$ are constants.

We call y_1 the first year of our calculations. If our starting year is equal to the year that exploitation started then we can assume virgin conditions for the population before that year. If catch series that extend back to y_1 are not available we can treat the catch during the years that no data are available as an uncertain random parameter (McAllister et al., 2001). If we assume that K_O is the virgin biomass then the number of fish in each age-class at the beginning of year y_1 will be:

(11)

$$N_{g,y_1,a} = \begin{cases} f_g \cdot R_0 & a = 1 \\ f_g \cdot R_0 \cdot \prod_{a'=1}^{a-1} S_{a'} & 1 < a \leq a_{\max} - 1 \\ f_g \cdot R_0 \cdot \dfrac{\prod_{a'=1}^{a_{\max}-1} S_{a'}}{1 - S_{a_{\max}}} & a = a_{\max} \end{cases}$$

where the number of fish of age 1 year old (recruits) under virgin conditions is:

(12)

$$R_0 = \frac{K_o}{\sum_g f_g \left[w_{g,1} + \sum_{a=2}^{a_{\max}-1} w_{g,a} \prod_{a'=1}^{a-1} S_{a'} + w_{g,a_{\max}} \dfrac{\prod_{a'=1}^{a_{\max}-1} S_{a'}}{1 - S_{a_{\max}}} \right]}$$

Alternatively, we can assume that the population is randomly distributed about its virgin size to account for uncertainties in recruitment. In this case equation (11) should be multiplied by $e^{e_a - s_r^2/2}$, where e_a accounts for process error: $e_a \sim N(0, s_r^2)$, except for the form of the equation that calculates *N* for the maximum age since it comprises a large number of age-classes which will effectively damp out the effects of process error.

3. PARAMETER ESTIMATION

A simple version of the model is used for our calculations in which the parameters virgin biomass, K_o, survival of pups at low densities ($1/a_1$ for the Beverton-Holt model), the constant of proportionality for each relative abundance series, q_j, the variance, s_j, for each relative abundance series (see below), and the catches prior to 1986 are treated as unknown parameters to be estimated. The model is fitted to the data using a Bayesian method and assigning a prior distribution to each of the estimated parameters of the model. The prior for $1/a_1$, $p(1/a_1)$, can be constructed based on existing estimates of shark survival and constraints imposed by the stock-recruitment relationship used each time, while information from previous assessment studies (when it is available) can be used for the construction of a prior for virgin biomass, *p*(*K*). In contrast, a non-informative prior distribution, $p(q_j)$, is used for *q's* and for *s* 's, p(s_j). We assume that the parameters are independent in the joint prior probability density function (pdf):

(13)

$$p(q_k) = p(A_k)\, p(K_k)\, p(q_{k_{j=1}})\, p(q_{k_{j=2}}) \ldots p(s_{k_{j=1}})\, p(s_{k_{j-2}}) \ldots$$

where q_k is the k^th potential combination of values for the uncertain parameters and $p(q_k)$ is the value of the joint prior pdf for this combination.

In order to construct the likelihood function we assume that all observations are independent and that the observed values from each abundance series, $I_{j,t}$, are log-normally distributed about the corresponding value predicted by the model, $q_j B_{j,t}$:

(14) $$I_{j,t} \sim \log normal(q_j B_{j,t}, s_j^{\,2})$$

where $B_{j,t}$ is the annual stock biomass that corresponds to observation $I_{j,t}$ and q_j is the constant of proportionality for the series that comes from fishery j and s_j is the lognormal standard deviation for residual errors between the observed and predicted values for each series of relative fish abundance. The loglikelihood function for one potential set of values for the uncertain parameters of the model, q_k, is (McAllister and Kirkwood, 1998, McAllister et al., 2001):

