SCRS/2001/073

Col.Vol.Sci.Pap. ICCAT, 54 (4): 1314-1332. (2002)

STATISTICAL CATCH-AT-LENGTH MODEL FOR PORBEAGLE SHARK (*LAMNA NASUS*) IN THE NORTHWEST ATLANTIC

S J Harley[1]

SUMMARY

*A variety of data types are available for the assessment of the Northwest Atlantic porbeagle shark (*Lamna nasus*) population. I describe an age- and sex-structured population dynamics model that fits to catch-at-length data and catch-per-unit-effort data from the fishery. This model provides an ideal environment for the exploration of the available data as it links the data via a dynamic model. This allows one to look for inconsistencies among data types and may provide insights into both population and fleet dynamics. A model of this general type could also be used in the formal assessment of the stock and has the advantage that by including much of available data into the estimation procedure, it may overcome some confounding from estimating key parameters outside of the model. A number of possible disadvantages of this approach are also discussed. Given the low fecundity of porbeagle sharks it is possible to derive spawner recruitment parameters from biological data, thus overcoming a common problem associated with forward projection models. I show how it is also possible to integrate mark-recapture data into the assessment model to improve the estimation of both annual and age-specific fishing mortalities. Preliminary results from this model were presented in the 2001 Canadian assessment of the stock (Campana, Marks, Joyce, and Harley (2001), Canadian Stock Assessment Secretariat Research Document 2001/067).*

RÉSUMÉ

Toute une variété de types de données est disponible pour l'évaluation du stock de requin-taupe commun de l'Atlantique nord-ouest. Le présent document décrit un modèle de dynamique des populations structuré par âge et par sexe qui s'ajuste aux données de prise par taille et de prise par unité d'effort de la pêcherie. Ce modèle offre un cadre idéal pour l'exploration des données disponibles, car il associe les données au moyen d'un modèle dynamique. Ceci permet de rechercher les incohérences entre les types de données et peut offrir des notions sur la dynamique de la population comme de la flottille. Un modèle de ce type général pourrait aussi servir pour l'évaluation formelle du stock, et présente l'avantage de pouvoir peut-être, en incorporant une grande partie des données disponibles dans le processus d'estimation, éliminer une partie de la confusion qui découle du fait d'estimer des paramètres-clés en-dehors du modèle. Un certains nombre d'inconvénients éventuels de cette approche sont également discutés. Vu la médiocre fécondité des requins-taupes, il est possible de calculer des paramètres géniteur/recrue d'après les données biologiques, ce qui permet de résoudre un problème courant lié aux modèles de projection forward. Le présent document montre comment il est possible d'intégrer des données de marquage-recapture dans le modèle d'évaluation pour améliorer l'estimation de la mortalité annuelle comme spécifique de l'âge. Les résultats préliminaires de ce modèle ont été présentés à l'évaluation canadienne de 2001 du stock (Campana, Marks, Joyce & Harley, 2001, Canadian Stock Assessment Secretariat Research Document 2001/067).

RESUMEN

Se dispone de una gran variedad de tipos de datos para la evaluación de la población del marrajo sardinero (Lamna nasus) del Atlántico Noroeste. En este documento se describe un modelo de dinámica de poblaciones estructurado por sexo y edad que se ajusta a los datos de

---

[1] Department of Biology, Dalhousie University, Halifax, Nova Scotia, CANADA B3H 4J1, E-mail: harley@mathstat.dal.ca

captura por clases de talla y a los datos de captura por unidad de esfuerzo de la pesquería. Este modelo proporciona un medio ideal para la exploración de los datos disponibles, ya que relaciona los datos a través de un modelo dinámico. Esto permite buscar contradicciones entre los diferentes tipos de datos y proporciona una idea de la dinámica de poblaciones y de la flota. Un modelo general de este tipo podría también utilizarse en la evaluación formal del stock y tiene la ventaja de que, al incluir la mayor parte de los datos disponibles en el procedimiento de estimación, se pueden superar algunas confusiones derivadas de la estimación de parámetros clave fuera del modelo. También se discuten numerosas desventajas posibles de este enfoque. Debido al bajo nivel de fecundidad del marrajo sardinero, es posible extraer parámetros de reclutamiento del stock reproductor de los datos biológicos, superando así un problema común asociado a los modelos de proyección de futuro. Se muestra también cómo es posible integrar los datos de marcado-recaptura en el modelo de evaluación para mejorar la estimación de las mortalidades por pesca tanto anuales como específicas por clase de edad. Los resultados preliminares de este modelo se presentaron en la evaluación del stock canadiense de 2001 (Campana, Marks, Joyce y Harley (2001), Documento Científico 01/067 Evaluación del stock de Canadá).

KEYWORDS

Stock assessment, population dynamics, long lining, shark fisheries, Lamna nasus,

1 INTRODUCTION

The porbeagle shark (*Lamna nasus*) population in the Northwest Atlantic has been the focus of considerable biological research in recent years (Campana et al. 1999). In particular, recent studies have focussed on reducing uncertainty in key biological process such as migration (i.e., stock structure) (Campana et al. 1999) and growth (Natanson et al. 2001). This recent research combined with observations from the population at near-virgin levels has provided sufficient data to apply quantitative methods to assess the stock (Campana et al. 2001).

In this paper I describe the age- and sex-structured model that formed part of the most recent Canadian assessment of the porbeagle stock in the Northwest Atlantic (Campana et al. 2001). I also outline the advantages and disadvantages of using this model as a tool to both explore the available data in a structured way, and provide estimates of stock status and yields.

Full details of the data and derivation of the biological parameters used here are described in full detail Campana et al. (2001) and are only briefly described here.

2 MODEL

The basic model dynamics are based on the generalized age-structured model Coleraine (Hilborn et al. 2000) while the mechanism for fitting to the catch-at-length data is that used in MULTIFAN (Fournier et al. 1990). The model projects the population forward in time removing catch and adding recruitment as opposed to the backwards projection used in Virtual Population Analysis (VPA) and its derivatives.

The available data motivated the structure of the model. Three sources of data were included in the model; total catches for the years 1961–2000, catch-per-unit-effort (CPUE) indices for immature and mature fish, and samples of the length frequency composition of the landings.

The fishery was separated into two components; (1) Scotian shelf fishery (Shelf), and (2) Grand Banks and the Gulf of St Lawrence (NFGulf). Each “fishery” represents different spatial and temporal strata and the size composition of the catch differs across these strata. All data was separated out by fishery.

Here I will use the subscripts, *a*, *t*, and *l*, for age, time (year), and length, and the superscripts *s* and *g* for sex and fishing gear. The model was independently developed in Excel for verification.

