

North American Journal of Fisheries Management



ISSN: 0275-5947 (Print) 1548-8675 (Online) Journal homepage: http://www.tandfonline.com/loi/ujfm20

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To cite this article: Martin W. Dorn (2002) Advice on West Coast Rockfish Harvest Rates from Bayesian Meta-Analysis of Stock–Recruit Relationships, North American Journal of Fisheries Management, 22:1, 280-300, DOI: 10.1577/1548-8675(2002)022<0280:AOWCRH>2.0.CO;2

To link to this article: <a href="http://dx.doi.org/10.1577/1548-8675(2002)022<0280:AOWCRH>2.0.CO;2">http://dx.doi.org/10.1577/1548-8675(2002)022<0280:AOWCRH>2.0.CO;2



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Advice on West Coast Rockfish Harvest Rates from Bayesian Meta-Analysis of Stock—Recruit Relationships

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Abstract.—Over the past two decades, populations of rockfish Sebastes spp. off the U.S. West Coast have declined sharply, leading to heightened concern about the sustainability of current harvest policies for these populations. In this paper, I develop a hierarchical Bayesian model to jointly estimate the stock-recruit relationships of rockfish stocks in the northeastern Pacific Ocean. Stock-recruit curves for individual stocks are linked using a prior distribution for the "steepness" parameter of the Beverton-Holt stock-recruit curve, defined as the expected recruitment at 20% of unfished biomass relative to unfished recruitment. The choice of a spawning biomass per recruit (SPR) harvest rate is considered a problem in decision theory, in which different options are evaluated in the presence of uncertainty in the stock-recruit relationship. Markov chain Monte Carlo sampling is used to obtain the marginal distributions of variables of interest to management, such as the yield at a given SPR rate. A wide range of expected yield curves were obtained for different rockfish stocks. The stocks of Pacific ocean perch S. alutus in the Gulf of Alaska and the Aleutian Islands are apparently the most resilient, with maximum sustainable yield (MSY) harvest rates greater than F_{30%} (the fishing mortality rate that reduces SPR to 30% of its unfished value) for all model configurations. In contrast, the MSY harvest rate for the West Coast stock of Pacific ocean perch was lower than $F_{70\%}$. The SPR rates at MSY for other stocks were clustered between F_{40%} and F_{60%} and depended on both the stock-recruit model (Beverton-Holt or Ricker) and the model for recruitment variability (lognormal or gamma). Meta-analysis results should be interpreted cautiously due to autocorrelation in the model residuals for several stocks and the potential confounding effect of decadal variation in ecosystem productivity. An $F_{40\%}$ harvest rate, the current default harvest rate for rockfish, exceeded the estimated F_{MSY} rate for all West Coast rockfish stocks with the exception of black rockfish S. melanops. A harvest rate of $F_{50\%}$ is suggested as a risk-neutral F_{MSY} proxy for rockfish. A more risk-averse alternative would be to apply an SPR harvest rate in the $F_{55\%}$ - $F_{60\%}$ range.

The rockfishes *Sebastes* spp. are a large number of closely related species found primarily in the northeastern Pacific Ocean, with about 71 species distributed from the Gulf of California to the Bering Sea. Over the past two decades, rockfish populations off the U.S. West Coast (Washington, Oregon, and California) have declined sharply (Ralston 1998). Declines were anticipated for stocks that had been lightly exploited previously (e.g., widow rockfish S. entomelas and yellowtail rockfish S. flavidus), since even sustainable harvesting would reduce these stocks by one-half to two-thirds relative to their unfished levels. However, several stocks have shown little evidence of stabilizing at these lower levels. Age-structured assessments show declines in recruitment as the spawning stock has declined, suggesting that compensatory processes in early life history are weak compared with those in other marine fish species. Moreover, the West Coast stock of Pacific ocean perch *S. alutus*, which was reduced to low abundance by overfishing in the 1960s, has shown no evidence of rebuilding after 30 years despite management policies designed to promote recovery. Such observations have led to heightened concern about the sustainability of current harvest policies for rockfish. In January 2000, the West Coast groundfish fishery was officially declared a "failure" by the U.S. Secretary of Commerce because of the precipitous decline in groundfish catches, making the fishery eligible for disaster relief funds

West Coast rockfish are managed by the Pacific Fishery Management Council using a fishery management plan developed to meet the requirements of the Magnuson-Stevens Fishery Conservation and Management Act and implementation guidelines established by the National Marine Fisheries

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Service. The management plan includes definitions of (1) a maximum sustainable yield (MSY) rule, that is, a constant fishing mortality rate that maximizes the long-term average yield $(F_{\rm MSY})$; (2) an optimum yield rule that reduces fishing mortality when stock size is below the mean biomass at $F_{\rm MSY}$ ($B_{\rm MSY}$); and (3) guidelines for reducing the optimum yield to account for uncertainty in stock status. Since obtaining a reliable estimate of the $F_{\rm MSY}$ for a particular fish stock is difficult, proxies are established for $F_{\rm MSY}$ and $B_{\rm MSY}$ based on spawning biomass per recruit (SPR).

In 1992, $F_{35\%}$ (the fishing mortality rate that reduces SPR to 35% of its unfished value) was adopted as a proxy for F_{MSY} for all West Coast groundfish based on work by Clark (1991). He showed that a large fraction of the potential yield from a typical groundfish stock could be obtained at this SPR rate across a discrete set of plausible stock-recruit relationships, including both Ricker and Beverton-Holt forms. In 1997, the $F_{\rm MSY}$ proxy for rockfish was reduced to $F_{40\%}$ based on several considerations, including concerns about the continuing decline of rockfish stocks and further work by Clark (1993) showing that the $F_{40\%}$ harvest rate would reduce the probability of low biomass if recruitment were highly variable or autocorrelated.

A harvest rate based on spawning biomass per recruit is explicitly intended to protect stocks from recruitment overfishing. An SPR-based harvest rate will also harvest unproductive stocks at lower rates than productive stocks, similar to an F = M (natural mortality rate) strategy (Clark 1991). However, rockfish as a group possess unique characteristics that distinguish them from other groundfish, including scarcity, ovoviviparity, sex differences in growth and mortality, long life spans, and high recruitment variability (Parker et al. 2000). The general advice of Clark (1991, 1993) may not provide sufficient guidance for establishing an $F_{\rm MSY}$ proxy for rockfish.

In this paper, I develop a hierarchical Bayesian model to jointly estimate the stock-recruit (S-R) relationships of all rockfish stocks in the northeastern Pacific for which stock-recruit data are available. Hierarchical Bayesian models were used by Liermann and Hilborn (1997) to assess depensation in S-R relationships. In a similar approach, Myers et al. (1999) used linear mixed models in a meta-analysis of S-R data to estimate the slope at the origin of the stock-recruit relationship. This work focused on characterizing

the mean and variability of various properties of the stock-recruit relationship in broad taxonomic groupings. I extend this work by considering management decisions, such as the choice of an SPR harvest rate, as a problem in decision theory in which different options are evaluated in the presence of uncertainty in the stock-recruit relationship (Thompson 1992). My purpose in using hierarchical Bayesian modeling is to pool information in order to more precisely estimate stock-recruit parameters (and F_{MSY} harvest rates) than is possible with independent stockspecific analysis, which often produces unreliable results. Markov chain Monte Carlo (MCMC) sampling is used to obtain the marginal distributions of variables of interest to management, such as the yield at a given SPR rate.

There are four steps involved in developing a hierarchical Bayesian model. (1) The Beverton-Holt S-R curve is reparameterized to allow the "steepness" (as defined by Mace and Doonan 1988) of the curve to be linked between stocks. (2) The posterior distribution of the parameters for the resulting S-R curves is formulated using conditional probability distributions for the S-R data (likelihood), the S-R parameters for individual stocks (prior), and the hyperprior, which is defined as the probability distribution of the parameters in the prior. (3) The marginal posterior distributions of the yield at a given SPR harvest rate are obtained using MCMC sampling from the posterior distribution. (4) Risk-sensitive estimates of F_{MSY} (i.e., risk-neutral or risk-averse estimates) are obtained using a loss function, the negative of which measures the societal benefits of the yield from the fishery. Alternative models for the mean S-R relationship (Ricker) and recruitment variability (gamma) are also evaluated using the hierarchical Bayesian approach.

