Use of an age-structured model for the stock assessment of blue shark in the North Atlantic.

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USE OF AN AGE-STRUCTURED MODEL FOR THE STOCK ASSESSMENT OF BLUE SHARK IN THE NORTH ATLANTIC

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SUMMARY

The paucity of exploitation and biological information for many pelagic shark species, such as blue shark (Prionace glauca), often thwarts the use of detailed population dynamics models for the simulation of the dynamics of those species and assessment of their status. A detailed age-structured population dynamics model is used here to describe the dynamics of blue shark population in the North Atlantic and evaluate the effects of exploitation on its stock size. Uncertainty in the understanding of blue shark dynamics and exploitation patterns due to limited data is incorporated using Bayesian statistics. The model is used to investigate the problems arising from the use of detailed population dynamics models in data poor cases. The potential of the statistical modeling framework to provide predictions about the status of blue shark population is examined and the sensitivity of the model predictions to the values of key input parameters is evaluated.

RÉSUMÉ

La pénurie d'informations relatives à l'exploitation et à la biologie de nombreuses espèces de requins pélagiques, telles que le requin peau bleue (Prionace glauca) contrarie souvent l'utilisation de modèles détaillés de dynamique des populations pour la simulation de la dynamique de ces espèces et l'évaluation de leur état. Un modèle détaillé de dynamique des populations structuré par âge est utilisé ici pour décrire la dynamique de la population de requin peau bleue dans l'Atlantique Nord et évaluer les effets de l'exploitation sur la taille de son stock. On incorpore à l'aide de statistiques bayésiennes l'incertitude dans la compréhension de la dynamique du requin peau bleue et dans les modes d'exploitation due aux données limitées. Le modèle est utilisé pour rechercher à déterminer les problèmes nés de l'emploi de modèles détaillés de dynamique des populations lorsqu'on dispose de peu de données. Le présent document examine le potentiel du cadre de modélisation statistique à prédire l'état de la population de requin peau bleue et évalue la sensibilité des prédictions du modèle aux valeurs des principaux paramètres d'entrée.

RESUMEN

La escasez de información sobre biología y explotación de varias especies pelágicas, como la tintorera (Prionace glauca), supone a menudo un obstáculo para la utilización de modelos detallados de dinámica de población para la simulación de la dinámica de estas especies y la evaluación sobre su estado. En este documento se utilizó un modelo detallado de dinámica de población estructurado por edad para describir la dinámica de la población de tintorera en el Atlántico norte y para evaluar los efectos de la explotación en el tamaño del stock. Se incorporó la incertidumbre en el conocimiento de la dinámica y de los patrones de explotación de la tintorera, debida a la escasez de datos, utilizando estadísticas bayesianas. El modelo se utilizó para investigar los problemas que se derivan de la utilización de modelos detallados de dinámica de población cuando se dispone de pocos datos. Se analiza el potencial del marco de

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modelación estadística para proporcionar predicciones sobre el estado de la población de tintorera y se evalúa la sensibilidad de las predicciones del modelo a los valores de los parámetros clave de entrada.

KEYWORDS

Stock assessment, Stochastic models, Age-structured population dynamics model, Bayesian statistics, By-catch, Blue shark

1. Introduction

Blue shark (*Prionace glauca*) is one of the main by-catches of longline fisheries targeting bluefin tuna, swordfish etc. in the Atlantic Ocean. Due to their low commercial value, blue sharks caught as by-catch are rarely landed. Fishermen have only recently started reporting the number of pelagic sharks caught as by-catch while a limited number of nations have developed relative abundance indices for blue shark in the Atlantic. As a result of these, there are many gaps in the basic catch statistics for this species. Furthermore, there are some aspects of blue shark dynamics which are poorly understood (i.e. recruitment process, age- and sex-dependent migration, etc). Although a stock assessment for the blue shark population in the Atlantic Ocean has not been conducted, both ICCAT and ICES have expressed interest in evaluating the effects of fishing on pelagic shark populations.

A detailed age-structured population dynamics model is presented here which could be used to describe the dynamics of blue shark population in the North Atlantic and evaluate the effects of exploitation on its stock size. Uncertainty in the understanding of blue shark dynamics and exploitation patterns due to limited data is incorporated using Bayesian statistics. This type of approach is general enough to allow for the use of all the available data for blue shark (i.e. catch, relative abundance indices, age-specific dynamics). On the other hand, the increase in the realism in the simulation of species dynamics requires a greater amount (and quality) of information than simpler population dynamics models.

The age-structured statistical framework is applied to existing exploitation and biological data for blue shark and the results are presented here. The potential of the statistical modelling framework to provide predictions about the status of blue shark population is examined and the sensitivity of the model results to the values of key input parameters and assumptions is evaluated.

2. Bayesian modeling framework

The modeling framework proposed here for the stock assessment of blue shark incorporates a detailed age-structured model for the simulation of the dynamics of this species and uses a Bayesian approach to fit the model to data. The age-structured population dynamics model is fleet disaggregated and allows for the simulation of sex-specific dynamics. It uses a fine time scale to calculate the changes in biomass and number of fish over time due to natural and fishing mortality. Stock-recruitment processes are explicitly simulated using either the Beverton-Holt or Ricker stock-recruitment relationship. The stock biomass under virgin conditions, pup survival at low population density, and catches prior to the first year for which catch statistics exist are estimated input parameters. A prior probability density function (pdf) is used for each of the estimated input parameters of the model and Bayesian statistical methods are used to fit the model to data and construct updated pdf's for these and other parameters of interest. A detailed description of the population dynamics model and the statistical method used for the analysis is presented in **Appendix 1**.