2.1 Dynamics

Abundance at age *a* and sex *s* is given by

$$N_{a,t}^{s} = \begin{cases} R_{a,t}^{s} & \text{for } a = 1 \\ N_{a-1,t-1}^{s} e^{-M_{a-1}^{s}} \left(1 - u_{a-1,t-1}^{s}\right) & \text{for } a = 2, \ldots, A-1 \\ N_{a-1,t-1}^{s} e^{-M_{a-1}^{s}} \left(1 - u_{a-1,t-1}^{s}\right) + N_{a,t-1}^{s} e^{-M_{a}^{s}} \left(1 - u_{a,t-1}^{s}\right) & \text{for } a = A \end{cases}$$

where M_a^s is the instantaneous rate of natural mortality, A is the plus-group, and $u_{a,t}^s$ is the exploitation rate for all gears combined given by,

$$u_{a,t}^{s} = \sum_{g} u_{a,t}^{s,g} \, .$$

The exploitation rate is separated into an age-specific component (assumed here to be constant over time within each fishery), and the exploitation rate of fully selected fish at year *t*

$$u_{a,t}^{s,g} = s_{a}^{s,g} u_{t}^{g} \, .$$

Here I assume that total catch for a gear type *g* is known without error and that fishing takes place in a short time period in the middle of the year. Thus, the annual exploitation rate for the fully selected age class is given by

$$u_{t}^{g} = \frac{C_{t}^{g}}{e^{-0.5M} \sum_{s} \sum_{a} s_{a}^{s,g} N_{a,t}^{s} w_{a}^{s}} \, .$$

2.2 Recruitment

The greatest limitation of the forward projection assessment approach is the reliance on a model between spawners and subsequent recruitment (though it is possible to estimate recruitment as independent parameters). The most commonly used model is the Beverton-Holt model. Often there is insufficient information in a single data set to accurately estimate the spawner recruitment model together with the other model parameters (Hilborn and Liermann 1998; Kehler 2001).

Given these problems, many researchers fix the parameter that defines the resilience of the population, i.e., how fast recruitment declines with decreasing abundance, and only estimate the 'carrying-capacity' parameter of the spawner recruitment curve. For species where estimates of (or ranges for) fecundity, frequency of spawning, and natural mortality are available, it is possible to derive the resilience parameter (and bounds for it) from these biological data. Such an approach has recently been attempted for the derivation of another productivity parameter, the intrinsic rate of increase, r_m, for sandbar sharks (*Carcharhinus plumbeus*) (McAllister et al. 2001). Thus it maybe possible to provide reasonable estimates for species such as sharks.

Assuming a Beverton-Holt spawner recruitment model with lognormal error structure, recruitment at age 1 is

$$R_{t} = \frac{S_{t-1}}{a + bS_{t-1}} e^{\left(e_{t} - s_{R}^{2} / 2\right)}$$

where S_t is the spawner abundance in year *t*, e_t is the recruitment deviate in year *t*, and s_R^2 is the standard deviation for the log recruitment deviates. The spawner-recruitment relationship parameters *a* and *b* are defined by

$$a = S_0 \frac{1-h}{4hR_0},$$
$$b = \frac{5h-1}{4hR_0},$$

where *h* is the steepness of the spawner-recruit curve, S_0 is the virgin spawner abundance, and R_0 is the average recruitment produced at equilibrium by an unfished population. The term "steepness" was first defined by Mace and Doonan (1988) and represents the recruitment, relative to recruitment at equilibrium in the absence of fishing, that occurs when spawner abundance has been reduced to 20% of its virgin level.

It is possible to further derive *h* in terms of the maximum reproductive rate ($\hat{a}$) (Myers et al. 1999),

$$h = \frac{\hat{a}}{4+\hat{a}}$$

where $\hat{a}$ is the number of spawners produced by each spawner over its lifetime at very low abundance (Myers et al. 1999). Using estimates of fecundity, maturity schedules, frequency of pupping, and natural mortality, a range of possible values for steepness can be determined. We assumed that mature females pup every year and produce around four age 0 pups. Using the female maturity ogive (parameters in Table 1), we can estimated *h* for a range of values of natural mortality (Table 2).

Recruitment variability for many bony fishes can be very high and deviations from the assumed spawner-recruitment model can be large and are often the result of multi-species interactions or environmental factors (or both). For large sharks, such as porbeagle sharks, low fecundity and high juvenile survival suggests that recruitment variability will be significantly less than that observed in bony fishes. Model runs where no recruitment variability is assumed (other than that related to spawner abundance) may be quite valid and allow more degrees of freedom for the estimation of other model parameters.

2.3 Initial conditions

I assume that the population was at an unfished equilibrium at the start of 1961. This strong assumption simplifies the model structure, but is likely to be valid for porbeagle sharks in the Northwest Atlantic. Numbers at age in the first year are

$$N_{a,1}^s = \begin{cases} 0.5R_0 & \text{for } a = 1 \\ N_{a-1,1}^s e^{-M_{a-1}^s} & \text{for } a = 2,\ldots,A-1 \\ N_{a-1,1}^s e^{-M_{a-1}^s} / \left(1 - e^{-M_a^s}\right) & \text{for } a = A \end{cases}$$

where R_0 is the recruitment in the virgin state. The virgin spawner abundance (in numbers) is

$$S_0 = \sum_{a=1}^{A} N_{a,0}^1 m_a^1$$

where m_a^1 is the proportion of females mature at age *a*.

2.4 Selectivity

The selectivity function implemented in the model was a double half-Gaussian function of age. The double half Gaussian curve has three parameters, the age at maximum selection (S_{full}), and the left (v_L) and right-hand (v_R) variances. This three-parameter curve allows considerable flexibility. Selectivity at age is

$$s_a^{s,g} = \begin{cases} \exp\left(\dfrac{-\left(a - S_{\mathrm{full}}^{s,g}\right)^2}{v_L^{s,g}} \right) & \text{for } a \le S_{\mathrm{full}}^{s,g} \\ \exp\left(\dfrac{-\left(a - S_{\mathrm{full}}^{s,g}\right)^2}{v_R^{s,g}} \right) & \text{for } a > S_{\mathrm{full}}^{s,g} \end{cases}$$

In order to fit to the CPUE indices for immature and mature individuals further selectivity curves were required for each maturity stage. These were derived from the original curves for each gear/sex assuming a knife-edge cut-off. Campana et al. (1999) assumed a length based cut-off of 200cm as a compromise between the different age at maturity of males and females. This reflects age an approximate age cut-off of 11 and 12 for females and males respectively.

2.5 Growth

In order to fit to catch-at-length data using an age-structured model, an age to length conversion is required. This conversion requires an assumption about the nature (e.g. lognormal versus normal) and extent (amount) of variability in length at age. Hilborn et al. (2000) assumed lognormal variability, while Fournier et al. (1990) assumed normal variability; after visual examination of the data, we have chosen to follow the approach of Fournier et al. (1990).

The proportion of fish of age a in length class l ($p_{a,l}$), is a function of the mean length-at-age (predicted by the von Bertalanffy growth function, VBGF) and the variance of the length-at-age,

$$p_{a,l}^{s}\left(l_a, \sigma_a^s\right) = \frac{\delta}{\sqrt{2\pi}\,\sigma_a^s} \exp\left\{ \frac{-\left(x_l - l_a\right)^2}{2\left(\sigma_a^s\right)^2} \right\}$$

where δ is the size of the length increment (chosen here to be 5cm) and $f_{l|a}^{s}$ denotes the length proportions at age.