Methods

Reparameterizing the Beverton-Holt Curve

The customary formulation of the Beverton–Holt curve for a single stock is

$$R = \frac{aS}{b+S};\tag{1}$$

R is the recruitment produced by spawning biomass S (or another proxy of the annual egg production of the stock). For a hierarchical model, it is necessary to parameterize the Beverton-Holt curve so that the parameters are comparable between stocks, and the parameters a and b in equa-

tion (1) do not meet this requirement. Instead of the customary formulation, I used R_0 , the expected recruitment for an unfished stock size of S_0 , and a parameter that measures the resiliency of the stock, h, defined as the proportion of R_0 that recruits when the stock is reduced to 20% of unfished biomass (i.e., the "steepness" parameter of Mace and Doonan 1988), that is,

$$hR_0 = \frac{a(0.2S_0)}{b + 0.2S_0}. (2)$$

For a steepness of 0.2, recruits are a linear function of spawners. For a steepness of 1.0, recruitment is independent of spawning biomass. The Beverton–Holt curve with parameters R_0 and h is

$$R = \frac{0.8R_0hS}{0.2\varphi_0R_0(1-h) + (h-0.2)S};$$
 (3)

 $S_0 = \phi_0 R_0$, and ϕ_0 is spawning biomass per recruit for an unfished stock, which is estimated independently using conventional spawning-biomass-perrecruit equations (Gabriel et al. 1989). All SPR calculations, including the estimate of ϕ_0 , used the fixed life history vectors (maturity, growth, natural mortality, and selectivity to the fishery) reported in the stock assessments. It is important to note that the standard SPR equations make an implicit assumption that all compensatory processes described by the stock—recruit relationship occur during early life history prior to recruitment. The potential density dependence of adult life history characteristics has not been evaluated in any North Pacific rockfish assessment.

The problem of jointly estimating the stock – recruit parameters for a taxon is addressed by modeling the relationships (if any) between the R_0 and h for the individual stocks using hierarchical priors, that is, by using probability distributions to describe the mean and variance of those parameters within the taxon. I do not use a hierarchical prior for R_0 because it measures the carrying capacity of the habitat occupied by the stock and would be unrelated between stocks.

The similarity of stocks in their response to harvesting was modeled by assuming that the logit of h_k , the steepness parameter for the kth stock, was normally distributed (after rescaling h_k into the interval [0, 1], $[h_k - 0.2]/0.8$, and simplifying), that is

$$\beta_k = \log_e \left(\frac{h_k - 0.2}{1 - h_k} \right), \qquad \beta_k \sim N(\mu, \tau^2). \quad (4)$$

For h_k in the interval (0.2, 1.0), the logit β_k ranges from $-\infty$ to $+\infty$.

Hierarchical Bayesian Modeling

A hierarchical Bayesian model describes the joint posterior distribution of the parameters with (1) the likelihood (the probability of the data given the parameters), (2) the prior (the probability distribution of the parameters), and (3) the hyperprior (the probability distribution for the parameters that determine the prior distribution; Gelman et al. 1995). The prior models characteristics of a parameter (i.e., the mean and variance) in a population, while the hyperprior assumes the role usually associated with the prior in Bayesian analysis. It quantifies prior beliefs about the parameters in the prior. A diffuse hyperprior can be used to reflect ignorance about these parameters.

A hierarchical model consists of conditional probability distributions that link data, Z, to parameters, Θ , and parameters to hyperparameters, Φ . The prior joint distribution of the parameters and hyperparameters is

$$p(\Theta, \Phi) = p(\Theta|\Phi) p(\Phi).$$
 (5)

The joint posterior distribution is obtained by Bayes' rule,

$$p(\Theta, \Phi \mid Z) \propto p(Z \mid \Theta, \Phi) p(\Theta, \Phi)$$

$$= p(Z \mid \Theta, \Phi) p(\Theta \mid \Phi) p(\Phi)$$

$$= p(Z \mid \Theta) p(\Theta \mid \Phi) p(\Phi) \qquad (6)$$

with the last equality because the data depend on the hyperprior only through the prior. The resulting joint posterior distribution is proportional to the product of the likelihood, the prior, and the hyperprior, as described in more detail below. The logarithm of the joint posterior distribution is typically used in posterior mode-finding routines and in MCMC sampling.

Likelihood $p(Z|\Theta)$.—The assumption of lognormal errors in S-R models is based on both theoretical considerations (Hilborn and Walters 1992) and empirical studies (Peterman 1981; Myers et al. 1995). A lognormal probability density for recruitment is

$$p[R \mid \hat{R}(S, R_0, \beta), \sigma^2] = \frac{1}{R\sqrt{2\pi}\sigma} \exp\left[-\frac{1}{2\sigma^2} \left(\log_e R - \log_e \hat{R} + \frac{\sigma^2}{2}\right)^2\right],$$
(7)

where $\hat{R}(S, R_0, \beta)$ is the expected recruitment as a

function of the S-R parameters and spawning biomass, and σ^2 is a shape parameter. Note that the mean of the lognormal variate is used here rather than the usual parameterization with the median, $m = \hat{R} \cdot \exp(-\sigma^2/2)$. This approach makes it possible to model the relatedness of the expected S-R curves for the rockfish stocks directly. When variability around the S-R curve differs substantially between stocks, as is the case for rockfish, comparisons between S-R parameters will be different depending on whether the comparison is between the mean or the median S-R relationship. Since management parameters, such as F_{MSY} , are based on the expected S-R curve, use of the mean was considered the most appropriate. For K stocks with n_k observations on the kth stock, the negative loglikelihood is proportional to

$$-\log_{e} L_{1} = \sum_{k=1}^{K} \sum_{i} [\log_{e} R_{ik} - \log_{e} \hat{R}_{ik} (S_{ik}, R_{0k}, \beta_{k}) + \sigma_{k}^{2}/2]^{2}/2\sigma_{k}^{2} + n_{k} \cdot \log_{e} \sigma_{k}.$$
(8)

Note that I assume no correlation in recruitment and no error in the estimates of spawning biomass, the usual simplifying assumptions in analyses of S-R data.

Prior $p(\Theta|\Phi)$.—Hierarchical structure was developed only for "steepness" parameters, h_k (through their logits β_k). For σ_k , a locally uniform prior on a logarithmic scale was used. A weak nonhierarchical prior was used for R_0 to prevent the estimate of R_0 from deviating too much from the recruitment observed at high spawning biomass for each stock. This prior had a minor effect on the posterior mode but curbed the tendency to sample extremely large values of R_0 from the posterior distribution during MCMC sampling for stocks with uninformative S-R data. The prior mean for the kth stock, \hat{R}_{0k} , was set to the average recruitment at spawning biomass that was greater than the median observed spawning biomass, and deviations from this prior were assumed to be normal, with a coefficient of variation (CV = SD/ mean) of 2.0. Because this prior (albeit very broad) was obtained from the data, there is some bending of Bayesian principles in this approach. Nevertheless, it was considered the most straightforward way to incorporate the legitimate prior information that rockfish stocks were close to a pristine state during the initial years of the assessment period, and it implicitly incorporates a temporal structure in the data that is not captured by the likelihood. The negative prior is proportional to

$$-\log_e L_2 = \frac{1}{2\tau^2} \sum (\beta_k - \mu)^2 + K\tau + \frac{1}{2} \sum \left(\frac{R_{0k} - \hat{R}_{0k}}{\text{CV} \cdot \hat{R}_{0k}} \right)^2.$$
 (9)

Hyperprior $p(\Phi)$.—The hyperprior specifies the probability distributions for μ and τ^2 . When possible, uninformative hyperpriors should be used to let the posterior distribution of μ and τ^2 reflect the information about these parameters that is contained in the data. For μ , a locally uniform prior was used to reflect the lack of knowledge about this parameter. To ensure a proper posterior distribution for τ^2 , it was necessary to assume a proper, but relatively uninformative, hyperprior for τ^2 . I assumed that the hyperprior for τ^2 followed a scaled, inverse chi-square distribution, the conjugate prior for a normal distribution scale parameter. The negative log hyperprior with a scaled, inverse chi-square distribution is proportional to

$$-\log_e L_3 = \left(\frac{\nu}{2} + 1\right) \log_e \tau^2 + \frac{\nu s^2}{2\tau^2}, \quad (10)$$

with parameters v and s^2 . This prior distribution can be regarded as providing the same information about τ^2 as v prior observations of $N(\mu, \tau^2)$ with a mean squared deviation of s^2 (Gelman et al. 1995). A hyperprior with parameters v=10 and $s^2=0.5$ was sufficient to bound τ^2 away from zero while still allowing the data to have a reasonable influence on the estimate. Experimentation with alternative values for v and s^2 suggested that the results were not particularly sensitive to this assumption.

The log joint posterior distribution is proportional to the sum of the log-likelihood, the log prior, and the log hyperprior,

$$L = \log_{e} L_{1} + \log_{e} L_{2} + \log_{e} L_{3}. \tag{11}$$

The posterior mode of the joint posterior distribution was obtained using the AD Model Builder nonlinear optimization software (Otter Research 1996).

