PRELIMINARY ASSESSMENT OF ATLANTIC WHITE MARLIN (*Tetrapturus albidus*) USING A STATE-SPACE IMPLEMENTATION OF AN AGE-STRUCTURED PRODUCTION MODEL

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SUMMARY

This paper illustrates the application of a state-space age-structured production model to Atlantic white marlin. An age-structured approach was applied to accommodate the possibility that the vulnerability of white marlin to the various fisheries changes with age. A state-space representation was employed to facilitate parameter estimation by accommodating Bayesian priors and inter-annual changes in parameters such as recruitment and catchability. The latter capability may prove especially useful inasmuch as the catchability coefficients appear to have increased during the early year of several of the CPUE time series. However, initial runs of the model in an attempt to duplicate the ASPIC and FISHLAB runs made by the 2000 SCRS indicate that the steepness parameter of the spawner-recruit relationship and the age at 50% vulnerability cannot be estimated reliably. This implies that an informative priors are required for these parameters before additional complexities are examined. The steepness parameter in particular has a strong influence on the model perception of the level of fishing mortality that can be sustained over the long term.

1. INTRODUCTION

This paper reports on the application of a state-space implementation of an age-structured production model (ASPM) to Atlantic white marlin. An age-structured approach was applied to allow the fecundity and vulnerability of white marlin to vary with age. A state-space representation was employed to facilitate parameter estimation by accommodating Bayesian priors and inter-annual changes in parameters such as the catchability coefficients and recruitment. The specific examples presented are purely illustrative and are not intended to form the basis for generating management advice. It is hoped, however, that discussions during the upcoming SCRS working group meeting will lead to a more useful model.

POPULATION DYNAMICS

The study period extends back to a time when the stock was near virgin levels such that the abundance N of each age class a at the beginning of the first month of the first year is given by

$$(1) \qquad N_{a,1,1} = \begin{cases} R_0 & \{\text{for } a = a_r\} \\ N_{a\text{-}1,1} e^{-M_a} & \{\text{for } a_r < a \leq A\} \\ N_{a\text{-}1,1} / (1 - e^{-M_a}) & \{\text{for } a = A\} \end{cases} .$$

where a_R is the age when the animal first recruits to the fishery, A is the plus-group representing age A and older fish, M is the natural mortality rate coefficient (yr^{-1}), and R_0 is the recruitment expected under virgin (unfished) conditions.

Abundance is updated at monthly intervals according to the recursion

$$N_{a,y,m+1} = N_{a,y,m} e^{-M_a \delta} - \sum_{i} C_{a,y,m,i} \tag{2}$$

where $N_{a,y,m}$ is the number of fish in age class a at the beginning of month m in year y, $C_{a,y,m,i}$ is the catch in numbers of fleet i, and δ is the duration of the time step in years (= 1/12). The abundance at the beginning of the first month of each subsequent year is modeled as

$$N_{a,y+1,1} = \begin{cases} \Psi(S_{y-a}) e^{\varepsilon_y} & a = a \\ N_{a-1,y,13} & a_R < a < A \\ N_{A-1,y,13} + N_{A,y,13} & a = A \end{cases} \tag{3}$$

$$S_y = \sum_{a=0}^{A} \rho_a E_a e^{-(F_y v_a + M_a) \tau_s} N_{a,y}$$

where the subscript 13 denotes the end of the 12th month (beginning of the next year). The initial abundance of the youngest age class is modeled as a Richer (1954) or Beverton and Holt (1957) function Ψ of spawning biomass (S):

$$(3) \qquad R = \begin{cases} R_0 \dfrac{S}{S_0} \alpha^{1-S/S_0} & \text{Ricker} \\ R_0 \dfrac{\alpha S/S_0}{1+(\alpha-1)S/S_0} & \text{Beverton and Holt} \end{cases} .$$

where α is the maximum lifetime reproductive rate α (see Appendix 1).

Deviations in recruitment from the expectation $\Psi(s)$, ostensibly due to fluctuations in the environment, are modeled as a first-order, lognormal autoregressive process,

$$\begin{aligned} r_y &= \Psi(s_{y-\alpha})\, e^{\varepsilon_y} \\ \varepsilon_y &= \rho\varepsilon_{y-1} + \eta_y \end{aligned} \quad , \tag{4}$$

where ρ is the correlation coefficient and η is a normal-distributed random variate having mean 0 and standard deviation σ_r. The 'random walk' model of Fournier et al. (1998) is a special case of the autoregressive model with ρ = 1.

The monthly catch of the *i*'th fishing entity (fleet) is computed as though it occurred as a pulse at the end of the month, after natural mortality and after the catch of fleets 1 through *i*-1:

$$C_{a,y,m,i} = F_{a,y,i}\left(N_{a,y,m} e^{-M_a \delta} - \sum_{k=1}^{i-1} C_{a,y,m,k}\right)\frac{\delta}{\tau_i} \tag{8}$$

where τ_i is the duration of the fishing season in years. The corresponding catch in weight is computed by multiplying (8) by the average weight at age $w_{a,y}$. Note that this formulation is only approximate when the fleets actually fish simultaneously rather than sequentially, but with monthly time steps the error is negligible.

The fishing mortality rate *F* is separated into components representing the age-specific relative-vulnerability *v*, annual effort expended *f*, and a catchability coefficient *q*:

$$F_{a,y,i} = q_{y,i} f_{y,i} v_{a,i} \tag{9}$$

The catchability coefficient *q* is the fraction of the most vulnerable age class that is taken per unit effort. Note that *q* may be allowed to vary from year to year rather than remain fixed in order to accommodate variations in the efficiency of the fishing process (see discussion of process errors below). The relative vulnerability coefficients *v* implicitly include factors such as gear selectivity, size limit regulations, and the fraction of the stock exposed to the fishery. They are modeled by a logistic selection curve:

$$v_{a,i} = \frac{1}{1 + e^{-(a - a_{50,i})/d_i}} \tag{10}$$

where $a_{50,i}$ is the age of 50% relative vulnerability for fleet *i* and d_i is the dispersion coefficient controlling the slope of the curve at $a_{50,i}$ (values of 0.2 or less effectively imply knife-edge selection).

Time series of catch per unit effort (CPUE) or fishery-independent abundance surveys are modeled as though the observations were made just before the catch of the fleet with the corresponding index *i*:

$$I_{y,m,i} = q_{y,i} \sum_a v_{a,i} \left(N_{a,y,m} e^{-M_{a,y}\delta} - \sum_{k=1}^{i-1} C_{a,y,m,k} \right) \frac{\delta}{\tau_i} \quad . \tag{11}$$

As for catch, the corresponding CPUE in weight is computed by multiplying (11) by $w_{a,y}$.

