Abstract—Priors are existing information or beliefs that are needed in Bayesian analysis. Informative priors are important in obtaining the Bayesian posterior distributions for estimated parameters in stock assessment. In the case of the steepness parameter (h), the need for an informative prior is particularly important because it determines the stock-recruitment relationships in the model. However, specifications of the priors for the h parameter are often subjective. We used a simple population model to derive h priors based on life history considerations. The model was based on the evolutionary principle that persistence of any species, given its life history (i.e., natural mortality rate) and its exposure to recruitment variability, requires a minimum recruitment compensation that enables the species to rebound consistently from low critical abundances (N_c). Using the model, we derived the prior probability distributions of the h parameter for fish species that have a range of natural mortality, recruitment variabilities, and N_c values.

A prior for steepness in stock-recruitment relationships, based on an evolutionary persistence principle

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Success in parameter estimation for stock assessment models often requires sufficient data and correct specification of prior distributions for the estimated parameters (Punt and Hilborn, 1997; Needle, 2002). This is especially true for successfully estimating stock-recruitment relationships with stock assessment models because there often are not sufficient data and there is considerable variability in stock-recruitment relationships. Even in the cases where there are sufficient data, these data can be very noisy and may not show a clear pattern for fitting stock-recruitment relationships (Hilborn and Walters, 1992; Williams and Shertzer, 2003; Munch et al., 2005). Yet, stock-recruitment relationships are important in making fisheries management decisions, especially for over-fished stocks such as widow rockfish (*Sebastes entomelas*), bocaccio (*Sebastes paucispinis*), and darkblotched rockfish (*Sebastes crameri*) along the west coast of the United States (He et al.[1]; MacCall[2]; Punt, 2003; Rogers[3]). Stocks with low values of steepness have low recruitment compensation; therefore stocks will take a long time to rebuild from over-fished status to desired management levels even though total allowable catches for these stocks are kept small (Mace and Doonan[4]).

In this study, we used a simple population model to derive prior distributions (referred to hereafter as "priors") for the steepness parameter (hereafter denoted h) (Mace and Doonan[4]). Prior distributions are probability distributions that represent existing information about parameters. The model was based on the principle that persistence of any fish species, given its life history and its exposure to recruitment variability,

[1] He, X., S. V. Ralston, A. D. MacCall, D. E. Pearson, and E. J. Dick. 2003. Status of the widow rockfish resource in 2003. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 138 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[2] MacCall, A. D. 2003. Status of bocaccio off California in 2003. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[3] Rogers, J. B. 2003. Darkblotched rockfish (*Sebastes crameri*) 2003 stock status and rebuilding analysis. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[4] Mace, P. M., and I. J. Doonan. 1988. A generalized bioeconomic simulation model for fish dynamics, 47 p. New Zealand Fishery Assessment Research Document 88/4. Fisheries Research Center, P.O. Box 297, Wellington, New Zealand.

would require a minimum recruitment compensation to allow the species to rebound from low abundances. We argue that distribution of the h parameter for any species could be determined from its life history and recruitment variability. Using the model, we derived the prior distributions of h for fish species that have a range of natural mortality, recruitment variabilities, and low critical abundance (N_c) values.

Methods

In calculating steepness priors, we used a simple population model with a Beverton-Holt stock recruitment relationship:

$$N_{(t)} = N_{(t-1)}e^{-M} + \frac{N_{(t-1)}}{\alpha + \beta N_{(t-1)}} e^{\left(R_{(t)} - \frac{\sigma^2}{2}\right)}, \qquad (1)$$

where $N_{(t)}$ = population size at year t;
   M = natural mortality;
   α and β = recruitment parameters; and
   $R_{(t)}$ = the logarithm recruitment residual at year t that follows a normal distribution of $N(0, \sigma^2)$, where σ is recruitment variability (Hilborn and Walters, 1992).

This model produces recruitments that are log-normally distributed, and a correction factor of $\frac{\sigma^2}{2}$ is applied to $R_{(t)}$. The correction factor is included because it is commonly used in stock assessments. The Beverton-Holt stock recruitment relationship can be reparametrized as (Mace and Doonan[4])

$$\alpha = \frac{N_0}{R_0} \frac{1-h}{4h} \qquad (2)$$

and

$$\beta = \frac{5h-1}{4hR_0}, \qquad (3)$$

where N_0 = virgin abundance at equilibrium;
   R_0 = virgin recruitment; and
   h = recruitment steepness.