(15) $$\ln L(I \mid q_k) = \sum_j \sum_t -\frac{1}{2c_j CV_{j,t}^2 s_j^2} \left(\ln \frac{I_{j,t}}{q_j B_{j,t,k}} \right)^2 - \ln \sqrt{c_j CV_{j,t}^2 s_j^2 2p}$$

where the annual estimate of the CV's for sampling error for each of the relative abundance series are used to weight s_j, the average value of $s_{j,t}$. The constant c_j is used to make the product of CV^2 and c_j sum to 1 (see McAllister et al., 2001). If catch-rate series are used as indices of relative fish abundance then $B_{j,t}$ denotes the exploited biomass that corresponds to $I_{j,t}$ (Punt and Walker, 1998):

(16) $$B_{j,t}^e = \sum_g \sum_a^{a_{\max}} w_{g,a+0.5} \cdot V_{g,j,a+0.5} \cdot (N_{g,t,a} \cdot S_a^{1/2} - \sum_{i=1}^{j-1} C_{g,t,a,i} - C_{g,t,a,j}/2)$$

The same equation, without the weight is used for the calculation of the exploited number of fish. Also the equation could be modified to account for abundance indices that apply to particular age classes or regions.

For each potential set of values for the unknown parameters q_k we calculate the value for the posterior probability density function:

(17) $$p(q_k \mid \mathrm{I}) \propto p(q_k) L(I \mid q_k)$$

The marginal posterior probability distribution for each of the parameters of interest is obtained with integration of the above expression.

4. MODEL IMPLEMENTATION

The values of the fixed parameters used by the model are given in Table 1. For the following calculations it was assumed that there is no spatial segregation of the species (all sharks live in the same area) and migration of sharks is not modelled. Estimates of the annual catches of blacktip shark are available for years 1986-1997 (Figure 1) together with seven relative abundance indices, one in biomass units and 6 in number of fish units (Table 2). The annual catch in the year 1998 is taken to be equal to the catch in 1997.

First we calculate the intrinsic rate of increase, r, under different assumptions about fish survival so we can find lower limits for the values of fish survival that can be used and investigate the relationship between survival rate and r. Two assumptions regarding survival are tested; survival that is the same for all age classes and survival that is the same for all age classes except the first one, the survival of one-year-old fish is fixed and is assumed to be smaller than the survival of older fish. This was done using a Leslie Matrix projection method (Ebert, 1999). For comparison, the values of the parameters that were used for these calculations are within the ranges of values used in the 1998 shark evaluation workshop (NMFS, 1998).

The baseline run of the model used an informative prior for pup survival at low densities (~lognormal[0.5, 0.2]) based on estimates of pup survival for blacktip and similar species in the wild (M. Heupel, Mote Marine Laboratory, pers. comm.; Manire and Gruber, 1993). Pups survival cannot be greater than the survival of 1-year-old fish or less than the survival of pups under virgin conditions. The baseline run also uses a weakly informative prior for virgin biomass (log(*B*o) ~ U[log($4x10^7$), log($4x10^8$)]). Due to the lack of information on catches before 1986, these are assumed to have been constant for the period 1975-1985 and are estimated by the model using an informative prior: $C_{1975-1985}$~Lognormal(302000, 0.5^2). Non-informative priors (uniform priors) were also used for q_j and s_j since no information is available for their values. Fixed parameter values for the baseline run included full fishing selectivity for all fish older than 3 years of age, an age of maturity of 6 years, a maximum age of 20 years, and a maximum fecundity of 5 pups per female.

We also ran the model with equal weighting of the CPUE data points, instead of inverse variance weighting (Eq. 15). Further sensitivity analyses were carried out by evaluating alternative scenarios regarding maximum number of pups per female (10 pups instead of 5 pups), type of stock-recruitment relationship (Equations 3-6), and using only one CPUE series at a time. Another alternative scenario included using an uninformative uniform prior for the virgin mature fish biomass *B*o; *B*o ~U[$4x10^7$ Kg, $4x10^8$Kg].