Average weight is computed as a power function of length, which in turn is computed as a von Bertalanffy function of age:

$$w_{ay} = \gamma \left[L_\infty \left(1 - e^{-k(a-t_0)} \right) \right]^\beta \tag{12}$$

The average weight for the plus-group depends on the age composition of the plus-group. However, to the extent that growth after the plus-age is approximately linear, the average weight may be calculated from the average age of the plus-group. Initially, it is assumed that the age composition of the plus-group is in equilibrium consistent with equation (6), in which case the average age of the plus-group at the beginning of the first year is

$$\bar{a}_{A,1} = A + \frac{e^{-(M_A+\phi_A)}}{\left(1 - e^{-(M_A+\phi_A)}\right)} \tag{13}$$

Subsequently, the age of the plus-group is updated as

$$\bar{a}_{A,y+1} = \frac{A N_{A-1,y,13} + \left(\bar{a}_{A,y} + 1\right) N_{A,y,13}}{N_{A,y+1,1}} \quad . \tag{14}$$

Similarly, the equilibrium spawning biomass per recruit for a given vector of fishing mortality rates at age (F) is computed

$$\theta_F = \sum_{a=\alpha}^{A-1} p_a E_a e^{-(Z_a\tau + \sum_{j=\alpha}^{a-1} Z_j)} + \frac{p_A E_A}{1 - e^{-Z_A}} e^{-(Z_A\tau + \sum_{j=\alpha}^{A-1} Z_j)} \tag{4}$$

where $Z_a = M_a + F_a$, τ is the fraction of the year elapsed at the time of spawning (= $t/12$). The virgin level (θ_0), which is used in equation (2) above, is obtained by setting $F_a = 0$.

3. STATE-SPACE IMPLEMENTATION

Process errors in the state variables and observation errors in the data variables (see Tables 1 and 2) are accommodated using the first-order autoregressive (AR1) model

$$\begin{aligned} g_{t+1} &= \mathrm{E}[g_{t+1}]\, e^{\varepsilon_{t+1}} \\ \varepsilon_{t+1} &= \rho \varepsilon_t + \eta_{t+1} \end{aligned} \quad , \tag{15}$$

where g represents any given state or observation variable, η is a normal-distributed random error with mean 0 and standard deviation σ_g, and E[g] denotes the value of g given by the deterministic components of the process or observation dynamics (equations 1-14). In the case of data, the g_t in (15) correspond to observed quantities, but in the case of states the g_t are unobserved and must be estimated along with the parameter vector.

For stability reasons, it is assumed that $\varepsilon_0 = 0$, leading to the negative log-density

$$-\log \mathrm{P}(g|\Theta,\mathbf{X}) = \frac{1}{2\sigma_g^2}\left[(\ln g_1 - \ln \mathrm{E}[g_1])^2 + \sum_{t=1}^{N-1}(\ln g_{t+1} - \ln \mathrm{E}[g_{t+1}] - \rho \ln g_t + \rho \ln \mathrm{E}[g_t])^2\right] + N \log \sigma_g \ , \tag{16}$$

where ρ_g is the correlation coefficient and σ_g^2 is the variance of $\log_e(\eta)$. In the present model, the variances of the process and observation errors are parameterized as multiples of an overall coefficient of variation parameter CV, i.e., $\sigma_g^2 = \log_e\left[(\lambda_g CV)^2 + 1\right]$. Note that the 'random walk' model of Fournier et al. (1998) is merely a special case of (15) with $\rho = 1$ and E[g_t] = g_0 (a time-invariant parameter).

The model was implemented using the nonlinear optimization package AD Model Builder (Otter Research Ltd., 2000), which provides facilities for estimating the mode and shape of posterior distributions formed by (16) and the negative logarithms of the priors.

4. APPLICATION TO WHITE MARLIN

Two runs were made that were essentially equivalent to the SCRS (2001) base-case runs with (i) a single composite CPUE series, and (ii) eight separate CPUE series. The catch and CPUE observations are assumed by the model to be unbiased, but imprecise. The annual catches from each fleet were assumed to be equally uncertain with constant coefficient of variation *CV* estimated by the model. The annual CPUE values for each fleet were assumed to be less certain than the catches, and were assigned coefficients of variation that were twice as large as the values estimated for the catch (i.e., 2*CV*). In the case of the composite model, the annual CPUE CV values were also multiplied by the GLM estimated standard errors (Table 8, SCRS 2001) scaled by the minimum value. The fleet-specific CPUE series were given equal weight.

Effort was allowed to vary from year to year essentially as a free parameter by allowing a relatively large process error (10*CV*) and moderate correlation (ρ = 0.5). No process error was allowed for the other state variables. The catchability coefficients q were estimated as time-independent constants in runs (i) and (ii). However, a third run was made with the composite series where the catchability coefficient was allowed to vary annually as a random walk process with coefficient of variation 2*CV*.

There was little basis upon which to formulate the priors for the estimated parameters, therefore I used uniform priors defined over a plausible range of values (see Table 3). The only exceptions were the natural mortality M and growth coefficients, which were held constant inasmuch as they are notoriously difficult to estimate from catch and CPUE time series alone. The value of M was set to 0.1, a low value reflecting the longevity of white marlin and related species (see SCRS 2001). The relationship between weight and length was modeled as estimated by Prager et al. (1995). The relationship between age and length for white marlin is poorly known, therefore von Bertalanffy growth coefficients were assumed to be approximately the same as for sailfish (*Istiophorus platypterus*) from the Gulf of California (Alvarado and Felix, 1998). This strategy, while inexact, should nevertheless be superior to assuming all age classes weigh the same as lumped-biomass production models do. Fish above age 9 were lumped together as a "plus" group.

5. RESULTS

5.1 Composite series

The constant and random-walk q models both fit the catch data rather well (Figure 1) inasmuch as the catch data were assumed to be about twice as precise as the CPUE information. The fit to the CPUE data by the constant q model was very similar to the fit provided by the equivalent ASPIC and FISHLAB logistic production models (SCRS 2001). The fit by the random-walk q model was much better as it could partly reconcile the simultaneous increase in catch and CPUE. The appraisals of stock status from both models were similar to those produced by ASPIC and FISHLAB. All suggest that the spawning biomass has declined well below the level associated with MSY and that the fishing mortality rate has increased to well above F_{MSY} (see Figures 2-4, Tables 4-5).

Most of the parameters appeared well determined, their estimates having CV's under 40%. However, the estimate for h tended toward the upper boundary of 0.95 and the estimate for a_{50} tended to the boundary of 3.0 (Figure 4). Moreover, minor changes in model structure or the order in which parameters were estimated could cause the estimate of h to swing to the lower boundary (as it does for the fleet-specific model below).

5.2 Fleet-specific series

The model fit to the catch data (Figure 5) is generally good except for a few years during the early part of the Japanese longline series. The fits to the CPUE data (Figure 6) were similar to the fits provided by the equivalent FISHLAB logistic production model (SCRS 2001). As was true for the composite runs above, the fleet-specific ASPM appraisal of stock status was similar to that of the SCRS FISHLAB model. Both models suggest the spawning biomass has declined below the level associated with MSY and that the fishing mortality rate has increased above F_{MSY} (see Figures 7-9, Table 4).