Obtaining Posterior Distributions Using the Markov Chain Monte Carlo Algorithm

To estimate $F_{\rm MSY}$ for a stock of interest, the marginal posterior distribution of the stock—recruit parameters for that stock is required; this is obtained by integrating the joint posterior distribution with respect to the other parameters. Rather than eval-

uating this difficult integral analytically, I used an MCMC algorithm to obtain random samples from the joint distribution. From these samples it is an easy matter to obtain empirical histograms that approximate the marginal distribution of any parameter of interest. The MCMC algorithm generates a Markov chain of random samples (i.e., each sample is conditionally dependent on the preceding sample) whose stationary distribution is the joint posterior distribution. Gelman et al. (1995) provides a good introduction to MCMC methods, including the Hastings-Metropolis algorithm provided in the AD Model Builder software (see the 30 January 1998 version of http://otter-rsch.com/ cc/cctoc.html for additional details). Marginal posterior distributions were obtained by subsampling every 200th sample from 500,000 cycles of the MCMC algorithm after an initial burn-in of 50,000 cycles.

To obtain a posterior predictive distribution for β_k (i.e., the distribution for an unobserved stock), it is necessary to integrate over μ and τ , the parameters that govern the distribution of β_k in the joint posterior distribution. This was done by augmenting the vector of β_k s in the hierarchical prior with an additional element with no associated S-R data and using MCMC sampling to obtain the posterior distribution of that element. A posterior predictive distribution was obtained for α_k in the Ricker model (described below) in the same way.

Decision-Theoretic Estimates of F_{MSY}

Let $(h_{(C)}, R_{0(C)})$ be a sample of the stock-recruit parameters for the stock of interest from the joint posterior distribution generated by the MCMC algorithm. For each sample, the equilibrium recruitment $R^{EQ}(p)$ is obtained using equation (3) for a sequence of harvest rates whereby SPR is reduced to a fraction, p, of unfished SPR $(p = 1.00, 0.99, 0.98, \ldots, 0.10)$,

$$R^{\rm EQ}(p) = \max \left(0, \, R_{0(C)} \frac{0.8 h_{(C)} p - 0.2[1 - h_{(C)}]}{p[h_{(C)} - 0.2]} \right). \tag{12}$$

Some combinations of SPR rate and the sampled stock—recruit parameters result in negative equilibrium recruitment, indicating that the SPR rate is not sustainable; hence the use of the "max" function in the above equation.

Equilibrium yield, $Y^{EQ}(p)$, and equilibrium spawning biomass, $S^{EQ}(p)$, at SPR rate p are

$$Y^{\text{EQ}}(p) = \eta_p R^{\text{EQ}}(p)$$
, and (13)

$$S^{EQ}(p) = p\varphi_0 R^{EQ}(p), \tag{14}$$

where η_p is the yield per recruit when the SPR is reduced to the fraction p of unfished SPR.

Risk aversion was explored by defining a loss function, the negative of which measures the societal benefits of the fishery yield, that is, the "utility." From a decision theoretic perspective, $F_{\rm MSY}$ can be regarded as the fishing mortality rate that minimizes risk, where risk is the expected loss. Thompson (1992) proposed a general loss function for fishery yield of the form

$$l(Y) = \frac{1 - Y^{\lambda}}{\lambda},\tag{15}$$

where λ is used to control risk aversion. Linear loss is obtained when $\lambda=1$, while the logarithmic loss is obtained in the limit as λ approaches zero. A linear loss function implies a risk-neutral approach, such that the expected yield is maximized, while any value of $\lambda<1$ implies risk aversion. Although logarithmic loss is often used as a default risk-averse approach, using it in this problem would exclude any SPR rate with a nonzero probability of zero yield, implying extreme risk aversion. Instead, I use $\lambda=0.5$ as an example of a risk-averse approach, which corresponds to maximizing the expected square root of yield.

A decision-theoretic estimate of the SPR rate at $F_{\rm MSY}$ is

$$SPR_{F_{MSY}} = \min_{p} E(l[Y^{EQ}(p)]). \tag{16}$$

The expected loss at a particular SPR rate is obtained by averaging the loss associated with the equilibrium yield for each of the MCMC samples drawn from the joint posterior distribution. Of course, the relationship of the SPR rate to yield and risk is of interest in addition to the point estimates.

Extensions

In the hierarchical Bayesian model, the Beverton–Holt curve with lognormal errors can be replaced with other stock–recruit relationships or alternative models for stock–recruit variability. Two important alternatives to consider are the Ricker S–R model and gamma errors.

Ricker S-R model.—Kimura (1988) reparameterized the Ricker curve in relation to R_0 , the expected recruitment for an unfished stock size of

TABLE 1.—Northeastern Pacific rockfish stocks used in meta-analysis of stock–recruit relationships. The SPR at F = 0 is the annual reproductive output per recruit for an unfished stock (i.e., fishing mortality = 0); it is defined variously as total spawning biomass (SB), female spawning biomass, or annual egg production (EP), and is not comparable between stocks; N indicates the number of years of stock–recruit data, and recruitment age is the age at which recruitment is estimated in the assessment model. Assessment models are abbreviated as follows: SS-age = stock synthesis age-based model (Methot 1989), SS-length = stock synthesis length-based model (Methot 1989), ADMB-age = AD Model Builder age-structured model, and ADMB-length = AD Model Builder size-structured model (Otter Research 1996).

| Species | Stock | Stock identi- fication code | Assessment model | Years | N |
|-----------------------------|---|--------------------------------|---------------------|-----------|-----|
| Chili pepper S. goodei | West Coast | CHILIPEPPER | SS-length | 1970-1997 | 28 |
| Bocaccio S. paucispinis | West Coast | BACACCIO | SS-length | 1969-1998 | 30 |
| Widow rockfish | West Coast | WIDOW | SS-age | 1970-1996 | 27 |
| Canary rockfish S. pinniger | West Coast | CANARY | SS-age, ADMB-length | 1967-1994 | 28 |
| Black rockfish S. melanops | Washington, northern Oregon | BLACK | ADMB-age | 1986–1992 | 7 |
| Yellowtail rockfish | West Coast | YELLOWTAIL | ADMB-age | 1967-1993 | 27 |
| Pacific ocean perch | West Coast | PERCHWUS | ADMB-age | 1956-1995 | 40 |
| | Goose Island Gully, British Columbia | PERCHGOOSE | ADMB-age | 1963–1988 | 26 |
| | Gulf of Alaska | PERCHGA | SS-age | 1977-1992 | 16 |
| | Aleutian Islands | PERCHAI | SS-age | 1962-1989 | 28 |
| | Eastern Bering Sea | PERCHEBS | SS-age | 1960-1996 | 37 |
| Total | | | - | | 294 |

 S_0 , and a curvature parameter, α . The Ricker curve with parameters R_0 and α is

$$R = \frac{S}{\varphi_0} \exp\left[\alpha \left(1 - \frac{S}{R_0 \varphi_0}\right)\right]. \tag{17}$$

Note that e^{α} is the potential increase in reproductive success relative to an unfished stock, so that additive changes in α imply multiplicative changes in reproductive success at low stock size. Steepness is not a useful concept for the domeshaped Ricker model because recruitment at 20% of unfished biomass can be greater than unfished recruitment (steepness > 1). I modeled the similarity of stocks in their response to harvesting by assuming that the curvature parameter for the kth stock was normally distributed,

$$\alpha_k \sim N(\mu, \tau^2).$$
 (18)

The hyperpriors for μ and τ^2 were the same as those developed for the Beverton–Holt curve.

Equilibrium recruitment for the Ricker curve is

$$R^{EQ}(p) = \frac{R_0}{p} \left(1 + \frac{\log_e p}{\alpha} \right). \tag{19}$$

Gamma likelihood.—Myers et al. (1995) recommend the gamma distribution as an important alternative to the lognormal distribution for recruitment variability. The gamma distribution parameterized by expected recruitment, \hat{R} , and a shape parameter, γ , is

$$p[R \mid \hat{R}(S, R_0, \beta), \gamma]$$

$$= \frac{1}{\Gamma(\gamma)} \left(\frac{\gamma}{\hat{R}}\right)^{\gamma} R^{\gamma - 1} \exp\left(-\frac{\gamma R}{\hat{R}}\right). \tag{20}$$

Data Sources

Stock-recruit data were obtained for 11 rockfish stocks in the northeastern Pacific Ocean. Sources included the stock assessments published by the Pacific and North Pacific Fishery Management Councils, Canada's Department of Fisheries and Oceans, and the Myers et al. (1995) database (Table 1). Assessment authors were also contacted to resolve discrepancies and obtain additional information. In assessments where results are presented for several alternative models, the model considered by the author as most appropriate was used. For the West Coast Pacific ocean perch stock, the assessment author reran the model without a prior on steepness and provided the resulting biomass and recruitment time series for use in the current analysis (J. N. Ianelli, Alaska Fisheries Science Center, personal communication). Although rockfish assessments are among the most comprehensive and technically advanced of all assessments, they are highly uncertain due to the difficulty of surveying highly aggregated fish populations that inhabit rocky areas and the infrequent survey schedule off the U.S. West Coast and Alaska.