2.6 Predicted values

Commercial CPUE (I_t^g) is assumed to be proportional to the vulnerable biomass in the middle of the year

$$I_t^g = q^g \, e^{-0.5M} \left(\sum_s \sum_a s_{a,t}^{s,g} \, N_{a,t}^s \, w_{a,t}^s \right) e^{\varepsilon_t}$$

The predicted length composition data is a function of the population age composition, age-specific selectivity ogive, and the length proportions at age.

$$P_{l,t}^{s,g} = \frac{\sum_{a} s_{a,t}^{s,g} f_{l|a}^{s} N_{a,t}^{s}}{\sum_{s}\sum_{a} s_{a,t}^{s,g} \sum_{l} f_{l|a}^{s} N_{i,t}^{s}}$$

2.7 Likelihood functions

We considered three likelihood functions to model the variability in the different data types. Here we choose to minimize the negative log-likelihood. For the CPUE data we considered both lognormal and the gamma likelihood functions.

For gamma errors, the negative log-likelihood is the sum of the individual likelihoods (ignoring constants),

$$L_{CPUE}^{g} = \sum_{i=1}^{nobs} (\log(\tilde{I}_t^g / I_t^g) - (\tilde{I}_t^g / I_t^g)) / f^g$$

where f^g is the assumed variance of the logarithm of the observed CPUE (assumed constant for all indices within a series), and $\tilde{I}_t^g$ is the observed CPUE in year *t*.

For lognormal errors, the negative log likelihood is,

$$L_{CPUE}^{g} = \sum_{i=1}^{nobs} \log f^g + \frac{1}{2} \log 2p + \left(-\frac{\log(\tilde{I}_t^g / I_t^g)^2}{2f^g} \right)$$

Fournier et al. (1990) examined different likelihood functions for length composition data. They presented a robustified normal log-likelihood for proportions. The negative log-likelihood for the length composition for gear *g* is

$$\begin{aligned} L_{LEN}^{s,g} &= -0.5 \sum_{t=1}^{nobs} \sum_{l=1}^{A_l} \log(2p(x_{l,t}^{s,g} + 0.1/A_l)) - \sum_{t=1}^{nobs} A_l \log(t) \\ &+ \sum_{t=1}^{nobs} \sum_{l=1}^{A_l} \log \left[\exp \left\{ -\frac{(\tilde{P}_{l,t}^{s,g} - P_{l,t}^{s,g})^2}{2(x_{l,t}^{s,g} + 0.1/A_l)t} \right\} + 0.01 \right] \end{aligned}$$

where A_l is the number of length classes, $\tilde{P}_{l,t}^{s,g}$ is the observed proportion of fish in a sample of length *l*, and t is the inverse of the number of fish in the sample. Fournier et al. (1990) based the variance $x_{l,t}^{s,g}$ on the predicted proportions,

$$x_{l,t}^{s,g} = P_{l,t}^{s,g}(1 - P_{l,t}^{s,g}).$$

The total objective function to be minimized is the sum of the negative log-likelihoods

$$F = L_{CPUE} + L_{LEN}.$$

2.7 Model implementation

The model was developed and implemented using AD Model Builder (ADMB) (Otter Research Ltd. 2000) ADMB is a set of C++ libraries that utilize automatic differentiation for fast and efficient non-linear model estimation. It is very useful for problems such as this because of its speed, ability to bound parameters in sensible ways, and estimate parameters in phases. It also provides three estimates of uncertainty in estimated parameters (and functions there of) via the Hessian matrix, likelihood profiling, and Bayesian posterior distributions.

3 EXAMPLE OF APPLICATION

Here I describe the base case model presented by Campana et al. (2001).

3.1 Biological parameters

Details of the key biological assumptions are provided in Table 1.

Sex-specific growth parameters (estimated from vertebrate ageing data) are provided by Natanson et al. (2001) (Table 1). They fitted the ageing data to the von Bertalanffy growth curve using least squares. As young porbeagle sharks have high growth rates, partial ages were used for younger fish. The length-weight relationship was provided by Campana et al. (1999) of the form

$$w_a^s = b_i^s \left(l_a^s\right)^{b_{ii}^s} .$$

Weighted least-squares (by the numbers-at-age) was used to determine the relationship between mean length-at-age and the standard deviation of length-at-age. This was done separately for males and females.

$$\sigma_a^s = c^s + d^s l_a^s$$

It was found that there was only a very slight increase in the standard deviation (σ_a^s) with the mean (Table 1).

Campana et al. (1999) reported 50% mature at ages 13 and 7 for females and males respectively. The maturity ogive was approximated with a logistic curve (Table 1), where maturity at age (by sex), m_a^s is

$$m_a^s = \frac{\exp\left(a + b \times \text{age}\right)}{1 + \exp\left(a + b \times \text{age}\right)} .$$

3.2 Model output

I have presented plots of the model output and diagnostics for the base case model described in Campana et al. (2001). Plots include reconstructed biomass trajectories (Figure 1), selectivity ogives (Figure 2), fit to the observed catch composition (Figures 3–5), and the fit to the CPUE data (Figure 6).

A range of sensitivity analyses were considered in the assessment such as alternative weighting for the different data types and alternative hypotheses regarding how the con-founding parameters, natural mortality and selectivity, change with increasing age. This second problem is of course relevant to most assessments (Thompson 1994).

4 DISCUSSION

Here I describe a statistical age-structured model that fits to catch-at-length data and apply this model to the Northwest Atlantic porbeagle shark stock. A model, such as that presented here, provides a useful framework for examining the wide range of data available.

A noted shortcoming of forward projection models is the requirement to specify a spawner-recruitment relationship; but because the fecundity of porbeagle sharks is very low (with high survival) it is possible to derive reasonable bounds for spawner recruitment parameters from life-history characteristics. Such an approach has recently been applied by McAllister et al. (2001) to two species of large coastal sharks found in the Atlantic Ocean.

A model that incorporates a variety of different data types has a number of advantages over separate analyses. Most importantly it ensures that the same assumptions are used when fitting to the different data types. Within the framework presented here it is also possible to "turn on and off" each of the data types.

There are three potential problems with integrated analyses. First, as different data types provide different information on population dynamics, e.g., catch-at-length data can provide information on selectivity and recruitment, while CPUE data provide information on trends in abundance, it is not always possible to estimate the parameters of the full model with each data type separately. It may be possible to fit to the CPUE data alone using biomass dynamic models. Investigations here suggest that the biomass level that will produce the maximum sustainable yield is about 55% of the virgin stock size. In this case a simple Schaefer surplus production model may be appropriate.

Second, the different statistical models assumed in the fitting of the various data types often contribute non-equal amounts towards the overall objective function of the model. Choosing weighting factors for the various likelihood components can be difficult (Quinn and Deriso 1999).

