

THE VARIABILITY AMONG POPULATIONS OF COHO SALMON IN THE MAXIMUM REPRODUCTIVE RATE AND DEPENSATION

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Abstract. Estimating parameters for population-dynamics models is a critical component in assessing extinction probabilities of populations. For many individual populations, key parameters will be poorly defined, and meta-analysis would provide a basis for estimating the parameters. Here, we introduce meta-analytical techniques to estimate the maximum reproductive rate, carrying capacity, and depensation in coho salmon on the west coast of North America. We used both nonlinear mixed-effects models and Bayesian techniques to estimate several population-dynamics models, including the Beverton-Holt and hockey-stick models, for 14 spawner–recruitment time series. The Beverton-Holt and hockey-stick mixed-effects models yielded equivalent fits to the data but gave very different estimates of α (the maximum rate at which female spawners can produce female smolts at low population sizes). The mean α for the Beverton-Holt mixed-effect model was 71.5 (1 SE = 1.2) female smolts per spawning female, whereas the hockey-stick estimate was 53.0 (1 SE = 1.14). We found little evidence for a general effect of depensation in coho salmon, unless fewer than one female per kilometer of river returned to spawn.

Key words: Allee effect; coho salmon; conservation; depensation; inverse density dependence; maximum reproductive rate; meta-analysis; population dynamics.

INTRODUCTION

A key ecological issue—perhaps the fundamental one in the estimation of extinction probabilities—is the nature of population dynamics at low population sizes. For fish, population dynamics are often described using well-known models, such as the Beverton-Holt (Beverton and Holt 1957) and more recently, the hockey stick and its generalizations (Barrowman and Myers 2000). These models estimate the maximum reproductive rate, i.e., the rate at which spawners can produce replacement spawners at low population sizes without fishing. When considering extinction dynamics, specifying the maximum reproductive rate and modeling depensation allows us to determine the capacity for growth and the speed with which populations recover from reduced sizes.

Usually, we lack any information at low population sizes, so that the estimation of extinction probabilities is extremely difficult. However, for coho salmon, a relatively large number of data sets are available in which the production of smolts is estimated at low population

abundance. Unfortunately, these time series are generally short and vary in quality.

We contend that, in order to make progress, information from many populations must be combined. This may be viewed as a form of meta-analysis. To do this, we must abandon the pretense that ecological parameters among populations are unrelated, and instead model them as being drawn from a common distribution. In statistical terms, rather than treating ecological parameters as population-specific values to be separately estimated, i.e., as fixed effects, we treat them as coming from a probability distribution with mean and variance to be estimated, i.e., as random effects. The resulting models are known as mixed-effects models or hierarchical models.

Meta-analytic investigations in ecology may have several different goals: to obtain overall estimates of ecological parameters, to explore heterogeneity in the information provided by different populations, and to provide predictions regarding populations for which no direct data are available. Additionally, mixed-effects models for meta-analysis can provide improved population specific estimates.

The chief goal of this work is to develop meta-analytical methods for the estimation of extinction probabilities under various management actions. We have had very good success using a meta-analytic approach on a variety of other problems (Myers et al. 1995a, Myers and Barrowman 1996, Myers 1997), and have

Manuscript received 30 May 2001; revised 17 June 2002; accepted 4 September 2002; final version received 15 October 2002. Corresponding Editor: L. B. Crowder.

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completed two recent meta-analytical studies for sockeye salmon (Myers et al. 1997a, 1998).

Here, we extend existing approaches to combining population parameters among populations, and apply these methods to coho salmon populations. We standardized all the populations considered so that they are all in the same units. This allows all the parameters to be compared among populations. In previous approaches, e.g., Liermann and Hilborn (1997), only a subset of population parameters were treated as comparable among populations.

Our analysis models the freshwater portion of coho life history, so that this information can be combined with independent data on survival at sea to produce improved management models. For example, in Southern British Columbia, coho salmon catches and escapements have declined in the last 20 years and there has been considerable disagreement on the causes of these declines (Walters 1993, Walters and Ward 1998, Beamish et al. 1999). However, it is clear that salmon survival at sea has greatly declined in recent years (Bradford et al. 2000). Our analysis of their freshwater survival can produce estimates of the mean and variation among populations, which can then be combined with long term data on survival at sea. Furthermore, we can produce improved population-specific estimates for individual rivers.

DATA

Our primary source of data is the compilation by Bradford et al. (1997). We have also obtained several more unpublished sources of data (Pacific Biological Station, Nanaimo, British Columbia, Canada, Salmon Archive, BL/2/5). In all, we have data on 14 populations of coho salmon. An in-depth analysis of these and related data is in Bradford et al. (2000).

We will estimate the production of female smolts per female spawner. Note, however, that our spawner units are always the number of female spawners per kilometer of stream, and the units for recruits are the number of female smolts produced per kilometer of stream. The lengths of streams ranged from ~1 km to 92 km, with a median of 7 km. Also, we assume that the sex ratio of smolts is 1:1 (Dittman et al. 1998). This puts data from all streams in common units, thus allowing comparisons among streams.