3. Parameter values and assumptions

The catch information and relative abundance indices used in the analysis are presented in **Tables 1** and **2**, respectively. By-catch data for the period 2000-2002 were not available and therefore, it was assumed that the by-catch for that period were the same as the by-catch in 1999. The values of the fixed input parameters of the model are shown in **Table 3**. A selectivity curve was developed for the commercial fishery which targets sharks or takes them as by-catch based on by-catch at age information from pelagic longlines. Two of the selectivity curves constructed based on by-catch at age information from two different sources (Japanese longline, American longline) are shown in **Figure 1**. A logistic curve was also used for the recreational fishery. For the construction of this curve it was assumed that selectivity for fish of age 6 or younger is one and declines for older fish to become zero for fish or age 10 or older.

The virgin biomass of the population was treated as an uncertain parameter and therefore, a prior distribution was constructed for its value. A uniform prior was selected for the virgin biomass of mature fish Uniform(1×10^6 Kg, 8×10^{11} Kg) to reflect the lack of information about the virgin biomass of the population. Similarly, a prior distribution was used for the survival of pups at low density, α ; beta(2,2). The prior used for α was slightly informative since it gave more probability to values close to 0.5 and did not allow for values which were greater than the survival of fish at age 1. Two more priors were used for the historical catches (recreational and commercial (by-catch)); $C_{com,hist} \sim N(6 \times 10^6 \text{ Kg}, (6 \times 10^6)^2)$ and $C_{rec,hist} \sim N(2 \times 10^5 \text{ Kg}, (2 \times 10^5)^2)$. The variance of the distributions was chosen such that considerable probability was given to a great range of values to reflect the paucity of information about historical catches. The historical catches are given in biomass since the catch data are also given in biomass. Calculations can be conducted either using the four priors described above or using only the priors for virgin biomass of mature fish and pup survival at low densities.

4. Results

The predictions of the model when all the CPUE series and the catch data were used are shown in **Table 4** (CPUE all) and **Figure 2**. When the values of the 4 uncertain parameters at the mode of the joint posterior pdf were used the model predicted that the current size of the population was approximately 21% of each virgin size (**Table 4**). However, the marginal probability distribution for the population depletion did not support such decrease (**Figure 2f**). The reason for that is that although the mode of the marginal posterior probability distribution for virgin biomass is at a relatively low value of the virgin biomass, considerable probability is given to values of virgin biomass which are much greater than the virgin biomass at the mode. This led to predictions about the current population size which were very close to the virgin size of the population. The model failed to provide a more precise estimate of the virgin size of the population probably because there was not enough information (or there was contradictory information) in the CPUE series and in the values of key biological parameters to support a smaller range of values for virgin biomass. For the same reason, the marginal posterior pdfs for the other three uncertain input parameters resembled their prior distributions (**Figure 2a-d**).

The model was also run using one CPUE series a time to examine whether it was lack of information in the CPUE series or the fact that the CPUEs provided contradictory information which led to such uninformative posterior pdf's. The values of the estimated parameters at the mode of the joint posterior probability distribution for each of the runs are shown in **Table 4**. For four out of the six CPUEs considered, the model failed to converge to a value for each of the uncertain input parameters which was neither the maximum nor the minimum allowed value of the corresponding parameter. CPUE series 1 and 6 were the only two series for which convergence of the model was possible. When CPUE 1 was used, the modal value for the virgin population biomass was much greater than that predicted when all the CPUEs were used. On the other hand, CPUE 6 seemed to support values for virgin biomass which were even smaller than the virgin biomass estimated when all the CPUEs were used for the calculations. The values of the other uncertain input parameters were less affected by the choice of CPUE series. The two CPUEs (CPUE 1 and CPUE 6) also supported much different population depletions. The modal value of the posterior pdf for depletion of the population when CPUE 1 was used was much smaller than that found when CPUE series 6 was used (**Table 4**).

Different combinations of CPUE series were also considered and the values of the estimated parameters at the mode of the joint posterior pdf for each of the combinations are given in **Table 5.** The greatest depletion was predicted when CPUE series 3 and 6 were used together, probably because the results were mainly influenced by CPUE 6. Despite these differences, in all cases, the modal values of the posterior pdfs for the three other uncertain input parameters (historical by-catch and recreational catches and pup survival at low population density) were very close to the modal value of the corresponding prior pdf.

The quality of catch statistics for blue shark is low mainly because by-catch information for the period before 1985 is not available and the information which exists for more recent years is incomplete. The uncertainty in the available catch statistics is believed to increase as we move to earlier years in the by-catch data series. For this reason, the model was run with a smaller set of by-catch data which included only the data for the period after 1993. The results of the calculations are given in **Table 6.** In all cases, the modal values for the biomass of sharks taken as by-catch in early years of exploitation were much smaller than those predicted when the complete series of commercial catches (by-catch) was used. However, when the smaller set of by-catch data was used (1993- 2002) the modal value for the historical by-catch (which, in this case, included the period from 1986-1992) was higher than the average value of reported by-catch over the period 1986-1992.

The calculations were also repeated assuming that the gears used in the fisheries which catch blue sharks were not age selective to examine how sensitive the model predictions were to the choice of gear selectivity. The results of the calculations are shown in **Table 7**. This assumption resulted in smaller population depletion in all of the cases considered. This was mainly the result of smaller predicted values for the historical commercial catches (by-catch). However, the model predictions for the historical commercial catches (by-catch) were much higher than those found when the smaller catch dataset was used (**Table 6**).