For the baseline and equal weighting case we approximated the posterior joint probability distribution using the SIR (sampling/importance resampling) algorithm (McAllister and Ianelli, 1997; McAllister et al., 2001; McAllister and Kirkwood, 1998). We used this distribution to calculate the marginal posterior probability distributions, mean values and CVs for virgin mature fish biomass, virgin number of fish, number of fish in 1998, pup survival at low density, and catch in the period 1975-1985. For the sensitivity analyses, we only present the point estimates with the highest posterior probability (the mode of the posterior distribution).

5. RESULTS

Figure 2 shows the values of *r* for different values of fish survival. The range of *r* values that can be used when pup survival is the same as for the rest of the age-classes is larger than when pup survival is reduced. Furthermore, the intrinsic rate of increase is much smaller with lower pup survival since a considerable number of pups die during the first year of their life. The results in the first case show that when survival is 0.9 the intrinsic rate of increase is equal to 0.11, which is close to the mean value of *r* that was calculated in the 1998 SEW.

The expected values of the estimated parameters using the two different weighting methods are presented in Table 3. According to the results with inverse variance weighting, shark exploitation has resulted in a 70% decrease in the fish population. The equal weighting method produced more optimistic results predicting a smaller relative decline in fish population (30%). Note that the difference between the number of fish under virgin conditions and in year 1998 was approximately the same for both methods, so the difference in depletion was caused by the different estimates of virgin number of fish. Figure 3 shows the decline in the exploited part of the population.

The posterior distributions for each of the estimated parameters have been calculated using the alternative weighting and equal weighting methods (Fig. 4). The inverse variance method produced tighter posterior distributions since it strongly downweighted those CPUE series characterised by a high variance and effectively ignored CPUE points that were inconsistent with the rest of the data and the modelled population dynamics (Fig. 3). However, inverse variance weighting could lead to biased results in case series with smaller sampling variance do not represent reality. On the other hand, the equal weighting method does not take into account the accuracy of the data and assigns equal weight to all CPUE points. This reduces the possibility that relevant information about trends in fish abundance will be overlooked but could increase the uncertainty in the estimated parameters. Hence, the equal weighting method has produced wider posterior distributions (Fig. 4) since the relative abundance series that were used for the calculation of the distributions had different (and even contradictory) trends (Fig. 3) resulting in considerable increase in the uncertainty in the estimated parameters.

A sensitivity analysis investigated the effects of alternative assumptions regarding input parameters on the dynamics of the population. The modal values of the estimated parameters are shown in Table 4. Although there were some differences in the values of the parameters for the different cases examined the level of the population depletion seemed not to be affected, with most of the results pointing to about a 75% depletion. Similarly, the results from the two alternative prior distributions for Bo suggest that the posterior distribution of Bo does not depend strongly on the prior distribution, implying that the CPUE data are informative about Bo.

Sensitivity analysis in which each CPUE series was fit separately has also be done (Table 5). The amount of depletion ranges from about 25% for series that have an upward trend (Fig. 4) to about 85% for series with a steep declining trend, highlighting the contradictory nature of the data. Improved data collection systems would be necessary to reduce this uncertainty in the assessment and consequent management advice.

6. DISCUSSION

Bayesian methods allow prior knowledge about parameter values to be incorporated into the model to make the best possible use of all the diverse types of data available. In the preliminary version of the model presented here, most of the parameters have been fixed at values found in the literature. This limits the model's ability to fit the CPUE data. It would be more appropriate to allow the model to fit many of the parameters, but use informative priors for these parameters based on experimental data. For example, instead of fixing adult survival at 0.85, the parameter could be given a prior distribution with a mean of 0.85 and a variance reflecting the uncertainty in the information about this parameter.

This paper describes a generalised model of shark population dynamics, including age-structure and selectivity data. The model could easily include migration and movement. This complexity in the model would allow the implications of size limits, area closures, and spatially complex fisheries to be modelled, allowing more sophisticated management of shark fisheries. However, this model requires much more information than simpler lumped biomass models. It is necessary to have some information on growth, fecundity, maturity, selectivity, and (if movement is considered) migration. Additionally the calculations showed that the quality of the catch-effort and relative abundance data is a very important factor when modelling advice is to be provided for the management of the shark fishery. Therefore better data collection methods could improve the accuracy in model predictions and management advice.

