Parameterizing age-structured models from a fisheries management perspective

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Abstract: Age-structured models are widely used in fisheries stock assessments and contain two very important parameters that determine the rate and amount of harvest that can be safely taken: the compensation rate in juvenile survival (κ) and the unfished biomass (B_o). These two parameters are often confounded. It is common for relative abundance indices to lack contrast, and the use of informative priors, or fixing at least one of these parameters, is necessary to develop management advice. Providing management advice proceeds by transforming estimates of biological variables such as B_o and κ into management variables such as the maximum sustainable yield (C^*) and the fishing mortality rate that would achieve this yield (F^*). There is no analytical solution for the transformation of B_o, κ to C^*, or F^* for age-structured models with commonly used stock–recruitment functions and therefore must be done numerically. The opposite transition, however, does have an analytical solution for both the Beverton–Holt and Ricker recruitment models with partial selectivities for all age classes. Use of these analytical solutions allows for age-structured assessment models to be directly parameterized in terms of the management variables C^* and F^*. The effects of informative priors on C^* and F^* on the results of the assessment model are completely transparent to management.

Résumé : Les modèles structurés en fonction de l'âge, qui sont couramment utilisés dans l'évaluation des stocks en pêches commerciales, contiennent deux variables très importantes qui déterminent le taux et l'importance de la récolte qui peut être réalisée sans danger, soit le taux de compensation dans la survie des jeunes (κ) et la biomasse non exploitée (B_o). Ces deux variables sont souvent confondues. Il arrive fréquemment que les coefficients d'abondance relative ne fassent pas la distinction et il est nécessaire, afin d'obtenir des avis de gestion, d'utiliser des informations a priori ou de corriger au moins une de ces variables. Pour fournir des avis des gestion, il faut transformer les estimations des variables biologiques, telles que B_o et κ, en variables de gestion, telles que le rendement soutenu maximal (C^*) et le taux de mortalité dû à la pêche qui produit ce rendement (F^*). Il n'existe pas de solution analytique pour la transformation de B_o, κ en C^*, ou F^* dans les modèles structurés en fonction de l'âge avec les fonctions de stock–recrutement en usage courant et il est ainsi nécessaire de le faire numériquement. La transformation inverse, cependant, possède une solution analytique, tant pour le modèle de recrutement Beverton–Holt que pour celui de Ricker, avec des sélectivités partielles pour toutes les classes d'âge. L'utilisation de ces solutions analytiques permet d'obtenir directement les variables de gestion C^* et F^* pour les modèles d'évaluation structurés en fonction de l'âge. Les effets des informations a priori au sujet de C^* et F^* sur les résultats du modèle d'évaluation sont complètement transparents dans une perspective de gestion.

[Traduit par la Rédaction]

Introduction

The overarching objectives of a fisheries stock assessment are threefold: (*i*) to estimate key population parameters that determine the population scale and productivity (e.g., unfished biomass, B_o, and the Goodyear compensation ratio (Goodyear 1980), here defined as κ, or the relative improvement in juvenile survival rate as the spawning stock biomass approaches zero); (*ii*) to estimate the current state of the population relative to a predefined reference point (usually B_o); and (*iii*) to provide short-term projections of the population state subject to alternative harvest policies or the application of a predefined harvest rule (i.e., management advice). The stock assessment process has evolved to also characterize the uncertainty in the management advice primarily through the use of Bayesian approaches (Punt and Hilborn 1997). It is obvious (but sometimes forgotten) that the process of proceeding through steps *i–iii* and ultimately providing sound management advice based on this process is conditional on the information in the available data. In steps *i* and *ii*, population dynamics models are often fitted to time series data on relative abundance (i.e., catch-per-unit-effort (CPUE) indices), and the ability to discern between a large, unproductive stock and a small, productive stock requires sufficient contrast in the abundance index (see Hilborn and Walters 1992). Step *iii* involves a transformation of population parameters calculated in the previous steps (e.g., B_o and the intrinsic rate of growth) into management parameters (e.g., target fishing rate (F^*) and maximum sustainable yield (MSY) (C^*)) and short-term projections of abundance.

Ricker (1975) first demonstrated that there was no analytical solution to transform population parameters to manage-

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ment parameters for relatively simple nonlinear models (e.g., Ricker stock–recruitment model). Schnute and Kronlund (1996) demonstrated that the opposite transition was possible, and later, Schnute and Richards (1998) extended this approach to age-structured models. The approach of Schnute and Richards (1998) assumed knife-edge recruitment and discrete mortality and, based on these assumptions, demonstrated that this inverse approach improved the statistical properties of characterizing uncertainty. This improvement in assessing uncertainty enhances communication between assessment scientist and resource managers because the parameters being evaluated by the assessment process are directly relevant to policy. Despite these statistical and communicative advantages, to our knowledge there has been no application of this approach in stock assessments.

A common situation in stock assessments is that the relative abundance data lack sufficient contrast that permit the joint estimation of productivity and population-scale parameters. Many of the data sets available to conduct stock assessments consists of one-way trips (persistent decline or increase in relative abundance) or no long-term trend information in relative abundance indices. In such circumstances, a common practice is to use prior information on productivity parameters or derive independent estimates for the constant that relates relative abundance to absolute abundance, or both. The reality of such a practice is that the policy parameter(s), such as the C^* or the F^* that achieves C^*, or both, are defined prior to fitting the models to time series data. There actually is some information about C^* in one-way trip data sets. Consider the simple Schaefer production model where MSY is defined as $C^* = rK/4$, where r is the intrinsic rate of growth and K is the carrying capacity. For one-way trip data sets, it is well known that r and K are not estimable (Hilborn and Walters 1992), but C^* may be well determined, as r and K are inversely correlated, and the estimate for C^* would be relatively stable as r and K trade off. However, if the relative abundance data show no trend over time, it becomes absolutely necessary to develop informative priors for population-scale parameters.

The principal difference between the simpler Schaefer model and the more complex age-structured model is that the relationship between productivity and F^* or bewteen B_o and C^* is not so transparent in complex, age-structured models. As such, the use of informative priors, or fixed values for scaling parameters, or stock productivity ultimately defines harvest policy in cases where relative abundance data are not informative about these key population parameters. A more transparent approach to this problem is to adopt the management-oriented approach, as first suggested by Schnute and Kronlund (1996), and parameterize age-structured models in terms of F^* and C^* directly. Under this parameterization, the sensitivity of policy parameters to prior distributions or fixed values is completely transparent in the decision-making process.

The main objective of this paper is to change the standard question of how likely are the B_o and κ parameters given the data to how likely are the C^* and F^* hypotheses given the data? Parameters such as B_o and κ ultimately define the harvest policies, yet it is easy to loose sight of this notion when the assessment model contains hundreds of additional parameters to explain, for example, variability in recruit-

ment, temporal changes in selectivity, catchability, and variability in growth. Using fixed values for these key population parameters can be easily overlooked when reviewers are forced to consider model sensitivity with respect to hundreds of nuisance parameters. Using fixed values for κ is equivalent to assuming fixed values for F^* (assuming some constant selectivity), and using fixed values for B_o or parameters that define the overall population scale is equivalent to assuming the overall population scale a priori.

In this paper, we derive analytical relationships between the policy parameters C^* and F^* and parameters that describe the instantaneous dynamics of an age-structured population. The method also allows for partial selectivity of specific age classes, including dome-shaped selectivity curves. We adopt a similar notation of Schnute and Kronlund (1996) and Schnute and Richards (1998) for comparison. All of the models presented here assume that fishing mortality and natural mortality occur simultaneously through the use of the Baranov catch equation. First, we first review the classical numerical transitions between $(B_o, \kappa) \Rightarrow (C^*, F^*)$ in a full age-structure model with Beverton–Holt-type recruitment. Second, we parameterize a full age-structured model using (C^*, F^*) as leading parameters and derive (B_o, κ) from (C^*, F^*) conditional on vulnerability and life-history parameters. We then derive the analytical solution for the $(C^*, F^*) \Rightarrow (B_o, \kappa)$ transition using the Ricker model. Finally, we apply the approach developed here to the Pacfic hake (*Merluccius productus*) data using the Beverton–Holt recruitment model and compare the uncertainty in parameter estimates with that of Helser and Martell (2007).

Age-structured model (B_o, κ)

To derive (C^*, F^*) from the unknown parameter vector Θ and independently derived life-history parameters Φ (defined in Table 1) in an age-structured population dynamics model, we first consider the steady-state conditions for a given fishing mortality rate F_e in an age-structured model (Table 1). In this paper, we assume that life-history parameters Φ are known; however, it is also possible to jointly estimate these parameters if necessary data are available. Note that the sequence of equations laid out in each of the tables describes the model structure and is also intended to represent the order of operations or pseudocode in which to implement the model in a given computer language. Source code for implementations in AD Model Builder (Otter Research Ltd., Sidney, British Columbia) and R (R Development Core Team 2006) are available from the first author upon request.