The final problem is introduced through the use of complex nonlinear models. Even with simple nonlinear models such as the Beverton-Holt spawner recruitment relationship, small amounts of bias are introduced to the estimation of parameters (Kehler 2001). Detailed simulation studies would be required with the introduction of more model complexity to ensure that parameter estimates were not badly biased.

4.1 Possible model extensions

The model described here is relatively simple and does not contain many of the additional components contained in either Coleraine (Hilborn et al. 2000) or MULTIFAN-CL (Fournier et al. 1998) on which it was loosely based. I have described some additions that could add further to the utility of this model.

4. 1.1 Integrated calculation of steepness for the Beverton-Holt model

Because the value of steepness is estimated as a strict function of a number of biological parameters it is not possible to "free-up" any of these parameters in the model without including the link to steepness. A more reasonable approach that could be considered for porbeagle sharks, is to incorporate the derivation of steepness inside the model. This would allow one to estimate natural mortality in the model while ensuring the continuity in the values of steepness used. Thus one could put priors on natural mortality and the uncertainty would be carried through into derived priors for steepness.

4.1.2 Estimation of growth

The original MULTIFAN and its successors estimate growth parameters inside the model from length frequency data and length-at-age observations (Fournier et al. 1998). For pelagic sharks, such as porbeagle, a high proportion of the potential growth span is achieved by the time they are born, this is likely to make it difficult to estimate growth accurately from length-frequency data alone. It may be useful to attempt to incorporate the estimation of growth into the model, however, it would be important to compare growth estimates calculated internally to those derived outside the model.

4.1.3 Mark-recapture data

Maunder (2001) described the benefits of incorporating mark-recapture data in the population dynamic model. The main benefit is that the tagged and un-tagged populations are modelled using the same population dynamics model. Also information in the mark-recapture data can be used to assist in the estimation of other population parameters, e.g., selectivity (Myers and Hoenig 1997), growth (Francis 1988), and natural mortality. Separate analyses could inadvertently use different assumptions, i.e., selectivity fixed in one analysis but estimated in another. To maximize efficiency the mark-recapture data should be in the same units as the population dynamics model. In our example here, we have an age- and sex-structured model. If we use **N** to represent the number of tagged individuals, the dynamics are given by

$$\mathrm{N}^{s}_{a+1,t+1} = \mathrm{N}^{a}_{a,t} e^{-M_a L}\left(1-u^{s}_{a,t}\right) + \mathrm{R}^{S}_{a+1,t+1}$$

where **R** is not recruitment rather the number of new releases in that age group that have survived initial mortality and tag loss, and *L* is the instantaneous rate of tag loss over time. The number of tagged individuals, **T**, caught each year is

$$\mathrm{T}^{s}_{a,t} = \mathrm{N}^{s}_{a,t} u^{s}_{a,t}$$

A poisson or multinomial likelihood is then used to model the observed and predicted number of recaptures (Hilborn 1990).

4.1.4 Estimation of yields

In an age-structured model, the maximum sustainable yield is a function of both life-history characters and age-specific fishing mortality (i.e., selectivity) imposed by the fishing fleet. Thus if the selectivity of the fleets change (or even the split in catch across fleets) MSY reference points also change. Presently I calculate these reference points outside of the model using model output, but for speed and simplicity these values should be calculated at the same time as the model. Thus we can use any of the methods provided in ADMB to provide estimates of uncertainty in these reference points.

5. CONCLUSIONS

The unique life-history strategy of large pelagic sharks such as porbeagle makes it possible to provide reasonable bounds for the important parameters required for stock assessment. For more fecund species such as tunas and marlins these approaches are less likely to pro-duce reasonable results and we must rely on meta-analytical techniques to provide “prior” information on key parameters (Myers et al. 1999; Millar and Meyer 2000).

Models such as that described here can provide an important tool for visualizing and modeling a wide variety of data types as is generally available in fisheries.

6. ACKNOWLEDGEMENTS

I would like to thank Steven Campana for provision of data and many useful discussions regarding parameter values and model structure, Bob O’Boyle for useful discussions and initiation of the project under which this work was undertaken, and Ransom Myers for his assistance in the derivation of steepness from life-history characters.

7. REFERENCES

CAMPANA, S., Marks, L., Joyce, W., and Harley, S. 2001. Analytical assessment of the porbeagle shark (*Lamna nasus*) population in the Northwest Atlantic, with estimates of long-term sustainable yield. Canadian Stock Assessment Secretariat Research Document 2001/067, Fisheries and Oceans, Canada.

CAMPANA, S., Marks, L., Joyce, W., Hurley, P., Showell, M., and Kulka, D. 1999. An analytical assessment of the porbeagle shark, *(Lamna nasus*) population in the Northwest Atlantic. Canadian Stock Assessment Secretariat Research Document 99/158, Department of Fisheries and Oceans Canada.

FOURNIER, D. A., Hampton, J., and Sibert, J. R. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore *Thunnus alalunga*. Can. J. Fish. Aquat. Sci. 55: 2105–2116.

FOURNIER, D. A., Sibert, J. R., Majkowski, J., and Hampton, J. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. 47: 301–307.

FRANCIS, R. I. C. C. 1988. Maximum likelihood estimation of growth and growth variability from tagging data. N. Z. J. Mar. Fresh. Res. 22: 42–51.

HILBORN, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci. 47: 635–643.

HILBORN, R., and Liermann, M. 1998. Standing on the shoulders of giants: learning from experience in fisheries. Rev. Fish Biol. Fisheries 8: 1–11.

HILBORN, R., Maunder, M., Parma, A., Ernst, B., Payne, J., and Starr, P. 2000. Coleraine: A generalized age structured stock assessment model.

KEHLER, D. G. 2001. Bias in linear and nonlinear mixed effects models. Master’s thesis, Dalhousie University, Halifax, Nova Scotia, Canada.

MACE, P. M., and Doonan, I. J. 1988. A generalized bioeconomic simulation model for fish population dynamics. N. Z. Fish. Assess. Res. Doc. 88/4.

MAUNDER, M. N. 2001. Integrated Tagging and Catch-at-Age ANalysis (ITCAAN). In Proceedings of the 17th Lowell Wakefield Fisheries Symposium: Spatial processes and management of fish populations. University of Alaska Sea Grant.

MCALLISTER, M. K., Pikitch, E. K., and Babcock, E. A. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. Can. J. Fish. Aquat. Sci. 58: 1871–1890.

MILLAR, R. B., and Meyer, R. 2000. Non-linear state space modeling of fisheries biomass dynamics by using Hastings-Metropolis within Gibbs sampling. Appl. Stat. 49: 327– 342.

MYERS, R. A., Bowen, K. G., and Barrowman, N. J. 1999. The maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. 56: 2404–2419.

MYERS, R. A., and Hoenig, J. M. 1997. Direct estimates of gear selectivity from multiple tagging experiments. Can. J. Fish. Aquat. Sci. 54: 1–9.