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LIST OF VARIABLES AND PARAMETERS

a	Age
g	Sex (f: female, m: male)
y_1	First year, it is assumed that the population in that year is equal to the virgin population
K_o	Virgin biomass
f_g	Fraction of pups of sex *g*
$w_{g,a}$	Weight of fish of age *a* and sex *g*
S_a	Survival in age *a*
$N_{g,t,a,r}$	Number of fish of age *a* and sex *g* in year t and area *r*
a_1, b_1	Constants of the Beverton-Holt stock recruitment formula
$L_{g,a}$	Length at age *a* of a fish of sex *g*.
P	Number of pups
Φ_a	Proportion of mature female fish at age *a*
$\overline{\Phi}_{a,t}$	Proportion of mature female fish at age *a* that mate in year *t*
$\overline{\overline{\Phi}}_a$	Number of pups per pregnant female of age *a*
t_g	Gestation period
$C_{t,j}$	Catch at year *t* using gear *j* (biomass units)
$C_{g,t,a,j}$	Catch at year t of fish of age *a* and sex *g* using gear *j* (number of fish)
$F_{t,j}$	Fishing effort that corresponds to gear *j* in year *t*
$H_{g,j,a}$	Selectivity at age *a* and sex *g* that corresponds to gear *j*
d_g, b_g	Constants of the weight-length relationship
$L_{\infty,g}$	Asymptotic length parameter of the VBGE for fish of sex *g*
k_g , $t_{o,g}$	Constants of the length at age relationship
$B^e_{j,t}$	Biomass that can be exploited by gear *j* in year *t*

Table 1. Values of the parameters that are fixed in the model (baseline case)

Parameters	Value	Reference
g	1= females, 2= males	
f_g	0.5 , g=1,2	
a_{max}	20 years	Branstetter, 1987; Killam and Parsons, 1989
a_{mat}	6 years	Killam and Parsons, 1989; Cortés, 1998
Φ_a	0, a<6 1, a>=6	
$\overline{\Phi}_a$	0.5	
$\overline{\overline{\Phi}}_a$	4, a<=9 5, a>9	
t_g	1	Castro, 1996
j	1	
$H_{g,j,a}$	1 a>=3	
$L_{\infty,g}$	195 cm, g=1 166.5 cm, g=2	Killam and Parsons, 1989
k_g	0.197, g=1 0.276, g=2	Killam and Parsons, 1989
$t_{o,g}$	-1.154, g=1 -0.884, g=2	Killam and Parsons, 1989
d_g	2.512×10^{-9}, g=1,2	Castro, 1996
b_g	3.1253, g=1,2	
S_a	0.75, a=1 0.85, a>=2	
y_1	1975	

Table 2: CPUE series (NMFS 1998). [1]biomass units, [2]fish number units

Year	Series 1[1]	Series 2[2]	Series 3[2]	Series 4[2]	Series 5[2]	Series 6[2]	Series 7[2]
1981			9.52				
1982			10.04				
1983			4.74				
1984			7.12				
1985			13.77				
1986			18.23				
1987			17.46				
1988			19.35				
1989			16.73			0.06	
1990			13.63				
1991			18.6			0.13	
1992		1.637	21.87				
1993	45.697	2.008		14.09			
1994	10.215	1.456		8.48	0.143		
1995	93.882	1.108		8.4	0.592		0.205
1996	133.368	1.118		9.21	0.333	0.03	0.121
1997	125.625	0.91		7.62	0.143		0.224
1998						0.13	

Table 3. Results for the baseline run (using inverse variance for weighting the CPUE series) and equal weighting for each CPUE series.