For the model represented in Table 1, we assume that growth (eqs. T1.4 and T1.5) is independent of density, vulnerability-at-age (eq. T1.6) is represented by a logistic curve, and fecundity-at-age (eq. T1.7) is proportional to body weight times the probability of being sexually mature at a given age. Assuming steady-state conditions, the lifetime reproductive output per individual recruit in an unfished population (unfished eggs per recruit) is simply the product of survivorship (eq. T1.8) and the mean fecundity-at-age; the sum of these products is the unfished eggs per recruit (eq. T1.10). These are also known as incidence functions, after Botsford and Wickham (1979) (see also Botsford

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Table 1. Steady-state, age-structured model assuming unequal vulnerability-at-age, age-specific natural mortality, age-specific fecundity, and Beverton–Holt-type recruitment.

Eq. No.	Model definitions
Parameters	
T1.1	$\Theta = (B_o, \kappa, M_a, \widehat{a}, \widehat{\gamma})$
T1.2	$B_o > 0;\ \kappa > 1;\ M_a > 0$
T1.3	$\Phi = (l_\infty, k, t_o, a, b, \dot{a}, \dot{\gamma})$
Age schedule information	
T1.4	$l_a = l_\infty \{1 - \exp[-k(a - t_o)]\}$
T1.5	$w_a = a(l_a)^b$
T1.6	$v_a = \{1 + \exp[-(\widehat{a} - a)/\gamma]\}^{-1}$
T1.7	$f_a = w_a\{1 + \exp[-(\dot{a} - a)/\dot{\gamma}]\}^{-1}$
Survivorship	
T1.8	$\iota_a = \begin{cases} 1, & a = 1 \\ \iota_{a-1}\exp(-M_{a-1}), & a > 1 \end{cases}$
T1.9	$\widehat{\iota}_a = \begin{cases} 1, & a = 1 \\ \widehat{\iota}_{a-1}\exp(-M_{a-1} - F_e v_{a-1}), & a > 1 \end{cases}$
Incidence functions	
T1.10	$\phi_E = \sum_{a=1}^{\infty} \iota_a f_a, \qquad \phi_e = \sum_{a=1}^{\infty} \widehat{\iota}_a f_a$
T1.11	$\phi_B = \sum_{a=1}^{\infty} \iota_a w_a v_a, \qquad \phi_b = \sum_{a=1}^{\infty} \widehat{\iota}_a w_a v_a$
T1.12	$\phi_q = \sum_{a=1}^{\infty} \dfrac{\widehat{\iota}_a w_a v_a}{M_a + F_e v_a}[1 - \exp(-M_a - F_e v_a)]$
Steady-state conditions	
T1.13	$R_o = B_o/\phi_B$
T1.14	$R_e = R_o\dfrac{\kappa - \phi_E/\phi_e}{\kappa - 1}$
T1.15	$C_e = F_e R_e \phi_q$

Note: To implement the Ricker type recruitment, substitute eq. T1.13 with eq. 6.

Fig. 1. (*a*) Equilibrium yield, (*b*) recruits, (*c*) biomass, and (*d*) spawner per recruit (ϕ_e/ϕ_E) versus instantaneous fishing mortality (F_e) for two different values of the recruitment compensation ratio ($\kappa = 12$, solid lines; $\kappa = 4$, broken lines). Vertical lines in each panel correspond to F^*; horizontal lines correspond to various reference points that would achieve C^*.

1981; Walters and Martell 2004), and we reserve the prefix ϕ to represent per-recruit incidence functions and use upper- and lower-case subscripts to denote unfished and fished conditions, respectively. The biomass per recruit is given by eq. T1.11, and eq. T1.11 subscript b is the yield per-recruit incidence function where both natural mortality and fishing mortality are assumed to occur simultaneously (note that $F_e\phi_q$ represents the yield per recruit). The unfished equilibrium age-1 recruits is given by eq. T1.12. In eq. T1.13, we assume that recruitment follows a Beverton–Holt-type relationship of the form
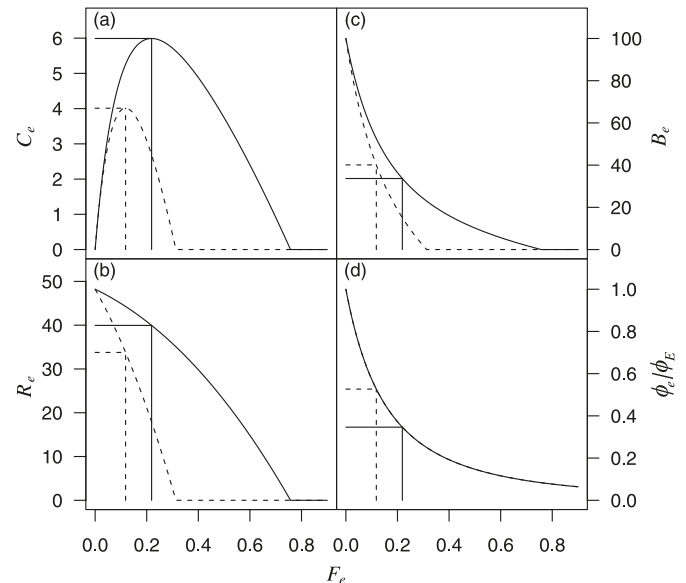
$$(1) \qquad R_e = \frac{s_o E_e}{1 + \beta E_e} = \frac{s_o R_e \phi_e}{1 + \beta R_e \phi_e}$$

where s_o is the maximum survival rate from egg E to age-1 recruit R, which can also be represented as $s_o = \kappa/\phi_E$. β is the density-dependent term defined as $\beta = (\kappa - 1)/(R_o\phi_E)$ in the unfished state. Substituting these expressions for s_o and β into eq. 1 yields

$$R_e = \frac{\kappa R_e \phi_e R_o}{R_o\phi_E + R_e\phi_e\kappa - R_e\phi_e}$$

and solving for R_e gives eq. T1.13. The overall yield C_e for a steady-state fishing mortality rate F_e is given by eq. T1.14.

There are two commonly used parameterizations of stock–recruitment models in use today. One is the so-called steepness parameterization, where steepness (h) is defined as the ratio of recruits produced at 20% of the unfished spawning stock biomass and the unfished spawning stock biomass (Mace and Doonan 1988). For the Beverton–Holt model, the values of h range between 0.2 and 1; for the Ricker model, values of h are >0.2. The second parameterization uses κ, which is defined as the relative improvement in survival from egg to recruit as the spawning stock biomass tends towards zero (Goodyear 1980). For both the Ricker and Beverton–Holt models, values of κ must be >1. There are simple analytical transformations to go from $\kappa \Leftrightarrow h$, and we derive these in Appendix B.

$(B_o, \kappa) \Rightarrow (C^*, F^*)$ transition

To determine (C^*, F^*) from (B_o, κ) and associated life-history parameters (eq. T1.3), the simplest approach is to plot C_e versus F_e and find the F_e value that maximizes C_e (e.g., Fig. 1). Furthermore, additional equilibrium values for recruitment (eq. T1.13), biomass ($B_e = R_e\phi_b$), or the ratio of spawners per recruit (SPR = ϕ_e/ϕ_E) versus F_e can be calculated and used to determine the ratios of fished states to unfished states that approximate a C^* fishing policy (Figs. 1*b*, 1*c*, 1*d*, respectively).

The exercise of plotting equilibrium yield versus fishing mortality rates to determine the optimal values for (C^*, F^*) is rarely performed in annual stock assessments. Instead, simple reference points such as B_{40} or SPR_{35} are used to approximate C^* and F^*. It is often assumed that these reference points are insensitive to the estimates of recruitment compensation. While SPR is a strict function of life-history

Table 2. Partial derivatives, based on components in Table 1, required for the numerical calculation of F^* and C^* using eq. 3.

Eq. No.	Partial derivatives
Mortality and survival	
T2.1	$Z_a = M_a + F_e v_a$
T2.2	$S_a = 1 - \exp(-Z_a)$
Survivorship	
T2.3	$\dfrac{\partial \widehat{\iota}_a}{\partial F_e} =$ $\begin{cases} 0, & a = 1 \\ \exp(-Z_{a-1})\left(\dfrac{\partial \widehat{\iota}_{a-1}}{\partial F_e} - \widehat{\iota}_{a-1} v_{a-1}{}^{a-1}\right), & a > 1 \end{cases}$
Incidence functions	
T2.4	$\dfrac{\partial \phi_q}{\partial F_e} = \displaystyle\sum_{a=1}^{\infty} f_a \dfrac{\partial \widehat{\iota}_a}{\partial F_e}$
T2.5	$\dfrac{\partial \phi_q}{\partial F_e} = \displaystyle\sum_{a=1}^{\infty} \dfrac{w_a v_a S_a}{Z_a}\dfrac{\partial \widehat{\iota}_a}{\partial F_e} + \dfrac{\widehat{\iota}_a w_a v_a^2}{Z_a}\left[\exp(-Z_a) - \dfrac{S_a}{Z_a}\right]$
Recruitment	
T2.6	$\dfrac{\partial R_e}{\partial F_e} = \dfrac{R_o}{\kappa - 1}\dfrac{\phi_E}{\phi_e^2}\dfrac{\partial \phi_e}{\partial F_e}$

parameters (independent of κ), the SPR level associated with MSY is sensitive to values of κ (Fig. 1*d*). As κ decreases, the corresponding SPR level that maximizes long-term yield increases. The SPR reference point is also sensitive to the age at first capture relative to the age at first maturity (Beddington and Kirkwood 2005).