An attempt was made to be as inclusive as possible when assembling the S-R data in order to

TABLE 1.—Extended.

| Species | Recruitment age | Average natural mortality | SPR at $F = 0$ | SPR units | Reference |
|-----------------------------|-----------------|---------------------------|----------------|-----------|---|
| Chili pepper S. goodei | 1 | 0.24 | 1.306 | EP | Ralston et al. 1998 |
| Bocaccio S. paucispinis | 1 | 0.20 | 1.289 | EP | MacCall et al. 1999 |
| Widow rockfish | 1 | 0.15 | 7.753 | EP | Ralston and Pearson 1997 |
| Canary rockfish S. Pinniger | 1 | 0.08 | 7.789 | Female SB | Crone et al. 1999, Williams et al. 1999 |
| Black rockfish S. melanops | 6 | 0.28 | 1.209 | Female SB | Wallace et al. 1999 |
| Yellowtail rockfish | 4 | 0.14 | 2.403 | Female SB | Tagart et al. 1997 |
| Pacific ocean perch | 3 | 0.06 | 6.155 | Female SB | Ianelli and Zimmerman 1998 |
| - | 7 | 0.05 | 18.144 | Total SB | Richards and Olsen 1996 |
| | 2 | 0.05 | 5.570 | Female SB | Heifetz et al. 1999 |
| | 3 | 0.05 | 5.729 | Female SB | Ito et al. 1999 |
| | 3 | 0.05 | 5.482 | Female SB | Ito et al. 1999 |
| | | | | | |

reduce the potential for bias due to subjective selection criteria (Englund et al. 1999). Assessments considered by their authors to be preliminary or to have given implausible results (e.g., northern rockfish Sebastes polyspinis; Courtney et al. 1999) and northern British Columbia yellowtail rockfish (Stanley and Haist 1997) were not used. Although a separate assessment was conducted for a putative "southern" canary rockfish stock (Williams et al. 1999), the biomass and recruitment estimates from this assessment were added to the time series for the northern stock to reflect the assessment author's conclusion that canary rockfish in this area probably did not constitute a separate stock.

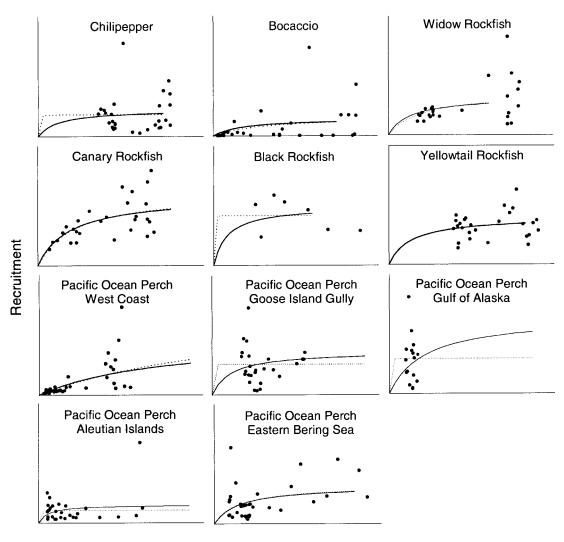
Life history and fishery selectivity information was used to estimate SPR and yield per recruit curves for each stock (Gabriel et al. 1989). General formulations of the SPR and yield-per-recruit equations that allow for age and sex differences in natural mortality, weight, proportion mature, and fishery selectivity were used. These computations were tailored to the characteristics of each stock using the same life history vectors and selectivity estimates used in the assessment to calculate SPR rates. Population response to harvesting on a per-recruit basis can be compactly characterized by (1) the spawning biomass per recruit for an unfished stock, ϕ_0 , and (2) a vector of yield per recruit (kg) as a function of the proportion of unfished SPR, η_p , where p = 1.00, 0.99, 0.98, ...,0.10. Note that the units of spawning biomass are

unimportant as long as the estimates of stock size are calculated the same way.

Results

The hierarchical Bayesian model produced credible S-R curves in comparison with independent estimates for each stock (Figure 1). When estimated independently, a steepness of 1.0 was obtained for 5 of the 11 stocks (chilipepper, black rockfish, and the Pacific ocean perch stocks in Goose Island Gully, the Gulf of Alaska, and the Aleutian Islands), implying that recruitment is unrelated to stock size. Several West Coast rockfish, including chilipepper, bocaccio, widow, and yellowtail rockfish, were estimated to be above the unfished equilibrium spawning biomass, S_0 , in the early 1970s due to favorable recruitment. For the hierarchical Bayesian model, estimates are shrunk towards the overall average steepness of approximately 0.65 (Figure 2). Estimated steepness for stocks with uninformative S-R data (e.g., chilipepper and bocaccio) show the largest shrinkage, while stocks with more informative S-R data (e.g., West Coast and Gulf of Alaska Pacific ocean perch stocks) show less shrinkage.

Empirical histograms of steepness, h_k , compiled from the MCMC samples, represent marginal posterior distributions of steepness and indicate how informative the data are concerning this critical parameter (Figure 3). Posterior distributions for several stocks are more informative than the rest.



Spawning biomass/Egg production

FIGURE 1.—Stock—recruit (S-R) data for 11 northeastern Pacific rockfish stocks. The solid lines are the Beverton—Holt S-R curves based on the posterior modes from a hierarchical Bayesian model; the dotted lines are the resulting curves when each S-R relationship is estimated separately. The right endpoints of the curves indicate the unfished equilibria (S_0) for all stocks except Gulf of Alaska Pacific ocean perch, for which the endpoint is 20% of S_0 .

The West Coast stock of Pacific ocean perch shows a low posterior mode for steepness (\sim 0.35), suggesting a weak compensatory response. Pacific ocean perch stocks from Goose Island Gully (central British Columbia coast) to the Aleutian Islands show high steepness (0.7–0.85), suggesting that they are more resilient than other rockfish stocks to the south. Canary rockfish also have a narrow posterior distribution for steepness, with a mode in the middle of the range (\sim 0.55). The remaining rockfish stocks show relatively flat posterior dis-

tributions, indicating that the S-R data are not highly informative.

Residual analysis indicated that the assumption of lognormal recruitment variability was reasonable. No severe patterns were evident when the log-scale residuals were plotted by year, although several moderate patterns were evident (Figure 4). Since 1990, the average of the residuals for West Coast rockfish stocks has been slightly negative. For Alaskan and British Columbian stocks, the residuals were strongly negative in the early 1970s;

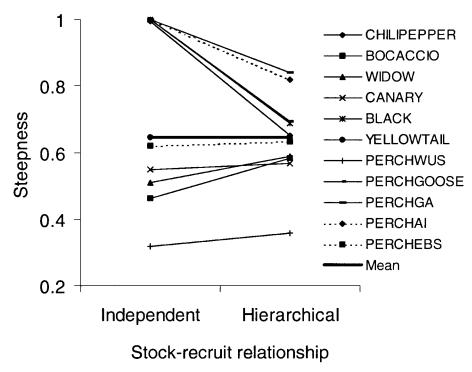


FIGURE 2.—Posterior mode estimates of steepness (h_k) when stock—recruit relationships are estimated separately and when they are estimated jointly with a hierarchical Bayesian model. Stock identification codes are given in Table 1.

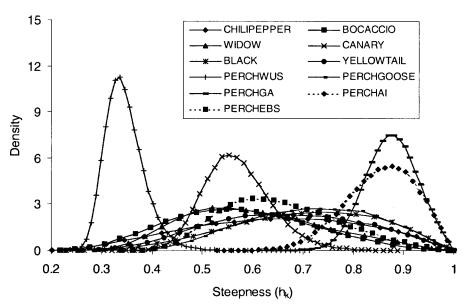
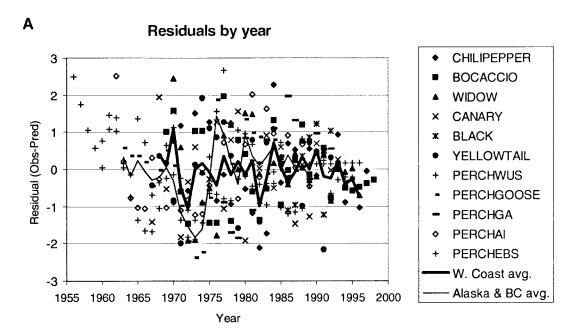


FIGURE 3.—Marginal posterior distributions of steepness for 11 rockfish stocks from a hierarchical Bayesian model. Stock identification codes are given in Table 1.