One of the biological processes which are not well understood is the stock-recruitment process. A Beverton-Holt stock-recruitment relationship was used for the calculations. However, the model was also run with a Ricker stock recruitment function. The results of these calculations are shown in **Table 8** for all the CPUEs combined and each of them separately. The analysis provided estimates of the modal values of the uncertain parameters only in two cases; when all the CPUE series were used and when only CPUE 2 was used for the calculations. In both cases, the predictions of the model were much different from those found with the Beverton-Holt stock recruitment function. The biggest difference was observed in the model predictions for the modal value of pup survival at low population densities. The value of the pup survival at low densities was expected to be affected by the choice of stock–recruitment function since this parameter is directly related to the stock recruitment function. The marginal posterior pdfs for the uncertain parameters were calculated using the Ricker stock recruitment function and all the CPUEs. The marginal posterior pdfs for the historical catches (commercial, recreational) and pups survival were the same as those found when the Beverton-Holt stock recruitment function was used (**Figure 2**). The marginal posterior pdf for the virgin biomass was similar to the one shown in **Figure 2** except for the mode which corresponded to a smaller value of the virgin biomass than that found when the Beverton-Holt stock recruitment function was used.

5. Discussion

The model predictions showed that the data to which the model was fitted did not provide much information about the values of the uncertain input parameters. Although the model predictions were mainly driven by the prior pdf's used, the analysis showed that the model predictions were affected by the choice of CPUE series. Contradictory information in the CPUE series might be a reason for this.

Blue sharks are caught in many fisheries as by-catch. For the biggest part of the analysis presented in this paper, it was assumed that the selectivity of the gear which corresponds to each fishery which catches blue sharks as by-catch was the same. This is partly the result of limited information about the by-catch taken by each fishery separately and/or about catches-at-age information for each fishery. However, the calculations using non-selective gears showed that the choice of gear selectivity could affect the model predictions.

The predicted modal values of pup survival at low densities were very sensitive to the choice of stock recruitment function. Given the lack of adequate information in the data to support either of the two stock – recruitment functions considered, other methods could be used to provide a better estimate of the value of this parameter (expert advice, meta-analysis etc.). Such methods could also be used to develop a (informative) prior for pup survival.

In general, although some differences in the model predictions were observed when different assumptions for key input parameters and biological processes were used, the model predictions were primarily driven by the priors. Given the uncertainty which characterises the catch information for the earliest years in the catch dataset, it is reasonable to treat the catch for those years as estimated parameters. However, this gives even more weight to the corresponding prior. Better catch statistics could assist in the elimination of this problem which could also lead to more precise model estimates for the status of blue shark stock.

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Table 1. Catch data available for blue shark in North Atlantic. The by-catch data are mainly from the longline fishery for tuna, swordfish, etc. (Anonymous 2002). The values for recreational and commercial fishery (targeting sharks) refer only to the U.S. recreational and commercial fisheries, respectively (E. Cortes, pers. comm.). Catches are given in Kg. For the calculations, it was assumed that the by-catch for the period 2000-2002 were the same as the by-catch in 1999.

Years	*By-catch*	*Recreational fishery*	*Commercial fishery*
1981	0	204273	0
1982	0	0	0
1983	0	605271	0
1984	0	106968	0
1985	0	340975	0
1986	1000	1111941	400
1987	526200	874268	0
1988	421160	354824	100
1989	480000	270502	0
1990	2129000	87085	254
1991	3029000	307818	0
1992	1767000	214341	470
1993	5750000	672161	7877
1994	5885000	21028	7820
1995	6786000	19245	3608
1996	6081000	277152	5399
1997	3466000	209917	1420
1998	25220000	252386	2870
1999	24263000	216426	155
2000	-	290752	612
2001	-	39403	3090
2002	-	30000	200

Table 2. CPUE series used for the calculations (Anonymous 2002; Brooks *et al.* 2004.).

Years	*CPUE 1*	*CPUE 2*	*CPUE 3*	*CPUE 4*	*CPUE 5*	*CPUE 6*
	N. Atl. JLL logbook	*U.S observers in JLL vessels*	*U.S. PLL logbooks*	*U.S. LPS*	*U.S. Pelagic observers*	*U.S. MRFSS*
1971	0.7819					
1972	1.1925					
1973	1.0384					
1974	2.1992					
1975	1.3323					
1976	0.8599					
1977	1.8199					
1978	1.9201	2.43				
1979	1.6581	1.77				
1980	3.2596	1.55				
1981	2.8504	1.09				0.87
1982	1.777	0.45				0.25
1983	1.5619	1.08				1.86
1984	0.9235	1.89				0.15
1985	0.9179	1.62				0.46
1986	2.2557	1.34	19.59	0.52		0.52
1987	1.6906	1.00	13.73	0.30		1.89
1988	1.0604	0.40	9.26	0.60		0.66
1989	1.2965		8.12	0.34		0.80
1990	1.3078		7.28	0.39		0.96
1991	1.0403		9.08	0.79		0.63
1992	1.9086		8.66	0.98	15.49	2.69
1993	2.5907		9.74	0.88	7.53	0.85
1994	2.8503		8.52	1.06	5.81	0.79
1995	2.4324		7.96	0.94	12.30	2.57
1996	2.6619		8.36	2.88	8.88	1.33
1997	2.136		7.57	2.05	2.93	
1998	1.8181		6.00	1.28	22.79	
1999	1.4182		4.65		11.98	
2000	1.3488		4.32		8.42	
2001			3.38		8.80	
2002			3.02		8.66	

Table 3. Population dynamics model input parameters (Skormal and Natanson 2003; Cortés 2002; Garcia-Cortés and Mejuto 2001; Castro and Mejuto 1995; E. Cortés pers. comm.)