SPAWNER-RECRUITMENT MODELS

We extend the nonlinear mixed model approach used by Myers et al. (2001) to include a wider range of spawner-recruitment functions and depensation. Let $R_{i,t}$ be recruitment in units of female smolts from cohort t from population i , and let $S_{i,t}$ be the number of female spawners that produced those smolts. For coho salmon, we primarily consider models in which recruitment is a nondecreasing function of spawner abundance, in contrast to models that display overcompensation such as the Ricker model. Coho salmon juveniles are ter-

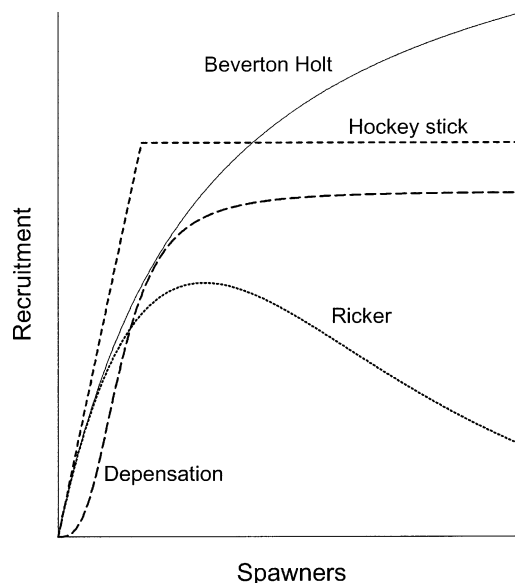


FIG. 1. The four spawner-recruitment curves considered in this paper.

ritorial (Sandercock 1991), and little density-dependent mortality appears to occur until territories have filled the habitat, i.e., the stream (Bradford et al. 1997, 2000, Barrowman and Myers 2000). In this case, we would expect survival to remain relatively constant until the habitat was close to being full, and then survival would decrease. This would result in recruitment being proportional to spawner abundance at low spawner abundance, and then leveling off at higher spawner abundance. We consider four spawner-recruitment functions (Fig. 1). In each case, the parameters of the function must be positive.

The Beverton-Holt model,

$$R_{i,t} = \frac{\alpha_i S_{i,t}}{1 + (S_{i,t}/K_i)}$$

seems to match the general compensatory population dynamics of coho salmon. The parameter α_i gives the slope at the origin, and is the maximum reproductive rate when multiplied by natural survival at sea. The parameter K_i is the spawner abundance corresponding to half the asymptotic recruitment (carrying capacity.) Barrowman and Myers (2000) showed that, for a single population, the Ricker model often gives more reasonable extrapolations of the slope at the origin than does the Beverton-Holt. Of the models considered, only the Ricker model shows overcompensation, i.e., recruitment declines at high spawner abundances. Barrowman and Myers (2000) and Bradford et al. (2000) also proposed the hockey-stick model:

$$R_{i,t} = \alpha_i \min(S_{i,t}, S_i^*)$$

where S_i^* is the spawner abundance at which density dependence has an effect. Barrowman and Myers

(2000) showed that the hockey-stick model typically gives reasonable extrapolations of the slope at the origin as well as matching the population dynamics of coho salmon. They also proposed two generalizations of the hockey stick that allow for a smoother transition between density-independent mortality and density-dependent mortality: the quadratic hockey stick (not presented here), and the smoother logistic hockey stick,

$$R_{i,t} = \alpha_i \theta_i \mu_i (1 + e^{-1/\theta_i}) \times \left\{ \frac{S_{i,t}}{\theta_i \mu_i} - \log \left[\frac{1 + e^{(S_{i,t} - \mu_i)/(\theta_i \mu_i)}}{1 + e^{-1/\theta_i}} \right] \right\}. \quad (1)$$

where θ_i is a smoothness parameter and μ_i is the inflection point of spawner abundance (Barrowman and Myers 2000).

A number of authors have expressed concern about depensatory dynamics (Courchamp et al. 1999, Stephens and Sutherland 1999). Myers et al. (1995a) investigated depensation for 128 fish populations using a modification of the Beverton-Holt model, which we call the type-1 depensatory Beverton-Holt model:

$$R_{i,t} = \frac{\alpha_i S_{i,t}^{\delta_i}}{1 + S_{i,t}^{\delta_i}/K_i}$$

where δ_i controls the extent of depensation. The parameter α_i has dimensions of recruitment per spawner in all of the models. Except for the depensation model, α_i gives the slope of the function at $S_{i,t} = 0$; it is crucial to setting the limits of overfishing (Mace 1994, Myers and Mertz 1998).

A second way to introduce depensation into a spawner-recruitment model is through multiplication by a term of the form

$$\frac{S_{i,t}}{S_{i,t} + d_i}.$$

We call models altered in this way type-2 depensatory models. The parameter d_i controls the extent of depensation; the original function is obtained when $d_i = 0$. The depensation parameter can be thought of as the number of female spawners per kilometer of stream needed to reduce the expected number of recruits by 50% relative to a model without depensation. This parameterization was used to obtain depensatory versions of the Beverton-Holt and logistic hockey-stick models.

INDIVIDUAL MODEL FITS

We will assume that within a population there is no autocorrelation in the recruitment residuals among years during the freshwater life-history stage (Bradford 1999). We also assume that the log-transformed deviations from the spawner recruitment curve are normal (Myers et al. 1999). Individual maximum likelihood fits of the Beverton-Holt model to these data are shown in Fig. 2.