	Inverse Variance Weighting			**Equal Weighting**		
	Expected Value	**SD**	**CV**	**Expected Value**	**SD**	**CV**
Virgin Biomass (Kg)	1.10×10^{8}	1.48×10^{7}	0.13	2.58×10^{8}	8.55×10^{7}	0.33
Catch 1975-1985 (kg)	2.05×10^{5}	7.05×10^{4}	0.34	2.30×10^{5}	7.97×10^{4}	0.35
Pup survival (y^{-1})	0.50	0.06	0.13	0.52	0.07	0.13
Terminal fish numbers (1998)	2.37×10^{6}	7.84×10^{5}	0.33	1.38×10^{7}	6.62×10^{6}	0.48
Virgin population fish numbers (1975)	8.52×10^{6}	1.14×10^{6}	0.13	1.99×10^{7}	6.59×10^{6}	0.33
Depletion	0.72			0.31		

Table 4. Results (modal values) of the first part of the sensitivity analysis. The different assumptions for each run are labelled at the top of each column. The baseline run has inverse variance weighting and parameter values given in Table 1. The sensitivity runs are identical to the baseline except for the changes shown.

	Baseline	Equal weighting	10 pups/female	Ricker stock recruit curve	Hockey Stick stock recruit curve	Pup survival 0.4	Uniform prior on Bo
-Log likelihood	54.47	36.03	54.37	54.46	53.89	54.33	55.66
Bo (kg)	9.86×10^{7}	1.63×10^{8}	7.85×10^{7}	9.81×10^{7}	8.55×10^{7}	1.06×10^{8}	1.02×10^{8}
Catch 75-85 (kg)	1.64×10^{5}	1.93×10^{5}	1.75×10^{5}	1.64×10^{5}	1.64×10^{5}	1.63×10^{5}	1.73×10^{5}
Pup survival (y^{-1})	0.48	0.48	0.47	0.48	0.50	0.40	0.47
Terminal fish numbers (1998)	1.80×10^{6}	6.60×10^{6}	1.47×10^{6}	1.79×10^{6}	1.71×10^{6}	1.91×10^{6}	1.92×10^{6}
Virgin population fish numbers (1975)	7.60×10^{6}	1.26×10^{7}	6.05×10^{6}	7.56×10^{6}	6.60×10^{6}	8.16×10^{6}	7.86×10^{6}
Depletion	0.76	0.47	0.76	0.76	0.74	0.77	0.76

Table 5. Results (modal values) of the second part of the sensitivity analysis. Each CPUE series was used alone for the model fit. All other inputs were the same as the baseline run.

	CPUE series 1	CPUE series 2	CPUE series 3	CPUE series 4	CPUE series 5	CPUE series 6	CPUE series 7
-Log likelihood	40.01	25.34	38.94	26.93	33.24	33.38	30.31
Bo (kg)	1.64×10^{8}	9.33×10^{7}	3.17×10^{8}	1.03×10^{8}	9.31×10^{7}	1.05×10^{8}	1.16×10^{8}
Catch 75-85 (kg)	2.00×10^{5}	1.91×10^{5}	1.93×10^{5}	1.93×10^{5}	1.92×10^{5}	1.93×10^{5}	1.95×10^{5}
Pup survival (y^{-1})	0.48	0.48	0.48	0.48	0.48	0.48	0.48
Terminal fish numbers (1998)	6.64×10^{6}	1.06×10^{6}	1.87×10^{7}	1.86×10^{6}	1.03×10^{6}	1.99×10^{6}	2.84×10^{6}
Virgin population fish numbers (1975)	1.27×10^{7}	7.19×10^{6}	2.45×10^{7}	7.97×10^{6}	7.18×10^{6}	8.10×10^{6}	8.93×10^{6}
Depletion	0.47	0.85	0.24	0.77	0.86	0.75	0.68