At equilibrium,

$$N_0 = N_0 e^{-M} + R_0 \qquad (4)$$

and

$$R_0 = DN_0, \qquad (5)$$

where D = death rate and is equal to $1 - e^{-M}$.
   We now introduce the persistence criterion. For a given h, the persistence criterion is defined as

$$p(n,t \mid h,T) = \Pr\left\{N_{(s)} > N_c \text{ for all } t \le s \le T \mid N_{(t)} = n\right\}, \quad (6)$$

where T = a time far into the future;
   n = a specific value of population size; and
   N_c = a critically low level of abundance, below which the population would have very high probability of extinction.

At $t = T$, $p(n,T \mid h,T) = 1$ if $n > N_c$ and $p(n,T \mid h,T) = 0$ otherwise. In addition, $p(n,t \mid h,T)$ satisfies the boundary condition that $p(N_c,t \mid h,T) = 0$ for all t.
   For times previous to T, $p(n,t \mid h,T)$ satisfies the stochastic iteration equation (Mangel and Clark, 1988; Clark and Mangel, 2000)

$$p(n,t \mid h,T) =$$
$$E_{R_t}\left\{p\left(ne^{-M} + \frac{n}{\alpha(h)+\beta(h)n} e^{R_t}, t+1 \mid h,T\right)\right\}, \qquad (7)$$

where E_{R_t} denotes the expectation over the stochastic processes associated with recruitment. We have indicated that the Beverton-Holt parameters depend upon steepness (as Eqs. 2–5 show, they also depend upon mortality M, which we hold to be a fixed value).
   Because the recruitment uncertainty is normally distributed and Equation 7 cannot be evaluated analytically, we used a discrete distribution for R_t $(=R_{(t)} - \frac{\sigma^2}{2})$ into K (=61) uniformly spaced values (r_k) between -3σ and 3σ, so that

$$\Pr\{R_t = r_k\} = \frac{\exp\left(-\frac{r_k^2}{2\sigma^2}\right)}{\sum_{j=1}^{K} \exp\left(-\frac{r_j^2}{2\sigma^2}\right)}. \qquad (8)$$

The iteration equation then becomes

$$p(n,t \mid h,T) =$$
$$\sum_{k=-3\sigma}^{k=3\sigma} \Pr\{R_t = r_k\}$$
$$\left\{p\left(ne^{-M} + \frac{n}{\alpha(h)+\beta(h)n} e^{r_k}, t+1 \mid h,T\right)\right\}. \qquad (9)$$

We solve Equation 9 backwards in time, starting at $t = T$–1 (Mangel and Clark, 1988; Clark and Mangel, 2000) until reaching $t = 1$. Assuming that the population starts at the deterministic steady state ($n=N_0$), we can then calculate the prior probability for each h value using Equation 9. Because h is bounded between 0.2 and 1, we used an interval of 0.005 so that a total of 161 solutions of Equation 9 are needed to produce the prior probability for h. We then used a logistic equation to fit 161 prior probability values to produce a derived h prior curve $\{\phi(h)\}$:

$$\phi(h) = \frac{\theta_1}{1 + \frac{(\theta_1 - \theta_2)}{\theta_2} e^{-\theta_3 h_1}}, \qquad (10)$$

Figure 1

Relative probability distributions of the steepness (h) prior for four different σ values with the parameter setting $M = 0.15$, $N_c = 0.1N_0$, and $T = 500$ years.

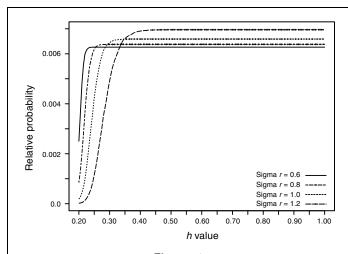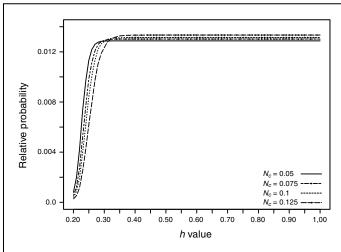**Figure 2**

Relative probability distributions of the steepness (h) prior for four different N_c values with the parameter setting $M = 0.15$, $\sigma = 1.0$, and $T = 500$ years.

where

$$h_1 = \frac{h - 0.2}{0.8} \qquad (11)$$

and θ_1, θ_2, and θ_3 are parameters for a logistic equation.

Note that the derived h priors produced above are relative probabilities, but that is what is needed for the assessment models and Bayesian priors.

