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ARTICLE

Evaluating evidence for alternative natural mortality and process error assumptions using a state-space, age-structured assessment model

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Abstract: State-space models explicitly separate uncertainty associated with unobserved, time-varying parameters from that which arises from sampling the population. The statistical aspects of formal state-space models are appealing and these models are becoming more widely used for assessments. However, treating natural mortality as known and constant across ages continues to be common practice. We developed a state-space, age-structured assessment model that allowed different assumptions for natural mortality and the degree of temporal stochasticity in abundance. We fit a suite of models where natural mortality was either age-invariant or an allometric function of mass and interannual transitions of abundance were deterministic or stochastic to observations on Gulf of Maine – Georges Bank Acadian redfish (*Sebastes fasciatus*). We found that allowing stochasticity in the interannual transition in abundance was important and estimating age-invariant natural mortality was sufficient. A simulation study showed low bias in annual biomass estimation when the estimation and simulation model matched and the Akaike imformation criterion accurately measured relative model performance, but it was important to allow simulated data sets to include the stochasticity in interannual transitions of abundance-at-age.

Résumé : Les modèles d'espace d'états séparent explicitement l'incertitude associée aux paramètres variables dans le temps non observés de celle qui découle de l'échantillonnage de la population. Les aspects statistiques des modèles d'espace d'états formels sont attrayants et ces modèles sont de plus en plus fréquemment utilisés pour les évaluations. Cependant, il demeure courant de traiter la mortalité naturelle comme étant connue et ne variant pas selon l'âge. Nous avons développé un modèle d'évaluation d'espace d'états structuré par âge qui permet différentes hypothèses concernant la mortalité naturelle et le degré de stochasticité temporelle de l'abondance. Nous avons calé une série de modèles dans lesquels la mortalité naturelle soit ne varie pas selon l'âge ou est une fonction allométrique du poids, et les transitions interannuelles de l'abondance sont déterministes ou stochastiques, sur des observations sur le sébaste acadien (*Sebastes fasciatus*) dans le golfe du Maine – banc de Georges. Nous avons constaté que le fait de permettre la stochasticité de la transition interannuelle de l'abondance est important et que l'estimation de la mortalité naturelle non variant pas selon l'âge est suffisante. Une étude de simulation a démontré un faible biais dans l'estimation de la biomasse annuelle quand l'estimation et le modèle de simulation coïncident et que le critère d'information d'Akaike mesurent avec exactitude la performance relative du modèle, mais il était important de permettre l'inclusion dans les ensembles de données simulés de la stochasticité dans les transitions interannuelles d'abondance selon l'âge. [Traduit par la Rédaction]

Introduction

Age-structured models for stock assessments have evolved from deterministic methods such as virtual population analysis to stochastic models such as statistical catch at age (SCAA) and more formal state-space models (Gulland 1965; Fournier and Archibald 1982; Mendelssohn 1988). The main difference between SCAA and state-space models is how process errors in time-varying parameters are modeled and estimated. Traditional SCAA models did not separate variance of the observations from those attributable to time-varying processes. Contemporary SCAA models may treat some parameters as stochastic, time-varying processes, but associated probability distributions are treated as penalties to the likelihood function for survey and catch observations (Legault and Restrepo 1999; Methot and Wetzel 2013). On the other hand, formal state-space models separate observation and process errors and maximum likelihood (ML) estimation can be performed by integrating over the unobserved state variables (Sullivan 1992; de Valpine and Hastings 2002).

Although the utility of state-space population models has been demonstrated (Buckland et al. 2004; Newman and Lindley 2006), they have rarely been used in management of commercial fish stocks until relatively recently. This may be partly attributable to the long run times required for fitting Bayesian state-space models, since the application of assessment models in management typically requires the ability to fit models with alternative assumptions within a few hours, or even faster. The implementation of the Laplace approximation to integrate over unobserved time-series variables for ML estimation in software such as ADMB (Fournier et al. 2012) and TMB (Kristensen et al. 2016) has facilitated increased speeds for fitting state-space models that are similar to contemporary SCAA models (e.g., Nielsen and Berg 2014).

As successively more advanced estimation approaches for age-structured assessment models have developed, the treatment of natural mortality as known and age- and time-invariant has remained widely practiced in stock assessment for management. The use of an unestimated constant value for natural mortality can lead to substantial bias in estimates of parameters in age-

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structured models, with unaccounted for temporal variation in natural mortality potentially being more serious (Deroba and Schueller 2013). The difficulties of estimating natural mortality within population models are well known (Vetter 1988; Quinn and Deriso 1999; Aanes et al. 2007). Ideally, data from well-designed tag-recovery experiments are available to be integrated with catch and relative abundance indices (Fournier et al. 1998; Hampton and Fournier 2001). However, assuming natural mortality to be known may be becoming a less frequent practice, even without tagging data (Lee et al. 2011).

Natural mortality rates are known to decrease with size or age, particularly at smaller sizes or younger ages of fish (Sette 1943; Pearcy 1962; Cushing 1974). Ursin (1967) developed an individual- and metabolically-based rationale for declining mortality rate with size that is well approximated by an allometric relationship. Peterson and Wroblewski (1984) also developed an allometric relationship to natural mortality from trophic size distribution properties. Lorenzen (1996) estimated parameters of the allometric relationship of natural mortality to individual body mass for different aquatic ecosystems as well as for each fish species within the various ecosystem types. Empirical individual mass at age estimates are routinely used in age-structured assessment models to form predictions of catch, index, or spawning stock biomass (SSB). Applying the allometric relationship to annually varying mass at age estimates is a fairly simple way to consider time- and (or) age-varying natural mortality with just one more parameter.

Here we develop a flexible state-space, age-structured model that allows age- and time-varying natural mortality and alternative assumptions about stochasticity in population abundance-at-age. As an example application, we fit a suite of models to observations on the Gulf of Maine (GOM) – Georges Bank (GB) Acadian redfish (*Sebastes fasciatus*) stock and compared the relative performance of the models using Akaike's (1973) information criterion (AIC) and Mohn's (1999) ρ. Natural mortality and process error assumptions vary among these models. We also conduct a simulation study to evaluate the statistical behavior of parameter estimation and accuracy of relative model performance using AIC.

Methods

State-space model

All notation we use is defined in Table 1. The definitions for probability models describing stochastic changes in abundance at age from one year to another are identical to those given in Miller et al. (2016). Log-abundance for ages and years greater than 1 are normally distributed conditional on the vector of numbers at age from the previous time step:

$$\log(N_{y,a})\,|\,\boldsymbol{N}_{y-1} \sim \mathrm{N}\left[f_a(\boldsymbol{N}_{y-1}), \sigma^2_{N,j}\right]$$

for $y > 1$ where $\mathrm{N}(x, y)$ indicates a normal distribution with mean x and variance y,

$$f_a(\boldsymbol{N}_{y-1}) = \begin{cases} \mu & \text{for} \quad a = 1 \\ \log\left(N_{y-1,a-1}\mathrm{e}^{-Z_{y-1,a-1}}\right) & \text{for} \quad 1 < a < A \\ \log\left(N_{y-1,a-1}\mathrm{e}^{-Z_{y-1,a-1}} + N_{y-1,a}\mathrm{e}^{-Z_{y-1,a}}\right) & \text{for} \quad a = A \end{cases}$$

$Z_{y,a} = F_{y,a} + M_{y,a}$ is the total mortality and A indicates the terminal age class (i.e., the "plus group"). We assume two different variance parameters (j = 1 or 2) for the abundance at age: one for the variance of annual deviations around mean log-recruitment μ and one for interannual transitions of abundance at older ages ($\sigma^2_{N,1}$ and $\sigma^2_{N,2}$, respectively). If $\sigma^2_{N,2} = 0$ for ages after recruitment ($a > 1$), interannual transitions in abundance at age are deterministic, like contemporary SCAA models.

We consider two alternative assumptions for natural mortality $M_{y,a}$. The first is the traditional assumption that natural mortality is constant across years and ages $M_{y,a} = M$. The second assumption is that natural mortality varies by age and potentially year via the allometric relationship to individual body mass:

$$\log(M_{y,a}) = b_0 + b_1 \log(W_{y,a}) \tag{1}$$

where $W_{y,a}$ represents the average mass of an individual fish at age a in year y.