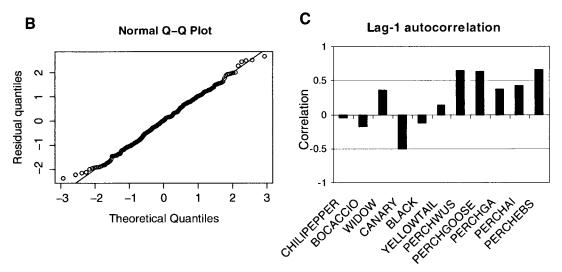


FIGURE 4.—Residual analysis (observed less predicted values) of the Beverton-Holt model with lognormal errors; (A) residuals by year, (B) quantile—quantile plot of the log-scale residuals against a standard normal distribution, and (C) lag-1 autocorrelation of residuals. The abbreviation BC stands for British Columbia. Stock identification codes are given in Table 1.

this was followed by several years of strongly positive residuals. A quantile—quantile plot of the log-scale residuals against a normal distribution suggested that the lognormal distribution was an appropriate model for recruitment variability. The lag-1 autocorrelation of the residuals showed some interesting differences between stocks. For Pacific ocean perch stocks, the lag-1 autocorrelation was strong (\sim 0.5) and consistently positive. For West

Coast stocks except Pacific ocean perch, the lag-1 autocorrelation was generally weak, and, in some cases, negative. Since the presence of autocorrelation could bias the estimated S-R curve, particularly with a short time series of data, there is a need for caution in drawing conclusions from the apparent strong compensation of the Pacific ocean perch stocks in Alaska and British Columbia and the apparent weak compensation of the West

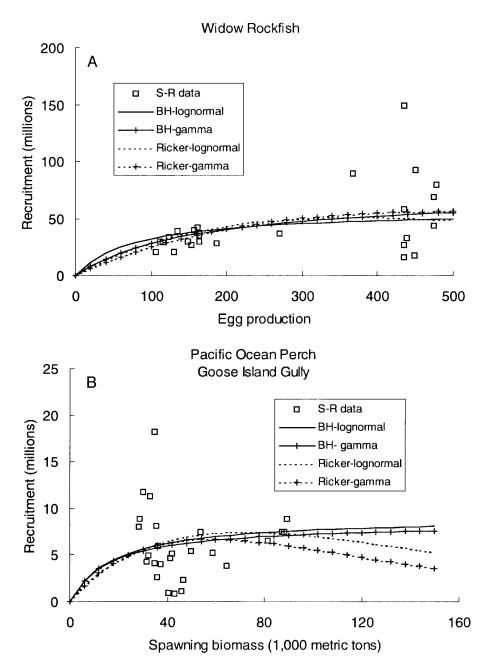


FIGURE 5.—Comparison of posterior mode stock—recruit curves for two different models (Beverton–Holt [BH] and Ricker) and recruitment error distributions (lognormal and gamma) for (A) widow rockfish and (B) Goose Island Gully Pacific ocean perch.

Coast Pacific ocean perch stock (see also Ianelli 2002, this issue).

Stock—recruit curves for the Beverton—Holt and Ricker models were similar, and both functional forms adequately described the mean relationship between stock size and recruitment (Figure 5). The Ricker model consistently estimated a lower initial slope for the S-R curve but predicted higher recruitment at intermediate stock sizes. Ricker curves for the stocks that appear to be more resilient (i.e., Goose Island Gully Pacific ocean perch) predict decreasing recruitment at high size,

TABLE 2.—Posterior mode log-likelihoods for two different stock-recruit relationships (Beverton-Holt and Ricker) and recruitment error distributions (lognormal and gamma) for a hierarchical model of rockfish stock-recruitment relationships. Bayesian information criteria (BIC) differences are relative to the Beverton-Holt model with lognormal error. Stock identification codes are given in Table 1.

| Stock identification - code and prior | Beverton-Holt | | | Ricker | | | |
|---------------------------------------|---------------|--------|----------------|-----------|----------------|--------|----------------|
| | Lognormal | Gamma | BIC difference | Lognormal | BIC difference | Gamma | BIC difference |
| CHILIPEPPER | -122.0 | -123.2 | -1.2 | -122.3 | -0.3 | -123.4 | -1.3 |
| BOCACCIO | -58.4 | -60.2 | -1.8 | -58.4 | 0.1 | -59.4 | -0.9 |
| WIDOW | -117.3 | -117.2 | 0.1 | -117.2 | 0.1 | -117.0 | 0.3 |
| CANARY | -24.4 | -24.2 | 0.2 | -24.8 | -0.4 | -24.7 | -0.2 |
| BLACK | -3.9 | -3.9 | 0.0 | -2.3 | 1.6 | -1.9 | 1.9 |
| YELLOWTAIL | -77.2 | -76.6 | 0.6 | -77.1 | 0.1 | -76.4 | 0.8 |
| PERCHWUS | -67.3 | -68.4 | -1.1 | -66.6 | 0.7 | -67.9 | -0.7 |
| PERCHGOOSE | -70.8 | -69.3 | 1.5 | -71.3 | -0.5 | -69.7 | 1.2 |
| PERCHGA | -78.7 | -77.8 | 0.9 | -78.8 | -0.1 | -78.0 | 0.7 |
| PERCHAI | -132.9 | -136.0 | -3.0 | -135.9 | -3.0 | -138.9 | -6.0 |
| PERCHEBS | -128.4 | -130.6 | -2.2 | -129.6 | -1.2 | -132.9 | -4.5 |
| R_0 prior | -45.3 | -45.5 | | -45.0 | | -45.2 | |
| Hierarchical prior | -11.8 | -14.3 | | -9.0 | | -10.4 | |
| Hyperprior | 0.6 | 0.4 | | 0.6 | | 0.7 | |
| Total | -937.8 | -947.1 | -9.1 | -937.8 | 0.1 | -945.1 | -7.1 |

which is not evident in the data. For the stocks with a weaker compensatory response (i.e., widow rockfish), the Ricker curve closely tracks the asymptotic Beverton-Holt curve (Figure 5). Lognormal and gamma error models resulted in similar S-R curves (Figure 5). For widow rockfish, the gamma error model estimated a lower steepness than the lognormal model, resulting in a predicted S-R curve that more closely passes though the cluster of points at 100–200 units of egg production. However, other than the gamma model's tendency to estimate a lower steepness, it was impossible to discern any consistent difference between the lognormal and gamma models.

Bayesian approaches to model comparison are based on the posterior probability of the model given the data, also called the integrated or marginal likelihood (Draper 1995). Although estimation of posterior model probabilities using asymptotic approximations and posterior simulation is an active area of research, no general approach is yet available for hierarchical models (Raftery 1996; Diciccio et al. 1997). The Bayesian information criterion (BIC) is a simple asymptotic approximation to the posterior model probability that can be used (with caution) for model comparison (Raftery 1995). The BIC is defined as $p(Z|\hat{\Theta})$ – $(d/2)\log_e n$, where $\hat{\Theta}$ is the posterior mode (maximum likelihood estimate), d is the number of parameters, and n is the number of observations. Since all the models considered here have the same number of parameters and observations, log-likelihoods at the posterior mode allow direct comparison of different stock-recruit and recruitment variability models. Raftery (1995) considers a difference of less than 2 in BIC values to be "weak" evidence in favor of the model with the higher value, a difference between 2 and 6 to be "positive" evidence, and a difference greater than 6 to be "strong" evidence.

The total log-likelihood for the Beverton-Holt model is nearly equivalent to that for the Ricker model with the same recruitment error assumption, and for individual stocks no consistent pattern is apparent (Table 2). For both the Beverton-Holt and Ricker S-R models, the total log-likelihood was higher for the lognormal error model than for the gamma error model, but the BIC differences were greater than 2 only for Pacific ocean perch stocks in the Aleutian Islands and the eastern Bering Sea. These results suggest that there is little reason to prefer either the Beverton-Holt or the Ricker model for the stock-recruit curve if they are given equal prior probability. The evidence is stronger for the lognormal recruitment error model than for the gamma error model, but it is not overwhelming.