Most of the parameters appeared well determined, their estimates having CV's on the order of 20% or less. However, the estimates for h and a_{50} tended toward their lower boundaries of 0.30 and 1.0, respectively.

6. DISCUSSION

The base ASPM models were unable to reconcile the early increase in CPUE with the simultaneous increase in catch, as was also true of the ASPIC and FISHLAB formulations. This was to be expected inasmuch as the CPUE and catch observations increase simultanously, which cannot be satisfactorily interpreted by those models unless either recruitment or catchability is allowed to deviate from the model expectations (e.g., via allowance for process error). Inasmuch as this increase is early in the time series, allowing for process errors in recruitment is of little help (one cannot estimate variations in recruitment prior to the date when the data begins). However, as is evident in Figure 1, allowing q to vary as a random-walk process enabled the model to better reconcile the two trends. This reconciliation, however, comes at the expense of less precise parameter estimates. None of the models were able to provide meaningful estimates of either the steepness h or the age of 50% selection a_{50}.

The estimate for h tended toward the upper boundary of 0.95 in the composite models and the lower boundary of 0.3 in the fleet-specific model. Moreover, seemingly minor changes in model structure or the order in which parameters were estimated could sometimes cause the parameter to swing to the lower boundary. The estimates for a_{50} similarly tended to the boundaries. Clearly this behavior is an artifice of insufficient data, implying that more informative priors are needed. Failing that, there is probably little chance of reliably estimating process deviations in the state variables.

There are several areas in which this analysis may be improved. The steepness, growth, vulnerability, and natural mortality parameters cannot generally be estimated from catch and effort data alone. There may be some chance of estimating natural mortality by incorporation of tag-recapture data (as in Porch et al., 2001). Likewise, the vulnerability vector would become estimable by incorporating age-composition data even if it is not available for every year (as required by a VPA). The steepness parameter may also become estimable with an index of the abundance of the youngest age class. If such auxiliary information is not available, then expert guidance will be required to develop reasonable priors.

Priors for h may be derived in principle from the meta-analyses of Myers et al. (1999) and Myers and Mertz (1998). Unfortunately, these analyses contain no information on Istiophorids. The closest phylogenetic groups in their analyses are a few scombrids, with h values ranging between 0.38 and 0.92, and a swordfish population with $h = 0.88$. There is also very little information on the natural mortality and growth of Istiophorids. The value of M was assumed to be low (around 0.10) based on the apparent longevity of the species, however empirical methods applied to striped marlin in the eastern pacific suggest much higher values between 0.4 and 1.3 (Hinton and Bayliff, 2002). The growth coefficients used here were borrowed from sailfish in the Gulf of California, but a possible alternative would be to use the coefficients estimated for striped marlin, which indicate a more rapid growth rate (see Hinton and Bayliff, 2002). Priors for the vulnerability coefficients, particularly a_{50}, may be derived from the length frequency data for the various fleets assuming one of the growth curves is appropriate (at least for the younger ages). If this is done it might also be possible to allow different selectivity curves for each fleet.

Finally, it would be useful to explore appropriate weighting schemes for each of the indices of abundance in the fleet-specific model. One possibility would be to use the weights already derived for the construction of the composite model. Another would be to use the estimates of the standard errors for each index, which would reflect inter-annual trends in samples sizes.

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REFERENCES

ALVARADO-Castillo, R., and Felix-Uraga, R. 1998. Growth of *Istiophorus platypterus* (Pisces: Istiophoridae) from the mouth of the Gulf of California. Rev. Biol. Trop. 46:115-118.

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.

HINTON, M. G., and Bayliff, W. H. 2002. Status of striped marlin in the Eastern Pacific Ocean in 2001, and outlook for 2002. Inter-American Tropical Tuna Commission. 3rd Meeting of the Scientific Working Group. Background paper A11. 24 pp.

MYERS, R. A., and G. Mertz. 1998. Reducing the uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. Fisheries Research 37:51-60.

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

OTTER RESEARCH LTD. 2000. An introduction to AD MODEL BUILDER Version 4.5. Box 2040, Sidney B.C. V8L 3S3, Canada. 141 p.

PORCH, C.E., S.C. Turner, and J.E. Powers. 2001. Virtual population analyses of Atlantic bluefin tuna with alternative models of transatlantic migration: 1970-1997 ICCAT Col. Vol. Sci. Pap. 52: 1022-1045.

PRAGER, M. H., Prince, E. E., and Lee, D. W. 1995. Empirical length and weight conversion equations for blue marlin, white marlin and sailfish from the North Atlantic Ocean. Bull. Mar. Sci. 56:201-210.

SCRS. 2001. Report of the fourth ICCAT billfish workshop. ICCAT Col. Vol. Sci. Pap. 53: 1-130.

Table 1. Stochastic equations used to define the state space age-structured production model, where the notation E is used to denote the value computed from the deterministic components of the model (equations 1-14).

Variables	Description
Process functions for state variables	
$M_{ay} = E[M_a]\, e^{-\varepsilon_{M,y}}, \quad \varepsilon_{M,y} = \rho_{M,y}\, \varepsilon_{M,y-1} + \eta_{M,y}$	natural mortality rate
$N_{\alpha y} = E[N_{\alpha y}]\, e^{-\varepsilon_{R,y}}, \quad \varepsilon_{R,y} = \rho_R\, \varepsilon_{R,y-1} + \eta_{R,y}$	recruitment of youngest age
$q_{iy} = E[q_{iy}]\, e^{-\varepsilon_{q\,i,y}}, \quad \varepsilon_{q,i,y} = \rho_{q,i}\, \varepsilon_{q,i,y-1} + \eta_{q,i,y}$	catchability for fleet *i*
$f_{iy} = E[f_{iy}]\, e^{-\varepsilon_{f\,i,y}}, \quad \varepsilon_{f,i.y} = \rho_{f,i}\, \varepsilon_{f,i,y-1} + \eta_{f,i,y}$	effort expended by fishery f
Observation functions for data variables	
$C_{ft} = \left(\delta q_{ft} E_{ft} \sum_{j=1}^{16} B_{t+j\delta}\right) e^{-\varepsilon_{C,f,t}}, \quad \varepsilon_{C,f,t} = \rho_{C,f}\, \varepsilon_{C,f,t-1} + \eta_{C,f,t}$	catch of fleet *i*
$I_{ft} = \left(\delta q_{ft} \sum_{j=1}^{16} B_{t+j\delta}\right) e^{-\varepsilon_{I,f,t}}, \quad \varepsilon_{I,f,t} = \rho_{I,f}\, \varepsilon_{I,f,t-1} + \eta_{I,f,t}$	CPUE of fleet *i*

Table 2. Time-independent parameters of the state-space age-structured production model and their use in the analyses of Atlantic white marlin.