Annual fully-selected fishing mortality rates were parameterized as deviations from the previous year:

$$\log(F_{y+1}) = \log(F_y) + \delta_y$$

where $y = 1, \ldots, T - 1$ and δ_y are the interannual, unpenalized deviations. Then year- and age-specific fishing mortality is defined by multiplying age-specific selectivity by annual fishing mortality, $F_{y,a} = s_{C,a}F_y$, where $s_{C,a}$ is selectivity at age for the fishing fleet that is based on a logistic form

$$s_{C,a} = \left[1 + \mathrm{e}^{-(a-a_{50,C})/k_C}\right]^{-1} \tag{2}$$

Observed log-aggregate relative abundance indices from survey d are also normally distributed:

$$\log(I_{d,y}) \sim \mathrm{N}\left[\log(\hat{I}_{d,y}), \sigma^2_{d,y}\right]$$

where observation error variances $\sigma^2_{d,y}$ are assumed known. The predicted relative abundance index at age a in year y is

$$\hat{I}_{d,y,a} = q_d s_{d,a} N_{y,a} \mathrm{e}^{-Z_{y,a}\phi_d}$$

where q_d is the fully-selected catchability from survey d, $s_{d,a}$ is the age-specific selectivity from survey d also based on the logistic form in eq. 2, and ϕ_d is the fraction of the year elapsed when survey d occurs. Separate logistic selectivity parameters ($a_{50,d}$ and k_d) are assumed for each survey. The predicted aggregated relative abundance index is just the sum over ages:

$$\hat{I}_{d,y} = \sum_{a=1}^{A} \hat{I}_{d,y,a}$$

Finally, the observed log-aggregate catches by the fishing fleet are also normally distributed:

$$\log(C_y) \sim \mathrm{N}\left[\log(\hat{C}_y), \sigma^2_{C,y}\right]$$

where observation error variances $\sigma^2_{C,y}$ are assumed to be known. The predicted catch-at-age given abundances at age is

$$\hat{C}_{y,a} = \frac{F_{y,a}}{Z_{y,a}}(1 - \mathrm{e}^{-Z_{y,a}})N_{y,a}W_{C,y,a} \tag{3}$$

where $W_{C,y,a}$ is the mass at age in the catch. The predicted aggregated annual catch is just the sum over ages:

$$\hat{C}_y = \sum_{a=1}^{A} \hat{C}_{y,a} \tag{4}$$

We assumed a multinomial distribution for the vector of frequencies at age for survey d in year y:

Table 1. Definition of terms.

a	Index for ages
y	Index for years
A	Last age class (“plus group”)
$\boldsymbol{N}_y$	Vector of abundance at age in year y
$N_{y,a}$	Abundance at age a in year y
μ	Mean log-recruitment after first year
$\sigma^2_{N,1}$	Variance of annual log-recruitment deviations from mean μ
$\sigma^2_{N,2}$	Variance in stochastic annual transition of abundance at age
$Z_{y,a}$	Total mortality rate at age a in year y
$F_{y,a}$	Fishing mortality rate at age a in year y
F_y	Fully-selected fishing mortality rate in year y
$M_{y,a}$	Natural mortality rate at age a in year y
δ_y	Interannual deviation between $\log(F_y)$ and $\log(F_{y+1})$
$s_{C,a}$	Selectivity at age a in the fishing fleet
$a_{50,C}$, k_C	Logistic selectivity parameters for age composition observation from the fishing fleet
d	Index for surveys
q_d	Fully-selected catchability for survey d
l_θ, u_θ	Lower and upper estimation bounds for a parameter θ
$s_{d,a}$	Selectivity at age a for survey d
b_0, b_1	Parameters in the allometric relationship of natural mortality to body mass
$W_{y,a}$	Average individual body mass of a fish at age a in year y
$a_{50,d}$, k_d	Logistic selectivity parameters for age composition observation from survey d
$I_{d,y}$	Observed aggregate relative abundance index in year y for survey d
$\hat{I}_{d,y}$	Predicted aggregate relative abundance index for survey d in year y
$\sigma^2_{d,y}$	Variance of observation errors for survey d in year y
$\hat{I}_{d,y,a}$	Predicted relative abundance index at age a in year y for survey d
ϕ_d	Fraction of the year elapsed when survey d occurs
C_y	Observed aggregate fishing fleet catch in year y
$\hat{C}_{y,a}$	Predicted fishing fleet catch (biomass) at age a in year y
$\hat{C}_y$	Predicted aggregate fishing fleet catch (biomass) in year y
$\sigma^2_{C,y}$	Variance of observation errors for fishing fleet catch in year y
$W_{C,y,a}$	Average individual body mass of a fish at age a in year y in fishing fleet catch
$\boldsymbol{n}_{d,y}$	Vector of observed age composition frequencies in year y from survey d
$E_{d,y}$	Sample size in the multinomial distribution for age composition observations in year y from survey d
$E_{C,y}$	Sample size in the multinomial distribution for age composition observations in year y for fishing fleet catch
$\tilde{C}_{y,a}$	Predicted fishing fleet catch (numbers) at age a in year y
$\tilde{C}_y$	Predicted aggregate fishing fleet catch (numbers) in year y
$\boldsymbol{p}_{d,y}$	Vector of observed age composition proportions in year y from survey d
$\hat{\boldsymbol{p}}_{d,y}$	Vector of predicted age composition proportions in year y from survey d
$\boldsymbol{p}_{C,y}$	Vector of observed age composition proportions in year y for fishing fleet catch
$\hat{\boldsymbol{p}}_{C,y}$	Vector of predicted age composition proportions in year y for fishing fleet catch
$\hat{p}_{d,y,a}$	Predicted proportion at age a in year y for survey d
$\hat{p}_{C,y,a}$	Predicted proportion at age a in year y for fishing fleet catch
$\boldsymbol{\theta}$	Vector of all parameters estimated by maximum likelihood (fixed effects)
$\boldsymbol{S}$	Vector of all state variables or random effects parameters (e.g., abundance at age)
$\mathcal{L}$	Joint likelihood of all parameters conditional on observations
$\mathcal{L}_i$	Likelihood component i
$\boldsymbol{D}$	Vector of all observations
$\rho(\theta)$	Mohn’s ρ for parameter θ
T	Number of years in the model
t	Index for years of data peeled for Mohn’s ρ
m	Total number of years peeled for Mohn’s ρ
$\rho_{y,t(\theta)}$	Relative difference of estimates for parameter θ in year y using data from years up to $T-t$ and T
$\mathrm{RD}_i(\theta)$	Relative difference of estimate and true value for parameter θ of simulated data set i

$$\boldsymbol{n}_{d,y} = E_{d,y}\boldsymbol{p}_{d,y} \sim \text{Multinomial}\,(E_{d,y}, \hat{\boldsymbol{p}}_{d,y}) \tag{5}$$

where $E_{d,y}$ represented the sample size and the age-specific elements of the vector $\hat{\boldsymbol{p}}_{d,y}$ are

$$\hat{p}_{d,y,a} = \frac{\hat{I}_{d,y,a}}{\hat{I}_{d,y}}$$

We also assume a multinomial distribution for the fishing fleet catch with sample size $E_{C,y}$ and proportions at age in the catch:

$$\hat{p}_{C,y,a} = \frac{\tilde{C}_{y,a}}{\tilde{C}_y}$$

where $\tilde{C}_{y,a}$ is the predicted number at age (i.e., eq. 3 with $W_{C,y,a} = 1$) and $\tilde{C}_y$ is analogous to eq. 4.

Parameter estimation

We define fixed effects $\boldsymbol{\theta}$ as parameters estimated by ML and random effects $\boldsymbol{S}$ as unobserved variables that are integrated out to obtain the marginal likelihood, which is maximized. All abundances at age and fully-selected fishing mortality in the first year

Table 2. Details of models fitted to Gulf of Maine – Georges Bank (GOM–GB) Acadian redfish (*Sebastes fasciatus*) data and assumed for simulation studies.

Model	Description
M1	Statistical catch at age (SCAA) model ($\sigma^2_{N,2} = 0$) with natural mortality fixed at $M_{y,a} = 0.05$
M2	SCAA model ($\sigma^2_{N,2} = 0$) with age- and time-invariant natural mortality estimated
M3	SCAA model ($\sigma^2_{N,2} = 0$) with an allometric relationship of natural mortality to body mass where b_0 is estimated and $b_1 = 0.305$ is assumed based on Lorenzen (1996)
M4	State-space model with stochastic interannual transitions of abundance at age ($\sigma^2_{N,2}$ estimated) and natural mortality fixed at $M_{y,a} = 0.05$
M5	State-space model with stochastic interannual transitions of abundance at age ($\sigma^2_{N,2}$ estimated) and age- and time-invariant natural mortality estimated
M6	State-space model with stochastic interannual transitions of abundance at age ($\sigma^2_{N,2}$ estimated) and an allometric relationship of natural mortality to body mass where b_0 is estimated and $b_1 = 0.305$ is assumed based on Lorenzen (1996)

($\boldsymbol{N}_1$ and F_1), mean log-recruitment (μ) and annual deviations in log-fully-selected fishing mortality (δ_y) after the first year, index catchability (q_d), all selectivity parameters ($a_{50,C}$, k_C, $a_{50,d}$, k_d), process error variances ($\sigma^2_{N,1}$, $\sigma^2_{N,2}$), and natural mortality parameters (M, b_0) are estimated as fixed effects. Recruits after the first year ($N_{y,1}$) and, depending on the model, abundance at older ages ($N_{y,a}$ for $a > 1$) are treated as random effects.

