A regional meta-model for stock-recruitment analysis using an empirical Bayesian approach

D.G. Chen and L. Blair Holtby

Abstract: A regional stock–recruitment meta-model is developed using a hierarchical Bayesian framework to combine information from multiple fish populations. The use of the meta-model is illustrated through analysis of the regional stock–recruitment parameters of the coho salmon (Oncorhynchus kisutch) within two large fisheries management units in southern and northern British Columbia. We construct our regional prior distribution from an analysis of all stock–recruitment data rather than by the more usual approach of assuming a prior distribution. That preliminary analysis indicated that the regional prior distribution for the two parameters of the Ricker model was bivariate normal–lognormal (NLN) with a high degree of correlation between the two Ricker parameters. Because this distribution had not been fully developed, we formulated the density function for the NLN distribution and proved some of its important properties. An empirical Bayesian approach was then used to estimate the regional distributions of the Ricker parameters and derived management parameters. Characterization of the distributional properties of productivity within management regions is a necessary step for resource managers seeking to prosecute mixed-stock fisheries while conserving population diversity.

Résumé : Nous avons mis au point un métamodèle de stock–recrutement régional à l’aide d’un cadre hiérarchique Bayésien dans le but de combiner les renseignements provenant de plusieurs populations de poissons. Nous proposons en exemple de notre métamodèle une analyse des paramètres régionaux de stock–recrutement de saumons coho (Oncorhynchus kisutch) provenant de deux grandes unités de gestion de la pêche dans le sud et le nord de la Colombie-Britannique. Nous avons basé la distribution régionale a priori sur une analyse de toutes les données de stock–recrutement au lieu de simplement assumer une distribution a priori comme on le fait couramment. Cette analyse préliminaire a révélé que la distribution régionale a priori des deux paramètres du modèle de Ricker est de type normal–lognormal (NLN) à deux variables avec un fort degré de corrélation entre les deux paramètres. Parce que la distribution n’avait pas été complètement décrite, nous avons calculé la fonction de densité de la distribution NLN et mis en lumière certaines de ses propriétés importantes. Une méthode empirique Bayésienne nous a ensuite permis d’estimer les distributions régionales des paramètres de Ricker et d’obtenir les paramètres de gestion. La caractérisation des propriétés de la distribution de la productivité dans une unité de gestion est une opération essentielle lorsque les gestionnaires d’une ressource cherchent à maintenir l’exploitation d’une pêche commerciale comprenant plusieurs stocks tout en conservant la diversité de la population.

Introduction

The management of mixed-stock fisheries has proven to be one of the most persistent and difficult problems facing resource managers. Such problems are most severe in anadromous species where fisheries occur in the ocean on numerous populations of differing productivities. Mixed-stock fisheries have been implicated in regional declines in most anadromous species, including all of the Pacific salmon (Oncorhynchus sp.), Atlantic salmon (Salmo salar), striped bass (Morone saxatilis), the river herrings (Alosa pseudoharengus and A. aestivalis), and shad (Alosa sapidissima).

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The threat to the stock diversity of Pacific salmon that such fisheries pose has long been recognized (Paulik et al. 1967; Ricker 1973; McDonald 1981). Nevertheless, despite extensive study of the problems posed by such fisheries and approaches to achieve optimal harvest while protecting stock diversity (Ricker 1958; Collie et al. 1990; Kope 1992), the failure to recognize and, more importantly, react appropriately to severe overfishing in intense and highly mixed-stock troll fisheries precipitated unprecedented closures of ocean coho salmon (O. kisutch) fisheries in Pacific Canada beginning in 1998 that remain in place.