Parameter	Value for WHM	Description
ϕ	0.0	negligible historical fishing mortality rate
M	0.1	arbitrary low value, constant for all ages.
R_0 , h	estimated	Beverton and Holt recruitment parameters
$q_{i,0}$	estimated	constant catchability coefficient for fleet i
$E_{f,0}$	mean of series	average effort expended by fleet i (C/CPUE)
d	0.2	logistic curve dispersion coefficient ~ knife edge
a_{50}	estimated	logistic curve age at 50% vulnerability
L	203.6	sailfish von Bertalanffy asymptotic length coeff. (cm)
k	0.08000	sailfish von Bertalanffy growth coeff.
t_0	-0.001500	sailfish von Bertalanffy age intercept
γ	0.5207E-08	weight-length curve multiplier (MT)
β	3.012	weight-length curve exponent
p_a	0, 1, 1, 1, 1	maturity vector
ρ_M	0	process correlation for M
ρ_{Rr}	0	process correlation for recruitment
$\rho_{q,i}$	1.0	process correlation for catchability for fleet i
$\rho_{f,i}$	0.5	process correlation for effort for fleet i
$\rho_{C,i}$	0	observation process correlation for catch of fleet i
$\rho_{I,i}$	0	process correlation for CPUE of fleet i
λ_M	0	relative process CV in M
λ_R	0	relative process CV in recruitment
$\lambda_{q,i}$	0	relative process CV in catchability for fleet i
$\lambda_{E,i}$	10.0	relative process CV in effort for fleet i
$\lambda_{C,i}$	1.0	relative observation CV for catch of fleet i
$\lambda_{I,i}$	2.0	relative observation CV for CPUE of fleet i
CV	estimated	coefficient of variation (controls absolute magnitude of variance)

Table 3. Priors used to constrain estimated parameters. Note that $\bar{I}_i$ denotes the geometric mean of the CPUE indices for each fishery.

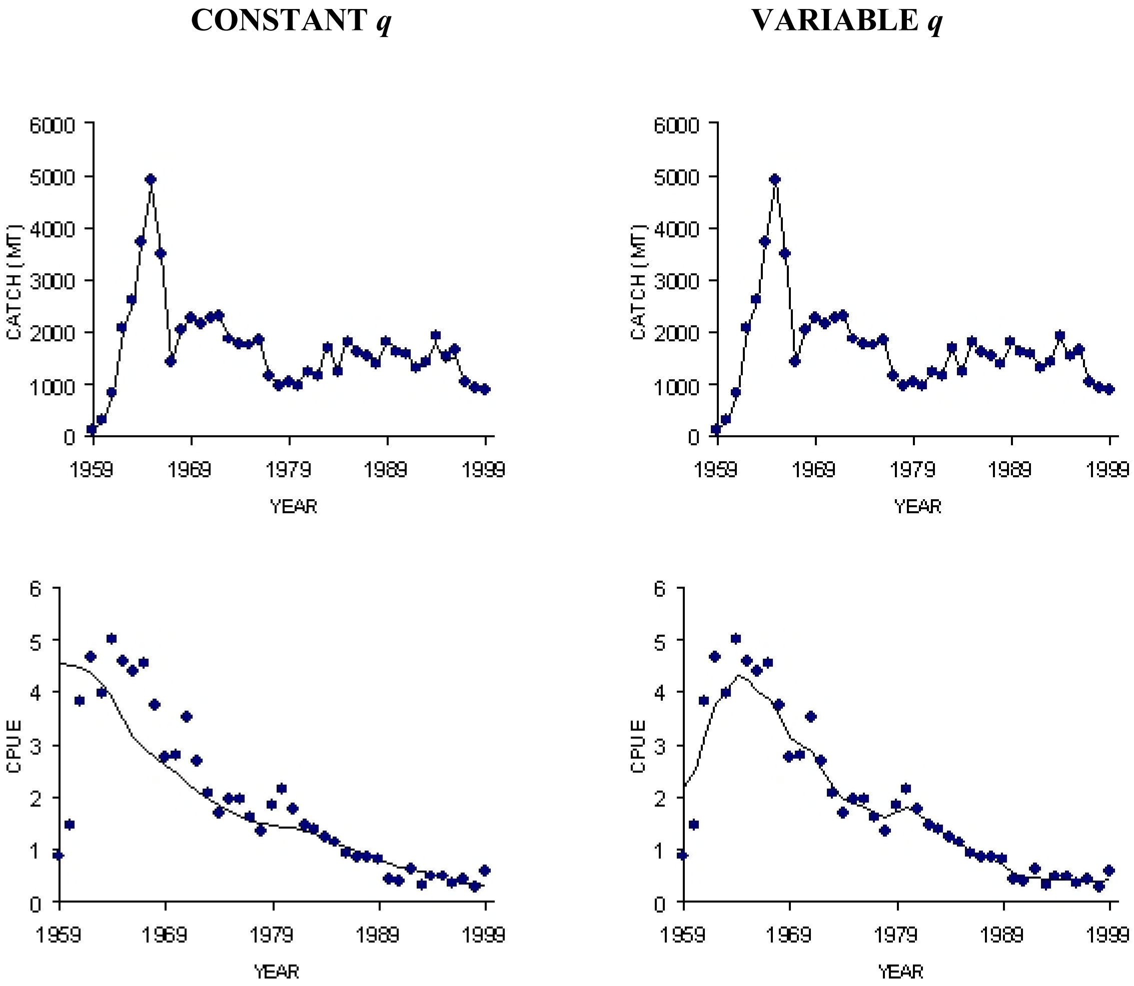
Parameter	**Prior**	**Rationale**
h	uniform(0.3, 0.95)	Relatively uninformative prior
R_0	uniform(10^4, 10^7)	Relatively uninformative prior
q_i	$\mathrm{uniform}\left(\frac{\bar{I}_i}{100\Omega}, \frac{\bar{I}_i}{0.1\Omega_i}\right)$	Probably $0.1\,\Omega_i < \Sigma_a v_{ia} N_{ay} < 100\,\Omega$ (Ω_i greatest observed annual catch by fleet i, Ω greatest annual catch of all fleets combined)
a_{50}	uniform(1, 3)	young fish are believed to be less vulnerable
CV	uniform(0.01, 2.0)	plausible range (1% to 200% CV)

Table 4. Parameter estimates from the various model formulations. Shaded cells indicate values at or near the limits imposed on the search algorithm.

Variable	Model configuration	Point estimates	Standard error	CV (%)
h	Composite	0.95		
	Composite with q dev.'s	0.95		
	Fleet specific	0.30		
R_0	Composite	462720	14084	3
	Composite with q dev.'s	512090	19619	4
	Fleet specific	648480	15053	2
a_{50}	Composite	3.00		
	Composite with q dev.'s	1.00		
	Fleet specific	1.00		
$F_{current}$	Composite	0.26	0.04	15
	Composite with q dev.'s	0.10	0.04	37
	Fleet specific	0.07	0.01	16
$S_{current}$	Composite	3875	451	12
	Composite with q dev.'s	9714	3572	37
	Fleet specific	12810	1428	11

Table 5. Estimates of management benchmarks from the various model formulations.