Comparisons of the posterior predictive distributions of β_k (the distribution for an unobserved stock) with the set of S-R relationships considered by Clark (1991) suggest that the range of S-R relationships considered by Clark (1991) is too optimistic for rockfish. Clark considered five S-R curves each for the Beverton-Holt and Ricker models that differed by the potential increase in reproductive success (R/S at the origin) relative to that of an unfished stock (R_0/S_0). Potential increases in reproductive success by factors of 4, 8, and

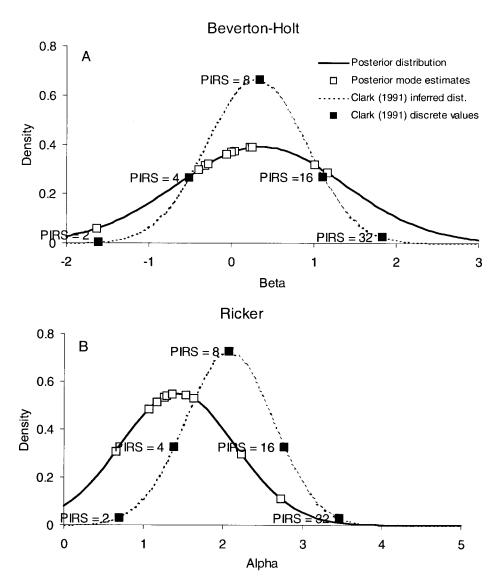


FIGURE 6.—Panel (**A**) shows the posterior predictive distribution of the logit transformed steepness (β_k) for the Beverton–Holt model for an unobserved stock. The location of the posterior mode estimates of β_k for 11 rockfish stocks are indicated on the distribution. The β_k for the discrete Beverton–Holt S–R curves considered by Clark (1991) and a distribution for β_k inferred from the discrete curves are also shown. The potential increase in reproductive success (R/S at the origin) relative to an unfished stock R_0/S_0 (PIRS) is indicated for each of the Clark (1991) alternatives. Panel (**B**) shows the posterior predictive distribution of the scaled slope at the origin (α_k) for the Ricker model.

16 (steepness = 0.50, 0.67, and 0.80, respectively) were considered plausible, while those by factors of 2 and 32 (steepness = 0.33 and 0.89, respectively) were considered implausible. The posterior predictive distributions are wider than the range considered by Clark (1991), and the posterior mode estimates for most rockfish are below the midpoint of the range, particularly for the Ricker model (Figure 6).

Stock—recruit steepness is a useful metric for the degree of compensation in the S-R relationship and is of potential use in stock assessment modeling and in Monte Carlo simulations to evaluate rebuilding plans and harvest policies. The posterior predictive distribution of steepness can be used as the prior probability distribution for an unobserved rockfish stock. To assist future rockfish assessment work, MCMC samples of the pos-

TABLE 3.—Prior probability distribution of steepness for an unobserved rockfish stock from a hierarchical Bayesian model with lognormal recruitment variability. Priors for Beverton–Holt and Ricker models are shown, along with an equally weighted combination of the priors for the two models. Prior probabilities for the posterior distribution of steepness were estimated by tabulating the number of Markov chain Monte Carlo samples in each bin.

| Bin lower | | | Probability | |
|-----------------------------|----------|-------------------|-------------|----------|
| bound and statis- tic | Midpoint | Beverton- Holt | Ricker | Combined |
| 0.20 | 0.225 | 0.003 | 0.028 | 0.016 |
| 0.25 | 0.275 | 0.012 | 0.052 | 0.032 |
| 0.30 | 0.325 | 0.024 | 0.072 | 0.048 |
| 0.35 | 0.375 | 0.038 | 0.087 | 0.062 |
| 0.40 | 0.425 | 0.054 | 0.104 | 0.079 |
| 0.45 | 0.475 | 0.066 | 0.112 | 0.089 |
| 0.50 | 0.525 | 0.075 | 0.114 | 0.094 |
| 0.55 | 0.575 | 0.083 | 0.106 | 0.094 |
| 0.60 | 0.625 | 0.093 | 0.095 | 0.094 |
| 0.65 | 0.675 | 0.100 | 0.078 | 0.089 |
| 0.70 | 0.725 | 0.105 | 0.060 | 0.083 |
| 0.75 | 0.775 | 0.100 | 0.043 | 0.072 |
| 0.80 | 0.825 | 0.093 | 0.028 | 0.061 |
| 0.85 | 0.875 | 0.077 | 0.015 | 0.046 |
| 0.90 | 0.925 | 0.054 | 0.006 | 0.030 |
| 0.95 | 0.975 | 0.024 | 0.001 | 0.012 |
| Mean | | 0.67 | 0.52 | 0.59 |
| SD | | 0.17 | 0.16 | 0.18 |

terior predictive distribution were tabulated (Table 3). For the Ricker model, steepness was estimated using $h = \exp(\alpha)/[\exp(\alpha) + 4]$, which converts the scaled slope at the origin for the Ricker model to steepness for a Beverton–Holt curve with the same scaled slope at the origin (Myers et al. 2002, this issue). The mean of the posterior predictive distribution of steepness was 0.67 for the Beverton–Holt model, 0.52 for the Ricker model, and 0.59 for an equally weighted combination of the two models.

For each level of SPR, MCMC sampling generates a probability distribution for equilibrium yield that reflects the effect of uncertainty in the stock-recruit relationship on yield. The probability distribution of equilibrium yield for a sequence of SPR harvest rates ranging from $F_{100\%}$ to $F_{10\%}$ was obtained for chilipepper, a stock with relatively uninformative S-R data (Figure 7). The expected yield (the average of the distribution of yield) increases, reaches a maximum, and then declines, as would occur for a fixed-parameter S-R relationship. However, uncertainty in the S-R relationship affects the distribution of yield in ways that are important to consider in providing management advice. The coefficient of variation (CV = 100 × SD/mean) of yield is relatively constant

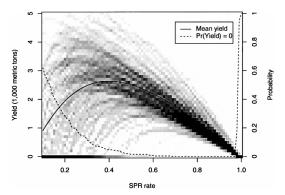


FIGURE 7.—Distribution of equilibrium yield (left scale) and probability of zero yield (i.e., an unsustainable harvest rate; right scale) for chilipepper obtained by Markov chain Monte Carlo sampling. For each spawning-biomass-per-recruit (SPR) harvest rate, the empirical distribution of the equilibrium yield is indicated by a gray-based scale, with black denoting the highest posterior probability.

when SPR is higher than the value at which yield is maximized (e.g., $\sim F_{41\%}$ for chilipepper), but it increases as SPR decreases further as a result of the increasing uncertainty in yield as the harvest rate increases. At harvest rates higher than $F_{\rm MSY}$, yield has a bimodal distribution in which either large equilibrium yields or stock collapse is possible. The probability of zero yield (stock collapse) increases monotonically from less than 0.05 at $F_{\rm MSY}$ to 0.63 at $F_{\rm 10\%}$.

A wide range of expected yield curves was obtained for different rockfish stocks (Figure 8). Pacific ocean perch stocks in the Aleutian Islands and Gulf of Alaska are apparently more resilient than other rockfish stocks, with the maximum expected yield occurring at a harvest rate exceeding $F_{30\%}$ for all models examined. The West Coast stock of Pacific ocean perch is at the other end of the range of resiliency, with the maximum expected yield occurring at a harvest rate lower than $F_{70\%}$. The SPR rates at MSY for other stocks were clustered between $F_{40\%}$ and $F_{60\%}$, depending on both the S-R model (Beverton-Holt or Ricker) and the model for recruitment variability (lognormal or gamma). The results are summarized in Table 4, where the maximum for a group of stocks was obtained by scaling each yield curve relative to its maximum and then averaging across stocks. A general ordering of models from the highest $F_{\rm MSY}$ to the lowest is (1) Beverton–Holt with lognormal error, (2) Ricker with lognormal error, (3) Beverton-Holt with gamma error, and (4) Ricker with gamma error. Risk-averse estimates of $F_{\rm MSY}$

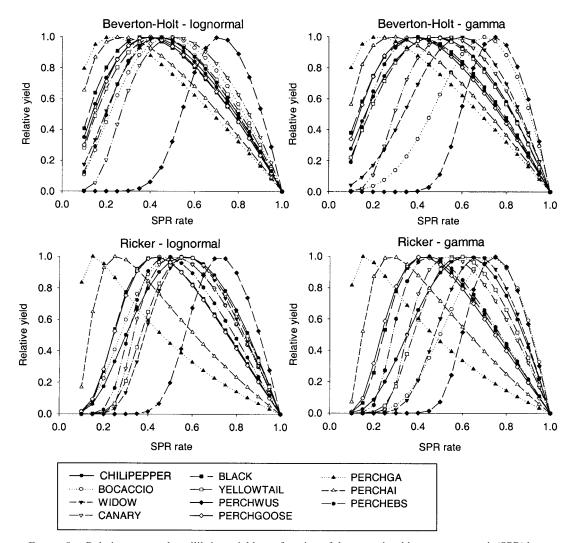


FIGURE 8.—Relative expected equilibrium yield as a function of the spawning-biomass-per-recruit (SPR) harvest rate for two different stock—recruit models (Beverton–Holt and Ricker) and error distributions (lognormal and gamma) for 11 rockfish stocks. Stock identification codes are given in Table 1.