Of the Pacific salmon, coho salmon are particularly susceptible to the problems of mixed-stock fisheries. Coho generally remain close to shore throughout their approximately 18-month life in the ocean and recruit to fisheries during their second summer in the ocean (Sandercock 1991). Feeding coho readily pursue moving lures, making them highly vulnerable to commercial and recreational troll fisheries. Coho salmon from many populations mingle in feeding areas (e.g., Argue et al. 1983; Pacific Salmon Commission 1994) and an ocean fishery can capture coho from nearly every population over a surprisingly large area. For
example, the intense troll fisheries off the west coast of Vancouver Island captured significant proportions (>25%) of the fish captured from nearly all coho populations in southern British Columbia (all streams draining the west coast of Vancouver Island and all streams draining into the Strait of Georgia and its inlets, including the Fraser River and its tributaries) and Washington (WA; all of the WA coast north of the Columbia River, including the Strait of Juan de Fuca and Puget Sound) (Pacific Salmon Commission 1994). Exploitation rates on coho salmon in ocean fisheries regularly exceeded 70% prior to stock collapses in the mid-1990s (e.g., Holthby et al. 1999; Irvine et al. 2000). The severity of the population declines within subregions was directly attributed to mesoscale differences in productivity (Holthby et al. 1999). Such subregional patterning of population decline is readily distinguished from the widespread declines in abundance that have occurred in the southern portions of coho range (e.g., Brown et al. 1994; Weitkamp et al. 1995; Beamish et al. 1999), which have generally been attributed to declines in the survival of juveniles entering the ocean caused by changes in ocean climate (Coronado and Hilborn 1998; Beamish et al. 2000) or to freshwater habitat loss and damage (e.g., Beechie et al. 1994; Bradford and Irvine 2000). The large declines in abundance in southern and northern coastal British Columbia (B.C.; Fig. 1) in the mid-1990s prompted the Canadian Department of Fisheries and Oceans, which is responsible for the management of anadromous species such as the Pacific salmon, to implement several policy and management initiatives aimed at conserving and rebuilding coho salmon populations. One of the policy initiatives was the development of a Wild Salmon Policy (WSP) (http://www-comm.pac.dfo-mpo.gc.ca/wsp-sep-consult/wsp/wsp.pdf). The WSP is structured around general principles derived from the precepts of conservation biology and precautionary management (DFO 2000). One of those principles requires that the many hundreds of coho populations will be aggregated, for management purposes, into a small number of conservation or management units (MU). The grouping of populations would be based on genetic and phenotypic similarities among the component populations but would also require that the component populations have similar fisheries profiles so that they are manageable as aggregates in mixed-stock fisheries.

Another principle of the WSP stipulates that a target and limit reference point would be established for each MU. Although it may be straightforward to determine such reference points for single populations, determining the reference points for a MU is more involved. When the fish are caught in mixed-stock fisheries, as is the case in coho salmon, any exploitation rate is unlikely to be optimal for all of the component populations. This is the classic mixed-stock fisheries problem. Setting the exploitation rate in such a situation would then become a public policy decision balancing diversity and harvest. To form such a policy decision, it is necessary both to describe the distribution of productivities within each MU and to model the consequences of policy options on the status of component populations within the MU.

In this paper, we describe the development of an empirical Bayesian approach for estimating the regional distributions of the two parameters of the Ricker stock–recruitment function and some associated management parameters (Hilborn and Walters 1992). We formally develop a new probability distribution (bivariate normal–lognormal or NLN) to accommodate both the different marginal distributions for $\alpha$ and $\beta$ and their correlation structure. We incorporate the NLN distribution into a hierarchical Bayesian model for estimation of the regional distribution of $\alpha$ and $\beta$. Our approach is empirical because we use sample data to estimate the unknown regional parameters in the NLN prior distribution rather than assuming a known prior distribution as would be done in a standard Bayesian analysis.

### Preliminary analysis for regional distributions

For Pacific salmon, stock–recruitment ($S-R$) analysis models the functional relationship between the escapement ($S$, i.e., the number of spawners) and the number of recruits that they produce ($R$) that are alive at some specified time ($t$), typically either immediately before the fishery, as is the case here, or at the inception of spawning. Coho salmon recruit to
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fisheries in their second summer in the ocean, and all fish that survive the fishery return to their natal streams to spawn in the fall of the same year. We assume that there is negligible natural mortality after the fishery begins and that recruitment is therefore the sum of escapement and catch. This is a conservative assumption for production modeling because it will underestimate recruitment and thus productivity.