It can be computationally difficult to evaluate the uncertainty in (C^*, F^*) because there is no analytical solution for the (B_o, κ) $\Rightarrow$ (C^*, F^*) transition. In cases where the uncertainty in (C^*, F^*) must be addressed, exact values for (C^*, F^*) can be obtained using numerical approaches (e.g., Newton–Raphson method). The optimal fishing mortality rate (F^*) corresponds to the zero derivative of eq. T1.14. This value can then be substituted back into eqs. T1.9, T1.10, T1.12, T1.14, and T1.15 to obtain C^*. Using the chain rule, the derivative of eq. T1.15 is given by

$$(2) \qquad \frac{\partial C_e}{\partial F_e} = R_e \phi_q + F_e \phi_q \frac{\partial R_e}{\partial F_e} + F_e R_e \frac{\partial \phi_q}{\partial F_e}$$

Using the Newton–Raphson method, F^* can be obtained numerically using

$$(3) \qquad F_{e+1} = F_e - \frac{R_e \phi_q + F_e \phi_q \frac{\partial R_e}{\partial F_e} + F_e R_e \frac{\partial \phi_q}{\partial F_e}}{\phi_q \frac{\partial R_e}{\partial F_e} + R_e \frac{\partial \phi_q}{\partial F_e}}$$

Analytical solutions for the partial derivatives in eqs. 2 and 3 are given in Table 2. Note that the use of eq. 3 requires an initial estimate of F_e and then an iterative approach must be used such that F_{e+1} converges to F_e. Equation 3 converges fairly quickly (approximately 10 to

15 iterations) and can be used to efficiently compute values of F^* and C^* from posterior samples of Θ.

Age-structured model (C^*, F^*)

In this section, our aim is to parameterize a full age-structured model in terms of (C^*, F^*), where C^* is roughly proportional to population scale (B_o), and F^* is a function of productivity (κ). In other words, rather than searching over values of B_o and κ when fitting models to time series data and then determining values of C^* and F^* after fitting, we parameterize the models directly in terms of C^* and F^* and then derive the values of B_o and κ that would be necessary to support (C^*, F^*) hypotheses, conditional on life-history parameters (Φ) and other model parameters in the vector Θ.

Assuming the same model structure outlined in Table 1, the first step in the (C^*, F^*) $\Rightarrow$ (B_o, κ) transition is to differentiate eq. T1.14 with respect to F_e, set the resulting equation equal to zero, and solve for κ. The end result of this transformation is given by the following (see Appendix A1 for derivation):

$$(4) \qquad \kappa = \frac{\phi_E}{\phi_e} - \frac{F^* \phi_q \frac{\phi_E}{\phi_e^2}\frac{\partial \phi_e}{\partial F_e}}{\phi_q + F^* \frac{\partial \phi_q}{\partial F_e}}$$

where the analytical solutions for the partial derivatives are specified in Table 2. To derive B_o from (C^*, F^*, κ), use

$$(5) \qquad B_o = \frac{C^* \phi_B (\kappa - 1)}{F^* \phi_q (\kappa - \phi_E / \phi_e)}$$

where ϕ_e and ϕ_q are evaluated at F^*. The results from eqs. 4 and 5 can then be substituted back into eq. T1.1 to be used in a standard age-structured model that is parameterized using B_o and κ as leading parameters.

There is constraint in the (C^*, F^*) $\Rightarrow$ (B_o, κ) transition in cases where the selectivity schedules are high for younger animals or growth overfishing. In such cases, F^* is independent of κ and much lower than the F that would maximize the yield per recruit. As the age at first capture decreases, the maximum sustainable fishing mortality rate decreases and recruitment compensation approaches infinity (for more details, see Forrest et al. 2008). In such cases, estimates of κ in eq. 4 will be negative; therefore, it is necessary to constrain κ to be greater than 1.0 when using nonlinear search procedures to estimate C^* and F^*.

Ricker formulation

To implement a Ricker-type stock–recruitment model of the form

$$R_e = s_o R_e \phi_e \exp(-\beta R_e \phi_e)$$

which can be rewritten in terms of R_o and κ as

$$(6) \qquad R_e = R_o \left[\frac{\ln(\kappa) - \ln(\phi_E / \phi_e)}{\ln(\kappa)}\right]$$

substitute eq. 6 into eq. T1.14 and proceed by differentiating this expression with respect to F_e, setting the resulting derivative equal to zero, and solving the expression for κ. For

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Table 3. Combined United States and Canadian landings (C_t; in 1000 tonnes) and relative abundance indices (I_t) from a fisheries-independent acoustic survey for Pacific hake (*Merluccius productus*) in the northeastern Pacific.

Year	C_t	I_t
1966	137.700	
1967	214.375	
1968	122.180	
1969	180.131	
1970	234.584	
1971	154.612	
1972	117.546	
1973	162.639	
1974	211.259	
1975	221.360	
1976	237.521	
1977	132.693	1.915
1978	103.639	
1979	137.115	
1980	89.936	2.115
1981	139.121	
1982	107.734	
1983	113.924	1.647
1984	138.441	
1985	110.401	
1986	210.617	2.857
1987	234.147	
1988	248.804	
1989	305.916	1.238
1990	259.792	
1991	307.258	
1992	296.910	2.169
1993	199.435	
1994	361.529	
1995	249.770	1.385
1996	306.075	
1997	325.215	
1998	320.619	1.185
1999	311.855	
2000	230.820	
2001	235.962	0.737
2002	182.911	
2003	205.582	1.840
2004	334.672	
2005	349.571	1.265
2006	347.270	

Fig. 2. Combined proportions-at-age in the United States and Canadian commercial fisheries for Pacific hake (*Merluccius productus*). The solid line represents the mean age of the landed catch, and each circle is proportional to the proportion-at-age landed in a given year. The vertical broken line indicates the year that age composition data were available from the Canadian fishery.
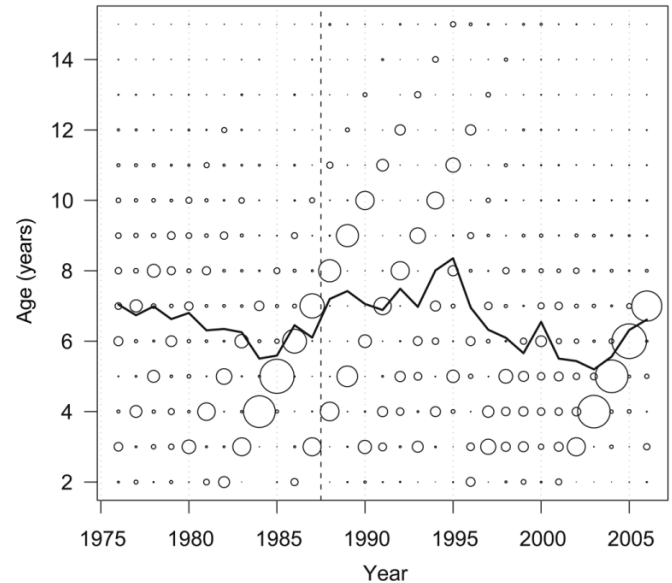
wise, all other partial derivatives defined in Table 2 are the same. Note also that ϕ_e and ϕ_q in eq. 7 are evaluated at F^*.

The unfished equilibrium biomass given (C^*, F^*, κ) is given by

$$(8) \qquad B_o = -\frac{\ln(\kappa)\phi_B\phi_e C^*}{\ln\left(\frac{\phi_E}{\kappa\phi_e}\right)\phi_q\phi_E F^*}$$

where ϕ_e and ϕ_q are evaluated at F^*.

Application to the Pacific hake stock

The Pacific hake (hereafter, hake) stock assessment is not atypical of many other assessments for groundfish species on the west coast of North America. Many of the groundfish species are assessed using age-structured models. Hake in this region undergo seasonal migrations, moving northward in the summer months into Canadian waters and moving southward in the winter months to spawn off the coast of Baja California and southern California. Hake are harvested by both United States (US) and Canadian (CAN) fishing fleets, and the composition of the CAN landings tends to contain larger and older individuals. The official stock assessment for hake assumes a single unit stock, but treats US and CAN fisheries separately to capture the interannual variation in migration of hake along the west coast of North America (Helser et al. 2006).

For the purposes of demonstration, we have greatly simplified the data and age-structured model in this application in comparison with the annual assessment that is conducted each year using Stock Synthesis II (Helser et al. 2006). A summary of the historical removals by US and CAN fisheries combined, as well as relative abundance indices for hake, are provided (Table 3). Aggregate age composition in-

the Ricker model, the recruitment compensation parameter κ can then be expressed as a function of F^* using

$$(7) \qquad \kappa = \frac{\phi_E}{\phi_e} \exp\left[-\frac{F^*\phi_q \frac{\partial \phi_e}{\partial F_e}}{\phi_q\phi_e + F^*\left(\phi_e \frac{\partial \phi_q}{\partial F_e} - \phi_q \frac{\partial \phi_e}{\partial F_e}\right)}\right]$$

Note to carry out the necessary algebra to derive eq. 7, the partial derivative of eq. 6 with respect to F^* must be substituted for eq. T2.6 in Table 2 (see Appendix A); other-

Table 4. Statistical catch-at-age model using the Baranov catch equation and C^* and F^* as leading parameters.