(maximum square root yield) were between 0 and 7 percentage points higher in SPR than risk-neutral estimates. Risk-averse estimates for stocks with uninformative stock—recruit curves (e.g., chilipepper and bocaccio) showed a greater reduction in harvest rate than stocks with informative stock—recruit curves (e.g., canary rockfish and Goose Island Gully Pacific ocean perch).

Results were also obtained for a hierarchical model that excludes all Pacific ocean perch stocks (Table 4). Although Pacific ocean perch stocks have longest time series of stock—recruit data, several factors motivated consideration of a model that excluded these stocks, including the strong

autocorrelation in model residuals and the lack of overlap between the range of Pacific ocean perch and that of West Coast rockfish. The results for this model indicated somewhat lower harvest rates at $F_{\rm MSY}$ (Table 4). When Pacific ocean perch stocks were excluded, the SPR at $F_{\rm MSY}$ for the remaining stocks increased 7 percentage points on average for the Beverton–Holt model but only 2 percentage points on average for the Ricker model.

Discussion

Uncertainty permeates harvest rate estimation, perhaps more so than in any other aspect of fisheries science. Bayesian methods, like the hierar-

TABLE 4.—The spawning biomass per recruit harvest rates at the maximum sustainable yield (MSY) for risk-neutral (maximum expected yield) and risk-averse (maximum square root yield, in parentheses) loss functions for hierarchical models using stock–recruit data for all rockfish stocks and West Coast rockfish stocks excluding Pacific ocean perch (POP) and two recruitment error distributions (lognormal and gamma). The MSY for a group of stocks was obtained by scaling each yield curve relative to its maximum, then averaging across the stocks in the group. Stock identification codes are given in Table 1.

| | | Beverton-Holt | | Ricker | |
|---------------------|---|---------------|---------|-----------|---------|
| Data used | Stock | Lognormal | Gamma | Lognormal | Gamma |
| All North Pacific | CHILIPEPPER | 41 (44) | 47 (54) | 57 (63) | 62 (68) |
| rockfish | BOCACCIO | 49 (52) | 70 (74) | 52 (58) | 73 (78) |
| | WIDOW | 45 (47) | 60 (62) | 57 (59) | 67 (70) |
| | CANARY | 51 (51) | 54 (54) | 52 (52) | 54 (54) |
| | BLACK | 37 (40) | 40 (44) | 43 (46) | 43 (46) |
| | YELLOWTAIL | 43 (46) | 47 (51) | 57 (59) | 59 (61) |
| | PERCHWUS | 71 (72) | 75 (75) | 72 (73) | 74 (75) |
| | PERCHGOOSE | 39 (39) | 38 (39) | 44 (44) | 42 (42) |
| | PERCHGA | 22 (22) | 22 (22) | 15 (15) | 16 (15) |
| | PERCHAI | 27 (27) | 29 (28) | 26 (26) | 28 (28) |
| | PERCHEBS | 43 (43) | 40 (40) | 48 (48) | 45 (45) |
| | Group 1: all stocks | 44 (53) | 55 (62) | 53 (59) | 61 (65) |
| | Group 2: West Coast rockfish except POP | 45 (47) | 56 (60) | 54 (57) | 67 (67) |
| West Coast rockfish | CHILIPEPPER | 49 (53) | 61 (66) | 60 (67) | 67 (72) |
| except POP | BOCACCIO | 53 (55) | 71 (73) | 56 (62) | 75 (80) |
| | WIDOW | 49 (51) | 63 (65) | 59 (61) | 68 (71) |
| | CANARY | 52 (52) | 56 (56) | 53 (53) | 54 (54) |
| | BLACK | 46 (49) | 55 (58) | 46 (50) | 47 (50) |
| | YELLOWTAIL | 50 (52) | 58 (60) | 59 (61) | 60 (61) |
| | All stocks | 50 (52) | 62 (65) | 56 (60) | 65 (69) |

chical models developed in this paper, are able to deal with uncertainty in a rigorous way. Nevertheless, there are potentially important sources of bias and uncertainty that could not be addressed with these methods. These sources of bias and uncertainty are discussed below to emphasize the need for caution when interpreting meta-analysis results.

The models developed in this paper treat stock and recruitment estimates from assessment models as though they were data. Although this is a standard assumption for S-R analyses, it is important to consider how this assumption could affect the results. Rockfish assessments are data poor, and equilibrium assumptions are often made to initialize the numbers-at-age matrix. The S-R estimates produced by such models are highly uncertain. Because biomass is linked to earlier recruitment in an assessment model, a spurious trend in stock size caused by an imprecise survey index may bias estimates of F_{MSY} . A good example is the yellowtail rockfish assessment (Tagart et al. 1997), which carried forward two scenarios that differed in the types of fishery-independent information used to tune the model. Depending on which scenario was considered correct, the estimated steepness in the S-R relationship was either 0.34 (indicating very weak compensation) or 0.65 (indicating that yellowtail rockfish is average for a rockfish stock).

Another potential source of bias in estimating S-R curves is a result of the time series nature of stock-recruit data. This bias is caused because high recruitments produce high spawning biomass and low recruitments produce low spawning biomass. Consequently, the stock sizes at which recruitments are observed are not controlled variables, as is required for S-R parameter estimates to be unbiased. A thorough discussion of time series bias can be found in Hilborn and Walters (1992). Usually this bias has the effect of flattening the S-R curve, so that stocks appear to be more resilient to harvesting than they actually are. Because most rockfish stocks have been fished from pristine to low levels without reversals in the biomass trend, rockfish S-R parameters may be relatively unaffected by this bias. The estimates of high steepness for the Pacific ocean perch stocks that have experienced a reversal in biomass trend are more questionable because of potential time series bias.

Climate variation has a potential influence on estimates of stock productivity. There is strong evidence of lower productivity in the California

current beginning in the 1970s (Roemmich and McGowan 1995; Francis et al. 1998; McGowan et al. 1998). Since this is also the period during which rockfish stocks were fished down from pristine levels, the effects of stock size and the environment on recruitment are confounded. Biased estimates of S-R steepness could result if environmentally caused declines in recruitment are attributed instead to declining stock size. By including rockfish stocks from British Columbia and Alaska, the meta-analysis averages to some extent over climate variation on the regional scale. However, because the geographic representation of rockfish stocks with full assessments is not balanced, this advantage of meta-analysis could not be fully realized. Additional S-R data at stock sizes that are informative with respect to steepness will become available for many West Coast rockfish stocks over the next decade, so future attempts to discriminate between these hypotheses may prove successful, particularly if changing environmental conditions provide the necessary contrast.

The approach of modeling environmental dependence by adding additional parameters to stock-recruit models has been used for singlestock models (citations in Quinn and Deriso 1999), although such practices have been characterized as "dangerous" due to the difficulty of excluding spurious correlations (Hilborn and Walters 1992). The objective of this paper was to estimate the mean stock-recruit relationships, which logically must exist even if decadal climate variation influrecruitment. If the time series stock-recruit data are too short to span the range of potential environmental states, as is arguably the case for rockfish, adding additional parameters will not correct the problem. Fishery managers and stakeholders should be made aware that evaluation of rockfish stock-recruit relationships is an ongoing process and that changing environmental conditions could alter estimates of the mean stock-recruit relationships and harvest rates based on those relationships. If decadal variation is a dominant feature of rockfish stock-recruit relationships, consideration should be given to harvest policies that perform well in those circumstances (Methot 1998). Modeling studies of fish stocks whose carrying capacity is affected by climate change suggest that fixed harvest rate policies based on F_{MSY} for the mean stock-recruit relationship may perform nearly as well as time-varying optimal controls with perfect knowledge of future environmental conditions (Walters and Parma 1996). Because a change in carrying capacity is only one of the possible effects of climate change (e.g., the steepness of the stock-recruit curve could also be affected), additional work is needed on the robustness of fixed harvest rate policies in the presence of climate change (Walters and Korman 1999).