NATANSON, L. J., Mello, J. J., and Campana, S. E. 2001. Validated age and growth of the porbeagle shark, Lamna nasus, in the western North Atlantic Ocean. Fish. Bull.

OTTER RESEARCH LTD. 2000. An introduction to AD Model builder Version 4: for use in nonlinear modeling and statistics. Otter Research Ltd.

QUINN, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Oxford University Press, New York. Thompson, G. G. 1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Can. J. Fish. Aquat. Sci. 51: 2654–2664.

Appendix 1: Summary of notation

SYMBOL	DESCRIPTION
Superscripts	
s	Sex: 1=females and 2=males
g	Gear type or fishery
Subscripts	
a	Age (A is the plus-group)
t	Time (years)
l	Length (A_l is the number of length intervals)
Growth	
l_a	Mean length at age as predicted by the VBGF
l_∞	Asymptotic length from the VBGF
k	Growth parameter from the VBGF
t_0	Hypothetical age at length zero
s_a	Standard deviation of lengths at age
c and d	Intercept and slope of the relationship between l_a and ó$_a$
ä	Size of the length increment
$p_{l,a}$	Proportion of fish of age a with length l
$f_{l\|a}^{s}$	Length proportions at age
w_a	Weight at age
b_i and b_{ii}	Length-weight relationship parameters
Maturity	
m_a^s	Proportion mature at age
A_{50}	Age at which 50% are mature
Dynamics	
M	Instantaneous rate of natural mortality
$N_{a,t}^{s}$	Numbers at age a and sex s at time t
S_t	Number of mature females at time t
R_0	Equilibrium recruitment (age 1) in an unfished population
R_t	Recruitment in year t
å$_t$	Log recruitment deviate in year t
s_R^2	Variance of the log recruitment deviates
a and b	Parameters of the Beverton-Holt curve
h	Steepness of the Beverton-Holt curve
â	Number of spawners produced per spawner over a lifetime
Fishery	
u_t^g	Exploitation rate for gear g in year t
C_t^g	Catch (in biomass) for gear g in year t
$s_a^{s,g}$	Relative selectivity of a fish of age a to gear g (scaled to a maximum of 1).
S_{full}	Age at full selectivity
v_R^g and v_L^g	Variance of the right-hand and left-hand limbs of the selectivity curve
q^g	Catchability coefficient for gear g

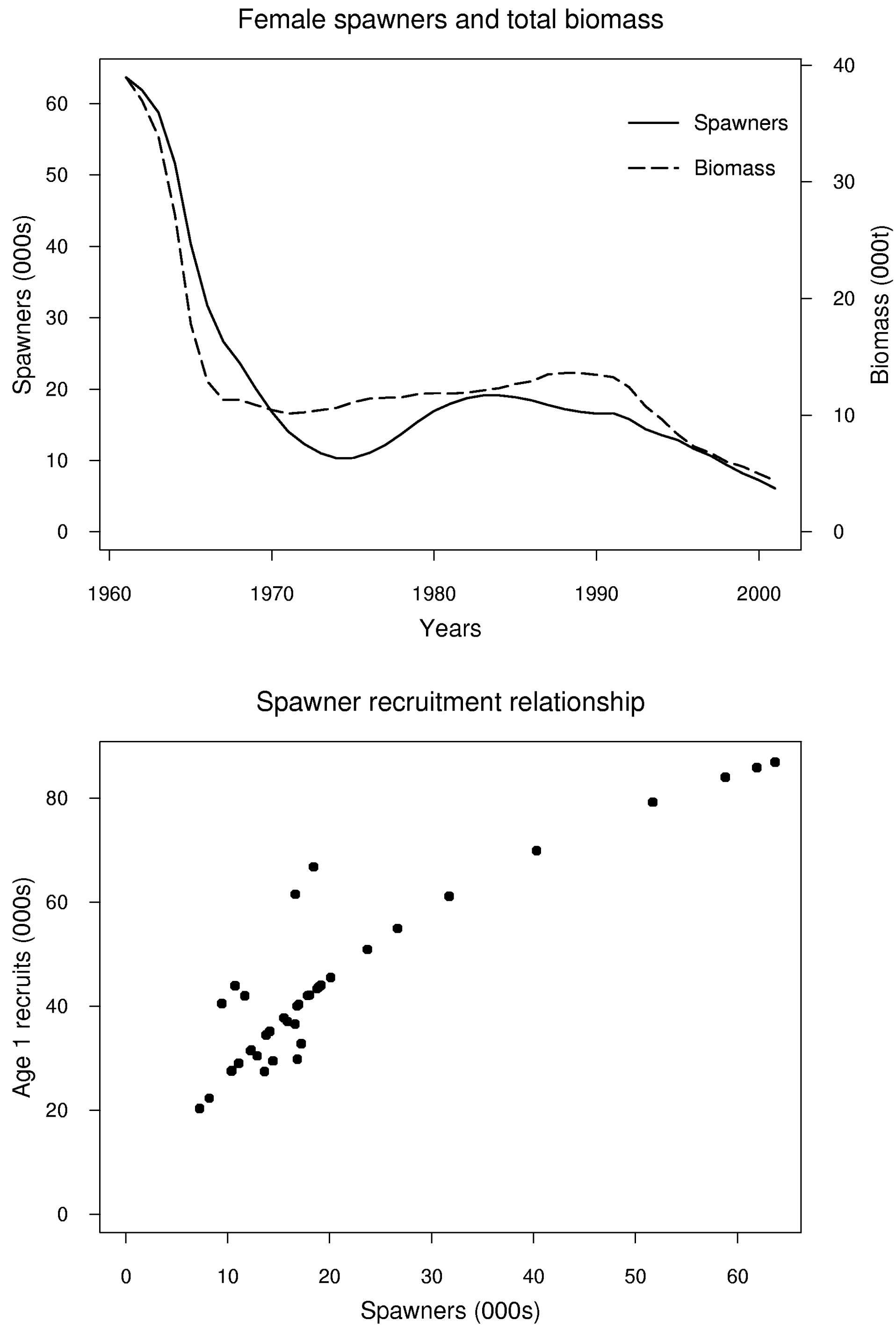
Predicted values	
$\tilde{I}_t^g$	Observed CPUE index
I_t^g	Predicted CPUE index
$\tilde{P}_{l,t}^{s,g}$	Observed proportion of fish at length l in a sample
$P_{l,t}^{s,g}$	Predicted proportion of fish at length l in a sample
Likelihoods	
L^g	Negative log-likelihood for gear *g*, CPUE or length composition (LEN)
f^g	Assumed variance of the logarithm of the CPUE indices for gear *g*
$x_{l,t}^{s,g}$	Variance for proportion at length
ô	Number of fish in length frequency sample

Table 1. Biological parameters assumed for the assessment model

Parameter	Females	Males	Combined
Growth			
l_∞	309.8	257.7	289.4
k	0.061	0.080	0.066
t_0	-5.90	-5.78	-6.06
Length-weight (cm to kg)			
b_i			$5E^{-5}$
b_{ii}			2.713
Growth variability			
c	12.06	11.05	8.42
d	$4.32E^{-4}$	$4.80E^{-3}$	0.258
Maturity			
A_{50}	13	7	
a	-13.57	-6.07	
b	1.042	0.75	
Natural mortality (M yr^{-1})			
Age 1			0.2
Immature			0.1
Mature	0.20	0.15	

Table 2. Estimates of steepness (h), based on values of natural mortality (for females). Fecundity is assumed to be 2 female pups per year and the assumed maturity ogive is given in Table 1.