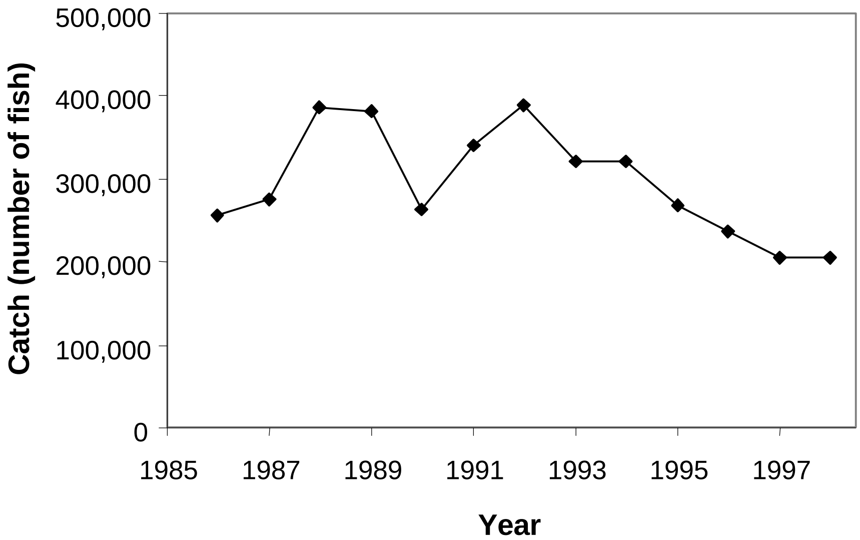

Figure 1. Estimated catch series for blacktip sharks (NMFS 1998)

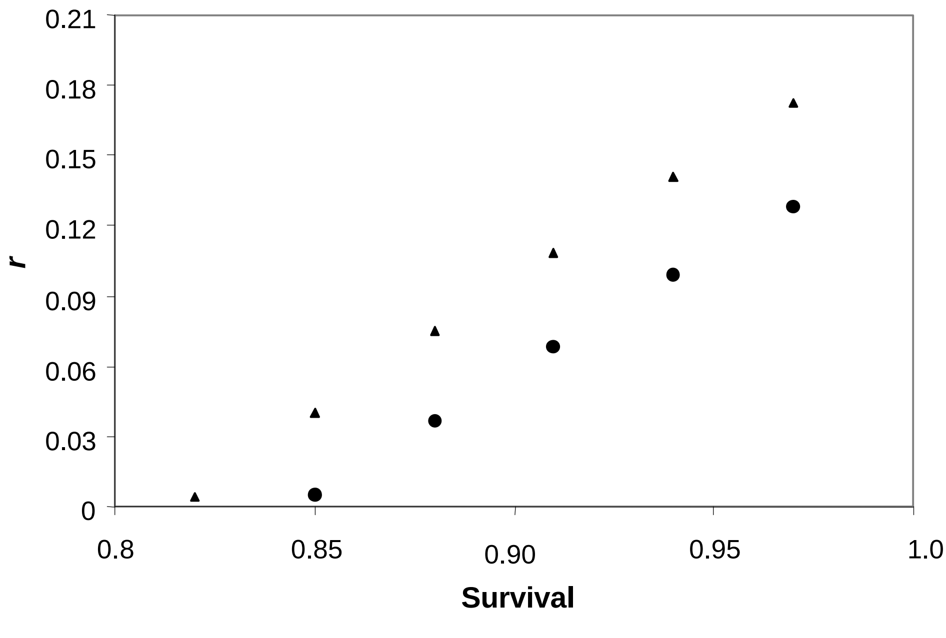

Figure 2 The values of *r* for different values of fish survival when the survival of fish is assumed to be the same for all fish (triangles) or the same for fish of age 1 or older but the survival of 0+ group is fixed and lower (circles).