The data sets vary tremendously in terms of information content due to differences in sample size and

the configuration of spawner observations. The data for two rivers, Bingham Creek and Qualicum River, suggest that the slope at the origin is arbitrarily large, i.e., $\alpha_i = \infty$ or equivalently $1/\alpha_i = 0$. Defining $\pi_i = 1/\alpha_i$, it can be shown (Barrowman 2000) that for $\hat{\pi}_i = 0$ to be a least-squares estimate of π_i , it is necessary that

$$\sum_{j=1}^{n_i} \log(R_{i,j}/\tilde{R}_i)/S_{ij} \geq 0$$

where \tilde{R}_i denotes the geometric mean of the observed recruitments in population i . Indeed this condition holds for Bingham Creek and Qualicum River, and in both cases, when α_i is not constrained to be positive, a numerical optimizer converges to a negative estimate. We conclude that, for these cases, the likelihood is maximized by an infinite slope at the origin. However, this is not credible: there cannot be more female smolts than the number of eggs produced by a female spawner, which though large (~ 3500), is certainly finite.

A formal model selection criterion can be used to choose the "best" model for the coho spawner-recruitment data. The Akaike Information Criterion (AIC) is commonly used for this purpose. Since each of the three models has the same number of parameters (two), choosing the model with the largest log likelihood is equivalent to using the AIC for model selection (Table 1).

In only one case (Deer Creek) is the maximized log likelihood for the Ricker model larger than that for the Beverton-Holt model. Summing the individual maximized likelihoods (last line of Table 1) shows that the Beverton-Holt model provides much better overall fitting of the data than the Ricker model. The comparison between the Beverton-Holt and the hockey-stick model is more equivocal. The AIC favors the Beverton-Holt for seven of the populations and the hockey stick for the other seven. For several populations, however, the maximized likelihood for the hockey stick is considerably larger than that for the Beverton-Holt.

MODELS

Mixed-effects Models

Our goal is to examine fits of spawner-recruitment models simultaneously for all 14 rivers; we thus need to consider the patterns of deviations of the observations of recruitment from the mean behavior model. Previous work has shown that, in the marine environment, recruitment deviations are correlated at separations of roughly 500 km (Myers et al. 1995b, 1997b) compared to < 50 km in the freshwater environment (Myers et al. 1997b). These results apply for coho salmon, for which freshwater survival is almost independent among years for populations > 20 km apart, but marine survival is correlated at a much greater spatial scale (Bradford 1999). Thus, in what follows we will assume that deviations from the spawner-recruitment relation-

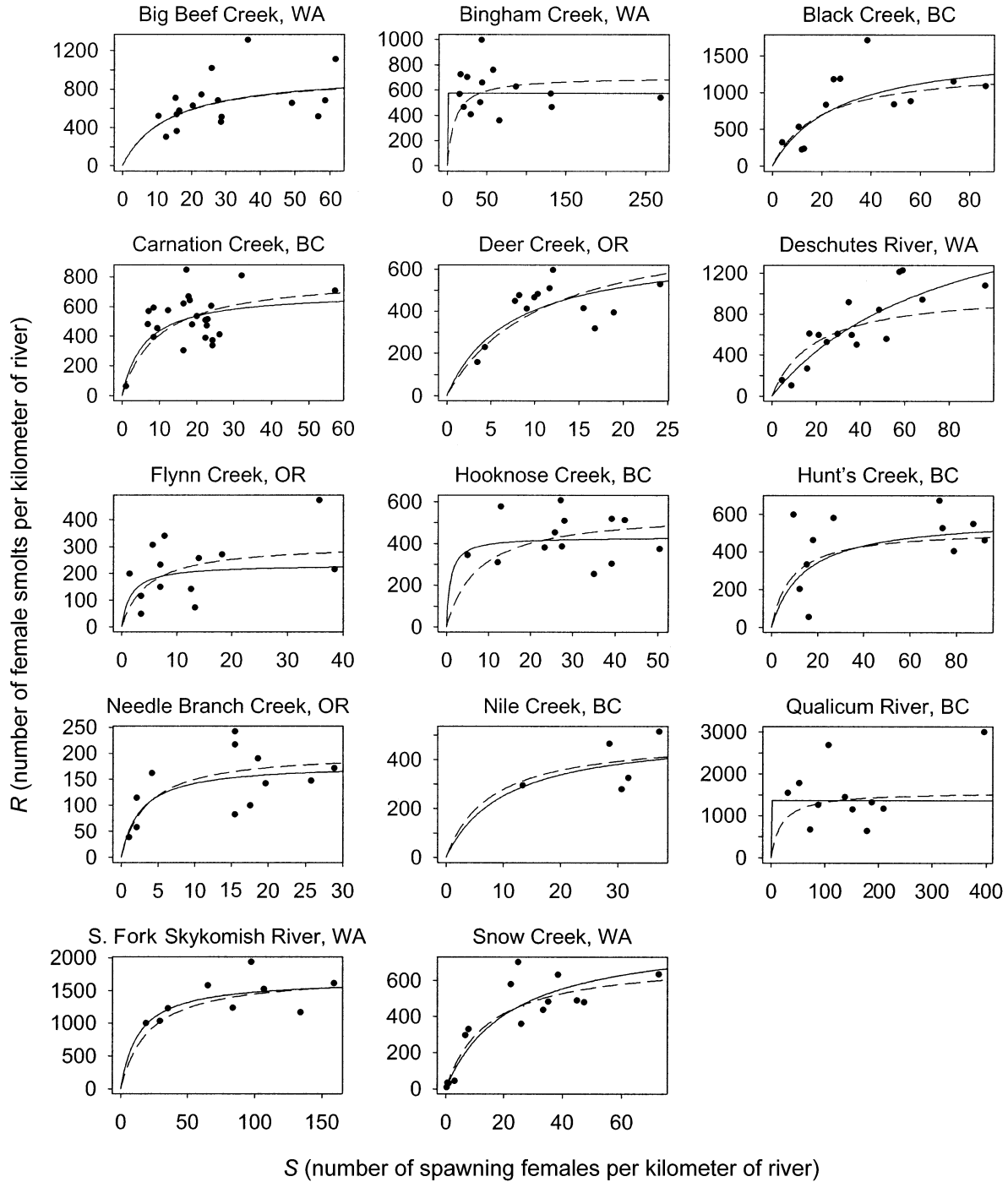


FIG. 2. Coho salmon data with superimposed fitted curves from individual maximum-likelihood fits of the Beverton-Holt model assuming a lognormal recruitment distribution (solid curves) and empirical Bayes curves from a mixed-model fit (dashed curves). Abbreviations are: WA, Washington State, OR, Oregon; and BC, British Columbia.