Age 1	Immature	Mature	Steepness
0.20	0.10	0.20	0.374
0.20	0.10	0.10	0.503
0.20	0.05	0.10	0.666
0.20	0.15	0.20	0.255



Female spawners and total biomass

Spawner recruitment relationship

Figure 1. Trends in biomass and spawner abundance (top), and the spawner recruitment relationship (bottom) for the base case model.

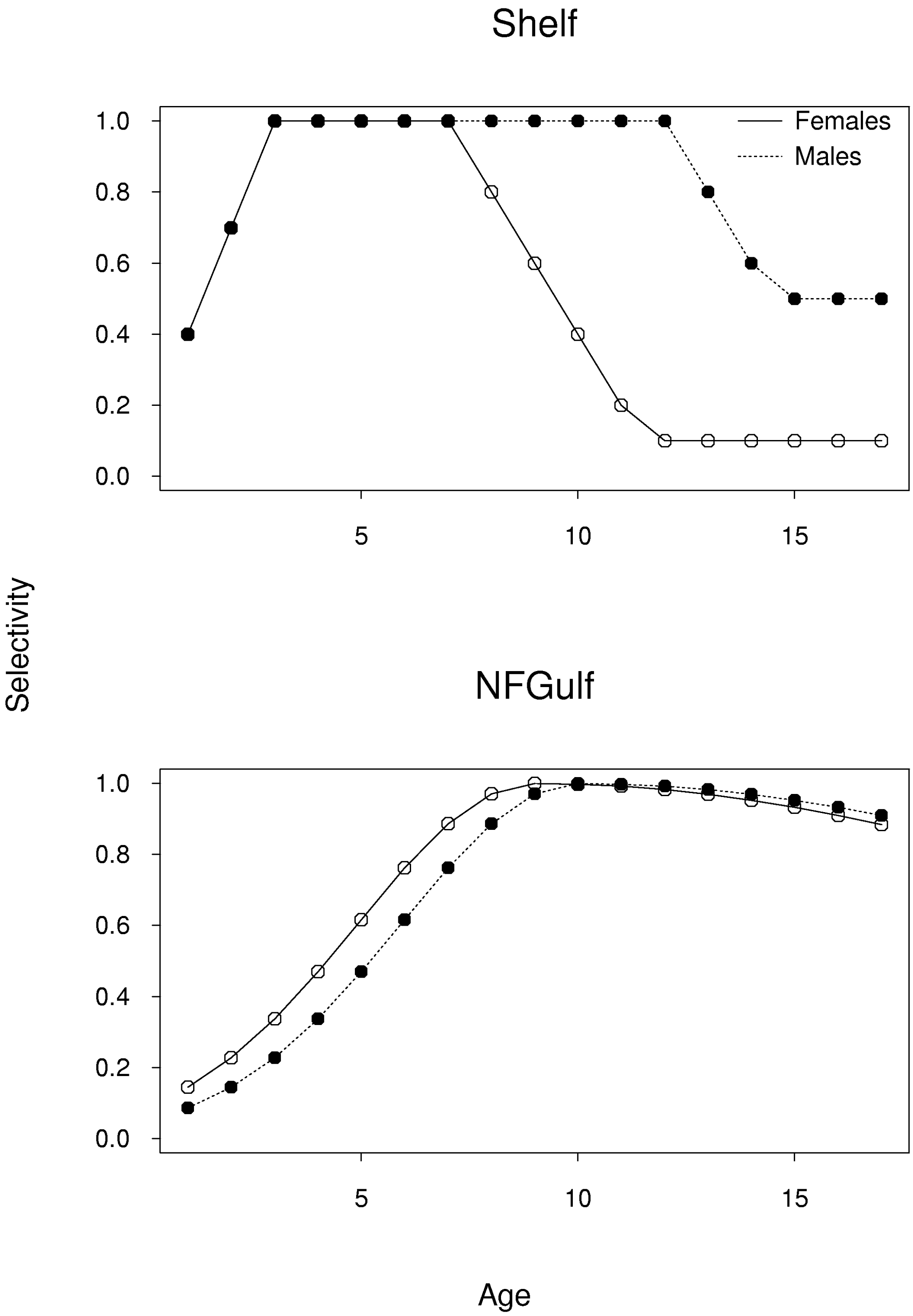


Figure 2: Age- and sex-specific selectivity curves fixed in the base case model.