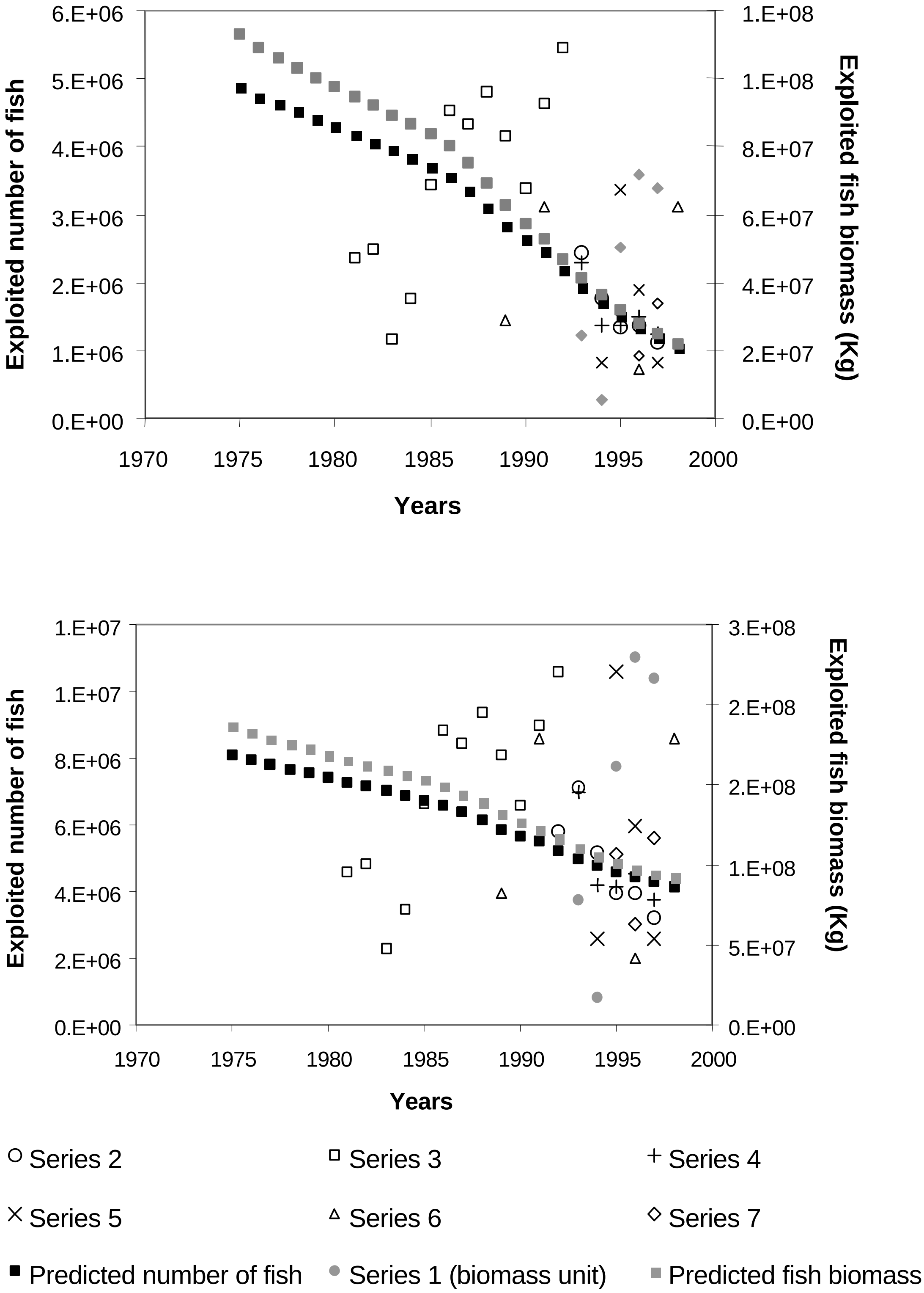

Figure 3 Model fits of population numbers and biomass for the inverse CV (upper figure) and equal weighting methods (lower figure)