Variable	Model configuration	Point estimates
MSY	Composite	985
	Composite with R dev.'s	1074
	Fleet specific	344
B_{MSY}	Composite	9363
	Composite with R dev.'s	13468
	Fleet specific	23588
F_{MSY}	Composite	0.110
	Composite with R dev.'s	0.081
	Fleet specific	0.014
B_{1999}/B_{MSY}	Composite	0.410
	Composite with R dev.'s	0.721
	Fleet specific	0.543
F_{1998}/F_{MSY}	Composite	2.320
	Composite with R dev.'s	1.183
	Fleet specific	5.270



CONSTANT *q*

VARIABLE *q*

Figure 1. Model fits to composite catch and CPUE series when *q* is assumed constant (left) or allowed to vary as a random walk (right).

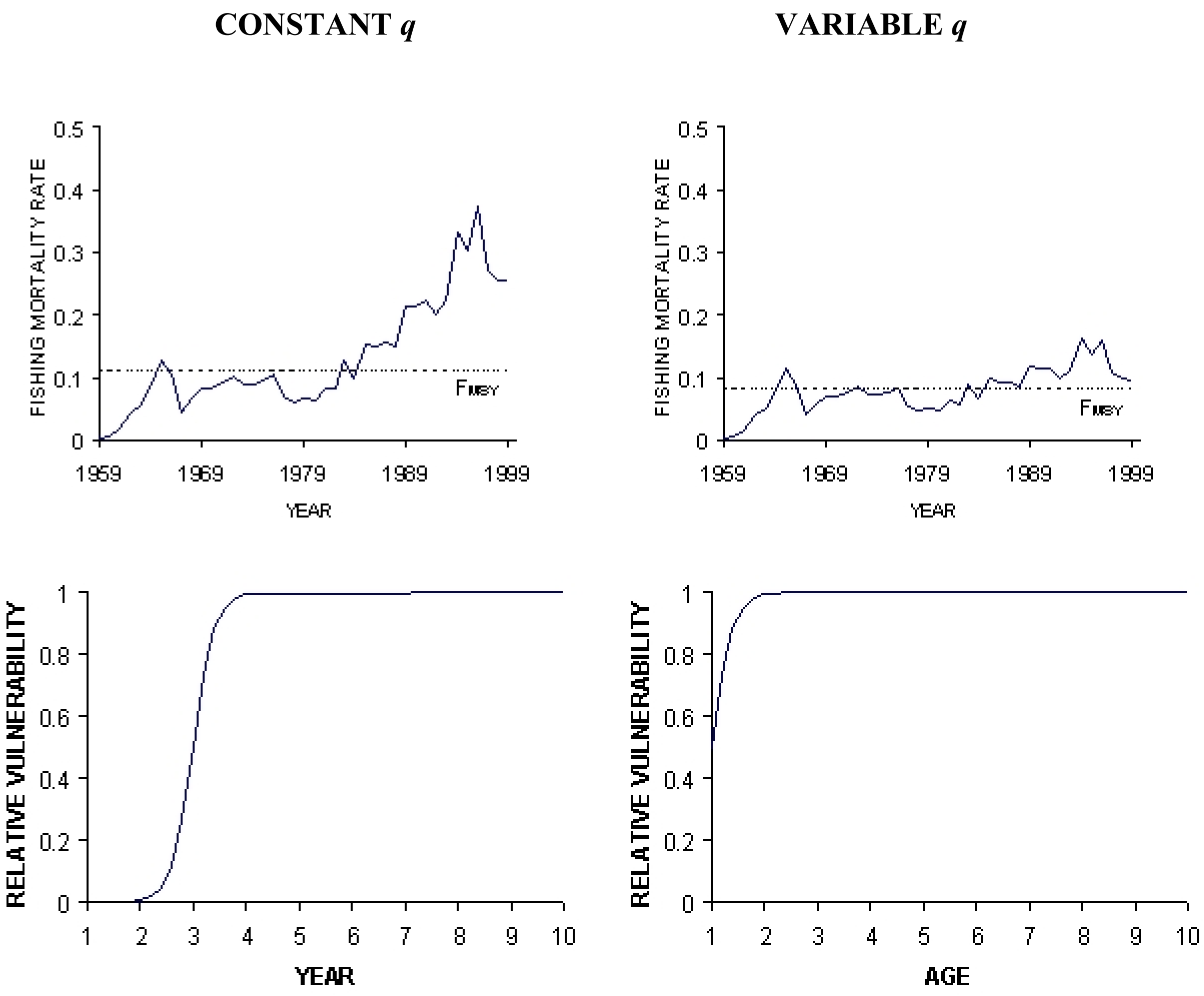


Figure 2. Estimated fishing mortality rates and selection curves for composite model when *q* is assumed constant (left) or allowed to vary as a random walk (right).

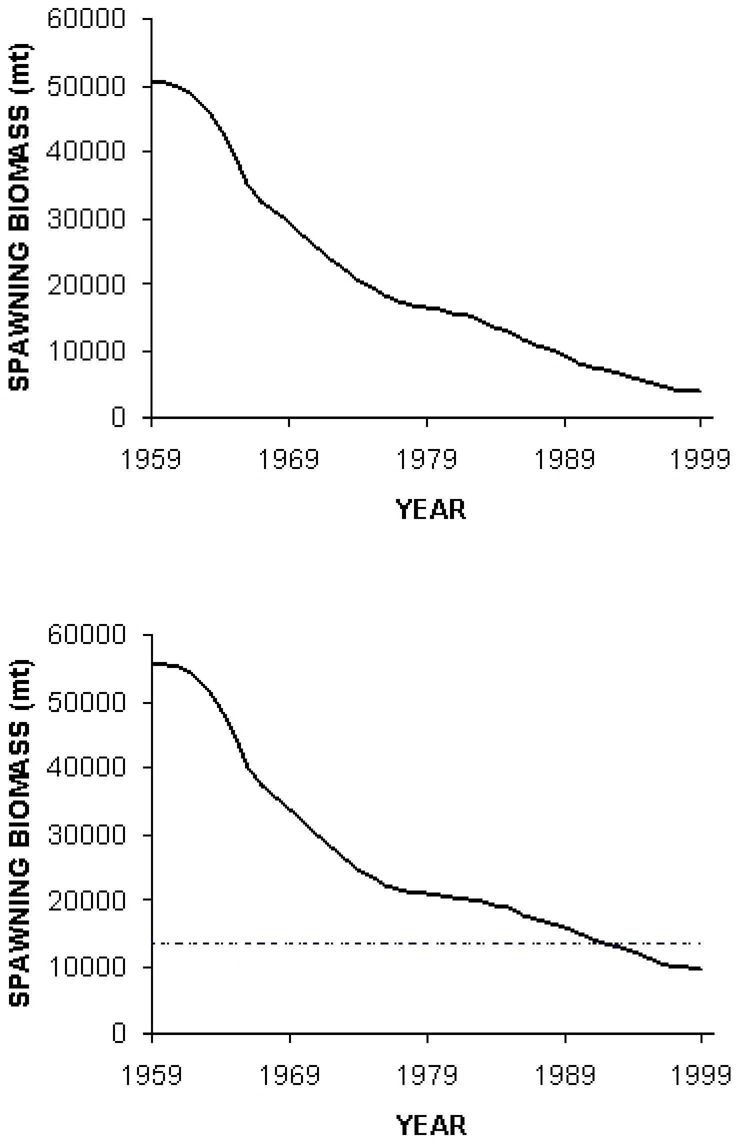


Figure 3. Estimated (modal) trends in spawning biomass from the composite model when q is assumed constant (top) or allowed to vary as a random walk (bottom). Dashed horizontal lines refer to the spawning biomass at MSY.