Parameter	*Value*	
Time step	3 months	
	females	*males*
Age at 50% maturity a_{50}	4.3 years	4 years
Age at 95% maturity a_{95}	5 years	4.5 years
Maximum age a_{max}	16 years	
Survival from natural causes of death	0.76 a=1 y 0.82 a=2 y 0.84 a=3 y 0.86 a=4 y 0.87 a=5 y 0.88 a=6 y 0.89 a=7 y – 8y 0.90 a=9 y – 12 y 0.91 a=13 y -16 y	
K	0.13	0.18
L_∞	310 cm FL	282 cm FL
t_o	-1.77 y	-1.35 y
b_g	3.2319	
d_g	8.04×10^{-7} length in cm (FL), weight in Kg	
Fecundity	-91.97 + 0.6052*FL	
Reproduction frequency	2 years	
Gestation period	1 year	
Sex ratio	1:1	

Table 4. Modal values of the 4 uncertain parameters (Mature fish biomas under virgin (v) conditions, historical commercial and recreational catches, and pups survival at low population density). The modal values for the current (c) size and biomass of the population as well as the depletion of the population in number of fish are also given below. The parameters that measure fish biomass are given in Kg. Historical catches are also given in Kg. "CPUE all" means that all the CPUEs presented in Table 2 were used. The modal values when only one CPUE at a time was used for the calculations are also presented. The results for CPUE 4 are not shown since the model did not converge. An asterisk next to the name of the CPUE means that the model converged at the minimum or maximum values of at least one of the uncertain parameters. For those cases, only the modal values of the 4 uncertain input parameters are presented.

	CPUE all	*CPUE 1*	*CPUE 2**	*CPUE 3**	*CPUE 5**	*CPUE 6*
Mat. fish biomass (v)	2.4E+08	4.3E+08	8.0E+11*	1.6E+08	8.0E+11*	1.8E+08
Mat. fish biomass (c)	4.8E+07	2.6E+08				7.6E+06
Historical by-catch	1.1E+07	8.4E+06	6.0E+06	1.0E+00*	6.0E+06	7.6E+06
Historical rec. catches	2.1E+05	2.1E+05	2.0E+05	1.7E+05	2.0E+05	1.8E+05
Pup survival at low population density	5.5E-01	5.2E-01	5.0E-01	5.0E-01	5.0E-01	5.3E-01
Number of fish (v)	3.9E+07	6.9E+07				3.0E+07
Number of fish (c)	8.3E+06	4.3E+07				1.9E+06
Number of mat. Fish (v)	2.8E+06	5.0E+06				2.1E+06
Number of mat. Fish (c)	7.0E+05	3.3E+06				1.2E+05
Total pop. depletion	0.21	0.62				0.06

Table 5. The model predictions (modal values, see Table 4 for an explanation of the parameters presented here) for different combinations of CPUEs.

	CPUEs 1 + 3 + 6	*CPUEs 1 + 3*	*CPUEs 3 + 6*
Mat. fish biomass (v)	1.9E+08	1.8E+08	1.9E+08
Mat. fish biomass (c)	2.1E+07	2.8E+07	1.7E+07
Historical Com. catches (by-catch)	7.7E+06	4.4E+06	7.2E+06
Historical rec. catches	2.1E+05	2.1E+05	2.1E+05
Pup survival at low pop. density	5.6E-01	5.3E-01	5.2E-01
Number of fish (v)	3.2E+07	3.0E+07	3.0E+07
Number of fish (c)	4.0E+06	5.1E+06	3.4E+06
Number of mat. Fish (v)	2.3E+06	2.1E+06	2.2E+06
Number of mat. Fish (c)	3.2E+05	4.0E+05	2.6E+05
Total pop. depletion	0.13	0.17	0.11

Table 6. Model predictions (modal values, see Table 4 for an explanation of the parameter presented here) for different combinations of CPUEs and when only the commercial catch (by-catch) data for the period 1993-2002 were used.

	CPUEs 1 + 3 + 6	*CPUEs 1 + 3*	*CPUEs 3 + 6*
Mat. fish biomass (v)	1.8E+08	1.7E+08	1.8E+08
Mat. fish biomass (c)	3.8E+07	3.5E+07	2.3E+07
Historical com. catches (by-catch)	2.0E+06	1.3E+06	3.1E+06
Historical rec. catches	2.3E+05	2.3E+05	2.1E+05
Pup survival at low pop. density	5.2E-01	5.1E-01	5.1E-01
Number of fish (v)	3.0E+07	2.8E+07	2.9E+07
Number of fish (c)	6.7E+06	6.2E+06	4.3E+06
Number of mat. Fish (v)	2.2E+06	2.1E+06	2.1E+06
Number of mat. Fish (c)	5.3E+05	4.8E+05	3.3E+05
Total pop. depletion	0.22	0.22	0.15

Table 7. Model predictions (modal values, see Table 4 for an explanation of the parameter presented here) for different combinations of the CPUEs and non selective gears for the commercial (by-catch and directed) and recreational fisheries.