The joint likelihood function is the product of the likelihood components defined in Appendix A:

$$\mathcal{L}(\boldsymbol{\theta}, \boldsymbol{S}|\boldsymbol{D}) = \prod_i \mathcal{L}_i$$

The joint likelihood is a function of fixed effects parameters $\boldsymbol{\theta}$ and random effects $\boldsymbol{S}$ representing the state variables (i.e., abundance at age) conditioned on all observations $\boldsymbol{D}$. We perform ML estimation of the fixed effects parameters with a Laplace approximation of the marginal log-likelihood function (Skaug and Fournier 2006):

$$\log\left[\int \mathcal{L}(\boldsymbol{\theta}, \boldsymbol{S}|\boldsymbol{D})d\boldsymbol{S}\right] = \log[\mathcal{L}(\boldsymbol{\theta}|\boldsymbol{D})]$$

using TMB (Kristensen et al. 2016) and R (R Core Team 2015) for implementing and fitting the state-space models. Specifically, we used the "nlminb" function in R to minimize the negative of the Laplace approximation of the marginal log-likelihood. Estimates of the random state variables are provided by the mode of posterior distributions of $\boldsymbol{S}$, conditioned on $\hat{\boldsymbol{\theta}}$. For a fuller description of variance estimation by the TMB package, see Kristensen et al. (2016).

Application to GOM–GB Acadian redfish

For demonstration purposes, we applied our model to the GOM–GB Acadian redfish stock. GOM–GB Acadian redfish have been primarily caught by trawl and gill net, and the National Marine Fisheries Service Northeast Fisheries Science Center annual bottom trawl surveys in the spring (1968–2014) and fall (1963–2014) are used for relative abundance indices of Acadian redfish (Miller et al. 2008; Linton 2015). Here we use the abundance indices, fishing fleet catches, and any associated age composition observations from 1969 to 2014. All observations and inputs we used to fit models can be obtained at www.nefsc.noaa.gov/saw/sasi/sasi_report_options.php. We used estimates of observation error variances ($\sigma^2_{C,y}$ and $\sigma^2_{d,y}$ for total catch and surveys) that are also used in the current assessment model. We also used the same assumptions for the sample sizes of the age composition observations. The uncertainties in total catch come from estimates of variance of the discard component, and those for the survey indices are based on the stratified random sampling design used for the Northeast Fisheries Science Center bottom trawl surveys.

We considered six alternative models for GOM–GB Acadian redfish (Table 2). We refer to the first three (M1–M3) as SCAA models because the only process error is in recruitment ($N_{y,1}$). The only difference from a traditional SCAA model is that the recruitment deviations are treated as random effects and the variance of these deviations ($\sigma^2_{N,1}$) is estimated. The second three models (M4–M6) are formal state-space models that treat the interannual transitions of abundance at age stochastically, and the variance of this process error ($\sigma^2_{N,2}$) is also estimated. The differences among models M1–M3 and among M4–M6 are in the assumptions for natural mortality. Models M1 and M4 assume a known age-invariant natural mortality of $M = 0.05$ (as in the assessment model currently used for management), models M2 and M5 estimate an age-invariant natural mortality rate, and models M3 and M6 estimate the scalar term of the allometric relationship to mass and constrain b_1 to the value estimated by Lorenzen (1996) for marine fish species (0.305). Although the general allometric relationship in eq. 1 allows interannual variation in natural mortality at age when mass at age changes over time, the mass at age for this stock is currently treated as constant over time because mass at age observations are not available over the entire time series (see Table S1[1]). Therefore, models M3 and M6 only allow variation in natural mortality with age for this application to GOM–GB Acadian redfish. In Table 3, we summarize numbers, initial values, and any bounds for parameters estimated by ML for each of the six models. Most parameters are estimated on a log-scale or a logit-scale to avoid boundary problems during estimation. The bounds are only necessary for the logit-transformed catchability and selectivity parameters. For example, the catchability for survey d is

$$q_d = l_{q_d} + \frac{u_{q_d} - l_{q_d}}{1 + e^{-\text{logit}(q_d)}}$$

where l_θ and u_θ are lower and upper bounds of parameter θ and logit(θ) is the actual parameter estimated in the model. The number of fixed effects parameters estimated by ML ranged between 82 and 84, depending on the assumptions of each model. We specified initial values of 10 for random numbers at age effects $\log(N_{y,a})$ after year 1.

Model performance

To evaluate the relative model performance, we used AIC and the measure of retrospective pattern, Mohn's (1999) ρ, to compare models. For AIC, we used the maximized marginal log-likelihood and the number of fixed effects parameters. We calculated Mohn's ρ as

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0035.

Table 3. Number, initial values, and any specified bounds for parameters estimated by maximum likelihood for each model fitted to the GOM–GB Acadian redfish data.

Parameter	M1	M2	M3	M4	M5	M6	Initial value	Bounds (l_θ, u_θ)
$\log(\mathbf{N}_1)$	26	26	26	26	26	26	10	
μ	1	1	1	1	1	1	10	
$\text{logit}(q)$	2	2	2	2	2	2	–8	(0, 1000)
$\log(F_1)$	1	1	1	1	1	1	–2	
δ_y	45	45	45	45	45	45	0	
$\text{logit}(a_{50,C})$	1	1	1	1	1	1	0	(–26, 26)
$\text{logit}(k_C)$	1	1	1	1	1	1	0	(0, 26)
$\text{logit}(a_{50,d})$	2	2	2	2	2	2	0	(–26, 26)
$\text{logit}(k_d)$	2	2	2	2	2	2	0	(0, 26)
$\log(M)$	0	1	0	0	1	0	log(0.05)	
$\log(b_0)$	0	0	1	0	0	1	log(0.05)	
$\log(\sigma_{N,1})$	1	1	1	1	1	1	0	
$\log(\sigma_{N,2})$	0	0	0	1	1	1	0	
Total	82	83	83	83	84	84		

$$\rho(\theta) = \frac{1}{m}\sum_{t=1}^{m}\frac{\hat{\theta}_{T-t,T-t}}{\hat{\theta}_{T-t,T}} - 1$$

where T is the terminal year of the data series, t is the number of years peeled off from the terminal year, m is the number of total years peeled off from the terminal year, and $\hat{\theta}_{T-t,y}$ is the estimate of a parameter for year $T - t$ from fitting the assessment model to data with terminal year y. We used $m = 5$ peels from the terminal year in Mohn's ρ for estimates of annual SSB and annual fully-selected fishing mortality, since Miller and Legault (2017) found Mohn's ρ to change negligibly with further peels. For illustrative purposes, we also define

$$\rho_{y,t}(\theta) = \frac{\hat{\theta}_{y,T-t}}{\hat{\theta}_{y,T}} - 1$$

as the relative difference of parameter estimates for year y using data up to years $T - t$ and T.

Simulation study

We performed a simulation study with two analogous components. For each component, we simulated 1000 sets of aggregate relative abundance and catch observations and corresponding age composition observations for each of six scenarios according to the assumptions of models in Table 1. The true parameter values used in the models are those estimated from the fits to the GOM–GB Acadian redfish data. The difference between the two components was how the population abundances at age were treated. In the first component, we conditioned on the abundance at age estimated from each fitted model so that the population abundance at age was the same for each simulated data set. For the second component, we allowed the abundance at age to be stochastic according to the assumptions of each model. Therefore, for the first three models, abundance at age was only stochastic through the annual recruitment process. For the latter three models, stochasticity of abundance at age also arises through the lognormal interannual transitions. We fit all six models to each simulated data set.

Given the results from these simulations, we performed two sensitivities. In the first sensitivity, we fit model M4 (fixed natural mortality) to the data simulated under model M5 using the estimated natural mortality rate from fitting M5 to the GOM–GB Acadian redfish data as the fixed, unestimated natural mortality rate. The second sensitivity was identical to the simulation scenario described where parameter estimates from fitting model M4 to the GOM–GB Acadian redfish data were used to simulate data and model M4 was also used to estimate parameters for these simulated data sets. However, we used restricted ML estimation by assuming flat priors and treating all parameters other than the process error variances as random effects (Harville 1974).

Table 4. Difference in the Akaike imformation criterion (AIC) from the model with the lowest value (ΔAIC) and estimates of Mohn's ρ for spawning stock biomass (SSB) and fully-selected fishing mortality (F) for each of the models fitted to the GOM–GB Acadian redfish observations.

	ΔAIC	SSB	F
M1	511.361	0.270	–0.187
M2	410.130	0.076	–0.030
M3	462.624	0.122	–0.071
M4	21.091	0.260	–0.188
M5	0.000	0.004	0.021
M6	13.351	0.068	–0.041

We used the median relative difference of parameter estimates and true values to estimate bias for a given scenario. The relative difference of a parameter estimate $\hat{\theta}_i$ from the true value θ_i for simulated data set i is

$$\text{RD}_i(\theta) = \frac{\hat{\theta}_i}{\theta_i} - 1$$

For results of a given model assumption and fitting scenario, we also calculated 95% confidence intervals of the median relative bias using the binomial distribution method (Thompson 1936). We used the fits to all models to evaluate the accuracy of AIC as a measure of relative model performance.