Results

Derived h prior curves for $M = 0.15$, $N_c = 0.1N_0$, and $T = 500$ years at four different values of recruitment vari-
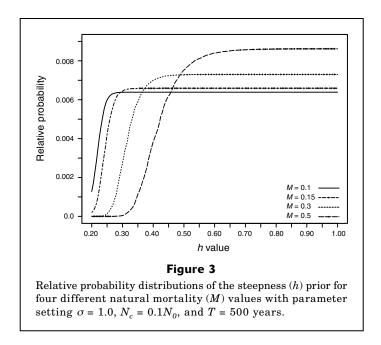
ability (σ) are shown in Figure 1. In general, the prior probability of h increased rapidly at low h values, and then remained at constant values at high h values. As expected, when recruitment variability (σ) increased, h values were higher to compensate for higher recruitment variability (Fig. 1). Table 1 shows parameter values of logistic curves fitted to derived h prior distributions as natural mortality (M) ranged from 0.05 to 0.7 and recruitment variability (σ) ranged from 0.2 to 1.6. These fitted curves would be convenient to use in stock assessment models for given natural mortality and recruitment variability, and values can be interpolated for intermediate cases. Derived h prior curves for four N_c values were plotted (Fig. 2). The figure shows patterns similar to those for recruitment variability, namely that as N_c values increase, h values are higher to increase recruitment potential for the population. Derived h prior curves for four natural mortality (M) values (M=0.1, 0.15, 0.3, and 0.5, respectively) are shown in Figure 3. As M values increase, h values also increase.

Discussion

This article presents a simple modeling approach that allows one to use life history criteria to derive steepness priors for a fish stock where no sufficient historical data could be used to establish reasonable stock recruitment relationships. The model used in this article requires a few assumptions, most of which could be inferred from the life history of the species. However, there is a shortcoming in our approach: a simple population model is used to derive h priors and then applied to the stock assessment model that is an age-structured population model. To derive h priors by using age-structured models would require some age-specific parameters, such as fecundity, growth, and possibly age-specific natural mortality rates. That is, "prior" information on these parameters for age-structured models is needed but in many cases they are not readily available (if they were, the entire stock assessment would be much easier). The parameters for age-structured models could be borrowed from stock assessment models, but applying priors back to stock assessment models could be deemed to be "double" uses of data (Minte-Vera et al., 2005). Our simple population model approach has been widely used in many other applications, such as in computing extinction risk in conservation biology (Hakoyama et al., 2000) and in simple production models in fisheries assessments (Mac-Call, 2002). In these applications, simple (non–age-structured) models were used for populations that are known to have age- or size-structures.

Although there are only a few parameters needed for the model, there are uncertainties in choosing ranges of values for each parameter. One of the important parameters in determining the priors is N_c, the parameter

Figure 3

Relative probability distributions of the steepness (h) prior for four different natural mortality (M) values with parameter setting $\sigma = 1.0$, $N_c = 0.1N_0$, and $T = 500$ years.

characterizing critical abundance. This parameter is more or less a theoretical concept that defines the lowest population abundance deemed to be viable, and its value interacts with the time horizon, T. Although we used a relatively large value of N_c, the associated time horizon was short (T=500 yr) in the evolutionary time scale. Because the stock-recruitment dynamics near the origin are nearly linear, a relatively large value of N_c is approximately equivalent to using a lower value of N_c over a longer time horizon. Also, Mangel and Clark (1988) showed that once the time horizon is sufficiently large, the distributions have the same shape and become stationary. Test runs on our models with large values of T (T=3000 yr) showed almost the same results. In a complex marine environment like that of the U.S. west coast, it would be very difficult to determine "true" values of N_c and T, which could be, for example, at a level where the Allee effect is likely to take place and over a time scale of major environmental change, respectively. However, the results indicated that the model is not very sensitive to the N_c values (Fig. 2). For a range of N_c/N_0 values from 0.05 to 0.125, the prior probability curves were very similar. In contrast, recruitment variability (σ) had much greater effects on the distributions of the prior probability (Fig. 1). As recruitment variability increases, minimum h values need to be significantly higher in order to ensure population viability. Stock assessment reports on other west coast groundfish species have indicated a very high recruitment variability in the past few decades, such as for bocaccio, (σ=1.0, MacCall[2]), and darkblotched rockfish, (σ=0.85, Rogers[3]). However, some recent stock assessment models for the west coast groundfish species have used a lower value of σ, such as 0.6 (Punt, 2003). In our example, if lower values of σ are used, the derived h prior curves will be very flat for h>0.23 (Fig. 2), in-

dicating that the population would be sustainable with very low h values.