ship are independent among populations for the freshwater part of the life history.

Our contention is that focusing on one population at a time can be misleading. In this section, we shall demonstrate how this can be avoided by incorporating the estimation of a spawner–recruitment model into a non-

linear mixed-effects model. Myers et al. (1999) used a similar approach for the Ricker model; however, thanks to the linearity of the Ricker model on the log scale, they were able to use linear mixed-effects models. As noted earlier, the Ricker model exhibits overcompensation. Therefore, for coho salmon, the Beverton-Holt

TABLE 1. Maximized log likelihoods for each of the coho salmon populations using the Ricker, Beverton-Holt, or hockey-stick models.

Population	Ricker	Beverton-Holt	Hockey stick
Big Beef Creek, WA	-4.6	-4.2	-4.2
Bingham Creek, WA	-7.2	0.3	0.3
Black Creek, BC	-5.3	-4.9	-4.4
Carnation Creek, BC	-12.4	-8.9	-5.6
Deer Creek, OR	3.5	2.5	7.6
Deschutes River, WA	-4.3	-3.8	-4.7
Flynn Creek, OR	-12.1	-9.7	-10.2
Hooknose Creek, BC	-0.8	1.0	1.1
Hunt's Creek, BC	-8.9	-8.2	-8.5
Needle Branch Creek, OR	-3.4	-2.1	-1.1
Nile Creek, BC	2.7	3.6	3.5
Qualicum River, BC	-8.1	-4.5	-4.5
S. Fork Skykomish River, WA	5.4	7.3	5.7
Snow Creek, WA	-4.9	-4.5	-3.4
Sum	-60.5	-36.3	-28.6

Note: The final row of the table gives the sum of the individual maximized log likelihoods for each model, providing an indication of which model provides the best overall fits.

model seems more appropriate, necessitating the use of nonlinear mixed-effects models.

We begin by developing a nonlinear mixed-effects model for the Beverton-Holt, and later generalize to the other spawner-recruitment models. Suppose we have M populations and suppose that for population i we have n_i observations. We assume additive normal observational errors in log recruitment, i.e., for the Beverton-Holt model,

$$R_{i,t} = \frac{\alpha_i S_{i,t}}{1 + (S_{i,t}/K_i)} e^{\varepsilon_{i,t}}$$

where $\varepsilon_{11}, \dots, \varepsilon_{Mn_M} \stackrel{i.i.d.}{\sim} N(0, \sigma^2)$. Dividing by α_i , we obtain

$$R_{i,t} = \frac{S_{i,t}}{1/\alpha_i + S_{i,t}/(R_{\max,i})} e^{\varepsilon_{i,t}}. \quad (2)$$

Note that $R_{\max,i} \equiv \alpha_i K_i$ is the asymptotic level of median recruitment. We prefer this parameterization because the asymptotic recruitment is well determined for many of the coho populations and has a direct biological interpretation.

Mixed models make additional assumptions by treating some or all of the parameters in Eq. 2 as random effects. Different versions of such models and the methods used for fitting them are discussed in the Appendix. Briefly, the basic model we use (model II) treats the logarithms of both α_i and $R_{\max,i}$ as being normally distributed.

Other models

We fitted models analogous to model II for the Ricker and logistic hockey-stick model with a smoothness parameter, θ , initially of 10. We also fitted three-parameter versions of model II for the type-1 and type-2 de-

pendent Beverton-Holt models and the logistic hockey-stick model. In each of these cases, we assumed that there was no among-population correlation in population parameters.

RAINDROP PLOTS

To display our results we use the recently introduced raindrop plot (N. Barrowman and R. Myers, *unpublished manuscript*). The raindrop plot provides a graphical gauge of the relative plausibility of different values, and is useful when conventional point estimates of parameters with confidence limits are not adequate. Conventional estimates are not appropriate when the likelihood is not approximately normal, as can occur with small sample sizes or nonlinear models. To understand how the individual raindrop shapes are obtained, consider Fig. 3, showing the profile log likelihood for α for Hunt's Creek, British Columbia.

A modification of the scheme for producing raindrop shapes can be used to display meta-analytic summaries showing confidence regions for the mean, estimated random-effect distributions, and Bayesian posterior and predictive distributions. In place of the log likelihood, we use the log-probability density. In other words, we use a raindrop based on the log density over the highest density region (Hyndman 1996).

RESULTS

We fitted nonlinear mixed models using the Beverton-Holt, logistic hockey-stick, and depensation spawner-recruitment models. Fitting was performed using the NLME software in S-PLUS (Statistical Sciences, Seattle, Washington, USA), which implements the method of Lindstrom and Bates (1990). The Beverton-Holt mixed model, described in detail earlier (model II), produced very reasonable individual estimates of log α and asymptotic recruitment (Fig. 2).