Eq. No.	Model definitions
Data	
T4.1	$C_t = C_t^{US} + C_t^{CAN}$
T4.2	$I_t, A_{t,a}, l_a, w_a, f_a$
Parameters	
T4.3	$\Theta = (C^*, F^*, M_a, \widehat{a}, \widehat{\gamma}, \{\omega_t\}_{t=1}^{T-1}, \rho, \vartheta^2)$
T4.4	$\sigma^2 = \rho\vartheta^2, \qquad \tau^2 = (1-\rho)\vartheta^2$
T4.5	$\vartheta^2 = \sigma^2 + \tau^2, \qquad \rho = \dfrac{\sigma^2}{\sigma^2 + \tau^2}$
Unobserved states	
T4.6	$\mathbf{N}_{t,a}, B_t, E_t, F_t$
Initial states ($t = 1$)	
T4.7	$v_a = \{1 + \exp[-(\widehat{a} - a)/\widehat{\gamma}]\}^{-1}$
T4.8	$\mathbf{N}_{t,a} = \dfrac{B_o}{\phi_B} \exp(-M)^{(a-1)}$
State dynamics ($t > 1$)	
T4.9	$E_t = \sum_a \mathbf{N}_{t,a} f_a$
T4.10	$Z_{a,t} = M_a + F_t v_a$
T4.11	$\widehat{C}_t = \sum_a \dfrac{\mathbf{N}_{t,a} w_a F_t v_a [1 - \exp(-Z_{t,a})]}{Z_{t,a}}$
T4.12	$F_{t_{i+1}} = F_{t_i} - \dfrac{\widehat{C}_t - C_t}{\widehat{C}_t'}$
T4.13	$\mathbf{N}_{t,a} = \begin{cases} \dfrac{s_o E_{t-1}}{1 + \beta E_{t-1}} \exp(\omega_t - 0.5\tau^2), & a = 1 \\ N_{t-1,a-1} \exp(-Z_{t-1,a-1}), & a > 1 \end{cases}$
T4.14	$B_t = \sum_a \mathbf{N}_{t,a} w_a v_a$
Residuals and predicted observations	
T4.15	$\varepsilon_t = \ln\left(\dfrac{I_t}{B_t}\right) - \dfrac{1}{n}\sum_{t \in I_t} \ln\left(\dfrac{I_t}{B_t}\right)$
T4.16	$\widehat{A}_{t,a} = \dfrac{\mathbf{N}_{t,a} \dfrac{F_t v_a}{Z_{t,a}}[1 - \exp(-Z_{t,a})]}{\sum_a \mathbf{N}_{t,a} \dfrac{F_t v_a}{Z_{t,a}}[1 - \exp(-Z_{t,a})]}$

Table 5. Assumed life-history parameters for Pacific hake (*Merluccius productus*).

Parameter	Value
Growth	
l_∞	55
k	0.25
t_o	−0.25
L or W	
a	6.54×10^{-6}
b	2.987
Maturity	
$\dot{a}$	2.65
$\dot{\gamma}$	0.05

Note: Length (*L*) is measured in centimetres; weight (*W*) is measured in in kilograms.

estimation of B_o, κ (or steepness as defined in Helser et al. 2006), and the scaling parameter q that relates the survey abundance to absolute abundance. To proceed with the stock assessment and provide management advice, κ and q have been fixed and only B_o is assumed unknown and estimated from the data. By fixing values of κ and q, the true uncertainty in B_o is underestimated and uncertainty surrounding subsequent management advice (e.g., estimates of MSY) is also underestimated.

The relative abundance indices for hake (I_t) are derived from fisheries-independent acoustic surveys that have been conducted every 2–3 years since 1977. Unfortunately, there is little informative contrast in this abundance index, and a few of the survey points have been heavily downweighted in the official stock assessment because of known problems with the historical surveys. In particular, the 1986 survey has been heavily discounted because of substantive differences in biomass estimates based on presurvey and postsurvey calibrations of the acoustic gear. Including the 1986 survey improves the overall contrast in the data series. In Helser and Martell (2007), each survey year is assigned a specific coefficient of variation (CV is set to 0.29 for surveys after 1992 and 0.5 for surveys prior to 1992). In this assessment, we treat all of the relative abundance indices with equal weight and estimate the CV in the surveys.

Age-structured model

The system of equations used in this age-structured model are provided in Table 4. The data consist of combined observed catches eq. T4.1, relative to abundance indices (I_t) assumed to be proportional to the vulnerable biomass seen by the commercial fisheries. Commercial landings and relative abundance indices between 1966 and 2006 are provided (Table 3). Observations on the age proportions landed in both the US and CAN fishery are denoted as $A_{t,a}$ in T4.2. Information on length-at-age, weight-at-age, and fecundity-at-age can be obtained from eqs. T1.4, T1.5, and T1.7, respectively, using the assumed life-history parameters specified in Table 5.

formation from the US and CAN fisheries are summarized in the form of bubble plots (Fig. 2). Age composition information from the CAN fishery are only available back to 1988. To construct the aggregated age composition matrix, we used a weighted average of the proportions-at-age landed in each fishery, where the weights are the proportion of the catch landed in each zone. Between 1984 and 1995, the catches were dominated by the 1980 and 1984 year classes, and in recent years, the 1999 year class has been dominant (Fig. 2). These exceptionally strong year classes have made it difficult to determine the underlying stock–recruitment relationship for hake.

Helser et al. (2006) noted that there is insufficient contrast in the relative abundance indices (I_t) that allow for the joint

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Table 6. Likelihoods and priors used in the statistical estimation of Θ from Table 4.

Eq. No.	Likelihoods and priors
Negative log-likelihoods	
T6.1	$\ell(\Theta)_1 = \sum_{t=1}^{T-1}\left[\ln(\tau) + \dfrac{\omega_t^2}{2\tau^2}\right]$
T6.2	$\ell(\Theta)_2 = \sum_{t \in I_t}\left[\ln(\sigma) + \dfrac{\varepsilon_t^2}{2\sigma^2}\right]$
T6.3	$\ell(\Theta)_3 = \sum_{t \in A_{t,a}}\sum_{a=2}^{A}\left(\ln(\varsigma) + \ln\left\{\exp\left[\dfrac{-(P_{t,a})^2}{2\varsigma^2}\right]\right\} + 0.01\right)$
	where $\varsigma = [\widehat{A}_{t,a}(1 - \widehat{A}_{t,a}) + 0.1/A]n$
	and $P_{t,a} = (A_{t,a} - \widehat{A}_{t,a})$
T6.4	$\ell(\Theta) = \sum_{i=1}^{3}\ell_i$
Prior distributions	
T6.5	$p(C^*) \sim \text{lognormal}(\mu = -0.8787, \sigma = 0.3960)$
T6.6	$p(F^*) \sim \text{lognormal}(\mu = -1.378, \sigma = 0.4697)$
T6.7	$p(M) \sim \text{lognormal}(\mu = -1.585, \sigma = 0.2435)$
T6.8	$p(\widehat{a}) \sim U(0, 14)$
T6.9	$p(\widehat{\gamma}) \sim U(0, 2)$
T6.10	$p(\rho) \sim \text{beta}(\alpha = 1.648, \beta = 10.1306)$
T6.11	$p(\vartheta^2) \sim \text{inverse gamma}(\alpha = 10.829, \beta = 13.368)$
Constraints	
T6.12	$\kappa > 1.0$
Posterior distribution	
T6.13	$P(\Theta) \propto \exp[-\ell(\Theta)]p(C^*)p(F^*)p(M)p(\rho)p(\vartheta^2)$

Estimated parameters denoted as Θ (eq. T4.3) include the C^* and F^* that achieves C^*. Here, we assume that the instantaneous natural mortality rate M is constant and age independent. Parameters for the vulnerability-at-age function are defined as the age and standard-deviation-at-age in which 50% of the fish are vulnerable to harvest ($\widehat{a}$, $\widehat{\gamma}$, respectively). Lognormal deviations from the mean stock–recruitment relationship are represented by ω_t. We assume that the total error ϑ is unknown and use variance-partitioning methods (see Schnute and Kronlund 2002; Deriso et al. 2007) to partition the observation and process errors using the ratio defined in eqs. T4.4 and T4.5. Note that the total variance in this mixed error model is estimable (Deriso et al. 2007), but the components of observation and process errors are not separable.

The unobserved states consists of a matrix of numbers-at-age ($N_{t,a}$), biomass that is vulnerable to harvest (B_t), annual egg production (E_t), and the instantaneous fishing mortality rate (F_e). The model is initialized by first calculating the vulnerabilities-at-age eq. T4.7, then computing κ and B_o using eqs. 4 and 5, respectively, for the Beverton–Holt model (or eqs. 7 and 8, respectively, for the Ricker model), then using eq. T4.8 to initialize the numbers-at-age in the population for $t = 1$ (note that $t = 1$ implies 1966 as the starting year).