Time series of coho escapement indices from populations within the Thompson River and its tributaries in southern British Columbia (SBC) (Fig. 2) and from populations within Statistical Area 6 in northern British Columbia (NBC) were used for this regional meta-model development. Escapement data from over 100 populations in NBC for the years 1950 to 1999 and 60 populations in SBC for the years 1975 to 1999 were available. Details of the data preparation are found in Holtby et al. (1999) for NBC and in Irvine et al. (2000) for SBC. Escapement estimates in SBC streams were corrected on a river-specific basis for observer efficiencies (Irvine et al. 2000), but no correction was possible in the NBC streams. No relationship between the correction factor and the size of the system was detected in the SBC systems. Stock-specific catch was estimated using estimates of the exploitation rate. We assumed that the annual exploitation rate was equal for all populations within each of the two regions. For NBC systems, the exploitation rate was derived from recoveries of coded-wire-tagged fish in ocean fisheries released from indicator stocks in the Skeena River from 1988 onward (Holtby et al. 1999). For the remaining years, the exploitation rate was estimated from records of total fishery effort in the ocean fisheries of northern British Columbia and southeast Alaska and empirical effort—exploitation rate relationships (Pacific Salmon Commission 2002). In SBC, exploitation rates were estimated from coded-wire-tagged releases from Thompson River and other southern British Columbian hatcheries (1975–1997) and direct estimates of the numbers of Thompson River fish in ocean fisheries (1998, 1999; Irvine et al. 2000).

In both areas and particularly in NBC, the data series were fragmentary in many systems. In NBC where there are two freshwater ages and adults return over 2 years from each brood year, the data for each population consisted of triplets of values where escapement had been indexed in a brood year and in both return years. In SBC, there is one freshwater age and all spawners return in the same year. Therefore, in SBC, the data consisted of pairs of values where escapement had been indexed in the brood year and the single return year. In both NBC and SBC, the escapement counts were treated as indices of escapement and not as absolute estimates of escapement. These data sets, and in particular the one from NBC, initially included all streams that had ever been enumerated, even if for only 1 year. Short periods of observation were common at the beginning of data collection. This suggested to us that those making the escapement estimates felt that estimates were particularly unreliable in those systems. The minimum standard for inclusion (five stock–recruitment observations) was developed in consultation with field staff familiar with these data. Stocks with five or fewer stock–recruitment observations were discarded, leaving 83 populations in NBC and 50 in SBC.

The most commonly used S–R models are the Ricker (1975) and the Beverton and Holt (1957) models. The Ricker model with a lognormal error term is used in this paper:

\[ R_t = S_t \exp(\alpha - \beta S_t) \exp(\epsilon_t) \]

where \( \alpha \) is the parameter measuring reproductive performance at low stock size with \( \exp(\alpha) \) being the maximum recruits per spawner and \( \beta \) is the parameter representing density dependence in juvenile survival rate; \( \epsilon_t \) is a normally distributed process error with mean 0 and standard deviation \( \sigma \). This model can be linearized as

\[ \log(R_t/S_t) = \alpha - \beta S_t + \epsilon_t \]

whereupon the parameters \( \alpha \) and \( \beta \) can be estimated by simple least-squares regression. Having estimates of \( \alpha \) and \( \beta \), fishery management parameters, such as \( S_{MSY} \) (the optimal stock size at maximum sustainable yield (MSY)) and \( S_{MSY} \) (exploitation rate), can be calculated based on the formulations from Hilborn (1985), Hilborn and Walters (1992), and Quinn and Deriso (1999).