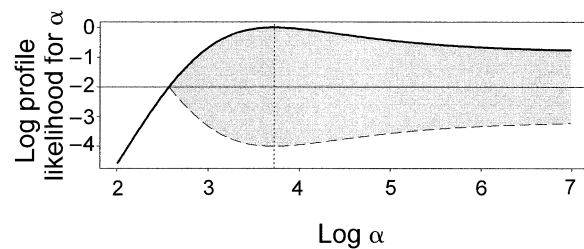


FIG. 3. Profile log likelihood for α for Hunt's Creek, British Columbia, showing how the raindrop shape is obtained. The profile log likelihood (solid curve) has been graphed with its maximum (indicated by the dotted vertical line) equal to 0. A drop in the log likelihood of ~ 2 (indicated by the horizontal line) is significant at the 0.05 level. In this case, the $\sim 95\%$ confidence interval for log α ranges from ~ 2.5 to infinity. By reflecting the part of the curve above -2 about the horizontal line, we obtain a symmetric region (shaded in the figure). The height of the region at a particular value of log α relative to the maximum height gauges the relative plausibility of that value.

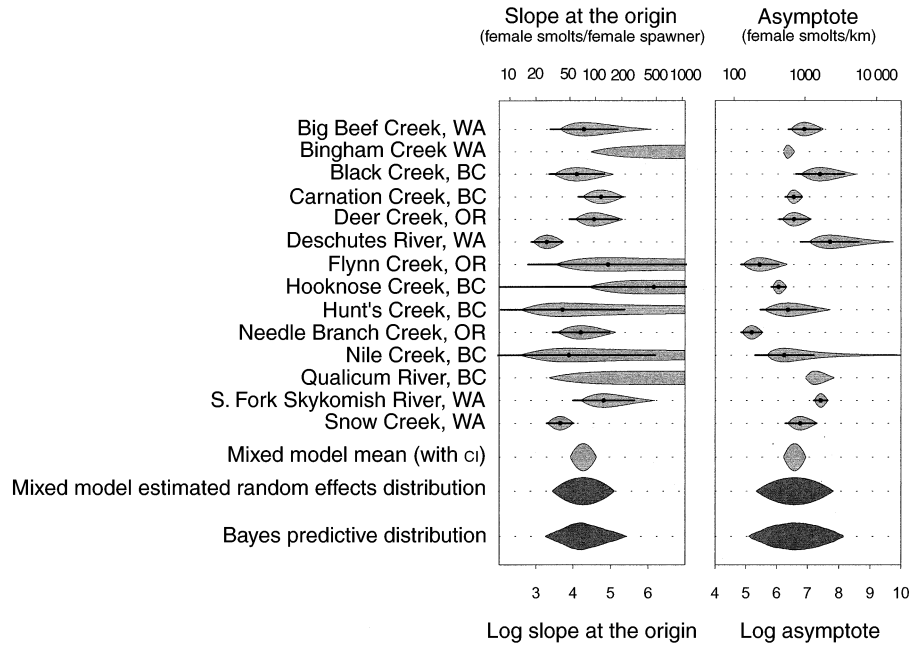


FIG. 4. Raindrop plots for the slope at the origin, α , and asymptotic level, R_{max} , in the Beverton-Holt model for the 14 coho salmon populations, together with meta-analytic summaries. The light-shaded raindrop shape for each population depicts a profile-likelihood-based 95% confidence interval for α for that population. The superimposed dot is the maximum-likelihood estimate obtained by nonlinear regression. Note that for two populations, convergence of the nonlinear least-squares algorithm was not obtained because of “ramping” behavior in the likelihood surface. In cases where convergence was obtained, an approximate asymptotic 95% confidence interval (based on nonlinear least squares theory) around the estimate is shown. The asymptotics are often poor in that the asymptotic confidence interval often does not match the profile-likelihood-based interval well. The three taller raindrop shapes at the bottom are meta-analytic summaries from the nonlinear mixed model, and should be interpreted differently from the raindrops for individual populations. The “mixed model mean (with CI)” represents the estimated mean $\log \alpha$ from the mixed model with a 95% confidence interval obtained from the asymptotic standard error of the mean. The two bottom raindrop shapes are shown darker to emphasize that they represent distributions: in place of the log likelihood, we use the log probability density, with a cutoff corresponding to a probability of 0.95. The “mixed-model estimated random effects distribution” represents the normal distribution with mean given by the estimated mean $\log \alpha$ from the mixed model, and variance given by the estimated variance of $\log \alpha$ obtained from the mixed model. The “Bayes predictive distribution” represents the induced prior from the Bayesian analysis (Efron 1996).

Raindrop plots for each population of $\log \alpha$ and asymptotic recruitment (Fig. 4) show the relative information content provided by each data set and their relation to the estimated means of the respective parameters. Maximum-likelihood estimates of the variability among populations (the “mixed-model esti-

mated random-effects distribution”) of $\log \alpha$ and asymptotic recruitment are also depicted.

The Beverton-Holt mixed model produced estimates of the mean (among populations) of $\log \alpha$ and asymptotic recruitment larger than the hockey-stick model (Table 2). Thus, even though the models fit the data

TABLE 2. Comparison of model fits.