In each year, state variables are updated using eqs. T4.9–T4.14. Note that the model is conditioned on the observed catch (C_t), and the analytical value of the instantaneous fishing mortality rate (F_t) is computed using Newton's method. The algorithm is initialized by setting $F_{t_1} = C_t/B_t$, then using Newton's method to update $F_{t_{i+1}}$ until the difference between the predicted catch and observed catch is minimal. The derivative of the catch equation ($\widehat{C}_t'$) is given by

$$\widehat{C}_t' = \sum_a \frac{N_a w_a v_a[1 - \exp(-M - F_t v_a)]}{M + F_t v_a}$$
$$- \frac{N_a w_a F_t v_a^2[1 - \exp(-M - F_t v_a)]}{(M + F_t v_a)^2}$$
$$+ \frac{N_a w_a F_t v_a^2 \exp(-M - F_t v_a)}{M + F_t v_a}$$

This algorithm converges rather quickly (5–7 iterations); however, we allow for a maximum of 30 iterations to occur and assess whether convergence was achieved by comparing the predicted and observed catches.

The final step in the age-structured model is computing the residuals between the relative abundance indices and the predicted catch-at-age proportions to be used in the negative log-likelihoods during parameter estimation or numerical integration of the posterior distribution. Here, we assume that the observation errors in the relative abundance index are lognormally distributed and are proportional to the vulnerable biomass defined by eq. T4.14. The residuals for the relative abundance indices are given by eq. T4.15, where the conditional maximum likelihood estimate for the scale parameter

Fig. 3. Three alternative prior densities for F^*. The lower 10th percentile is equal to $0.6M = 0.132$ for all three models, and the 90th percentiles correspond to $2M$, $1.6M$, and $1.2M$ for runs A (solid line), B (broken line), and C (dotted line), respectively.
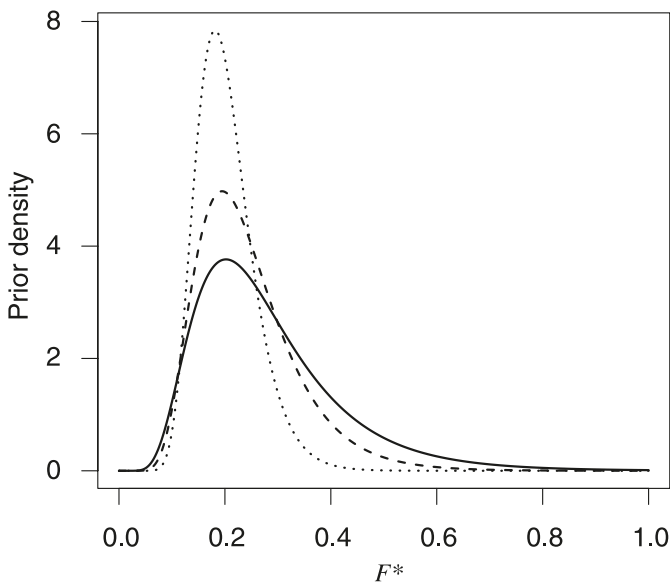
($\ln(q)$) is used (see Walters and Ludwig 1994). The predicted proportions-at-age for each year is the ratio of catch in numbers-at-age divided by the total catch in numbers (eq. T4.16).

Likelihoods and prior distributions

Parameter estimation was carried out using AD Model Builder (Otter Research Ltd., Sydney, British Columbia). Recruitment deviations (ω_t) were assumed to be lognormally distributed, with an unknown variance to be estimated from the data, and the negative log-likelihood of the recruitment deviations is given by eq. T6.1. The ω_t parameters represent the process error component in this model. Observation errors in the relative abundance index (I_t) were also assumed to be lognormally distributed with an unknown and assumed constant variance. The negative log-likelihood of the acoustic survey is given by eq. T6.2 (Table 6).

Hake are a schooling species, and individuals in each school are nearly uniform in size. Therefore, it was necessary to down-weight the age composition information because age composition samples are likely to be biased owing to the tendency for the fishery to target specific age–size classes (Fournier and Archibald 1982). We use a robust normal approximation to the mulitnomial likelihood (see Fournier et al. 1990 for details) for the proportion-at-age data, with an effective sample size of $n = 50$ in eq. T6.3 for all years of available catch-at-age data. The effective sample size for the age composition data was determined through an iterative process whereby a comparison between the root mean squared error for ω_t and ε_t was compared with the estimates of τ and σ. The sample size was then adjusted such that the root mean squared errors were approximately equal to the standard deviations in the observation errors and process errors.

Informative, lognormal prior distributions were used for C^*, F^*, and M where the log means and log standard deviations are defined by eqs. T6.5–T6.7 (Table 6). To derive the

means and standard deviations for the lognormal prior distribution, we choose arbitrary 10th and 90th percentiles for each parameter and fit a lognormal distribution to these values. Since 1966, the combined landings for the US and CAN fisheries has averaged 216 867 t, and since 1996, it has averaged 286 427 t. Recent estimates of C^* from Helser et al. (2006) are 639 900 t with a 95th confidence interval of (582 000 – 690 000 t). The prior for C^* was constructed by setting the 10th and 90th percentiles equal to [0.25, 0.69], representing 250 000 and 690 000 t, respectively. The prior for F^* was constructed assuming [0.138, 0.46] for the 10th and 90th percentiles, which is roughly $0.6M$ to $2M$ for hake (assuming $M = 0.23$). Bounded uniform prior distributions were assumed for the selectivity parameters eqs. T6.8 and T6.9. The prior distribution for M was constructed assuming [0.15, 0.28] as the 10th and 90th percentiles.

To examine the influence of the assumed prior distribution for F^* on estimates of C^* and all other model parameters, we also explored two additional prior distributions for F^* (Fig. 3). For the two subsequent runs, we assume the lower 10th percentile for F^* was equal to $0.6M$ and reduced the 90th percentiles to $1.6M$ and $1.2M$, respectively. We denote these are runs A–C, representing three alternative prior distributions where the 90th percentiles for F^* range from $2M$ to $1.2M$.

For the variance parameters ρ and ϑ^2, the beta and inverse gamma distributions were used as priors. The beta distribution and inverse gamma distribution are the conjugate prior distributions for binomial distributions and normal variances, respectively (Gelman et al. 1995). In the Helser and Martell (2007) assessment, variances for error terms were assumed to be known and fixed at 0.29 for the observation error CV and 1.13 for the process error CV. This corresponds to a ratio of 0.2 for observation error to total error (or $\rho = 0.2$ under the eq. T4.5 definition). In deriving the α and β parameters in eq. T6.10 for this assessment, we assume a rather wide distribution for the ρ with a mode equal to 0.0663 and 0.275 for the 90th percentile. The assumed total variance ϑ^2 from Helser et al. (2006) was equal to 1.36 ($\sigma_R = 1.131$, and the CV for the acoustic surveys was assumed at 0.29 for recent years). To derive α and β in eq. T6.11, we assumed an expected value for $\vartheta = 1.36$, and the CV in this estimate was assumed at 0.1.

There are certain combinations of C^* and F^* along with selectivity parameters that lead to severe growth overfishing. Under growth-overfishing conditions, estimates of κ become negative; therefore, it was necessary to constrain κ to be greater than 1 (eq. T6.12). If estimates of $\kappa < 1.01$, a large penalty that was proportional to the difference was added to the objective function such that the objective function remained differentiable with respect to F^*.

Marginal posterior distributions for model parameters were constructed by sampling (eq. T6.13) using a Metropolis–Hastings algorithm. The Metropolis–Hastings algorithm is a Markov chain Monte Carlo (MCMC) method for a randomly walking through parameter (Gelman et al. 1995). A marginal posterior distribution for each parameter or derived variable was constructed from 4000 systematic samples of the joint posterior distribution taken from an MCMC chain of length 500 000, where the first 100 000 iterations were discarded to allow for convergence. Conver-