	CPUE all	*CPUEs 1 + 3 + 6*	*CPUEs 1 + 3*	*CPUEs 3 + 6*
Mat. fish biomass (v)	2.5E+08	2.0E+08	1.8E+08	2.0E+08
Mat. fish biomass (c)	5.6E+07	2.9E+07	3.7E+07	2.3E+07
Historical com. catches (by-catch)	1.0E+07	7.0E+06	3.4E+06	7.2E+06
Historical rec. catches	2.1E+05	2.1E+05	2.0E+05	2.0E+05
Pup survival at low pop. density	5.7E-01	5.6E-01	5.2E-01	5.2E-01
Number of fish (v)	4.1E+07	3.3E+07	3.0E+07	3.2E+07
Number of fish (c)	9.3E+06	4.9E+06	6.2E+06	3.9E+06
Number of mat. fish (v)	3.0E+06	2.4E+06	2.2E+06	2.3E+06
Number of mat. fish (c)	7.4E+05	3.8E+05	4.6E+05	3.0E+05
Total pop. depletion	0.23	0.15	0.21	0.12

Table 8. Model predictions (modal values, see Table 4 for an explanation of the parameters presented here) when a Ricker stock-recruitment relationship is assumed to describe the recruitment process. "CPUE all" means that all the CPUEs presented in Table 2 were used. The modal values when only one CPUE at a time was used for the calculations are also presented. An asterisk next to the name of the CPUE means that the model converged at the minimum or maximum values of at least one of the uncertain parameters. For those cases, only the modal values of the 4 uncertain input parameters are presented.

	CPUE all	*CPUE 1**	*CPUE 2*	*CPUE 3**	*CPUE 4**	*CPUE 5**	*CPUE 6*
Mat. fish biomass (v)	1.5E+08	8.0E+11*	1.1E+08	2.1E+08	8.0E+11*	8.0E+11*	8.0E+11*
Mat. fish biomass (c)	2.9E+07		3.9E+06				
Historical com. catches (by-catch)	1.0E+07	6.0E+06	7.4E+06	1.4E+06	6.0E+06	6.0E+06	6.0E+06
Historical rec. catches	2.0E+05	2.0E+05	2.1E+05	2.0E+05	2.0E+05	2.0E+05	2.0E+05
Pup survival at low pop. density	0.18	0.50	0.67	0.02*	0.50	0.50	0.50
Number of fish (v)	2.4E+07		1.7E+07				
Number of fish (c)	5.5E+06		2.4E+06				
Number of mat. Fish (v)	1.7E+06		1.3E+06				
Number of mat. Fish (c)	4.6E+05		7.2E+04				
Total pop. depletion	0.23		0.14				

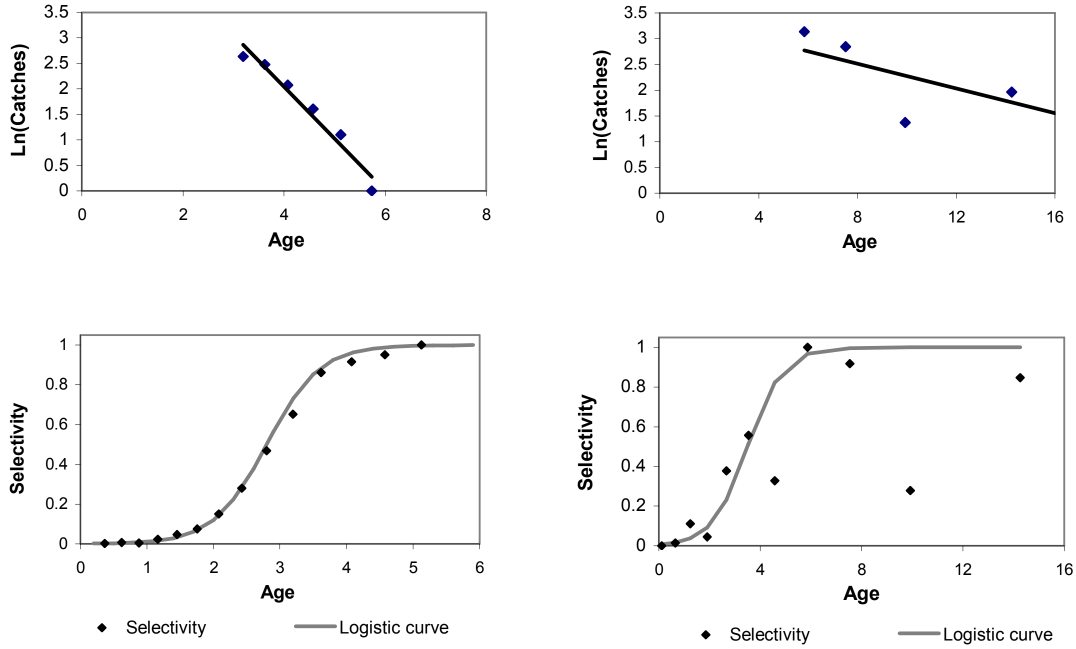

Figure 1. Selectivity curves (second row) constructed from catch at age information (first row). *Left column*: Catches and selectivity for Japanese longline vessels fishing in western North Atlantic (Matsushita and Matsunaga 2001). *Right column*: Catches and selectivity for U.S. longline vessels operating in the western North Atlantic (Beerkircher 2004).