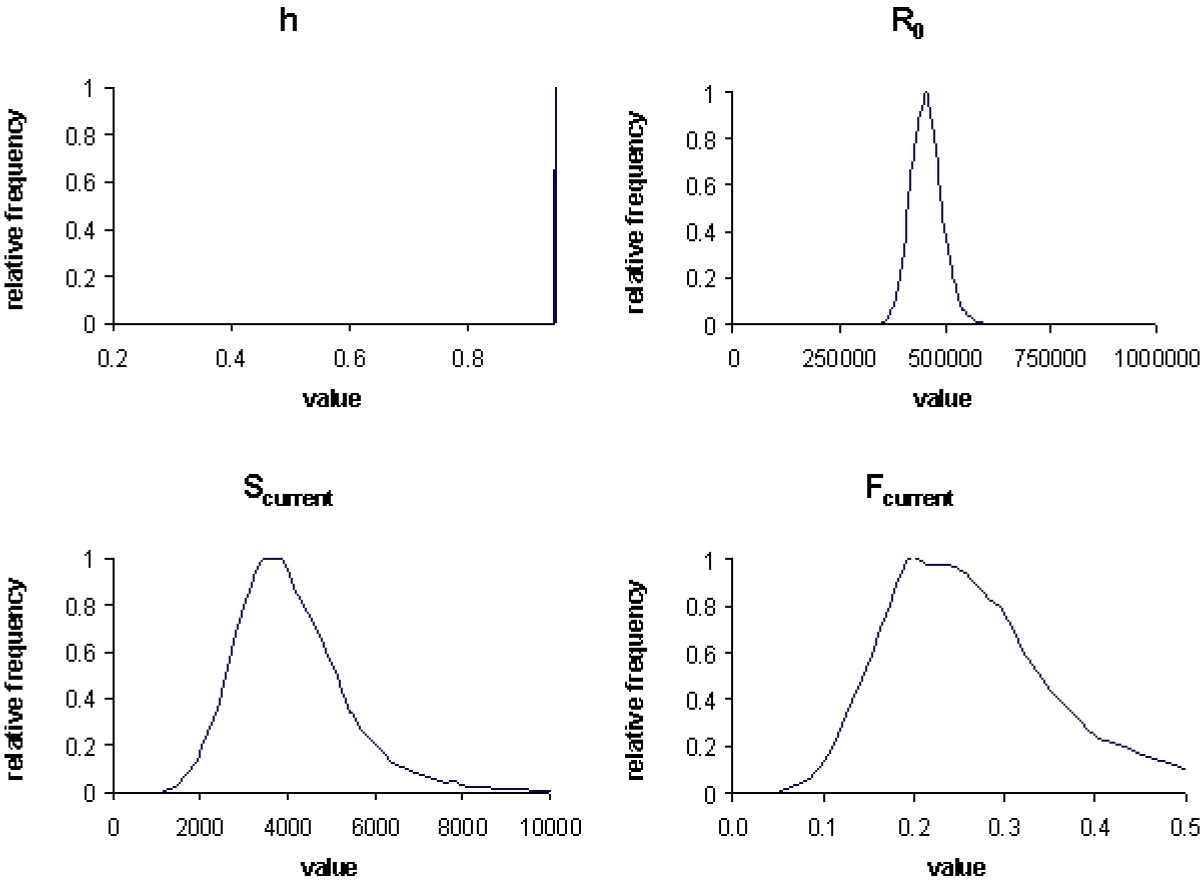


Figure 4. Posterior distributions of steepness, maximum recruitment, current (1999) spawning biomass and current fishing mortality rate from the composite ASPM with constant *q*.