Fig. 4. Guassian kernel densities of marginal posterior distributions (black lines) and prior distributions (shaded lines) for (*a–g*) model parameters and (*h* and *i*) two derived quantities (B_o and steepness *h*) from model runs A (solid line), B (broken line), and C (dotted line). Posterior densities are based on 4000 systematic samples from a Markov chain Monte Carlo (MCMC) chain of length 500 000, where the first 100 000 are discarded to allow for convergence.
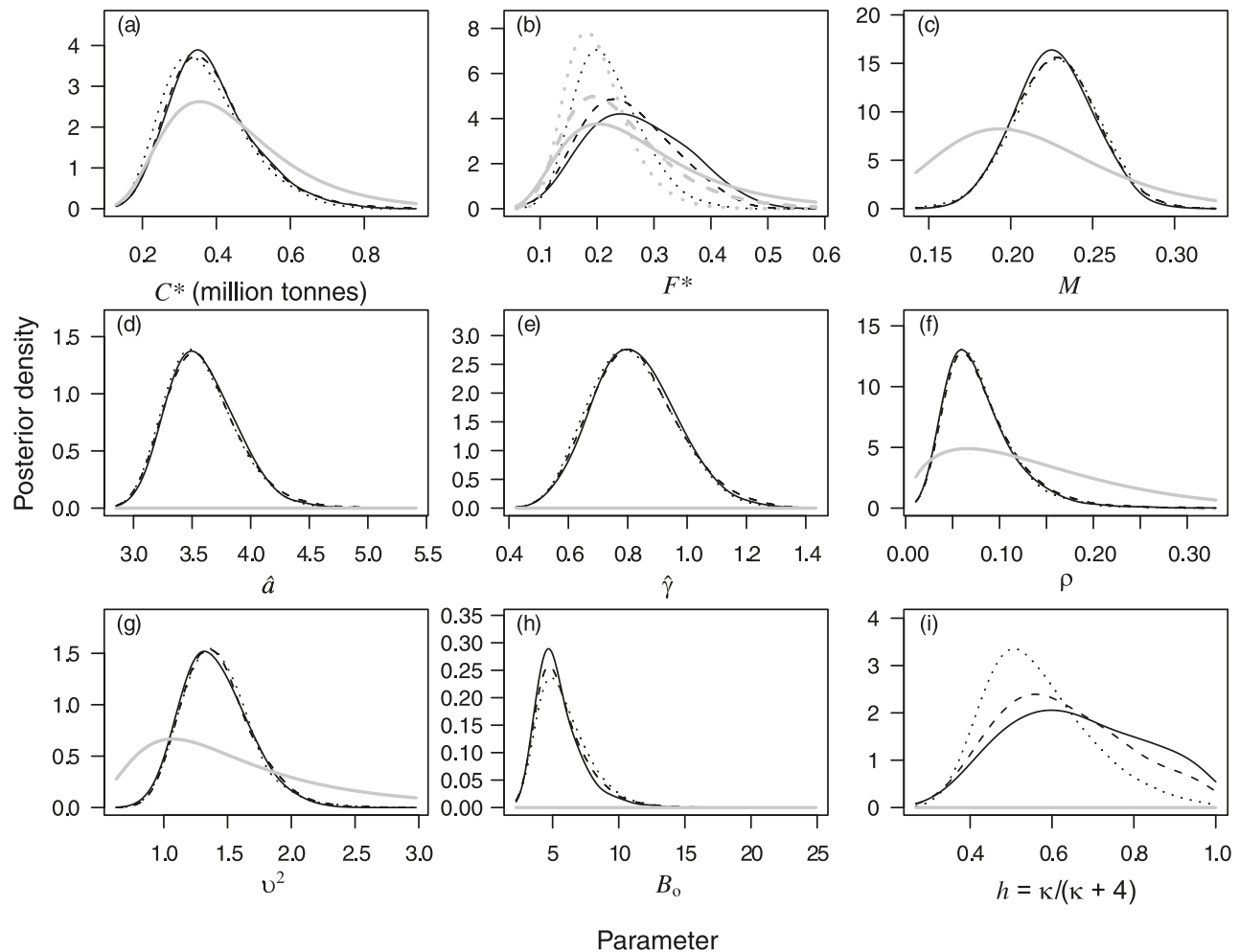
Results

The marginal posterior distributions for all model parameters with the exception of the annual recruitment deviations ω_t for each of the three alternative prior densities assumed for F^* are illustrated (Fig. 4). In addition, the marginal posterior distributions for the derived quantities B_o (Fig. 4*h*) and steepness *h* (Fig. 4*i*) are also presented for comparison with the results in Helser and Martell (2007). Among the three alternative prior densities for F^*, there is very little influence on the overall posterior density for C^* or *M*, which are two key parameters that describe the underlying production relationship. Similar distributions were also obtained for selectivity parameters ($\hat{a}$, $\hat{\gamma}$) and the variance parameters (ρ, ϑ^2) among the three alternative prior densities for F^*. The resulting estimates of the selectivity parameters are insensitive to the assumed prior density on F^* ($\hat{a}$ and $\hat{\gamma}$ are largely determined by the age composition information and are positively correlated with *M* (Table 7)).

The marginal posterior distribution for C^* is influenced

by the assumed prior density for C^* (Fig. 4*a*); we conducted additional runs with a uninformative prior distribution for C^* and note here that the marginal posterior distribution has a slightly larger CV and the mode was slightly less than that shown in Fig. 4*a*. More importantly, however, is that C^* was fairly insensitive to alternative prior distributions on κ, and there is only a very weak positive correlation between C^* and F^* (Table 7).

The prior densities for F^* strongly influence the marginal posterior densities for F^* (Fig. 4*b*); this reflects the absence of information in the relative abundance index to discern between a large unproductive stock and a small productive stock. Moreover, the resulting estimates of recruitment compensation (κ) or steepness (*h*) reflect a wide range of uncertainty (Fig. 4*i*), and the modes of all three distributions are considerably less than the assumed value of *h* = 0.75 in Helser and Martell (2007). Recall that steepness is derived from estimates of F^*, life-history parameters, and the vulnerability schedule. Runs A and B assume a fairly wide prior density for F^*, and high values of F^* imply high values of *h*. However, this is conditional on the age at first capture or the estimated selectivity parameters in the model. As

gence was assessed using the diagnostic tools provided in the coda package in R (R Development Core Team 2006).

Table 7. Correlations among estimated model parameters for model runs A–C.

	C^*	F^*	M	$\widehat{a}$	$\widehat{\gamma}$	ρ	ϑ^2
Run A							
C^*	1						
F^*	0.281	1					
M	0.507	–0.091	1				
$\widehat{a}$	–0.107	0.139	0.411	1			
$\widehat{\gamma}$	–0.155	0.119	0.261	0.888	1		
ρ	–0.084	0.001	–0.021	0.058	0.054	1	
ϑ^2	0.13	–0.047	0.121	0.069	0.066	–0.117	1
Run B							
C^*	1						
F^*	0.235	1					
M	0.51	–0.148	1				
$\widehat{a}$	–0.081	0.162	0.436	1			
$\widehat{\gamma}$	–0.146	0.15	0.283	0.895	1		
ρ	–0.096	0.022	–0.045	0.081	0.084	1	
ϑ^2	0.122	–0.045	0.103	0.03	0.03	–0.13	1
Run C							
C^*	1						
F^*	0.158	1					
M	0.525	–0.19	1				
$\widehat{a}$	–0.138	0.064	0.425	1			
$\widehat{\gamma}$	–0.193	0.077	0.263	0.884	1		
ρ	–0.069	0.025	–0.01	0.078	0.069	1	
ϑ^2	0.128	–0.065	0.106	0.019	0.024	–0.142	1

the selectivity curve shifts towards younger age classes, the resulting estimate of M decreases (i.e., making the stock less productive and larger in scale; see correlations in Table 7), and the standard deviation in selectivity ($\widehat{\gamma}$) also decreases (i.e., selectivity becomes more knife-edge). In run C, the relative probability of high values of h decrease dramatically. Again, this is an artifact of the joint effects of selectivity and natural mortality; had the fishery targeted smaller fish, the posterior density for h would shift upwards.

Age composition data are informative about total mortality rates, size selectivity parameters, and relative abundance of each cohort. In this assessment, we assumed that the selectivity curve is an asymptotic function, and this assumption permits the joint estimation of natural mortality and selectivity. There was some positive correlation between M and C^* and strong positive correlation between the selectivity parameters $\widehat{a}$ and $\widehat{\gamma}$ (Table 7). The mean of the marginal posterior distribution for M is roughly equal to the expected value of its corresponding prior distribution. Thus, the specified prior for M can influence the overall scale of the population when survey information lacks sufficient contrast to resolve the underlying production function.
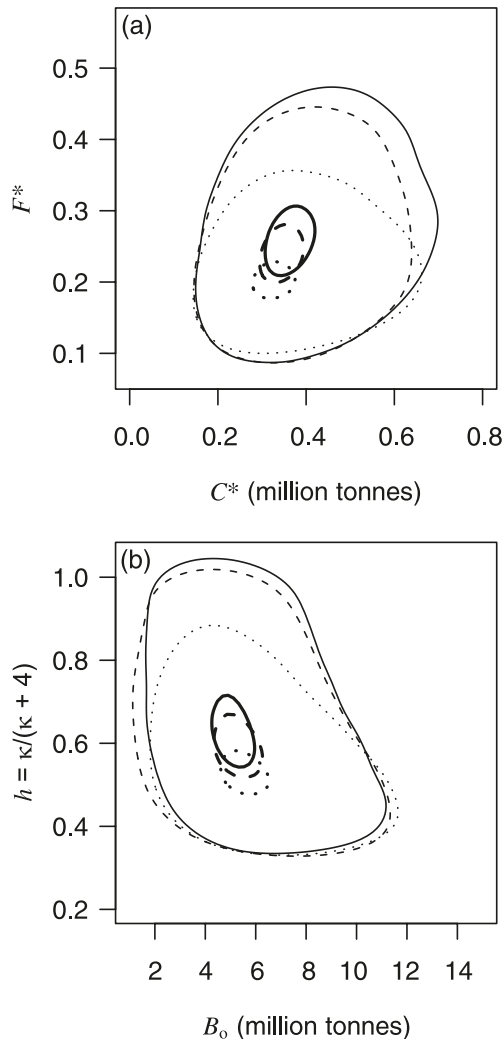
Progressively increasing the amount of information in the prior density for F^* decreases the confounding between F^* and C^* (Table 7) and slightly increases the confounding between C^* and M. The three alternative prior densities for F^* that we chose for this example have different expected values (0.25, 0.22, and 0.19 for runs A–C, respectively), and the modes of the marginal posterior distributions for F^* are roughly equal to the expected values of the prior densities. The resulting 20% posterior density region for F^* also de-

creases as the prior information increases; however, the ranges of uncertainty for C^* do not decrease in a substantial manner for runs A–C (Fig. 5a). Transition to B_o and h show a progressively shrinking joint posterior density as the prior information on F^* increases; however, the uncertainty in B_o is comparable for all three prior densities of F^*. We also tried decreasing the amount of prior information on C^* and found that the uncertainty for B_o and C^* increases slightly, but the shift in the resulting posterior distributions are downward (i.e., lower values for C^* and B_o were more likely). Similar results were also obtained when we progressively increased information in the prior density for M. The overall effect of fixing M is to increase the possible confounding between B_o and κ, creating more of a defined ridge in the joint posterior distribution.