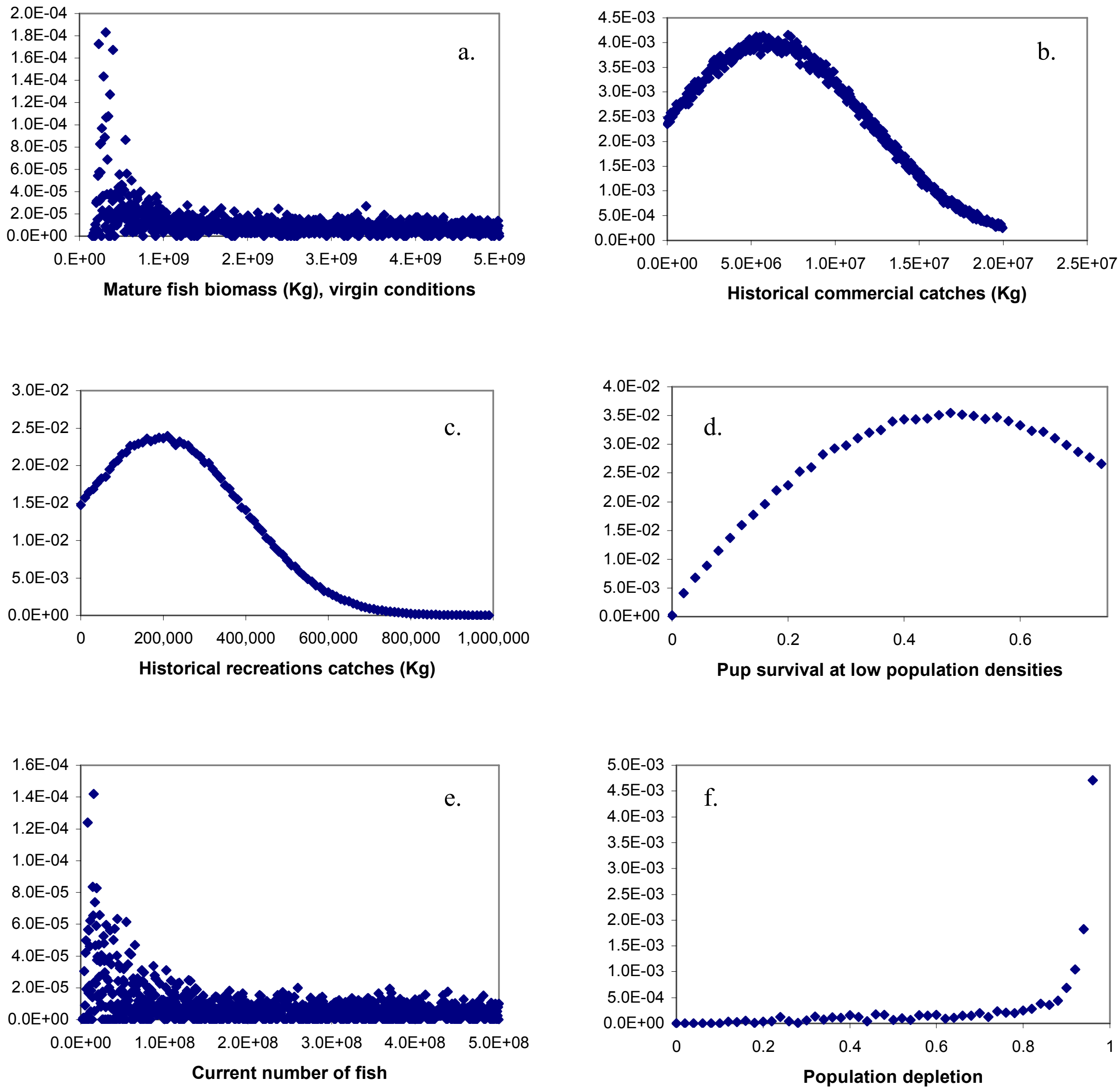

Figure 2. Marginal posterior probability distributions for a: mature fish biomass under virgin conditions (prior pdf: Unif(1×10^6 Kg, 8×10^{11} Kg)), b: historical commercial (by-catch) catches (prior pdf: N(6×10^6 Kg, $(6 \times 10^6)^2$)), c: historical recreational catches (prior pdf: N(2×10^5 Kg , $(2 \times 10^5)^2$)), d: pup survival at low population densities (prior pdf: beta(2,2)), e: current population size, and f: population depletion.

Appendix 1

1. Bayesian modeling framework

1.1 Population dynamics model

The model simulates the dynamics of the blue shark population and calculates the changes in the population size due to natural and fishing mortality. It uses a 3-month time step for the calculations and thus, each year comprises of 4 time steps. Starting from the number of fish, $N^b_{g,y,t,a}$, of sex, *g*, in each age class, *a*, at the beginning of each time step, *t*, and year, *y*, we can calculate the number of fish in each age class at the end of the same time step, $N^e_{g,y,t,a}$, if the annual survival at age, S_a, of the population from natural causes of death and the number of fish, $C_{g,y,t,a}$, of sex, *g*, from each age class, *a*, that die at time step, *t*, due to fishing with gear, *j*, are known:

(A1.1) $$N^e_{g,y,t,a} = \begin{cases} (N^b_{g,y,t,0} \cdot S_a^{1/8} - C_{g,y,t,a})S_a^{1/8} & a = 0, t = t_p + 1 \\ (N^b_{g,y,t,a} \cdot S_a^{1/8} - C_{g,y,t,a}) \cdot S_a^{1/8} & a \geq 1 \end{cases},$$

where $N^b_{g,y,t_p+1,0} = f_g \cdot N_{0,y}$ is the number of pups of gender, *g*, born in year, *y*. $N_{0,y}$ is the number of pups born in year, *y*, f_g is the fraction of pups of sex, *g* and t_p is the time step when pupping is taking place. It is assumed that pupping is taking place at the end of the pupping season and the survival per year of fish in age class, *a*, S_a, is constant. Pups are vulnerable to fishing which takes place in the middle of each time step. The number of fish caught at time step, *t*, in year, *y*, with gear, *j*, $C_{y,t,j}$, is equal to one fourth of the corresponding annual catches unless non-uniform temporal distribution of fishing is simulated. Catches, $C_{g,y,t,a,j}$, of fish of age *a* and sex, *g*, in year, *y*, and time step, *t*, with gear, *j*, are taken in a pulse in the middle of each time step, after the population has experienced natural mortality for half of the time period which corresponds to one time step (Punt and Walker, 1998):