Results

All six models we fit to the GOM–GB Acadian redfish data converged, with an invertible Hessian providing variance estimation of parameters estimated by ML. Using AIC as a measure of relative model performance, the state-space models (M4–M6) outperformed the SCAA models that only allowed variation in recruitment (M1–M3) (Table 4). Within each class of models (state-space or SCAA), those that allowed natural mortality to be estimated performed better than those where it was assumed to be 0.05, as in the current assessment model (Linton 2015). However, imposing the allometric relationship for natural mortality performed worse than age-invariant natural mortality for both SCAA and state-space models. The model with the lowest AIC (M5) resulted in an estimated natural mortality rate of 0.14 (SD = 0.02); the corresponding estimate from the SCAA version (M2) was nearly the same. Estimates of abundance, fishing mortality, and survey catchability at age from model M5 are provided in the supplementary materials.

Retrospective patterns as estimated by Mohn's ρ were relatively minor for SSB and fully-selected fishing mortality with absolute values ≤0.27 for all models (Table 4). The SCAA and state-space models with natural mortality fixed (M1 and M4) performed similarly and had the highest Mohn's ρ estimates (in absolute value) of the models we considered. Mohn's ρ estimates were lowest in absolute value for models where age-invariant natural mortality was estimated (M2 and M5), with those for the state-space model negligibly lower. The models with natural mortality estimated also exhibited an increasing trend in the natural mortality estimates with additional years of data (e.g., 0.12–0.14 for M5) that

Fig. 1. Relative difference of annual spawning stock biomass (SSB) and fully-selected fishing mortality (*F*) estimates from five peels and corresponding estimates from the full data set for each of the six models in Table 2.

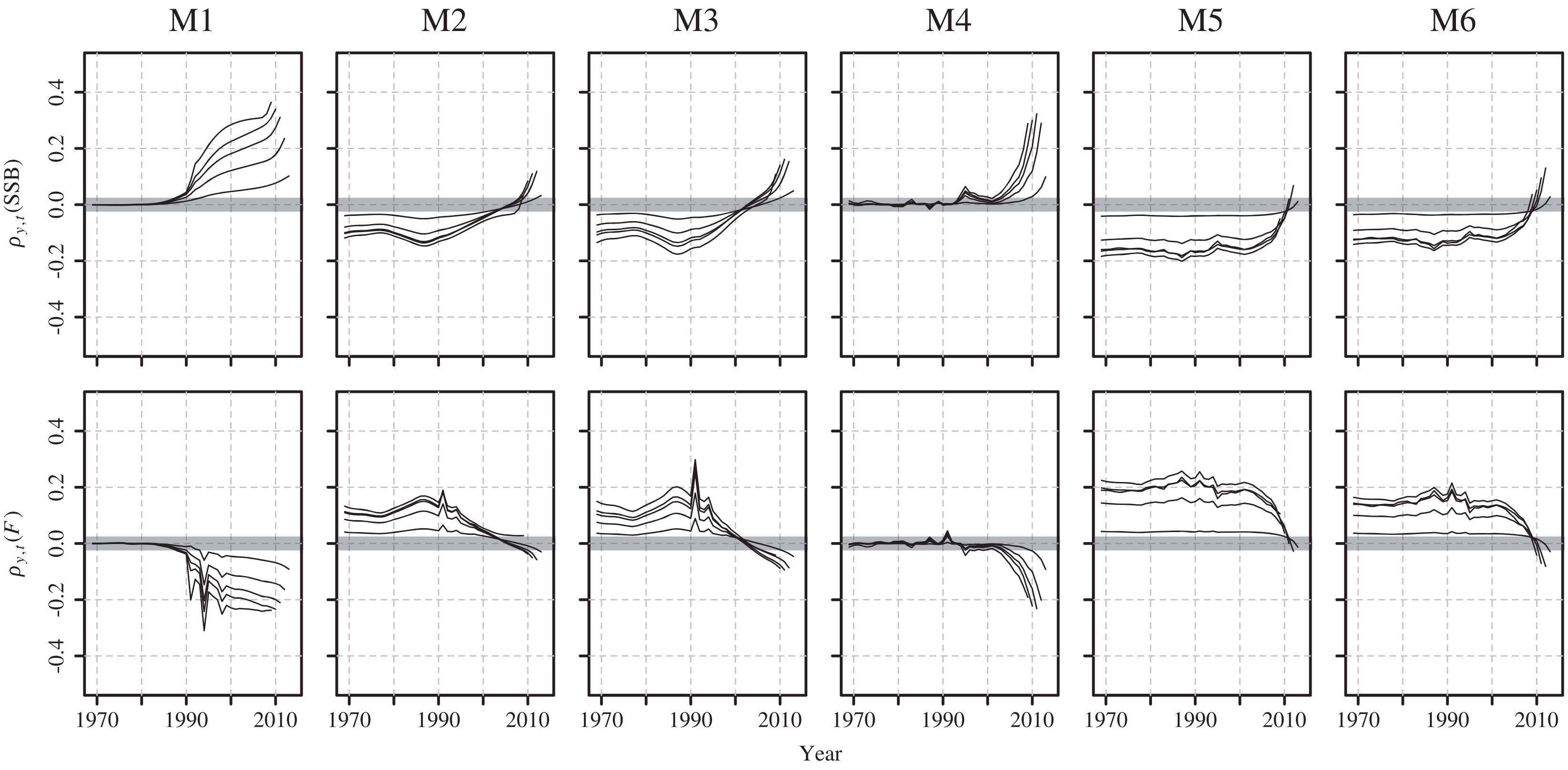


Fig. 2. Annual estimates of SSB$_y$, F_y, and recruitment ($N_{y,1}$) and 95% confidence intervals for each of the six models in Table 2.

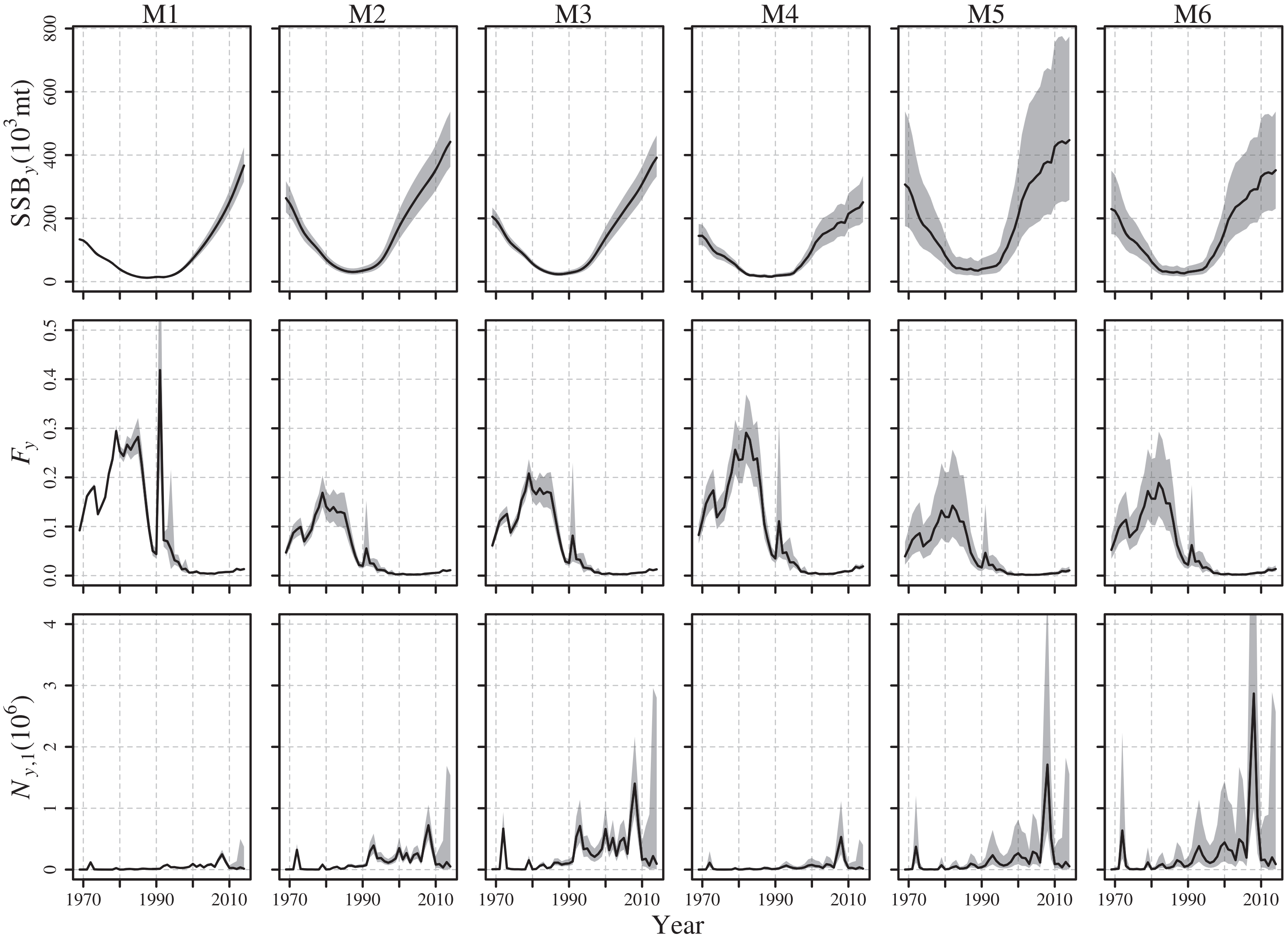


Table 5. Convergence of models fitted (columns) to data sets simulated assuming parameters estimated by each model (rows) and conditioned on estimated abundance at age.