Barrowman and Myers (2000) suggested that the Ricker and Beverton–Holt models poorly fit the stock–recruitment data for coho salmon. Their assertion was justified for the Beverton–Holt model, and in our preliminary tests, the Beverton–Holt model did give unrealistically high estimates of the slope at the origin (\( \alpha \)) and was not considered further. In the case of the Ricker model, support for their assertion (Barrowman and Myers 2000, their fig. 2) was, in our opinion, tenuous. Our experience is similar to that of Myers et al. (1999), who concluded that the Ricker model usually provides reasonable estimates of \( \alpha \) for management purposes. We briefly examined some three-parameter S–R models. The results of those analyses did suggest that there was some nonlinearity in the Ricker fits. However, examination of many of the individual fits showed no consistent patterning in the residuals, and we concluded that the Ricker model was adequate for these data. Other S–R functions (e.g., the hockey stick; Barrowman and Myers 2000) were not considered, although our framework could be readily extended to other S–R functions.

When extended to a region, the Ricker model (eq. 1) becomes \( y_i = \ln(R_i/S_i) = \alpha_i - \beta_i S_i + \epsilon_i \), where \( \epsilon_i \sim N(0, \sigma^2) \) and \( t = 1 \) to \( n_i \) (dependent on population \( i \)), and \( i = 1 \) to 83 for NBC and \( i = 1 \) to 50 for SBC. The Ricker model (eq. 1) was fit to each population independently (Figs. 3a, 3b). For NBC coho, the Ricker \( \alpha_i \) are centrally distributed around 1.5 (Figs. 3a, 4a) and the Ricker \( \beta_i \) is highly skewed toward lower values (Fig. 4b). The distributions of \( \alpha_i \) and \( \beta_i \) are similar in SBC (Figs. 3b, 4e, 4f), although the average values of both parameters are greater in SBC. In both NBC and SBC, both \( \alpha_i \) and \( \ln(\beta_i) \) are normally distributed (Figs. 4d, 4h). This is confirmed by the Kolmogorov–Smirnov distribution test (Table 1).

Regional meta-model

Our primary interest is in the regional populations from which the 83 and 50 populations (NBC and SBC, respectively) were drawn rather than in the individual populations. Independently fitting the Ricker model to the individual population results in a set of parameters estimates \( \alpha_i \) and \( \beta_i \),
within-sample estimates of $\sigma^2_{\alpha}$ and $\sigma^2_{\beta}$ for each of the two regions but does not provide a basis for inference about the two regional populations. These estimates are presumably drawn from regional populations with regional means $\alpha_R$ and $\beta_R$, and among-stock true variances $\sigma^2_{\alpha}$ and $\sigma^2_{\beta}$. Furthermore, these regional Ricker parameters $\alpha_i$ and $\beta_i$ should be correlated with the regional coefficient $p$. The process of estimating the regional parameters can be accomplished with
a two-stage hierarchical Bayesian model where stage 1 consists of fitting a Ricker model (1) with lognormally distributed errors to each individual population \(i = 1\) to \(K\) (83 for NBC and 50 for in SBC) and stage 2 estimates the regional Ricker parameters \(\alpha_i\) and \(\beta_i\) that are distributed as a bivariate NLN distribution. Therefore the regional meta-model can then be formulated as

\[
\begin{align*}
\text{Ricker model for each stream } i: \\
&\ln y_{Rit} = \frac{R_{it}}{S_{it}} = \alpha_i - \beta_i S_{it} + \varepsilon_{it} \\
&\varepsilon_{it} \sim N(0, \sigma^2_S); i = 1, \ldots, K; t = 1, \ldots, n_i \\
\text{Regional prior distribution: } \\
&(\alpha, \beta) \sim \text{NLN}(\alpha_R, \sigma^2_{\alpha}, \beta_R, \sigma^2_{\beta}, \rho)
\end{align*}
\]