(A1.2) $$C_{g,y,t,a,j} = (N^b_{g,y,t,a} \cdot S_a^{1/8} - \sum_{j'}^{j-1} C_{g,y,t,a,j'}) \cdot v_{g,a,j} \cdot u_{y,t,j},$$

where $v_{g,a,j}$ denotes vulnerability of fish of age *a* and sex, *g*, to gear *j*, and $u_{y,t,j}$ is the exploitation rate per gear, *j*, at time step, *t*. The assumption underlying this equation is that fishing using different gears is a successive process such that, at any given time, fish are caught with only one gear. If the catch per fishing period and gear, are known then the exploitation rate for each fishing period, $u_{y,t,j}$ is (Punt and Walker, 1998):

(A1.3) $$u_{y,t,j} = \frac{C_{y,t,j}}{\sum_g \sum_a v_{g,a,j} \cdot \left[N^b_{g,y,t,a} \cdot S_a^{1/8} - \sum_{j'=1}^{j-1} C_{g,y,t,a,j'} \right]}$$

The catches in biomass could also be calculated using equation 2 and the weight at age relationship. Fish weight at age *a*, is expressed as a function of fish length, $L_{g,a}$:

(A1.4) $$w_{g,a} = d_g (L_{g,a})^{b_g},$$

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

(A1.5) $$L_{g,a} = L_{\infty,g} \cdot (1 - e^{-k_g(a - t_{o,g})}),$$

where, $L_{\infty,g}$, is the theoretical maximum asymptotic length of fish of sex, g, and k_g , $t_{o,g}$, are constants. The biomass of the exploitable population per gear at each time step, t, is calculated by using an equation similar to equation 2:

(A1.6) $$B^{expl}_{y,t,j} = \sum_g \sum_{a=0}^{a_{max}} \left(N_{g,y,t,a} \cdot S_a^{1/8} - \sum_{j'}^{j-1} C_{g,y,t,a,j'} \right) \cdot v_{g,a,j} \cdot w_{g,a(t)}$$

The exploitable number of fish for each gear is calculated using the same equation but without multiplying by the weight of the fish at each age class. The exploitable biomass/number of fish per gear and year are found as the mean of the exploitable biomass/number of fish per time step over a year period.

Apart of the number of males and females in each age group, the model also calculates the mature fish at each time step. The model allows for multi-annual reproductive cycles thus, the number of females which give birth each year could be a fraction of the number of mature female fish in the same year. A bi-annual reproduction cycle has been chosen for the calculations based on information about the biology of blue shark. Females are assumed to pup at the second time step of each year after a gestation period of one year. The number of the gravid females in the middle of each year, y, is equal to the fraction of gravid females at the beginning of year, y, that survive to give birth. The number of pups is calculated by multiplying the number of the gravid females in the middle of the year by the expected number of pups per female:

(A1.7) $$N_{0,y} = \frac{1}{2} \sum_{a(t=t_p)} N_{g=fem,\, y,\, t=t_p, a} \cdot \phi_{g=fem,\, a-1} \cdot \overline{\Phi}_a$$

where, $\phi_{g,a}$, is the proportion of fish of age a and sex, g, that are mature and $\overline{\Phi}_a$, is the number of pups per pregnant female of age a. The value of the latter parameter could depend on the age or size of the fish or be constant. A logistic curve is used to describe the proportion of fish at age a which are mature:

(A1.8) $$\phi_{g,a} = \frac{1}{1 + e^{(-k_g \cdot (a - a_{50_g}))}},$$

where a_{50_g} is the age at 50% maturity and k_g is a constant which can be calculated if the ages at 50% and 95% maturity are known.

The survival of pups at age 0 is assumed to be density dependent and is calculated using a stock-recruitment function. Two types of density dependence are simulated using the Beverton-Holt and Ricker stock-recruitment functions. According to the Beverton-Holt stock – recruitment function, the annual survival of sharks of age 0 at different density levels and under no exploitation conditions is:

(A1.9) $$S_{0,y} = \frac{R_y}{N_{0,y}} = \frac{1}{\alpha + \beta \cdot N_{0,y}}$$

According to the Ricker stock-recruitment function the survival of pups during the first year of their life assuming that only natural mortality occurs, is:

(A1.10) $$S_{0,y} = \frac{R_y}{N_{0,y}} = \gamma \cdot e^{-\delta \cdot N_{0,y}}$$

1.2 Virgin conditions

The fraction of total fish population which is in each age class under virgin conditions is determined by the survival of fish from natural causes of death. Therefore, if the survival at age and the total number, $N_{y_v,t}$, or biomass of fish, $B_{y_v,t}$, before any exploitation takes place is known the number of fish of age, *a*, at the beginning of each year, y_v, can be calculated as follows:

(A1.11)
$$N_{g,y_v,t=1,a} = \begin{cases} f_g \cdot R_{y_v,t=t_p} \cdot S_a^{1/2} & a = 1 \\ f_g \cdot R_{y_v,t=t_p} \cdot \prod_{a'=1}^{a-1} S_{a'} \cdot S_a^{1/2} & 0 < a \le a_{\max} - 1 \\ f_g \cdot R_{y_v,t=t_p} \cdot \dfrac{\prod_{a'=1}^{a_{\max}-1} S_{a'}}{1 - S_{a_{\max}}} \cdot S_{a_{\max}}^{1/2} & a = a_{\max} \end{cases}$$