	M1	M2	M3	M4	M5	M6
M1	998	997	999	0	0	0
M2	998	995	996	1	0	0
M3	995	996	994	0	0	0
M4	993	992	984	981	986	986
M5	994	991	987	980	978	979
M6	992	987	988	983	980	974

Table 6. Convergence of models fitted (columns) to data sets simulated assuming parameters estimated by each model (rows) and stochastic abundance at age.

	M1	M2	M3	M4	M5	M6
M1	1000	995	995	0	0	1
M2	996	1000	996	208	0	0
M3	996	993	998	35	0	0
M4	958	886	894	975	978	980
M5	969	965	964	979	982	979
M6	976	955	976	972	978	976

Table 7. Frequencies of models fitted (columns) with lowest AIC to data sets assuming parameters estimated by each model (rows) and conditioned on estimated abundance at age.

	M1	M2	M3	M4	M5	M6
M1	750	104	146	0	0	0
M2	0	953	47	0	0	0
M3	0	63	937	0	0	0
M4	0	0	0	0	1000	0
M5	0	0	0	0	1000	0
M6	0	0	0	0	1000	0

Table 8. Frequencies of models fitted (columns) with lowest AIC to data sets assuming parameters estimated by each model (rows) and stochastic abundance at age.

	M1	M2	M3	M4	M5	M6
M1	753	107	140	0	0	0
M2	0	963	37	0	0	0
M3	0	59	941	0	0	0
M4	0	0	0	703	120	177
M5	0	0	0	0	805	195
M6	0	0	0	16	189	795

generally resulted in a corresponding trend in the population size (Fig. 1).

Trends in annual estimates of SSB, fully-selected fishing mortality, and recruitment were similar for all models, but the scale and range of estimates differed (Fig. 2). The scale of annual SSB estimates was greatest for models where invariant natural mortality was estimated (M2 and M5). There is greater uncertainty in SSB estimates for models M2 and M3 than for M1 and for M5 and M6 than for M4 because of the natural mortality being estimated rather than fixed.

Comparing models with the same natural mortality assumption, SSB estimates from the state-space model are also more uncertain because of the process error in the interannual transitions in the abundance at age. Ratios of coefficients of variation (CVs) for annual SSB estimates ranged from 0.08 to 0.73, from 0.32 to 0.49, and from 0.29 to 0.54 for models M1 to M4, M2 to M5, and M3 to M6, respectively. Fully-selected fishing mortality estimates for recent years (2000–2014) were low for all models (0.002–0.018), but annual estimates prior to this were greatest for models M1 and M4. The higher fully-selected fishing mortality in models with lower SSB estimates is expected given the same catch data.

There is also a large difference in the 1991 fully-selected fishing mortality estimate from model M1. This fishing mortality rate is also estimated much higher in the GOM–GB Acadian redfish assessment, which uses a similar SCAA model (Linton 2015); however, the uncertainty in this estimate is larger than for other years due to large uncertainty in the corresponding catch observation. The scale and variation of recruitment estimates were greatest for models assuming an allometric relationship of natural mortality to individual mass (M3 and M6) because of the higher natural mortality imposed at younger aged individuals in the population.

Simulation study

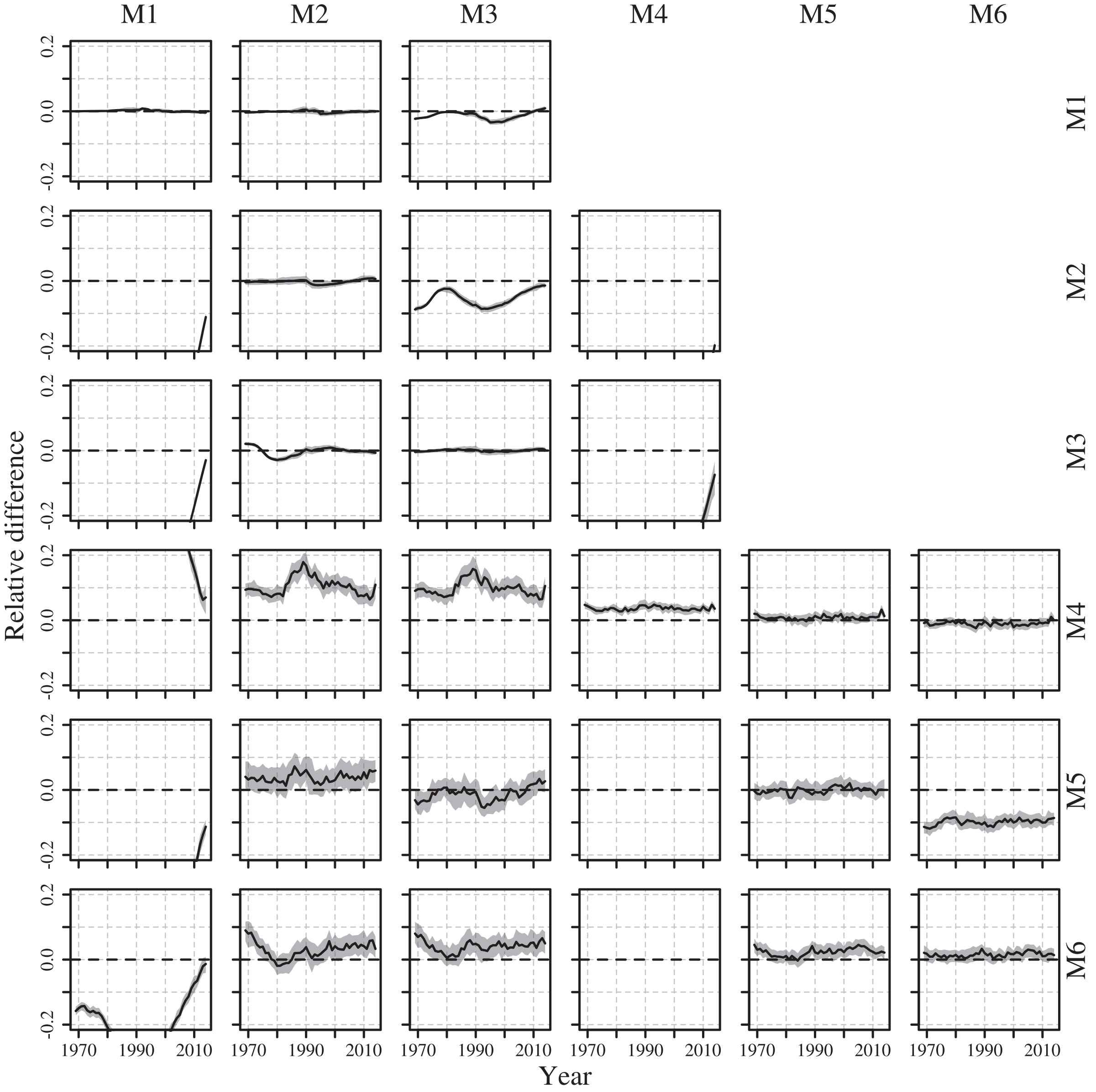
Convergence of fitted models (as indicated by the nlminb flag only) depended on the type of fitted model and whether stochasticity in abundance at age was simulated. Fits of state-space models (M4–M6) to data simulated under models M1–M3 understandably did not converge because of the impossibility of estimating process error variances when process errors do not exist (Tables 5 and 6). When data were simulated from state-space models (M4–M6), lack of convergence was generally infrequent (<4.5%) whether SCAA type models (M1–M3) or state-space models were fitted or whether stochasticity in the abundance at age was simulated. The SCAA-type models (M1–M3) converged for a high percentage of data sets for all assumed models whether or not stochasticity in the abundance at age was simulated, but the convergence rate was slightly greater when SCAA models were assumed to simulate data sets. However, lack of convergence was greater when models M2 (11.4%) and M3 (10.6%) were fitted to data simulated assuming model M4 with stochasticity in numbers at ages. This was likely due to the misspecified fixed natural mortality rate for the fitted model and the much wider variation in the realized population sizes of the data sets.