The ability to estimate parameters that specify the observation error variance and process error variance owes to having both age composition information and relative abundance indices. The marginal posterior distributions for ρ and ϑ are largely determined by the assumed weight assigned to the effective sample size in eq. T6.3 in addition to the specified prior distributions. Decreasing the effective sample size for the age composition data shifts the marginal distributions for ϑ and ρ upwards, increasing the total errors. There was very little correlation between the variance parameters and all other model parameters (Table 7). As the effective sample size is reduced in eq. T6.3, the variance parameters are more influenced by the specified prior distributions, in particular the ratio between observation errors and process errors (ρ).

Helser and Martell (2007) make very different assump-

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Fig. 5. Contour plots of the highest 20% and 90% posterior density regions of (a) (C*, F*) and (b) (B_o, h) for the three alternative prior densities for F* (run A, solid line; run B, broken line; run C, dotted line). Contours were constructed from 4000 systematic samples from the Markov chain Monte Carlo (MCMC) chain of length 500 000, where the first 100 000 were discarded for burn-in.

growth. The most significant difference between the two models is in the estimates of MSY (or C*). Estimates of MSY from Helser and Martell (2007) are 536 600 t and in this study are 387 254 t (Table 8). This difference is due in part to the much lower estimates of B_o than what was estimated in Helser and Martell (2007). Estimates of F* are slightly lower in this study because of lower estimates of steepness than what was assumed in Helser and Martell (2007).

Discussion

The main motivation for this paper is to change the question from how likely are B_o and κ given the data to how likely are estimates of C* and F* given the data. We have demonstrated that the reverse transformation of management parameters to population parameters has an analytical solution for an age-structured model with age-specific selectivities and instantaneous mortality rates. This creates both a statistical advantage through reduced confounding (as demonstrated by Schnute and Kronlund 1996) as well as opportunities to develop informative priors for management parameter directly for cases in which relative abundance information lacks sufficient contrast to resolve the B_o, κ trade-off. It also allows for direct comparison of how likely current catches are relative to alternative hypotheses about MSY. We feel that this parameterization of age-structure models will greatly enhance communication with fisheries managers and industry partners.

In the traditional forward-projecting, age-structured stock assessment model, it is necessary to estimate two key population parameters (B_o and κ) to develop management parameters (C* and F*) that are used in harvest control rules (e.g., the 40:10 harvest control rule). To reliably estimate κ, it is necessary to observe the recruitment response at low spawner abundance. Generating such observations may be undesirable because this would call for deliberate over-fishing of the stock, and additional statistical problems such as time-series bias (Myers and Barrowman 1995) or measurement error (Walters and Ludwig 1981; Rivot et al. 2001) may not guarantee that such a deliberate overfishing experiment would yield the correct answer. However, there are alternative approaches to estimating F* for iteroparous species that are independent of knowing the underlying stock–recruitment relationship (e.g., Beverton and Holt 1957; Walters and Martell 2002; Beddington and Kirkwood 2005). Based on growth information, size-selectivity, and estimates of natural mortality, reasonable estimates of F* can be obtained from simple yield-per-recruit analysis. These alternative methods for estimating the fishing mortality that maximizes yield per recruit do not require observations over a wide range of stock sizes; however, these methods are sensitive to changes in growth, natural mortality, or selectivity over time. The main point is that reasonable priors can be developed for F* from simple life-history information (growth and natural mortality) and basic information on the age at first capture; whereas developing reasonable priors for the slope of the stock–recruitment curve may be much more difficult.

The current practice of estimating B_o and κ by fitting models to uninformative time-series data can lead to mis-

tions about the age composition data and the form of the selectivity parameters; therefore, the results of this study are not directly comparable. However, the number of estimated model parameters in Helser and Martell (2007) is nearly double the number of estimated parameters in this study; yet, estimates of uncertainty are very precise in Helser and Martell (2007) by comparison (Table 8). The high precision owes to assuming fixed values for steepness and the scaling parameter for the acoustic survey, as well as fixed values for the variance parameters. Estimates of unfished spawning stock biomass and the spawning stock biomass at MSY are not that different between the two models; however, the uncertainty in these estimates are significantly larger in this study (Table 8). Estimates of the current depletion state are much more conservative in this study owing to lower estimates of the initial unfished states. Furthermore, mean body weights in the hake populations have declined considerably since the late 1970s, and this model assumes constant

Table 8. Comparison of reference points and current states for Pacific hake (*Merluccius productus*) with estimates obtained from Helser and Martell (2007) and this study.

Quantity	Helser and Martell (2007)		This study	
	Estimate	95% CI	Median	95% CI
Unfished spawning stock biomass (1×10^6 t)	3.567	3.112–4.023	3.145	1.829–6.593
Unfished total biomass (1×10^6 t)	8.702	NA	6.678	3.853–14.154
Unfished 3+ biomass (1×10^6 t)	7.321	NA	6.291	3.659–12.188
Spawning stock biomass at MSY (1×10^6 t)	0.986	0.773–1.203	1.23	0.667–2.768
Spawning stock biomass in 2006 (1×10^6 t)	1.241	0.906–1.576	2.18	0.843–6.028
Spawning stock depletion in 2006 (%)	34.8	27.7–41.9	69.20	33.3–128.49
Instantaneous fishing rate at MSY (F^*)	0.282	NA	0.241	0.129–0.415
MSY (C^*) (t)	536 600	468 853 – 595 015	387 254	217 146 – 736 138

Note: MSY, maximum sustainable yield.

guided discussions about developing informative priors for unobserved quantities (e.g., scaling parameters for acoustic surveys or selectivity parameter for dome-shaped selectivity curves). Currently, most stock assessment models that are used for guiding decision makers undergo a review process, either through an internal panel (e.g., Stock Assessment Review (STAR) Panel) or an external review. During this review process, members of the stock assessment teams are usually required to perform a series of additional analysis such that members of the review panel can further understand the sensitivity of management outcomes to alternative assumptions about model structure or the data. Presumably these requests are carried out to determine robustness of the management advice; however, often these requests are carried out because of concerns with the present management advice. In cases where it is absolutely clear that the abundance indices are not informative about the underlying stock production function, we recommend that the discussion begins with an honest admission of a reasonable long-term average yield that first meets conservation objectives and second satisfies the economic constraints of industry and then proceeds to ask how likely are the data given these objectives and constraints. The outcome of such a process can go in two possible directions: (*i*) both the conservation objectives and economic constraints are within the same domain and yield recommendations are straightforward; or (*ii*) economic constraints are beyond the conservation objectives and industry must adapt to lower yield options through cost reduction or enhancing product value. The latter scenario would provide clear incentives for industry partners to develop more efficient solutions that are compatible with management objectives.

The hake data is a great example of the challenges that stock assessment scientists and decision makers must face when a fisheries-independent survey lacks information to reliably estimate the productivity and population scale. To cope with these data challenges, typical responses have included fixing parameters (such as the steepness parameter) or using informative prior distributions based on the results of meta-analysis of similar species. Indeed, the work of Myers et al. (1999) has greatly improved our understanding of recruitment compensation and has been a valuable resource for developing informative priors. However, recruitment compensation defines the rate at which we can safely harvest a population; it does not define the absolute amount

that can be safely removed. The absolute amount that can be safely removed is defined by the population scale, usually defined as the unfished spawning stock biomass. Unfished states are very rarely observed in fisheries, and this quantity must be estimated from time-series data that are often suspect, missing, or even that are estimated from other independent statistical models (e.g., see Maunder 2001). Furthermore, there are very few stock assessments that have a relative abundance index for the entire history of the fishery. If, however, the model is parameterized in a management-oriented approach, then information from historical removals can be used to develop informative priors for population scale. Even one-way trip data contain information on overall scale; in this case, B_o and κ are negatively confounded and the resulting estimates of C^* are fairly well determined over a wide range of likely B_o and κ values. The overarching message here is that it is difficult to determine if one-way trip data come from a large unproductive stock or a small productive stock; in either case, estimates of C^* are roughly the same. Thus, it seems much more intuitive to derive overall population-scale parameters from C^* and F^*.