Model	Maximized approximate log likelihood	Log α			Log R_{max}			Log depensation parameter		
		Mean	SE	SD	Mean	SE	SD	Mean	SE	SD
Beverton-Holt (BH)	-116.1	4.27	0.18	0.43	6.58	0.18	0.64			
Logistic hockey stick (LHS)	-116.4	3.97	0.13	0.32	6.35	0.17	0.62			
Type-1 depensatory BH	-116.1	4.08	0.22	0.38	6.51	0.18	0.61	0.13	0.10	0.03
Type-2 depensatory BH	-115.9	4.34	0.21	0.40	6.57	0.19	0.63	-2.01	1.52†	1×10^{-7}
Type-2 depensatory LHS	-116.3	3.99	0.15	0.33	6.35	0.17	0.61	-3.29	3.77†	0.003

Notes: SE, standard error of estimated mean; SD, standard deviation of random effect. Note that for the depensation models, α does not have the interpretation of slope at the origin. The logistic hockey stick (LHS) and its depensatory version both used a smoothness parameter $\theta = 10$.

† The maximum-likelihood estimates are not normally distributed. Treating depensation as a fixed effect and examining profile likelihoods reveals an undefined lower boundary and a 95% upper boundary (from a χ^2 approximation) of -0.38 for the Beverton-Holt (BH) model and -0.73 for the LHS model.

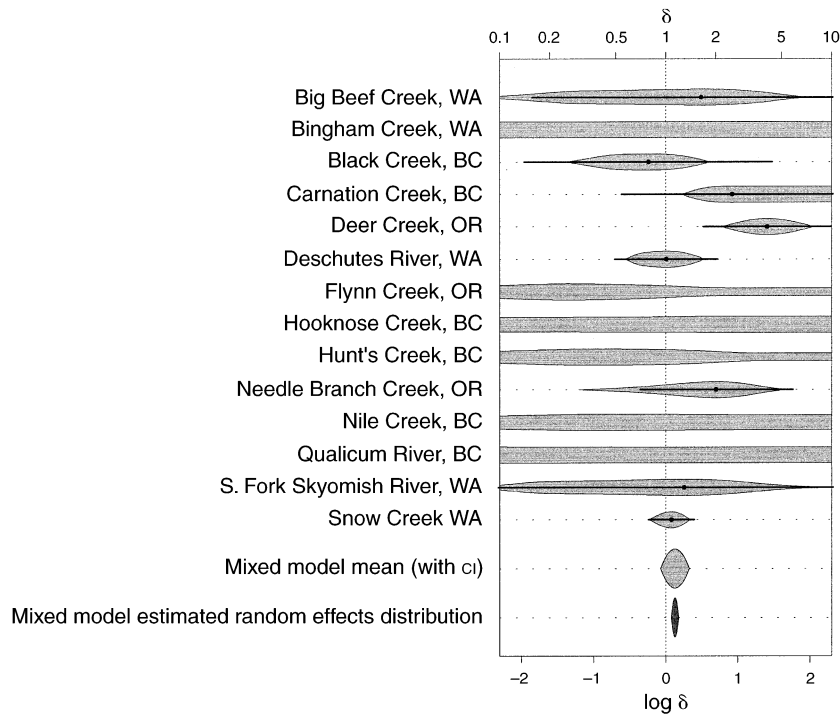


FIG. 5. Raindrop plot for the depensation parameter, δ , for the type-I depensatory Beverton-Holt model for the 14 coho salmon populations, together with meta-analytic summaries (see Fig. 4 for details).

equally well, the hockey-stick model suggests that coho should be managed much more conservatively than does the Beverton-Holt model. The random-effects distribution is shifted up for the Beverton-Holt compared to the hockey-stick model. However, both models predict roughly the same lower limit for α : 95% of the populations are estimated to have an α between 30 and 169 for the Beverton-Holt model, while the range for the hockey stick is between 28 and 68.

We do not give details on the Ricker model for reasons given earlier. Note, however, that the maximized log likelihood of the Ricker mixed model was very similar to that of other models fit to the data (Table 2).

DEPENSAATION MODELS

In the nonlinear mixed models previously discussed, there were two random effects, the log slope at the origin, $\log \alpha$, and the log asymptotic level. For the depensation models, we also treated $\log \delta$ or $\log d$ as a random effect. Note that for these models, α can no longer be interpreted as the slope at the origin.

Most data sets contained almost no information on depensation (Fig. 5), and in no case was the addition of depensation in the mixed-effect model close to being statistically significant by a likelihood ratio test. Also, in all cases, the mean level of depensation estimated was very small.

The other two models of depensation, the depensatory Beverton-Holt and depensatory hockey stick, show similar results (Table 2). In each case, they show

that the mean depensation appears to occur only at very low population densities, i.e., at 0.13 and 0.037 female spawners per kilometer of river. Even the upper 95% confidence limit for the mean depensation (derived from the profile log likelihood) is $d = 0.68$ females per kilometer of river, and $d = 0.48$, respectively (Table 2). This implies that, on average, depensation can only occur at very low population densities. At these population densities, some streams used in the analysis would have no fish at all, so that depensation would occur trivially.

BAYESIAN ANALYSIS AND ROBUSTNESS ANALYSIS

For robustness, we repeated the above analyses using a fully Bayesian analyses. In general, we found the results similar to the mixed-model results, so we only give the results for the Beverton-Holt model in detail. Vague priors were used for the means of $\log \alpha$ and $\log K$ (normal with mean 0 and variance 10 000). Approximately uninformative priors for the variance components were specified in terms of precision = 1/variance, using a gamma distribution with shape parameter 0.001 and scale parameter 1000. Markov chain Monte Carlo (MCMC) sampling was performed with BUGS software (Bayesian inference Using Gibbs Sampling; Gilks et al. 1994, 1996). For this model, BUGS uses Metropolis-within-Gibbs sampling, which requires bounded ranges for the $\log \alpha$, and $\log K$, random effects. The ranges applied were (0.5, 10) for $\log \alpha$; and (-30, 30)

for $\log K_r$. Neither the priors used nor the bounded ranges applied had a strong influence on the results.