The lowest AIC was always obtained for models with the correct assumptions about stochasticity in the interannual transitions of abundance at age (SCAA versus state-space), whether or not the data sets included stochasticity in abundance at age (Tables 7 and 8). However, AIC only accurately determined the correct natural mortality assumption among state-space models for data sets where the stochasticity in abundance at age was accounted for in simulated data sets. For more detailed results from the simulation study, we focus on the component that included stochasticity in abundance at age in the simulated data sets.

When the simulated and fitted models matched, median bias of annual SSB estimates was at most 5%. The bias was worst for model M4 (3%–5%), the state-space model when natural mortality was fixed at the true value (Fig. 3). Curiously, the bias was absent or negligible when natural mortality was estimated (fitting M5 to data simulated under M4). To verify that this was not due to an error in the simulation, we performed the first sensitivity described above in the simulation study methods. We fit models to data simulated assuming M5 but fixing natural mortality at the higher value estimated from the original data ($M = 0.14$). Fits of these models also produced a similar slight positive bias in SSB estimates. There was also evidence of a smaller positive bias in some of the annual SSB estimates under model M6, but otherwise, bias was negligible when the simulated and fitted model matched.

When simulated data and fitted models did not match, bias in SSB estimation was variable. The worst bias occurred when model M1 was fitted to data simulated under any of the other scenarios (extremes of −71% and 73% for data simulated under M2 and M4, respectively) and when model M4 was fitted to data assuming models M5 and M6 (extremes of <−56% and <−40%, respectively). Both M1 and M4 assume a natural mortality of 0.05 and bias would be expected when assuming the incorrect natural mortality rate when the true estimated natural mortality was higher, as estimated in models M2 and M5. Although the bias was relatively

Fig. 3. Median relative difference and 95% confidence intervals of SSB estimates from fitting each of the six models (columns) in Table 2 to data sets simulated according to assumptions of each of the models (rows) and stochastic abundance at age. Missing plots correspond to fitted models that did not converge for the simulated data sets.



large when the natural mortality was correctly assumed known and stochasticity of interannual transitions in abundance at age was ignored (fitting model M1 to data simulated assuming model M4), estimation bias was relatively modest (1%–8%) when natural mortality was estimated (M2 or M3 fitted to data simulated under models M5 or M6). Patterns in estimation bias for annual fully-selected fishing mortality were similar to the results for SSB, although opposite in sign as one would expect (Fig. 4); with a given catch history, higher abundance requires lower harvest rates and vice versa to best fit the data.

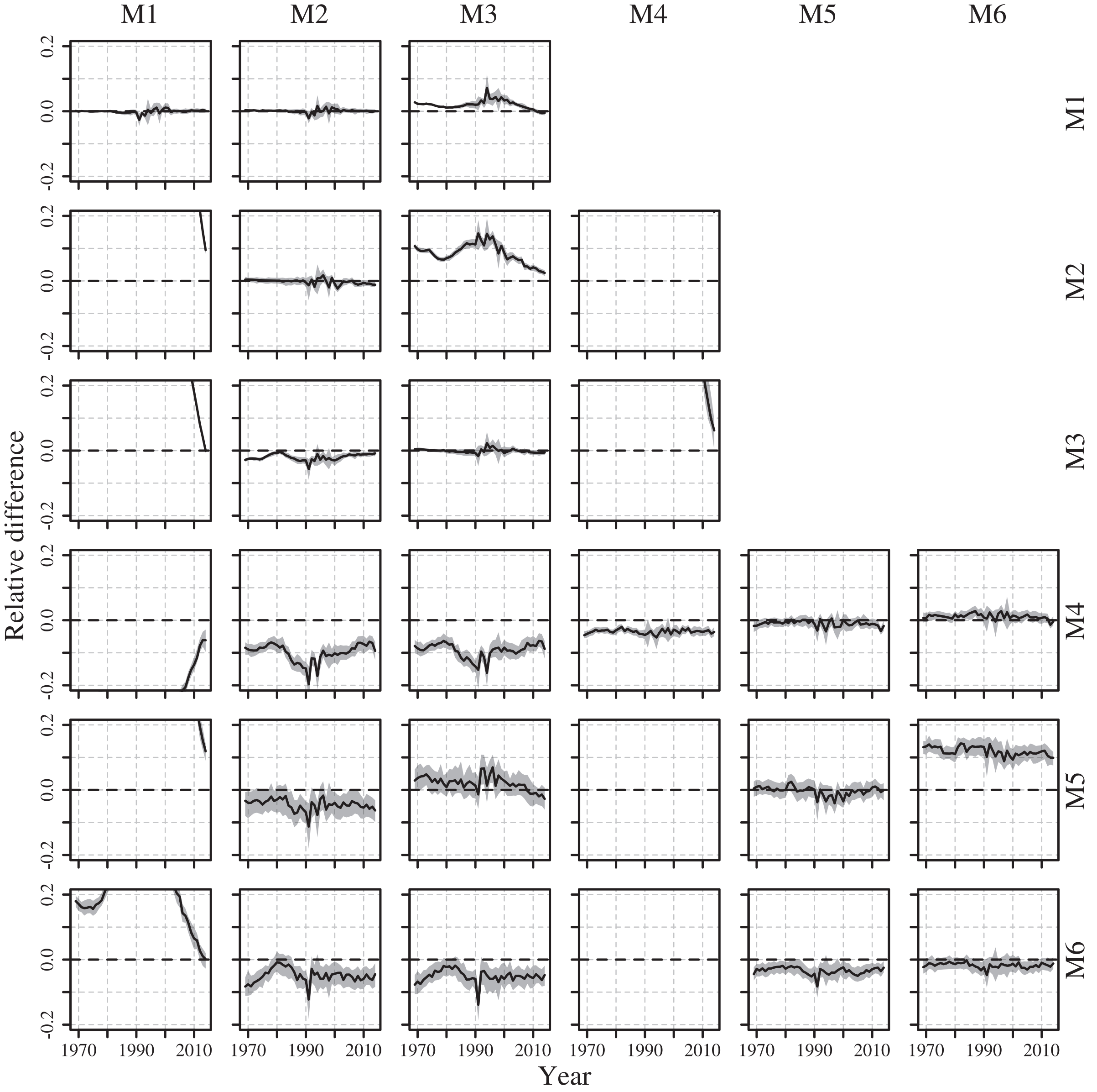
As expected with ML estimation, we found negatively biased estimation of variances for recruitment and interannual transitions of abundance at age (Fig. 5). However, the bias (–14% to –16%) was only considerable for the variance of interannual transitions ($\sigma^2_{N,2}$) in the state-space models M4–M6. We performed restricted ML estimation of these variances as described for the second sensitivity in the simulation study methods for the M4 simulated data sets to verify that ML was the cause; median relative bias of the restricted ML estimation for $\sigma_{N,2}$ was 0.9% (95% confidence interval: 0.2%–1.5%).

Bias in estimation of natural mortality parameters was evident in the state-space models (–4% and –5% for models M5 and M6, respectively) but median bias of estimation in the SCAA models was negligible (–0.2% and –0.3% for models M2 and M3, respectively) and confidence intervals included zero. Median bias of ML estimates for other parameters is provided in the supplementary materials.

Discussion

Of the six models we considered for GOM–GB Acadian redfish, we found that the state-space models (M4–M6) outperformed the SCAA models (M1–M3) with respect to AIC and that the best performing model (M5) also exhibited negligible retrospective pattern. We also found that estimating a constant natural mortality rate performed better, based on AIC, than the allometric relation-

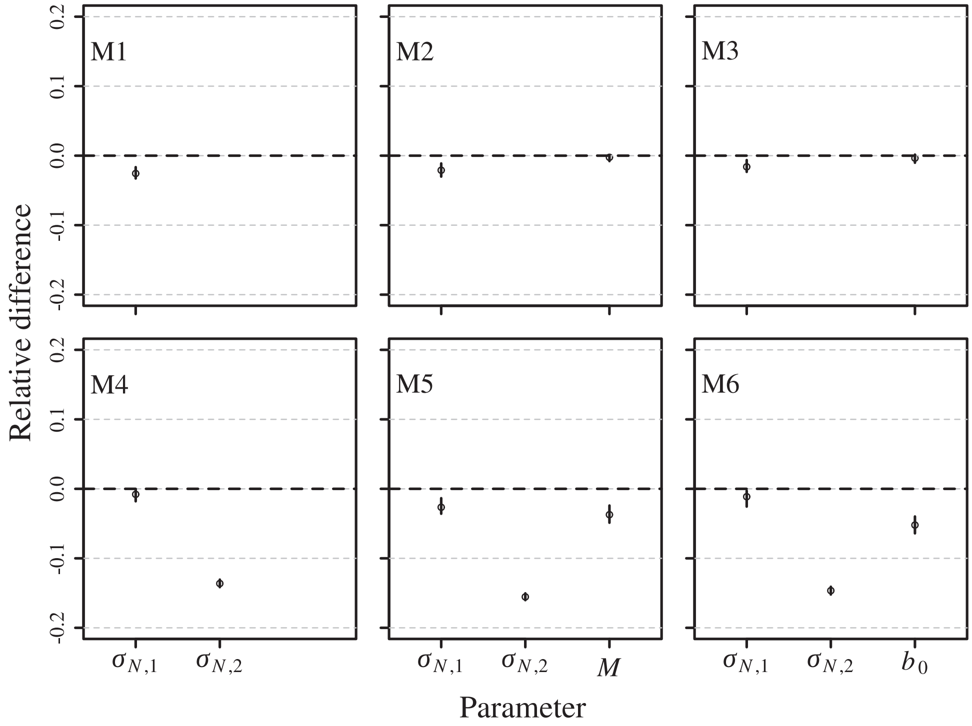
Fig. 4. Median relative difference and 95% confidence intervals of *F* estimates from fitting each of the six models (columns) in Table 2 to data sets simulated according to assumptions of each of the models (rows) and stochastic abundance at age. Missing plots correspond to fitted models that did not converge for the simulated data sets.