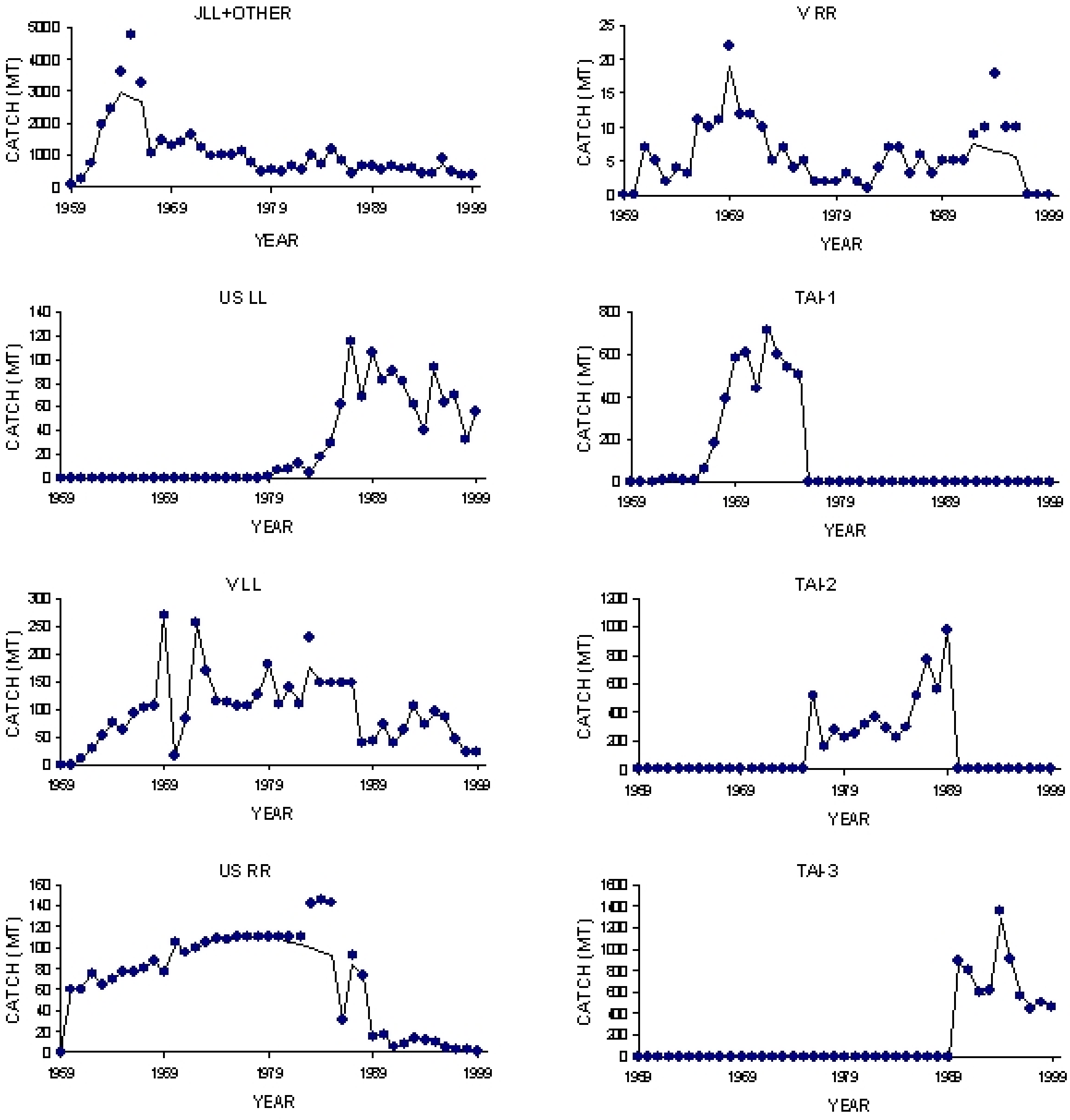


Figure 5. Model fits to fleet-specific catches.

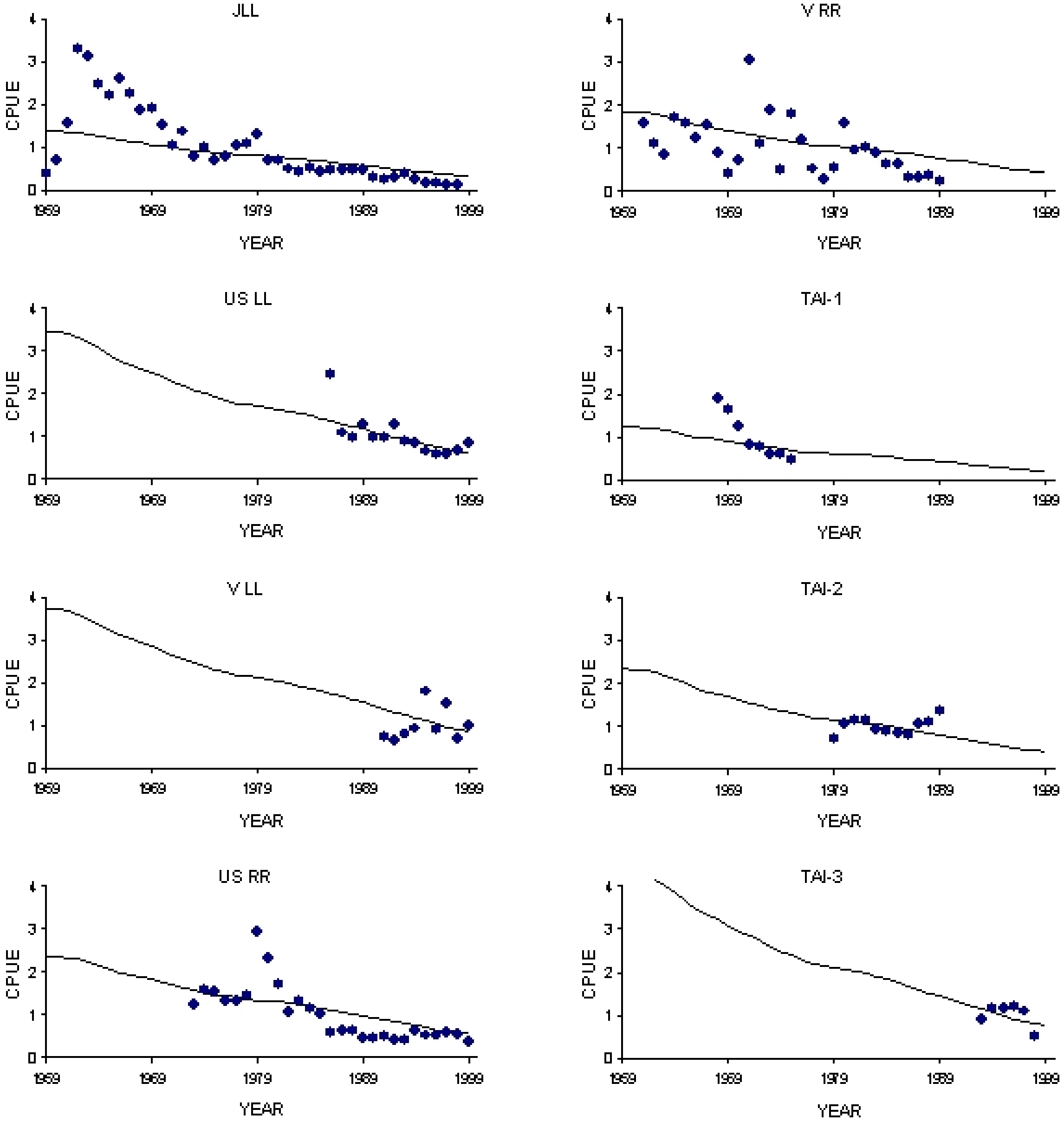


Figure 6. Model fits to fleet-specific CPUE series.

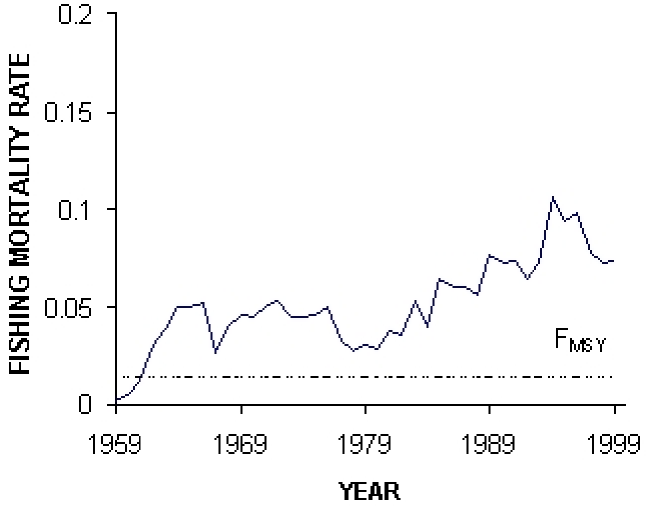


Figure 7. Estimated trends in overall fishing mortality rate and selection curve for composite model.