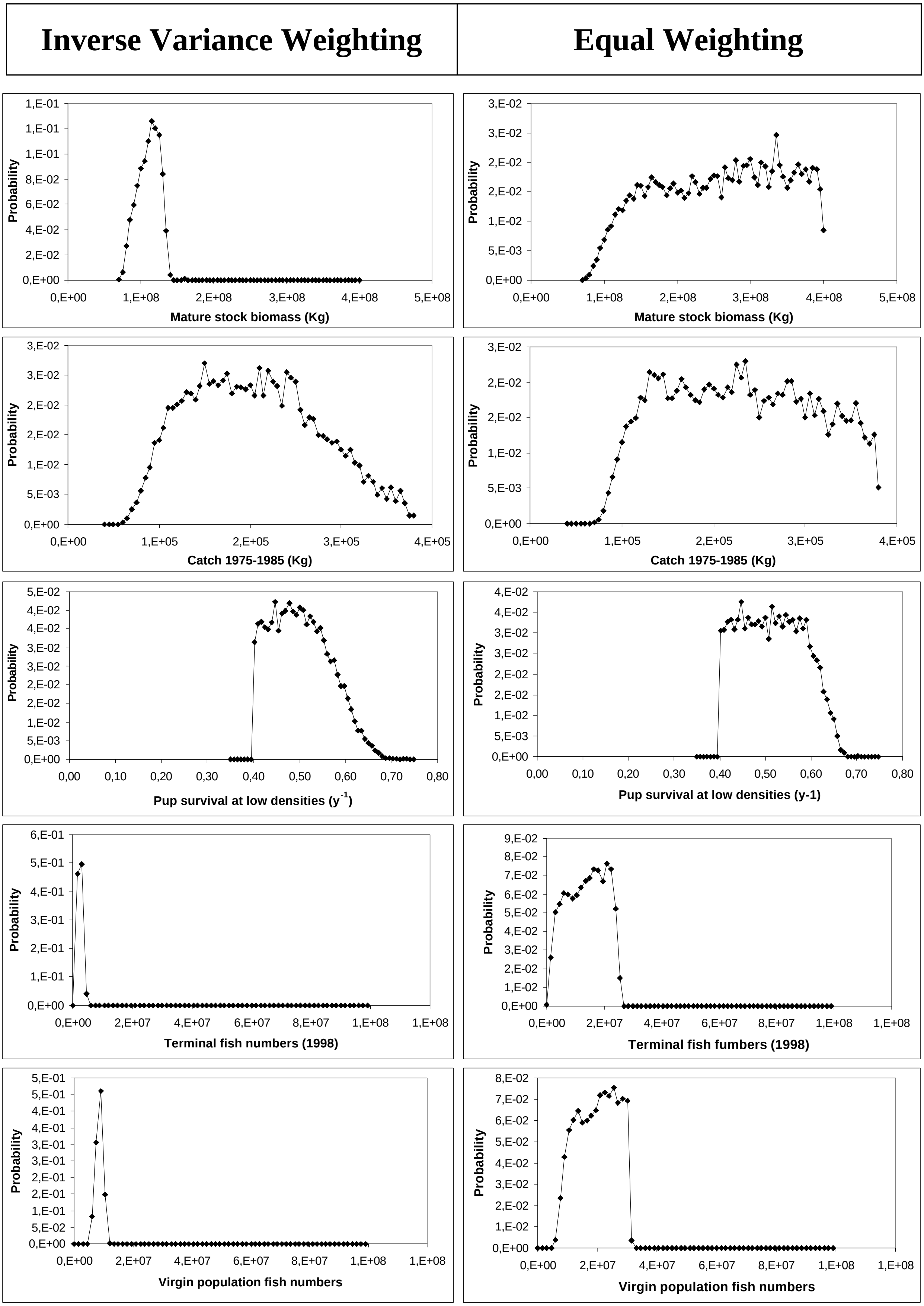

Figure 4. Posterior probability distributions of mature stock biomass under virgin conditins, catch from 1975-1985, pup survival,number of fish in 1998 and virgin number of fish, fitted with inverse variance weighting (left) or equal weighting (right).