ship of natural mortality to mass. Initially, we attempted estimating both of the allometric coefficients (b_0 and b_1), but estimates of b_1 would tend to zero, yielding the constant natural mortality model (M2 or M5), which, of course, provided a better fit to the data. The natural mortality rate estimated from model M5 (0.14) is approximately three times the value assumed in the current assessment used to provide management advice for GOM–GB Acadian redfish (e.g., Linton 2015) and is fairly precise (CV = 0.13). We found less retrospective pattern in SSB and fully-selected fishing mortality when natural mortality was estimated, whether the SCAA-like model or the state-space model was used to fit the data. This is consistent with the finding by Miller et al. (2008) of less retrospective patterns in SSB and fully-selected fishing mortality with a higher natural mortality rate of 0.1 in a previous assessment using an SCAA model. The same natural mortality rate is also used in assessment models for other Atlantic redfish stocks, but a higher value of $M = 0.1$ has previously been used for at least one golden redfish (*Sebastes marinus* or *Sebastes norvegicus*) stock and a declining natural mortality rate at age (0.2 at age 1 to 0.05 at age 5) is used for another golden redfish stock (ICES 2012). The lower value of 0.05 is surely an approximation, but the difference between that and our estimate from model M5 does not seem to be attributable to precision of the estimate. Rather than there truly being a higher natural mortality for this stock, the “extra” mortality could be due to various issues such as unreported harvest or net migration from the area considered for the stock. Furthermore, some variation in this rate over time is likely, although we did not consider such models here.

Although the allometric relationship for natural mortality did not apply to GOM–GB Acadian redfish, we found in our simulation study that such a relationship is estimable and AIC accurately determined it as best when it existed. Application of these models to other stocks would be helpful to see whether the allometric relationship performs better for certain types of life histories. Other parameterizations of natural mortality such as with density-dependent effects (Beverton and Holt 1957, Section 7.3; Powers

Fig. 5. Median relative difference and 95% confidence intervals of process error standard deviation ($\sigma_{N,1}$ and $\sigma_{N,1}$) and natural mortality parameter (M and b_0) estimates from data sets simulated assuming the same assumptions as the fitted model and stochastic abundance at age.



2014) would also result in time-varying natural mortality and the estimability of such assumptions should be investigated.

There was also a substantially lower uncertainty in SSB and fully-selected fishing mortality estimates for SCAA models than state-space models with the same natural mortality assumptions. The CVs of SSB estimates from SCAA models with any of the natural mortality assumptions were between 92% and 27% lower than the corresponding estimates from state-space models. The CVs for annual SSB estimates from the last GOM–GB Acadian redfish assessment using an SCAA model had the same range (0.01–0.11) as those from the most similar model M1 we fit.

We found that AIC performed well in that the correct model had the lowest AIC for a high percentage of the simulated data sets in each scenario. Furthermore, it was important to simulate the random effects associated with the stochasticity of the abundance at age of the population to evaluate the accuracy of AIC. Other simulation studies involving state-space models have also accounted for this variation (de Valpine and Hastings 2002; de Valpine and Hilborn 2005; Pedersen et al. 2011). The simulation study also found that marginal likelihood-based AIC was especially accurate in differentiating SCAA-type models from state-space models where there was stochasticity in the interannual transitions in the abundance at age.

Another important finding from the simulation study was that using SCAA models when data are generated with process error in the interannual transitions in abundance at age resulted in poor estimation of SSB and fully-selected fishing mortality. The bias was particularly pronounced when natural mortality was assumed known for the SCAA model (M1 assumed for M4-based simulations), a widely used assessment model parameterization for fisheries management.

Together, the relative differences in estimated precision of the SSB estimates from the SCAA and state-space models and the results from the simulation study have potentially important implications, at least for GOM–GB Acadian redfish. These results would imply that only considering SCAA models would result in both biased estimation of annual SSB estimates and an incorrect perception of much greater precision in the estimates. We did not calculate standard errors of parameter estimates for each of the fits to simulated data because this would greatly increase the computation time, but we suspect this is a general result. Of course, whether these findings apply to other stocks remains to be investigated.

In a study evaluating estimability of natural mortality in SCAA models, Lee et al. (2011) found that the proportion of good fits ranged between 76% and 100% for all but one of the 12 simulation scenarios they considered, using the value of the maximum gradient at convergence as a criterion of utility of the model fit. Although we simply used the convergence flag that the nlminb function returns, our convergence rates (89%–100%) are consistent with these for many scenarios we considered, including those with stochasticity in abundance at age and mismatches between the model used to simulate and fit the data sets. Understandably, the only scenarios that resulted in poorer convergence were those where state-space models were fit to data simulated with deterministic interannual transitions of abundance at age.

Simulation testing of the accuracy of model selection methods is not common in the fisheries literature. Focus of these studies has mostly been on differentiating stock–recruitment models (de Valpine and Hastings 2002; Wang and Liu 2006; Zhou 2007) and, as we have here, assessment models (but see Helidoniotis and Haddon (2013) for an application to growth models). The poor ability of AIC to determine the correct state-space models when data sets were conditioned on the estimated abundance at age seems appropriate because the fitted models assume two sources of stochasticity (observation and process error) when there is only observation error in the simulated data sets. The accuracy of AIC for models M2 and M3, which assumed deterministic transitions in abundance at age, was nearly perfect whether or not simulated data sets included stochasticity in recruitment. These results are consistent with those found by Helu et al. (2000) for Stock Synthesis models in a comparable simulation study. However, in a simulation study comparing Bayesian assessment models, Jiao et al. (2012) found much poorer accuracy of the deviance information criterion (as low as 2.5%) than we found for AIC in any of the six scenarios. Wilberg and Bence (2008) found better accuracy using the deviance information criterion comparing Bayesian models for lake whitefish with different assumptions on fishing fleet catchability. Cadigan (2016) performed a simulation study to self-test the statistical performance of the best state-space model that he fit to northern cod observations. The simulations conditioned on the abundance at age estimated from the original model fits are analogous to the first type of simulated data sets we analyzed where the fitted model matched the simulation model. Interestingly, Cadigan (2016) found bias in some annual SSB estimates greater than 10%, which is larger than we found for the state-space models we fit to data sets that also included stochasticity in the abundance at age. Variation in these results is likely a function of the differences in informativeness of the data to each of the models and the life and harvest histories of the stocks simulated, which indicates that such simulation tests should be carried out for candidate models when assessing fish stocks for management purposes.

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References

Aanes, S., Engen, S., Saether, B.-E., and Aanes, R. 2007. Estimation of the parameters of fish stock dynamics from catch-at-age data and indices of abundance: can natural and fishing mortality be separated? Can. J. Fish. Aquat. Sci. **64**(8): 1130–1142. doi:10.1139/f07-074.

Akaike, H. 1973. Information theory and the maximum likelihood principle. *In* The 2nd International Symposium on Information Theory. *Edited by* B.N. Petrov and F. Csàki. Akademiai Kiàdo, Budapest. pp. 267–281.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish and Fisheries Series No. 11, fascimile reprint 1993. Chapman and Hall, London.

Buckland, S., Newman, K., Thomas, L., and Koesters, N. 2004. State-space models for the dynamics of wild animal populations. Ecol. Model. **171**(1–2): 157–175. doi:10.1016/j.ecolmodel.2003.08.002.

Cadigan, N.G. 2016. A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. Can. J. Fish. Aquat. Sci. **73**(2): 296–308. doi:10.1139/cjfas-2015-0047.

Cushing, D.H. 1974. The possible density-dependence of larval mortality and adult mortality in fishes. *In* The early life history of fishes. *Edited by* J.H. Blaxter. Springer-Verlag, New York. pp. 103–111.

de Valpine, P., and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. Ecol. Monogr. **72**(1): 57–76. doi:10.1890/0012-9615(2002)072[0057:FPMIPN]2.0.CO;2.

de Valpine, P., and Hilborn, R. 2005. State-space likelihoods for nonlinear fisheries time-series. Can. J. Fish. Aquat. Sci. **62**(9): 1937–1952. doi:10.1139/f05-116.