The Bayes predictive distribution was calculated for the slope at the origin and the asymptote (Fig. 4). In both cases, the fully Bayes predictive distributions are wider than the mixed-model estimate of the random-effects distribution. This is expected for theoretical reasons, i.e., the fully Bayes predictive distribution incorporates all of the uncertainty in the parameter estimates (Efron 1996). However, the Bayes predictive distributions are only slightly wider than the mixed-model estimates, which suggests that the simpler-to-calculate mixed-model estimates are adequate approximations. Similar results were obtained for other models.

For robustness, we also considered a variety of modifications of the mixed-effects models: alternative estimates of smoothness for the logistic hockey stick and correlations among the random effects. In no case did these modifications significantly improve the fit, or lead to any important changes in the results.

DISCUSSION

In this paper, we carried out parallel analyses using nonlinear mixed-effects models and fully Bayes approaches, extending the nonlinear mixed-model approach used by Myers et al. (2001) to include a wider range of spawner–recruitment functions and depensation. A related model for depensation was developed by Liermann and Hilborn (1997), however their approach differed in two important ways. First, they treated only a subset of population parameters as comparable among populations. Second, rather than a mixed-model or fully Bayes approach, they used a hybrid Bayesian approach involving several approximations. Notably, the nonlinear mixed-effects model approach we have described is much simpler to implement.

Critical to our analysis is that all model parameters are in units that can be compared among populations. The α is in units of female smolts produced per female spawner, R_{\max} is in units of female smolts produced per kilometer of river, and the depensation parameter is either a dimensionless number (δ) or the spawner abundance per kilometer of river, for which the expected recruitment is one-half what it would be if there were no depensation (d). This “unit comparability” is indispensable for meta-analytic models. Model fits to individual rivers can produce nonsensical results, e.g., infinite α or carrying capacity (Barrowman and Myers 2000).

This study shows that the choice of model can markedly affect one's interpretation of the data, even though the goodness of fit of the models are almost identical. The Beverton-Holt mixed-effects model shows a median slope of 71.5 female smolts to female spawners, while the logistic hockey stick shows a median slope of 53. This difference has important consequences for the estimation of extinction probabilities, and for the

optimal management of the species. Since it is hard to imagine how density dependence could keep increasing at very low densities, the hockey-stick estimate may be preferred.

The individual and mixed-model fits were dramatically different. For example, in Table 1, the sum of the maximized likelihoods for the hockey-stick model was greater than for the Beverton-Holt fits. However, this was not the case in the overall fit of the mixed-effect models, which gave virtually identical fits (Table 2). This difference is important, and the mixed effects results are probably more biologically and statistically meaningful because they incorporate realistic constraints on the differences among populations.

The estimate of the mean $\log \alpha$ depends upon whether a depensatory model is used (Table 2). In other words, the estimation of $\log \alpha$ is not independent of the estimation of the depensatory term. This creates a problem if empirically derived prior distributions for depensation are applied to models in which the parameters were estimated in the absence of a depensatory term. For example, Liermann and Hilborn (1997) produced predictive distributions for depensation, which could theoretically be used as priors in a Bayesian risk assessment. What is actually needed in this case is a joint prior for the depensatory parameter and $\log \alpha$, thus magnifying the complexity of the problem considerably. Although the effect of including a depensatory factor on the estimation of α is small in our case, the estimates of the mean do differ in the depensatory and nondepensatory models (Table 2). This problem is more acute with modifications of the Beverton-Holt than the hockey stick.

CONCLUSIONS

Meta-analytic techniques provide a way to obtain estimates for populations where little is known. In the case of the coho salmon, we were able to obtain estimates of α , the rate at which female spawners can produce female smolts at low population sizes (and thus critical to predicting extinction) for each stream, as well as an estimate of the variance of α . This information could be incorporated directly into an extinction model, thus overcoming the difficulties highlighted by Routledge and Irvine (1999) about imprecise predictions.

We also have provided an improved approach to estimating depensation. Our estimates of depensation provide much-improved quantitative information compared to previous approaches. For example, we have obtained estimates of the population size where depensation will occur, whereas previous approaches have provided much less useful information (Myers et al. 1995a).

Also, we have demonstrated that you cannot estimate depensation independently from other model parameters. That is, models that include a depensation parameter change the meaning of the other parameters, and

the parameters cannot be considered independent a priori. This results in a difficulty in practice in applying Bayesian population dynamic models that include depensation.

Considerable effort has been devoted to the development of both analytical and simulation models that estimate extinction probabilities of natural populations (Lande 1993, Ludwig 1996, Fagan et al. 1999). On the whole, these models suffer from a lack of plausible parameter values, as there is often very little data available. Instead, parameters are drawn from distributions without firm empirical bases and the conclusions are difficult to apply in specific cases (Foley 1994, Johst and Wissel 1997). This problem is particularly acute for parameters that describe population dynamics at low population sizes. Moreover, it is the dynamics at low sizes that are of greatest import when estimating extinction risk.