One of the more important difference between the assessment of hake presented here and that of Helser and Martell (2007) is that this assessment assumes an asymptotic selectivity curve. In Helser and Martell (2007), dome-shaped selectivity curves are assumed for both the US and CAN fisheries and also for the acoustic survey. This feature of the assessment model adds 12 additional unknown parameters to be estimated from the data, as well as assumes that there is some fraction of the older age classes that will never enter the fishery or be seen by the survey. These older or cryptic fish are still maintained in the calculations of spawning stock biomass and probably account for the differences between the two estimates of unfished spawning stock biomass in Table 8. The concern, at least with the hake stock, is that spawning stock biomass can be artificially created by assuming more of a dome in the selectivity function. Alternatively, biased estimates of the M can also have the same affect. Although the assessment for hake presented in this stock assessment does not assume a dome-shaped selectivity curve, we do admit a wide range of uncertainty in M rather than assuming a fixed value. We also note here that using a fixed value for M results in a much stronger correlation between B_o and κ; this results in much less uncertainty in the estimate of C^*.

In comparison with Helser and Martell (2007), there is a much wider range of uncertainty for all model parameters in this assessment of hake. The interpretation of our approach for developing prior distributions could be considered naïve, and indeed it is. Our purpose here was to demonstrate that these data for hake are completely uninformative about the overall population-scale and recruitment compensation. When management requires an estimate of absolute abundance to apply harvest control rule, it is absolutely necessary to incorporate prior information on scaling parameters such as q or B_o itself. When it is absolutely necessary to fix scaling parameters or use informative priors, the process should properly reflect the uncertainty (or at minimum some uncertainty) such that the risk of management options can be properly quantified.

An alternative to the management-oriented approach that we present here would be to develop informative priors for B_o and κ directly and then proceed with model fitting and deriving reference points C^* and F^* required for decision making. However, it is not absolutely clear how priors on B_o and κ would affect estimates of C^* and F^* because of structural assumptions in the model (e.g., the form of the stock–recruitment relationship), confounding with additional nuisance parameters, and assumed variance ratios. For example, if the variance in process errors (ω_t in our example) is sufficiently large, then the shape of the stock–recruitment function is completely determined by the prior information, which ultimately defines C^* and F^*. In contrast, if the variance of the process errors is sufficiently small, then the shape of the stock–recruitment relationship is more influenced by the available data and the associated observation errors. Seeing the effect of the informative priors on estimates of C^* and F^* is confounded with nuisance parameters and the assumed variance ratio. Seeing the effect of informative priors on C^* and F^*, however, is much more transparent. Rivot et al. (2001) warn against using management-oriented approaches for parameterizing stock assessment models because they change the structural assumptions of the model. This is also true for the age-structured model presented here, and we also carry the same warning. In particular, the change in the structural assumptions does not permit growth overfishing as a viable long-term sustainable option. In cases where there has been strong growth-overfishing, estimates of κ are likely to be infinitely large, leading to optimistic management advice.

Acknowledgements

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Appendix A. Relationship between recruitment compensation (κ) and steepness (h)

Steepness is defined as the ratio of the resulting recruitment between unfished conditions and when egg production is reduced to 20% of its unfished state.

$$h = \frac{f(0.2\phi_E)}{f(\phi_E)}$$

Beverton–Holt model

To derive h from κ, first begin by substituting the Beverton–Holt model for $f(E)$ in the expression above and simplify:

$$
\text{(A1)} \qquad
\begin{aligned}
h &= \frac{\left(\dfrac{0.2aE}{1 + 0.2bE}\right)}{\left(\dfrac{aE}{1 + bE}\right)} \\[2mm]
&= \frac{0.2(1 + bE)}{1 + 0.2bE}
\end{aligned}
$$

Next, substitute $b = (\kappa - 1)/E$ into eq. A1:

$$\text{(A2)} \qquad h = \frac{0.2\kappa}{0.8 + 0.2\kappa} = \frac{\kappa}{4 + \kappa}$$

The reverse transformation is given by

$$\text{(A3)} \qquad \kappa = \frac{4h}{1 - h}$$

Ricker model

Substitute the Ricker model into the definition of h and simplify:

$$
\text{(A4)} \qquad
\begin{aligned}
h &= \frac{0.2aE \exp(-0.2bE)}{aE \exp(-bE)} \\[2mm]
&= \frac{0.2 \exp(-0.2bE)}{\exp(-bE)} \\[2mm]
&= 0.2 \exp(0.8bE)
\end{aligned}
$$

Next, substitute $b = \ln(\kappa)/E$ for b in eq. A4 and simplify:

$$
\text{(A5)} \qquad
\begin{aligned}
h &= 0.2 \exp[0.8 \ln(\kappa)] \\
&= 0.2\kappa^{4/5}
\end{aligned}
$$

and the reverse transformation is given by

$$\text{(A6)} \qquad \kappa = (5h)^{5/4}$$

Appendix B. Parameter derivations

Beverton–Holt model

The derivation of eq. 4 starts with substituting eqs. T1.13 and T2.6 into eq. 2:

$$\text{(B1)} \qquad \frac{\partial C_e}{\partial F_e} = R_o \phi_q \frac{\kappa - \phi_E/\phi_e}{\kappa - 1} + F_e \phi_q \frac{R_o}{\kappa - 1} \frac{\phi_E}{\phi_e^2} \frac{\partial \phi_e}{\partial F_e} + F_e R_o \frac{\kappa - \phi_E/\phi_e}{\kappa - 1} \frac{\partial \phi_q}{\partial F_e}$$

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Setting eq. B1 equal to 0 and solving for κ yields

$$0 = \left(\kappa - \frac{\phi_E}{\phi_e}\right)\phi_q + F_e\phi_q\frac{\phi_E}{\phi_e^2}\frac{\partial\phi_e}{\partial F_e} + F_e\left(\kappa - \frac{\phi_E}{\phi_e}\right)\frac{\partial\phi_q}{\partial F_e}$$

$$-F_e\phi_q\frac{\phi_E}{\phi_e^2}\frac{\partial\phi_e}{\partial F_e} = \left(\kappa - \frac{\phi_E}{\phi_e}\right)\left(\phi_q + F_e\frac{\partial\phi_q}{\partial F_e}\right)$$

$$\kappa = \frac{\phi_E}{\phi} - \frac{F_e\phi_q\frac{\phi_E}{\phi_e^2}\frac{\partial\phi_e}{\partial F_e}}{\phi_q + F_e\frac{\partial\phi_q}{\partial F_e}}$$

To prove eq. 5, start with

(B2) $B_o = R_o\phi_B$

Then solve eq. T1.13 for R_o and substitute the result into eq. B2:

(B3) $B_o = \dfrac{R_e(\kappa - 1)}{\kappa - \phi_E/\phi_e}\phi_B$

and solve eq. T1.14 for R_e and substitute this expression into eq. B3, which is equivalent to eq. 5 when $C_e = C^*$ and $F_e = F^*$.

Ricker model

As with eq. 5, the derivation of eq. 7 starts by substituting eq. 6 and its corresponding partial derivative with respect to F_e into eq. 2, setting this expression equal to zero, and solving for κ. The partial derivative of eq. 6 with respect to F_e is

(B4) $\dfrac{\partial R_e}{\partial F_e} = R_o\phi_E\left[1 + \ln\left(\dfrac{\phi_E}{\kappa\phi_e}\right)\right]\phi_e^{-2}[\ln(\kappa)]^{-1}\dfrac{\partial\phi_e}{\partial F_e}$

Let $H = \ln\left(\dfrac{\phi_E}{\kappa\phi_e}\right)$ and substitute eqs. B4 and B6 into eq. 2, set the expression equal to zero, and solve for κ:

$$0 = -\frac{HR_o\phi_E\phi_q}{\ln(\kappa)\phi_e} + \frac{F_e\phi_qR_o\phi_E(1+H)}{\phi_e^2\ln(\kappa)}\frac{\partial\phi_e}{\partial F_e} - \frac{HR_o\phi_eF_e}{\ln(\kappa)\phi_e}\frac{\partial\phi_q}{\partial F_e}$$

$$0 = -H\phi_q + \frac{F_e\phi_q(1+H)}{\phi_e}\frac{\partial\phi_e}{\partial F_e} - HF_e\frac{\partial\phi_q}{\partial F_e}$$

$$\frac{F\phi_q(1+H)}{\phi_e}\frac{\partial\phi_e}{\partial F_e} = H\phi_q + HF_e\frac{\partial\phi_q}{\partial F_e}$$

(B5)

$$H = \ln\left(\frac{\phi_E}{\kappa\phi_e}\right) = \frac{F_e\phi_q\frac{\partial\phi_e}{\partial F_e}}{\phi_q\phi_e + F_e\phi_e\frac{\partial\phi_q}{\partial F_e} - F_e\phi_q\frac{\partial\phi_e}{\partial F_e}}$$

$$\kappa = \frac{\phi_E}{\phi_e}\exp\left(-\frac{F_e\phi_q\frac{\partial\phi_e}{\partial F_e}}{\phi_q\phi_e + F_e\phi_e\frac{\partial\phi_q}{\partial F_e} - F_e\phi_q\frac{\partial\phi_e}{\partial F_e}}\right)$$