Deroba, J.J., and Schueller, A.M. 2013. Performance of stock assessments with misspecified age- and time-varying natural mortality. Fish. Res. **146**(1): 27–40. doi:10.1016/j.fishres.2013.03.015.

Fournier, D.A., and Archibald, C.P. 1982. A general theory for analyzing catch-at-age data. Can. J. Fish. Aquat. Sci. **39**(8): 1195–1207. doi:10.1139/f82-157.

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**(9): 2105–2116. doi:10.1139/f98-100.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A., and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Opt. Methods Softw. **27**(2): 233–249. doi:10.1080/10556788.2011.597854.

Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. ICES CM 1965, Document 3.

Hampton, J., and Fournier, D.A. 2001. A spatially, disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Mar. Freshw. Res. **52**(7): 937–963. doi:10.1071/MF01049.

Harville, D.A. 1974. Bayesian inference for variance components using only error contrasts. Biometrika, **61**(2): 383–385. doi:10.1093/biomet/61.2.383.

Helidoniotis, F., and Haddon, M. 2013. Growth models for fisheries: the effect of unbalanced sampling error on model selection, parameter estimation, and biological predictions. J. Shellfish Res. **32**(1): 223–235. doi:10.2983/035.032.0129.

Helu, S.L., Sampson, D.B., and Yin, Y. 2000. Application of statistical model selection criteria to the Stock Synthesis assessment program. Can. J. Fish. Aquat. Sci. **57**(9): 1784–1793. doi:10.1139/f00-137.

ICES. 2012. Report of the benchmark workshop on redfish (WKRED 2012), 1–8 February 2012, Copenhagen, Denmark. ICES CM 2012/ACOM:48.

Jiao, Y., Smith, E.P., O'Reilly, R., and Orth, D.J. 2012. Modelling non-stationary natural mortality in catch-at-age models. ICES J. Mar. Sci. **69**(1): 105–118. doi:10.1093/icesjms/fsr184.

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B.M. 2016. TMB: automatic differentiation and Laplace approximation. J. Stat. Softw. **70**(5): 1–21. doi:10.18637/jss.v070.i05.

Lee, H.-H., Maunder, M.N., Piner, K.R., and Methot, R.D. 2011. Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. Fish. Res. **109**(1): 89–94. doi:10.1016/j.fishres.2011.01.021.

Legault, C.M., and Restrepo, V.R. 1999. A flexible forward age-structured assessment program. Col. Vol. Sci. Pap. ICCAT, **49**(2): 246–253.

Linton, B. 2015. Acadian redfish. *In* Operational assessment of 20 northeast groundfish stocks, updated through 2014. US Dept. Commer. Northeast Fish. Sci. Cent. Ref. Doc. 15-24. pp. 130–139.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. **49**(4): 627–647. doi:10.1111/j.1095-8649.1996.tb00060.x.

Mendelssohn, R. 1988. Some problems in estimating population sizes from catch-at-age data. Fish. Bull. **86**(4): 617–630.

Methot, R.D., and Wetzel, C.R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish. Res. **142**(1): 86–99. doi:10.1016/j.fishres.2012.10.012.

Miller, T.J., and Legault, C.M. 2017. Statistical behavior of retrospective patterns and their effects on estimation of stock and harvest status. Fish. Res. **186**(1): 109–120. doi:10.1016/j.fishres.2016.08.002.

Miller, T.J., Mayo, R.K., Travers, M., and Col, L. 2008. Gulf of Maine – Georges Bank Acadian redfish. *In* Assessment of 19 northeast groundfish stocks through 2007: Report of the 3rd Groundfish Assessment Review Meeting (GARM III), Northeast Fisheries Science Center, Woods Hole, Massachusetts, 4–8 August 2008. US Dept. Commer. Northeast Fish. Sci. Cent. Ref. Doc. 08-15. pp. 658–692.

Miller, T.J., Hare, J.A., and Alade, L.A. 2016. A state-space approach to incorporating environmental effects on recruitment in an age-structured assessment model with an application to southern New England yellowtail flounder. Can. J. Fish. Aquat. Sci. **73**(8): 1261–1270. doi:10.1139/cjfas-2015-0339.

Mohn, R. 1999. The retrospective problem in sequential population analysis: an investigation using cod fishery and simulated data. ICES J. Mar. Sci. **56**(4): 473–488. doi:10.1006/jmsc.1999.0481.

Newman, K.B., and Lindley, S.T. 2006. Accounting for demographic and environmental stochasticity, observation error, and parameter uncertainty in fish population dynamics models. N. Am. J. Fish. Manage. **26**(3): 685–701. doi:10.1577/M05-009.1.

Nielsen, A., and Berg, C.W. 2014. Estimation of time-varying selectivity in stock assessments using state-space models. Fish. Res. **158**(1): 96–101. doi:10.1016/j.fishres.2014.01.014.

Pearcy, W.G. 1962. Ecology of an estuarine population of winter flounder *Pseudopleuronectes americanus* (Walbaum). Parts I–IV. Bull. Bingham Oceanogr. Coll. **18**(1): 1–78.

Pedersen, M.W., Berg, C.W., Thygesen, U.H., Nielsen, A., and Madsen, H. 2011. Estimation methods for nonlinear state-space models in ecology. Ecol. Model. **222**(8): 1394–1400. doi:10.1016/j.ecolmodel.2011.01.007.

Peterson, I., and Wroblewski, J.S. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. **41**(7): 1117–1120. doi:10.1139/f84-131.

Powers, J.E. 2014. Age-specific natural mortality rates in stock assessments: size-based vs. density-dependent. ICES J. Mar. Sci. **71**(7): 1629–1637. doi:10.1093/icesjms/fst226.

Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sette, O.E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: early life history, including growth, drift, and mortality of the egg and larval populations. Fish. Bull. **50**: 149–237.

Skaug, H.J., and Fournier, D.A. 2006. Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. Comp. Stat. Data Anal. **51**(2): 699–709. doi:10.1016/j.csda.2006.03.005.

Sullivan, P.J. 1992. A Kalman filter approach to catch-at-length analysis. Biometrics, **48**(1): 237–257. doi:10.2307/2532752.

Thompson, W.R. 1936. On confidence ranges for the median and other expectation distributions for populations of unknown distribution form. Ann. Math. Stat. **7**(3): 122–128. doi:10.1214/aoms/1177732502.

Ursin, E. 1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board Can. **24**(11): 2355–2453. doi:10.1139/f67-190.

Vetter, E.F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. **86**(1): 25–43.

Wang, Y., and Liu, Q. 2006. Comparison of Akaike information criterion (AIC) and Bayesian information criterion (BIC) in selection of stock–recruitment relationships. Fish. Res. **77**(2): 220–225. doi:10.1016/j.fishres.2005.08.011.

Wilberg, M.J., and Bence, J.R. 2008. Performance of deviance information criterion model selection in statistical catch-at-age analysis. Fish. Res. **93**(1–2): 212–221. doi:10.1016/j.fishres.2008.04.010.

Zhou, S. 2007. Discriminating alternative stock–recruitment models and evaluating uncertainty in model structure. Fish. Res. **86**(2–3): 268–279. doi:10.1016/j.fishres.2007.06.026.

Appendix A

Joint likelihood components

The joint likelihood component for log-abundance at age is

$$\mathcal{L}_1 = \prod_{y=2}^{T}\prod_{a=1}^{A}\frac{1}{\sqrt{2\pi}\sigma_{N,j}}\mathrm{e}^{\frac{1}{2\sigma^2_{N,j}}(\log N_{y,a} - f(\mathbf{N}_{y-1}))^2}$$

where $j = 1$ when $a = 1$ and $j = 2$ otherwise. The joint likelihood component function for log-aggregate fishing fleet catch observations is

$$\mathcal{L}_2 = \prod_{y=1}^{T}\frac{1}{\sqrt{2\pi}\sigma_{C,y}}\mathrm{e}^{\frac{1}{2\sigma^2_{C,y}}(\log C_y - \log\hat{C}_y)^2}$$

The joint likelihood component for the multinomial distribution for the age composition data (eq. 5) from the fishing fleet catch is

$$\mathcal{L}_3 = \prod_{y=1}^{T}\left(E_{C,y}!\prod_{a=1}^{A}\frac{\hat{p}_{C,y,a}^{n_{C,y,a}}}{n_{C,y,a}!}\right)$$

Similarly, the joint likelihood component for log-aggregate relative abundance indices for survey d (there are two surveys used in the model) is

$$\mathcal{L}_{3+d} = \prod_{y=1}^{T}\frac{1}{\sqrt{2\pi}\sigma_{d,y}}\mathrm{e}^{\frac{1}{2\sigma^2_{d,y}}(\log I_y - \log\hat{I}_y)^2}$$

and the joint likelihood component for the multinomial distribution for the age composition data for survey d is

$$\mathcal{L}_{5+d} = \prod_{y=1}^{T}\left(E_{d,y}!\prod_{a=1}^{A}\frac{\hat{p}_{d,y,a}^{n_{d,y,a}}}{n_{d,y,a}!}\right)$$