Meta-analytic techniques are crucial for estimating the among-population variability in population parameters, which are needed for conservation and management models. With these techniques, we have the capability of estimating not only the means of ecological parameters, but their spread as well. The populations whose parameters are at the extremes, and which may be more susceptible to extinction, may be the ones we care about the most.

ACKNOWLEDGMENTS

We thank Mike Bradford and Rick Routledge for helpful suggestions. The work was supported by the Killam Foundation, Natural Sciences and Engineering Research Council of Canada (NSERC), and the National Center for Ecological Analysis and Synthesis (NCEAS) which is supported by NSF.

LITERATURE CITED

- Barrowman, N. J. 2000. Nonlinear mixed effects models for meta-analysis. Dissertation. Dalhousie University, Halifax, Nova Scotia, Canada.
- Barrowman, N. J., and R. A. Myers. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:665–676.
- Beamish, R. J., G. A. McFarlane, and R. E. Thomson. 1999. Recent declines in the recreational catch of coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia are related to climate. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:506–516.
- Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. MAFF Fisheries Investigations Series II **19**:533.
- Bradford, M. J. 1999. Temporal and spatial trends in the abundance of coho salmon smolts from western North America. *Transactions of the American Fisheries Society* **128**:840–846.
- Bradford, M. J., R. A. Myers, and J. R. Irvine. 2000. Reference points for coho salmon harvest rates and escapement goals based on freshwater production. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:677–686.
- Bradford, M. J., G. C. Taylor, and J. A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production. *Transactions of the American Fisheries Society* **126**:49–64.
- Courchamp, R., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* **14**:405–410.
- Dittman, A. H., T. P. Quinn, and E. C. Volk. 1998. Is the distribution, growth, and survival of juvenile salmonids sex biased? Negative results for coho salmon in an experimental stream channel. *Journal of Fish Biology* **53**:1360–1368.
- Efron, B. 1996. Empirical Bayes methods for combining likelihoods. *Journal of the American Statistical Association* **91**:538–565.
- Fagan, W. F., E. Meir, and J. L. Moore. 1999. Variation thresholds for extinction and their implications for conservation strategies. *American Naturalist* **154**:510–520.
- Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* **8**:124–137.
- Gilks, W. R., S. Richardson, and D. J. Spiegelhalter, editors. 1996. Markov chain Monte Carlo in practice. Chapman and Hall, London, UK.
- Gilks, W. R., A. Thomas, and D. J. Spiegelhalter. 1994. A language and program for complex Bayesian modeling. *Statistician* **43**:169–178.
- Hyndman, R. J. 1996. Computing and graphing highest density regions. *American Statistician* **50**(2):120–126.
- Johst, K., and C. Wissel. 1997. Extinction risk in a temporally correlated fluctuating environment. *Theoretical Population Biology* **52**:91–100.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**:911–927.
- Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1976–1985.
- Lindstrom, M. J., and D. M. Bates. 1990. Nonlinear mixed effects models for repeated-measures data. *Biometrics* **46**:673–687.
- Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* **6**:1067–1076.
- Mace, P. M. 1994. Relationships between common biological reference points used as threshold and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:110–122.
- Myers, R. A. 1997. The role of meta-analysis in the study of recruitment variation in fish populations. Pages 575–596 in R. C. Chambers and E. A. Trippel, editors. Early life history and recruitment in fish populations. Chapman and Hall, London, UK.
- Myers, R. A., and N. J. Barrowman. 1996. Is fish recruitment related to spawner abundance? *Fishery Bulletin* **94**:707–724.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995a. Population dynamics of exploited fish stocks at low population levels. *Science* **269**:1106–1108.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. The maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:2404–2419.
- Myers, R. A., M. J. Bradford, J. M. Bridson, and G. Mertz. 1997b. Estimating delayed density-dependent mortality in sockeye salmon (*Oncorhynchus nerka*); a meta-analytic approach. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2449–2463.
- Myers, R. A., B. R. MacKenzie, K. G. Bowen, and N. J. Barrowman. 2001. What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1464–1476.
- Myers, R. A., and G. Mertz. 1998. The limits of exploitation: a precautionary approach. *Ecological Applications* **8**(Supplement):S165–S169.

- Myers, R. A., G. Mertz, and N. J. Barrowman. 1995b. Spatial scales of variability in cod recruitment in the North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 1849–1862.
- Myers, R. A., G. Mertz, and J. M. Bridson. 1997b. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1400–1407.
- Myers, R. A., G. Mertz, J. M. Bridson, and M. J. Bradford. 1998. Simple dynamics underlie sockeye salmon (*Oncorhynchus nerka*) cycles. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:2355–2364.
- Routledge, R. D., and J. R. Irvine. 1999. Chance fluctuations and the survival of small salmon stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1512–1519.
- Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 395–446 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. DBC, Vancouver, British Columbia, Canada.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* **14**:401–405.
- Walters, C. J. 1993. Where have all the coho gone? Pages 1–8 in L. Berg and P. Delaney, editors. *Proceedings of the Coho Workshop*, Nanaimo, British Columbia, May 26–28, 1992. Department of Fisheries and Oceans, Habitat Management Sector, Vancouver, British Columbia, Canada.
- Walters, C. J., and B. Ward. 1998. Is solar radiation responsible for declines in marine survival rates of anadromous salmonids that rear in small streams? *Canadian Journal of Fisheries and Aquatic Sciences* **55**:2533–2538.

APPENDIX

A description of models and methods for combining population dynamics data is available in ESA's Electronic Data Archive: *Ecological Archives* A013-012-A1.