Pacific ocean perch is represented by five stocks from south to north: West Coast, Goose Island Gully, Gulf of Alaska, Aleutian Islands, and eastern Bering Sea. All were severely overfished by distant-water fleets in the 1960s and 1970s. It is interesting to note that stocks near the center of the range have increased in abundance and have S-R curves with high steepness. Stocks at the northern and southern limits of the range, namely, the West Coast and eastern Bering Sea stocks, have been slow to rebuild and have S-R curves with low steepness. The abundance of these peripheral stocks may be governed more by environmental conditions that expand or shrink favorable habitat than by density-dependent processes, suggesting that sustainable harvesting of these stocks may be problematic. These geographic differences in stock resiliency are accounted for in a hierarchical model, which assumes a probability distribution of stock-recruit "steepness" for the taxon but allows the data to determine how broad that distribution should be. It would also be possible to explicitly model the decline in resilience toward the edges of a species' range by including a covariate for steepness, such as distance from the geographic center of the species. In evaluating a harvest rate for a group of stocks, membership in the group should be considered carefully. Harvest rates that rely primarily on stock-recruit data from stocks in the center of a species' range may be inappropriate for peripheral stocks.

The estimates of mean steepness that I obtained for rockfish (range, 0.52–0.67) are lower than the estimates for the families Clupeidae (~0.7) and Gadidae (~0.8) obtained by Myers et al. (2002) in a meta-analysis of steepness for broad taxonomic groups. Myers et al. (2002) also found a positive correlation between steepness and longevity but noted that the genus *Sebastes* was an apparent exception to this pattern. Differences in life history traits and reproductive biology between rockfish and the well-studied species in the North Atlantic are a possible explanation for the lower steepness for rockfish.

When considering alternative target harvest rates for rockfish, meta-analysis results should be interpreted cautiously due to the problems discussed above. Rather than using the point estimates of F_{MSY} for any stock, it may be better to use meta-analysis results in a more advisory way to evaluate whether the current harvest policy requires modification and make an informed decision about the direction and magnitude of that change. This decision can be guided by two factors: whether or not the proposed SPR harvest rate is less than the point estimate of F_{MSY} and whether or not a large percentage of the potential yield can be obtained at that harvest rate. Since several additional years of data or revision of the assessment model could substantially change the $F_{\rm MSY}$ estimates for individual stocks, these estimates are unlikely to be stable in the sense that a similar analysis conducted 5 years from now would produce a similar estimate. An SPR harvest rate based on stock-recruit data for a group of stocks should show more stability over time, but it could lead to overharvesting some stocks and underharvesting others. Given the problematic nature of many rockfish assessments and the stock-recruit "data" derived from those assessments, some grouping of rockfish stocks seems warranted when establishing target harvest rates. As time series of stock-recruit data for individual stocks become longer, it should be possible to reduce the level of aggregation.

Another difficult issue is the extent to which stock—recruit data from Pacific ocean perch stocks should be considered when recommending target harvest rates for West Coast rockfish. The overlap between the range of Pacific ocean perch and West Coast rockfish is not extensive, and autocorrelation in the stock-recruit residuals for Pacific ocean perch stocks suggests a potential bias. On the other hand, Pacific ocean perch stocks have life history traits that are similar to those of West Coast rockfish and occur in a region where productivity increased after the mid-1970s regime shift, in contrast to the California Current system. The increase in recruitment for Gulf of Alaska and Aleutian Island Pacific ocean perch stocks after the regime shift are important for the understanding the potential effects of climate variation on West Coast rockfish.

My results suggest that SPR harvest rates in the $F_{40\%}-F_{60\%}$ range should be considered for West Coast rockfish. An $F_{40\%}$ harvest rate exceeded the $F_{\rm MSY}$ rate for all West Coast stocks and all sets of model assumptions except for black rockfish in the Beverton–Holt S–R model. After excluding West Coast Pacific ocean perch, only 4 of the 24 combinations of stock and stock–recruit model assumptions indicated that $F_{\rm MSY}$ was lower than $F_{60\%}$. For a model using only West Coast S–R

data, none of the $F_{\rm MSY}$ rates were higher than $F_{\rm 40\%}$ and 6 of the 24 combinations of model and stock indicated that F_{MSY} was lower than $F_{60\%}$. For West Coast rockfish as a group, models with lognormal error resulted in SPR harvest rates ranging from $F_{45\%}$ to $F_{56\%}$. An SPR harvest rate of $F_{50\%}$ is suggested as a reasonable compromise value for a risk-neutral F_{MSY} proxy for West Coast rockfish. Placing greater emphasis on models with gamma error and limiting S-R data to West Coast stocks would lead to recommendations in the $F_{55\%} - F_{60\%}$ range. A default harvest rate may not be appropriate for all rockfish stocks. The West Coast stock of Pacific ocean perch had the lowest estimated steepness of all rockfish stocks, suggesting that the stock's compensatory response to harvesting is unusually weak. A lower harvest rate may be advisable for this stock. As assessments for other rockfish stocks are updated, the appropriateness of any default F_{MSY} proxy should be evaluated to determine whether a further adjustment is warranted for the stock in question.

Although Canadian and Alaskan rockfish stocks were not specifically an objective of this investigation, a few comments follow. For the Goose Island Gully Pacific ocean perch stock, the current harvest policy setting F = M corresponds to an $F_{49\%}$ harvest rate (Richards and Olsen 1996). Although the F_{MSY} rate is higher, the loss of longterm yield from this policy is probably less than 5%. The F = M harvest rate could be considered a risk-averse harvest policy for this stock. For Pacific ocean perch stocks in Alaska, a default $F_{40\%}$ harvest policy is used. Hierarchical model results for all model configurations suggest that this rate is lower than the F_{MSY} for both the Gulf of Alaska and the Aleutian Island stocks. For the Beverton-Holt S-R curve, the loss of long-term yield for the Gulf of Alaska stock was approximately 12% at an $F_{40\%}$ harvest rate; for the Aleutian Islands stock, it was around 7%. The eastern Bering Sea stock has been slower to rebuild than other Alaska stocks and may be less resilient to harvesting. Hierarchical model results suggest that harvest rates in the $F_{45\%}$ – $F_{50\%}$ range may be more appropriate than the current $F_{40\%}$ policy.

Since the analysis presented in this paper focuses on equilibrium yield, it does not assess the effect of recruitment variability on the stability of the stock and associated yield. This may not be a serious shortcoming because, as Clark (1985) notes, "simply passing from a deterministic model to a related stochastic model is likely to have very little quantitative effect on the outcome of an op-

timization analysis." However, a lower fishing mortality rate would reduce the fluctuations in yield and abundance caused by recruitment variability (Quinn et al. 1990). An $F_{\rm MSY}$ harvest policy does not consider the potential benefits to the stock, the fishing industry, and ecologically dependent species that a lower harvest rate would generate by reducing annual variability. Future work on harvest policies should consider the potential benefits of "fluctuation aversion" (as well as those of risk aversion with respect to uncertainty in the S-R relationship).

The use of maximum expected square root yield as a risk-averse objective is an arbitrary, though reasonable, choice for this problem. It is intended primarily as an example of how to obtain a harvest rate that is formally risk averse in the presence of uncertainty in the S-R relationship and to encourage consideration of risk aversion in management decisions. For the risk-averse loss function considered here, the SPR harvest rate increased between 0 and 7 percentage points from the riskwith stocks with neutral rate, stock-recruit relationships showing the greatest change. It is important to note that the harvest control rule recently adopted by the Pacific Fishery Management Council for West Coast groundfish (the 40:10 rule) reduces the harvest rate at low stock size and is an alternative way to reduce the risk of overharvesting. The appropriate level of risk aversion in marine resource management is an open question. One can hope that experience, particularly those instances when uncertainty did not result in appropriately risk-averse decision making, will lead to improved decisions in the future. Science can help achieve societal goals by clearly demonstrating the probable consequences of decisions and by ensuring that policies are applied consistently. Harvest policy guidelines developed by the National Marine Fisheries Service are designed to maintain stocks at the crest of their production curves as required by the Magnuson-Stevens Fishery Conservation and Management Act. As broader ecosystem concerns become increasingly important, policies that further reduce the cumulative human impact on marine ecosystems will be required (NRC 1999).

Acknowledgments

Alec MacCall inspired this inquiry into the sustainability of harvest policies for West Coast rockfish and made suggestions that improved this paper. Jim Ianelli generously provided advice on modeling approaches. I thank Ransom Myers, Ray

Hilborn, Jon Brodziak, and Grant Thompson for comments on an earlier version. A draft of this paper was reviewed at a harvest policy workshop convened by the Scientific and Statistical Committee of the Pacific Fishery Management Council. The harvest policy review panel members, Stephen Ralston (chair), James Bence, William Clark, Ramon Conser, Thomas Jageilo, and Terrance Quinn II are also acknowledged.

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