Other methods for deriving h priors include using expert opinion, borrowing values from other taxonomically or ecologically related species, and using regional meta-analysis (Myers, 1998, 2001; Chen and Holtby, 2002; Dorn, 2002; Millar, 2002; Myers et al., 2002). For example, Myers et al. (2002) used an empirical Bayesian approach to derive prior distributions for steepness for nine species. As compared to our method, their method, based on a combined method of taxonomic and ecological criteria, still requires the collection of biological data from related species, as well as expert opinions on the life history of each species, which are somewhat "subjective" values. Dorn (2002) used Bayesian meta-analysis to derive stock-recruitment relationships for a group of west coast groundfish species. He used the results from the previous stock assessments for widow rockfish and other west-coast groundfish species and indicated that the prior distribution for steepness for widow rockfish could have a median value around 0.72 and a probability of 0.0033 for h≤0.225. This result could indicate that our method is more conservative because our method indicates much lower median value for widow rockfish-like species. Minte-Vera et al. (2005) also suggested that the priors derived by Dorn (2002) might not be appropriate for stock assessments that include the same data that were used in the meta-analysis to derive priors.

We believe that the method used in our study provides a scientific way of estimating the prior for steepness and avoids the pitfall of imposing a preconception of what the true distribution is thought to be. For example, it seems reasonable that very high values of h will not be likely because of tradeoffs between individual survival

Table 1

Parameter values of logistic curves fitted to derived h prior distributions for different natural mortality (M) and recruitment variability (σ). Parameters are listed in the order of θ_1, θ_2, and θ_3 (see Eq. 10). For some combinations of natural mortality and recruitment variability, distributions were uniform or could not be fitted.

Recruitment variability	Natural mortality									
	0.05	0.1	0.15	0.2	0.25	0.3	0.4	0.5	0.6	0.7
0.2	Uniform distribution	Uniform distribution	Uniform distribution	Uniform distribution	Uniform distribution	1.0000 669.60 0.9289	1.0000 443.00 0.8046	1.0000 306.13 0.6662	1.0000 282.66 0.5015	1.0000 278.16 0.3724
0.4	Uniform distribution	0.9994 139.90 0.9800	1.0000 248.40 0.7973	1.0000 223.60 0.5585	1.0000 196.43 0.3739	1.0000 199.3 0.2146	0.9999 182.22 0.08619	0.9999 157.82 0.04454	0.9999 148.63 0.02264	0.9997 145.48 0.01154
0.6	Uniform distribution	1.0000 149.70 0.7552	1.0000 133.60 0.3895	1.0000 116.74 0.1791	0.9998 109.86 0.08069	0.9995 105.32 0.03805	0.9992 89.55 0.01543	0.9988 78.79 0.007602	0.9985 69.29 0.005074	61.48 0.003861
0.8	1.0000 83.00 0.9259	1.0000 93.13 0.4317	1.0000 84.25 0.1376	0.9997 76.29 0.04540	0.9992 68.73 0.02022	0.9990 65.53 0.01197	0.9982 48.84 0.005796	0.9972 40.51 0.003745	0.9959 34.03 0.003041	0.9943 29.12 0.002722
1.0	1.0000 75.30 0.9526	1.0000 64.42 0.1929	0.9995 57.52 0.04464	0.9987 48.77 0.1700	0.9980 41.44 0.009240	0.9970 35.57 0.006199	0.9944 27.15 0.003906	0.9902 21.58 0.003076	0.9830 17.71 0.002680	0.9709 14.97 0.002402
1.2	1.0000 69.36 0.5920	0.9995 48.16 0.07182	0.9983 38.71 0.01844	0.9967 30.90 0.009036	0.9946 25.38 0.005819	0.9915 21.26 0.004420	0.9801 15.75 0.003134	0.9543 12.64 0.002243	0.9011 11.01 0.001320	0.8085 10.34 0.0005882
1.4	1.0000 47.79 0.2024	0.9983 35.06 0.02504	0.9956 25.81 0.009163	0.9913 19.87 0.005647	0.9835 15.94 0.004010	0.9697 13.39 0.003087	0.9025 10.74 0.001373	0.7428 10.25 0.0003183	0.4973 10.88 0.00003683	0.2428 12.62 0.0000016
1.6	0.9992 39.09 0.03001	0.9955 25.03 0.008900	0.9883 17.22 0.004923	0.9716 13.22 0.003340	0.9338 11.08 0.001971	0.8585 10.25 0.0008686	0.5463 10.75 0.00005315	0.2027 12.90 0.00000079	0.02790 16.85 0.00000001	Not fitted

and reproduction, but that tradeoff should be shown, not imposed. The methods used in the present study can be extended to address this tradeoff (i.e., Mangel and Clark, 1988; Clark and Mangel, 2000), but that is a subject for another study. However, for many overfished stocks that need stock-recruitment relationships for rebuilding analysis, this method is especially appropriate because it indicates the ability of the population to recover from low abundance. For other depleted stocks, use of prior probability distributions based on this method can provide useful information on how quickly the populations could be rebuilt under various management policies.

Acknowledgments

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