$R_{y_v,t}$ denotes number of recruits under virgin conditions and is calculated from the total number or biomass of fish of age 1 or older under virgin conditions:

(A1.12)
$$R_{y_v,t=t_p} = \frac{B_{y_v,t=t_p}}{\sum_g f_g \left[w_{g,a=1} + \sum_{a=1}^{a_{\max}-1} w_{g,a(t=t_p)} \prod_{a'=1}^{a-1} S_{a'} + w_{g,a_{\max}(t=t_p)} \dfrac{\prod_{a'=1}^{a_{\max}-1} S_{a'}}{1 - S_{a_{\max}}} \right]}$$

The summation over age will be limited to only the ages which are equal to or greater than the age at maturity if the virgin biomass of mature fish is used instead of the total biomass of the population of fish of age 1 or older. Similarly, the weight in the above expression will be omitted if the total number of fish of age 1 or older is used instead of the total biomass. The number of pups born under virgin conditions are calculated using equation (7) once the number of fish in each age class has be found.

1.3 Statistical framework

According to the Bayesian theorem, if $p(\theta_n)$ is the joint prior probability density function for a set of values of the estimated parameters, θ_n then the value for the posterior probability density function for this set of values, given the data, *I*, is:

(A1.13)
$$p(\theta_n \mid I) \sim p(\theta_n) * L(\mathrm{I} \mid \theta_\mathrm{n})$$

where $L(\mathrm{I} \mid \theta_\mathrm{n})$ is the likelihood function for this set of values of the uncertain parameters of the model.

The model assumes that catch data are known without error and that the error in the relative annual population abundance series is available. The observed values, $I_{j,k,y}$, of each relative abundance series, *k*, from fishery, *j*, are assumed to be independent of each other and log-normally distributed about the corresponding model predicted values:

(A1.14)
$$I_{j,k,y} \sim \log normal(q_{j,k} N_{y,j}^{\exp l}, {\sigma_{j,k}}^2)$$

A constant of proportionality, $q_{j,k}$, is used to express the model predicted values, $N_{y,j}^{\exp I}$, to the same units as the units used for the corresponding relative abundance series. $\sigma_{j,k}$ is the lognormal standard deviation for residual errors between the observed and predicted values for each series of relative fish abundance.

The model uses two different weighting methods to calculate the weight which is given to each relative abundance series; inverse CV weighting and equal weighting. If the inverse CV weighting method is used the likelihood function for all the sets of observed values and for one potential set of values for the parameters of the model, θ_n, is (McAllister and Kirkwood 1998):

(A1.15) $$\ln L(I \mid \theta_n) = \sum_j \sum_k \sum_y -\frac{1}{2c_k CV_{k,y}^2 \sigma_{j,k}^2}\left(\ln \frac{I_{j,k,y}}{q_{j,k} B_{j,y,k}}\right)^2 - \ln\sqrt{I_{j,k,y} \cdot c_k CV_{k,y}^2 \sigma_{j,k}^2 2\pi},$$

where the annual estimate of the CV for each abundance series is used to express the sampling error for each observation of the relative abundance series, k. In the above equation, each relative abundance series point is given a weight based on the error which characterises it. A constant, c_k, is used to make the sum of the square of CV's of each series equal to 1. The alternative weighting method (equal weighting) assumes that each point has the same weight regardless of the observation error which characterises it. The expression for log-likelihood in this case is:

(A1.16) $$\ln L(I \mid \theta_n) = \sum_j \sum_k \sum_y -\frac{1}{2\sigma^2}\left(\ln \frac{I_{j,k,y}}{q_{j,k} B_{j,y,k}}\right)^2 - \ln\sqrt{2\pi \cdot I_{j,k,y} \cdot \sigma^2}$$

The posterior joint probability distribution of the estimated parameters is approximated using the SIR (sampling/importance resampling) algorithm.

Table A1.1. Parameters used in the statistical modelling framework.

Symbol	*Parameter*
α	Constant of the Beverton-Holt stock recruit function
A	Age
a_{50_g}	Age at 50% maturity
β	Constant of the Beverton-Holt stock recruit function
b_g	Constant of the weight-length equation
γ	Constant of the Ricker stock recruit function
$C_{g,y,t,a}$	Number of fish of sex, *g*, from each age class, *a*, that die at time step, *t*, due to fishing with gear, *j*
δ	Constant of the Ricker stock recruit function
d_g	Constant of the weight-length equation
f_g	The fraction of pups of sex, *g*
$\overline{\Phi}_a$	Number of pups per pregnant female of age *a*
$\phi_{g,a}$	Proportion of fish of age *a* and sex, *g*, that are mature
g	Gender
j	Gear
k_g	Constant of the length at age function
$L_{\infty,g}$	The theoretical maximum asymptotic length of fish of sex, *g*
$N_{g,y,t,a}$	Number of fish of sex, *g*, in each age class, *a*, at time step, *t*, and year, *y*
$q_{j,k}$	Constant of proportionality
R_y,	Number of recruits
S_a	Annual survival at age
t	Time step
t_p	Time step when pupping is taking place
$t_{o,g}$	Constant of the length at age function
$u_{y,t,j}$	Exploitation rate per gear, *j*, at time step, *t*
$v_{g,a,j}$	Vulnerability of fish of age *a* and sex, *g*, to gear, *j*
y	Year