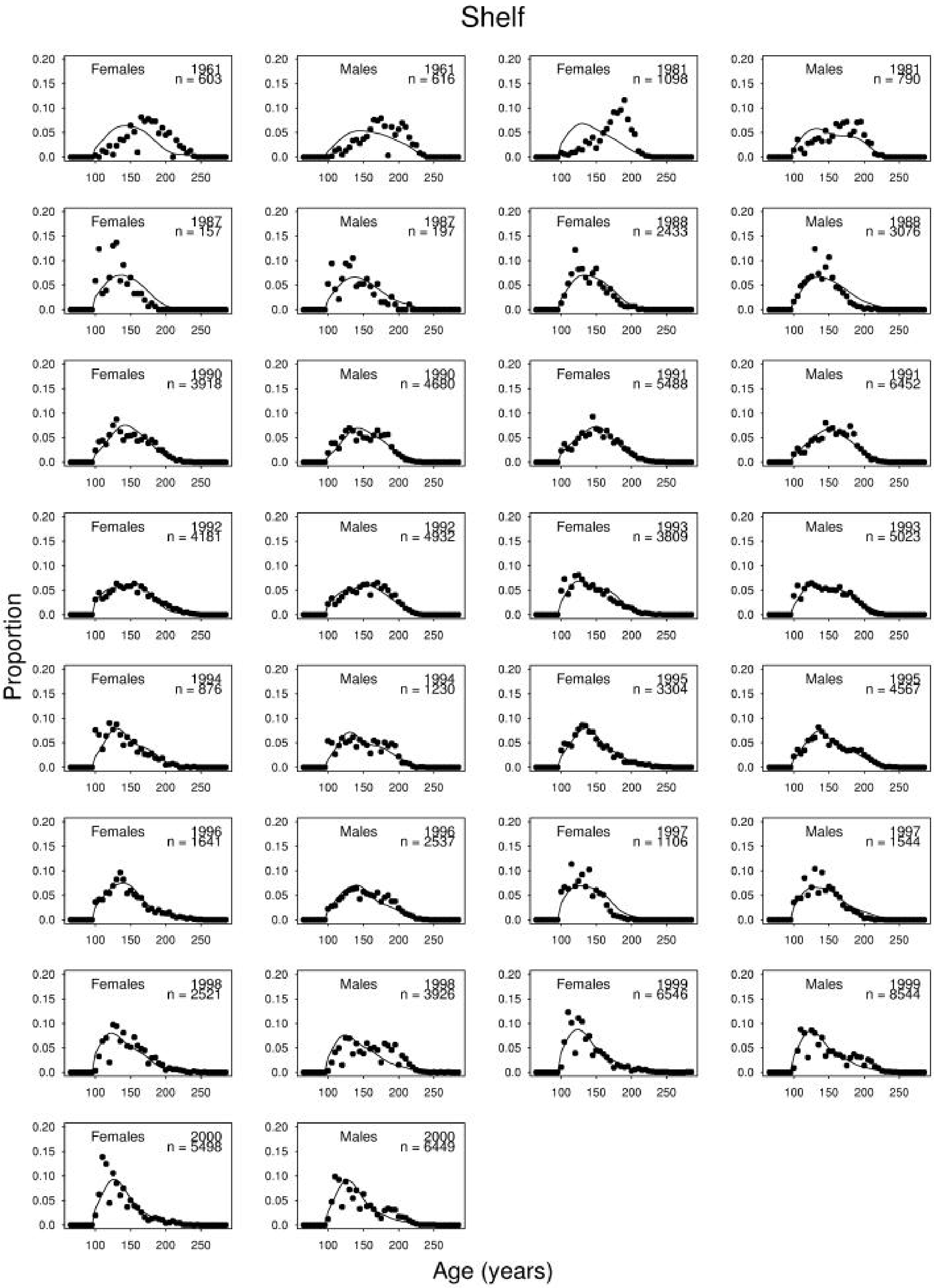


Figure 3: Observed (points) and predicted (solid line) proportions-at-length from the commercial catches for the Scotian Shelf fishery.

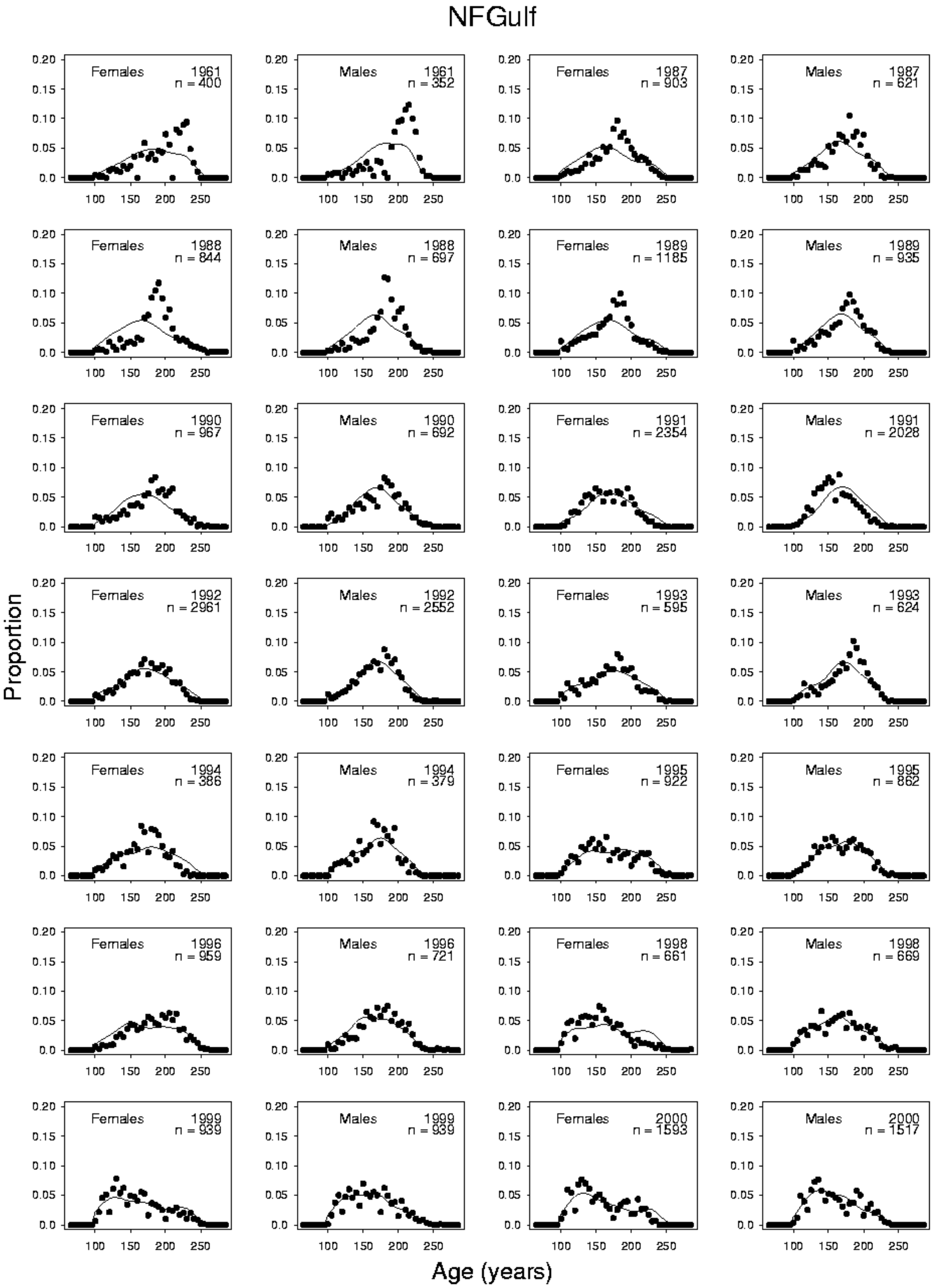


Figure 4: Observed (points) and predicted (solid line) proportions-at-length from the commercial catches for the Newfoundland and Gulf of St Lawrence fishery.