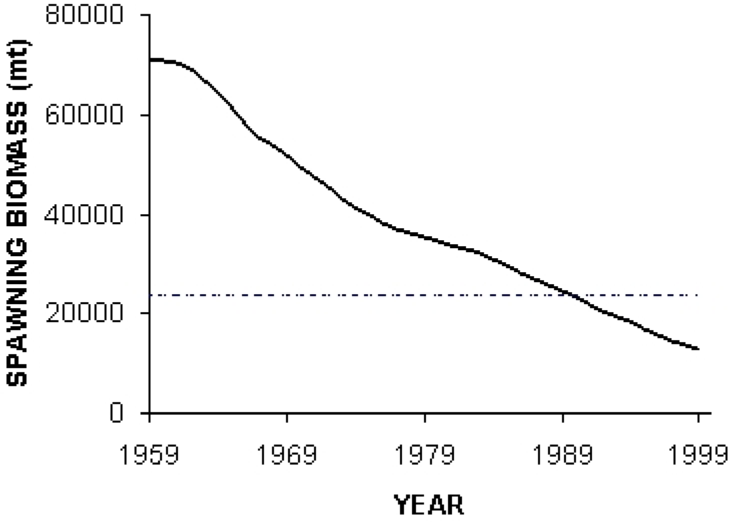


Figure 8. Estimated (modal) trends in spawning biomass from the fleet-specific model. Dashed horizontal line refers to the spawning biomass at MSY.

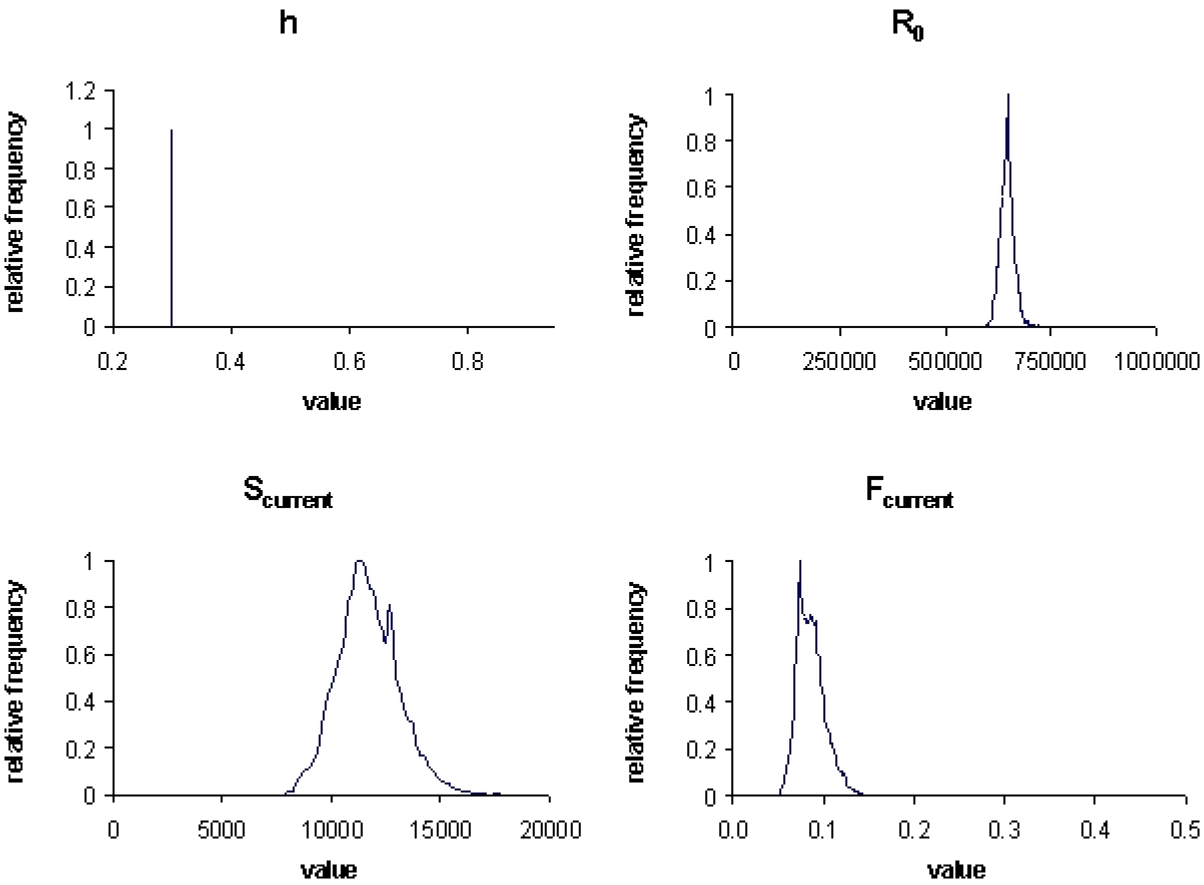


Figure 9. Posterior distributions of steepness, maximum recruitment, current (1999) spawning biomass and current fishing mortality rate from the fleet-specific ASPM.

Appendix 1: Reparameterized spawner-recruit relationships

The number of young fish recruiting to a population is often related to the aggregate fecundity of the spawning stock using one of two functional forms:

(A.1) $$R = \begin{cases} aSe^{-bS} & \text{Ricker} \\ \dfrac{abS}{b+S} & \text{Beverton and Holt} \end{cases} .$$

The parameter *a* is the slope of the curve at the origin and the parameter *b* controls the degree of density dependence. Notice that the domain of both functions extends from zero to infinity, whereas in practice there must be some limitation on *S* even in the absence of fishing owing to environmental constraints. This being so, we obtain

(A.2) $$a\frac{S_0}{R_0} = \begin{cases} e^{bS_0} & \text{Ricker} \\ 1 + S_0 / b & \text{Beverton and Holt} \end{cases}$$

The ratio S_0/R_0 represents the maximum expected lifetime fecundity of each recruit and *a* represents the survival of recruits in the absence of density dependence. Accordingly, the product $\alpha = aS_0/R_0$ may be interpreted as maximum possible number of spawners produced by each spawner over its lifetime (Myers et al. 1998).

The dimensionless character of α makes it useful for interspecies comparisons, or for borrowing values from species with similar life history strategies. Solving for *b* in terms of α one obtains

(A.3) $$b = \begin{cases} \log_e \alpha / S_0 & \text{Ricker} \\ S_0 \ / (1 - \alpha) & \text{Beverton and Holt} \end{cases}$$

Substituting (A.3) into (A.1) gives

(A.4) $$R = \begin{cases} aS\alpha^{-S/S_0} & \text{Ricker} \\ \dfrac{aS_0}{1 + (\alpha - 1)S/S_0} & \text{Beverton and Holt} \end{cases}$$

and, since $a = \alpha R_0/S_0$,

$$(\text{A.5}) \quad R = \begin{cases} R_0 \dfrac{S}{S_0} \alpha^{1-S/S_0} & \text{Ricker} \\ R_0 \dfrac{\alpha S/S_0}{1+(\alpha-1)S/S_0} & \text{Beverton and Holt} \end{cases}.$$