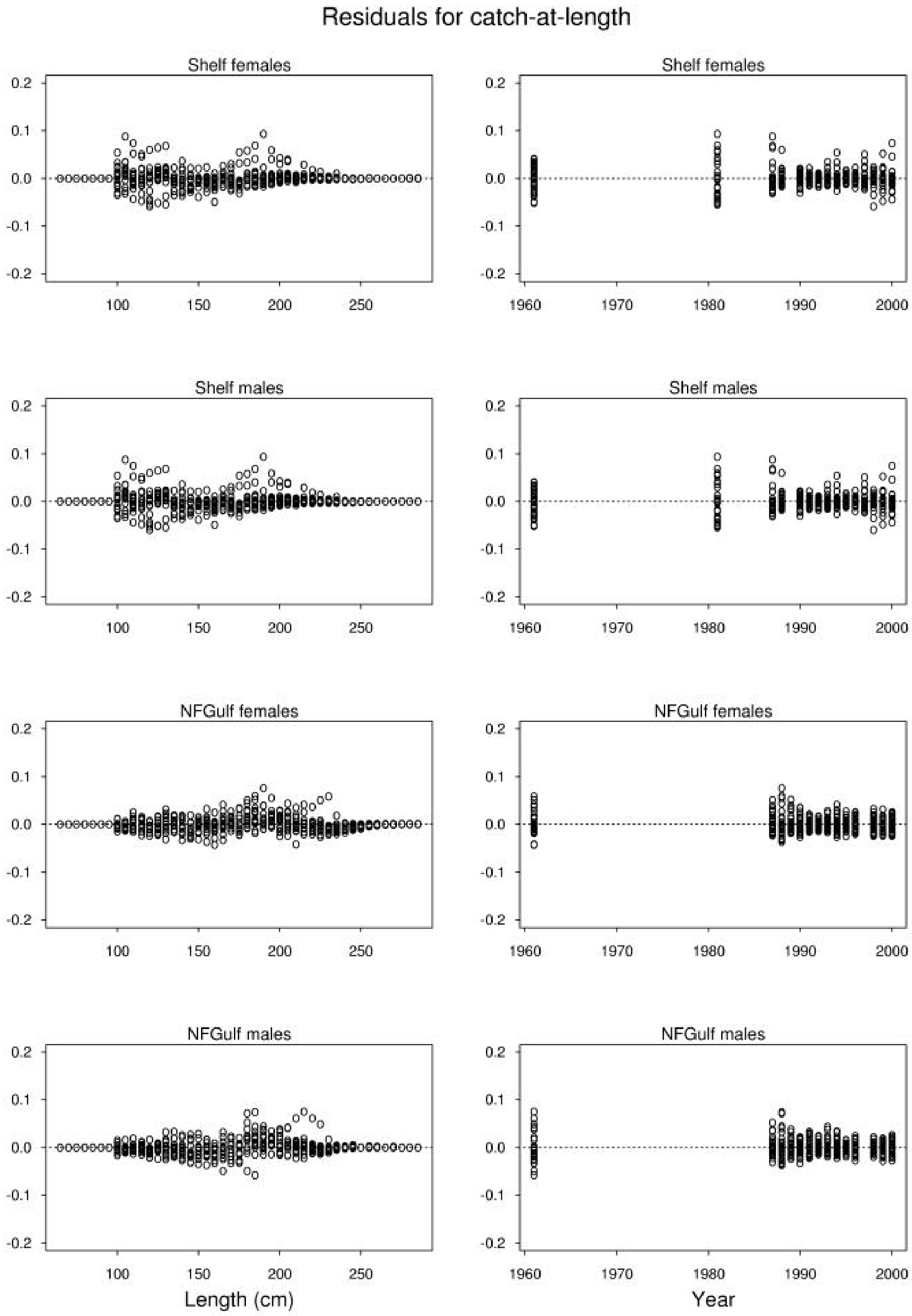


Figure 5: Residuals from fitting to the catch-length data by year and size.

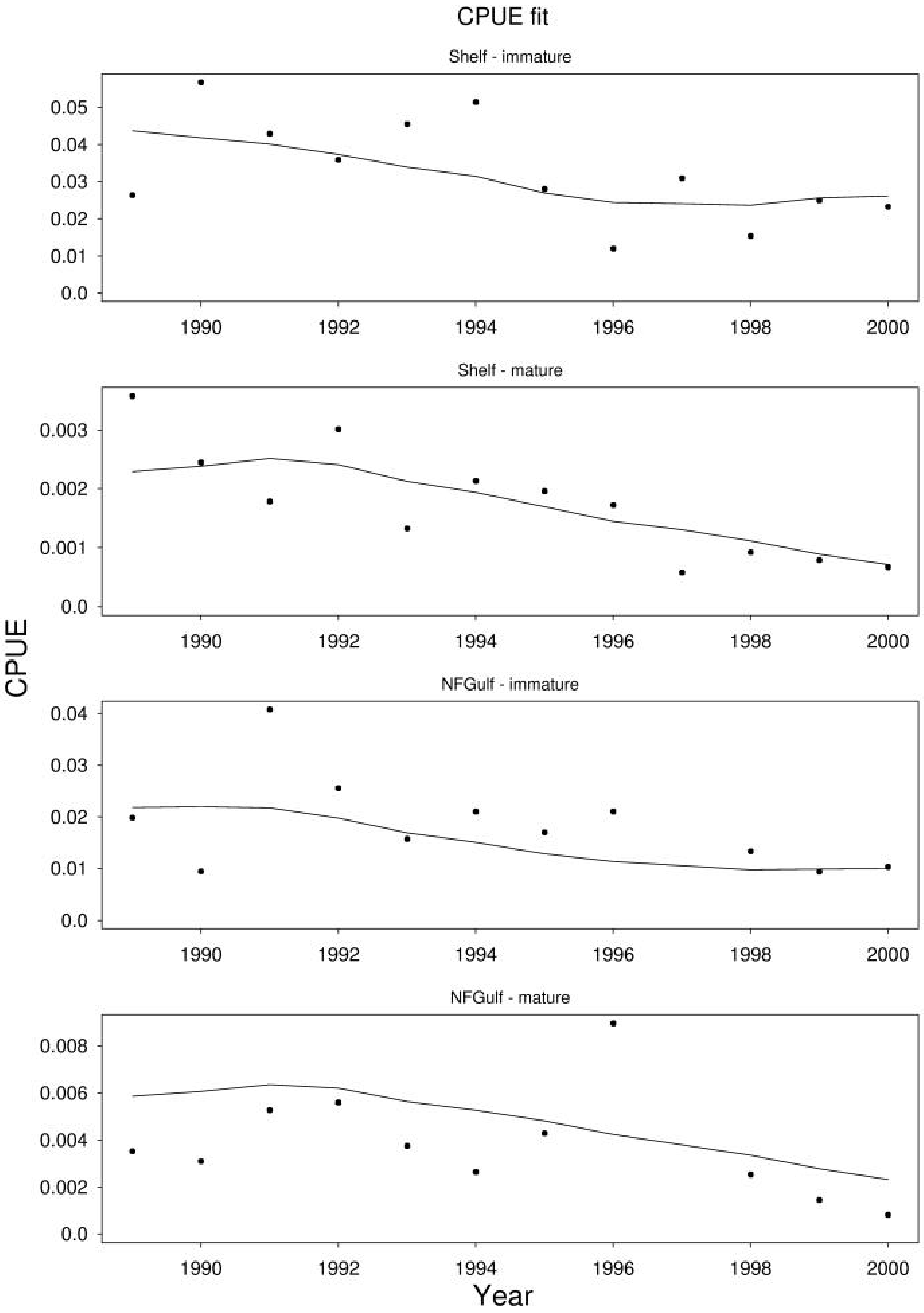


Figure 6: Observed (points) and predicted (solid line) CPUE for immature and mature fish by fishery.