We present a graphical description of this two-stage hierarchical model (Fig. 5). In model 2 (eq. 2), NLN(\(\alpha, \beta\); \(\alpha_R, \sigma^2_{\alpha}, \beta_R, \sigma^2_{\beta}, \rho\)) denotes the joint bivariate NLN distribution.
Because this distribution is not formally formulated, we propose and prove (Appendix A) the NLN with a density function defined as 

\[
dNLN(\alpha, \beta; \alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2, \rho) = \\
\frac{1}{2\pi \sigma_{\alpha} \sigma_{\beta}} \exp \left\{ -\frac{1}{2(1-\rho^2)} \left[ \frac{\alpha - \alpha_R}{\sigma_{\alpha}} - \rho \left( \frac{\ln \beta - \ln \beta_R}{\sigma_{\beta}} \right) \right]^2 \right\} \\
- 2\rho \frac{\alpha - \alpha_R}{\sigma_{\alpha}} + \frac{\ln \beta - \ln \beta_R}{\sigma_{\beta}} + \frac{\ln \beta - \ln \beta_R}{\sigma_{\beta}} \right\}
\]

where \( \alpha_R \) and \( \sigma_{\alpha}^2 \) are the mean and variance parameters for \( \alpha \); \( \beta_R \) and \( \sigma_{\beta}^2 \) are the mean and variance for \( \ln(\beta) \); \( \rho \) is the correlation coefficient for \( \alpha \) and \( \beta \); and 

\[
\rho = \frac{\sigma_{\alpha} \exp(\sigma_{\beta}^2) - 1}{\sigma_{\beta}}
\]

The notation \( dNLN \) denotes the density function for the NLN distribution. A similar notational shorthand where “d” is prefixed to the name of the distribution has been used elsewhere in this paper, for example, “dNorm” denotes the density function of the normal distribution.

The posterior distribution of \( \alpha \) and \( \beta \) conditional on the \( S-R \) data and the regional prior distribution (eq. 3) would then be

\[
\alpha, \beta | S_{it}, y_{it}, \alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2, \rho \\
\propto d\text{Norm}(y_{it}; \alpha - \beta_S, \sigma_i^2) \\
\times d\text{NLN}(\alpha, \beta; \alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2, \rho)
\]

This posterior distribution (eq. 4) could also be used to provide corrected estimates of the \( (\alpha, \beta) \) pairs using the regional information to provide a more biologically reasonable value for each stock by combining information from both the region and the stock itself (Myers and Mertz 1998).

We have shown that the conditional distribution of \( \alpha | \beta \) is also normally distributed with mean \( \alpha_R + \rho \frac{\sigma_{\alpha}}{\sigma_{\beta}} (\ln \beta - \beta_R) \) and variance \( \sigma_{\alpha}^2 (1 - \rho^2) \) (see Appendix A). With simple mathematical manipulations, we can prove that

\[
\alpha, \beta | S_{it}, y_{it}, \alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2, \rho \\
\propto d\text{Norm}(y_{it}; \alpha - \beta_S, \sigma_i^2) \\
\times d\text{NLN}(\alpha, \beta; \alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2, \rho) \\
= d\text{Norm}(y_{it}; \alpha - \beta_S, \sigma_i^2) \\
\times d\text{Norm}(\alpha, \alpha_R + \rho \frac{\sigma_{\alpha}}{\sigma_{\beta}} (\ln \beta - \beta_R), \sigma_{\alpha}^2 (1 - \rho^2)) \\
\times d\text{LNNorm}(\beta; \beta_R, \sigma_{\beta}^2)
\]

**Empirical Bayesian estimation**

The dependence of the posterior distribution (eq. 5) on five unknown regional parameters \( (\alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2, \rho) \) effectively precludes the implementation of a fully Bayesian hierarchical approach. However, an empirical Bayesian approach can be developed in which the observed \( S-R \) data are used to estimate the distribution of the regional parameters (Carlin and Louis 1998).

Because the primary objective is to obtain the regional distribution, the \( S-R \) parameters \( \alpha \) and \( \beta \) are nuisance parameters; therefore, these parameters can be integrated out with the marginal likelihood function to estimate the regional parameters \( (\alpha_R, \sigma_{\alpha}^2, \beta_R, \sigma_{\beta}^2) \):
\[ L(\alpha_R, \sigma^2_\alpha, \beta_R, \sigma^2_\beta, \rho) \]

\[ = \prod_{i=1}^{K} \prod_{j=1}^{n_i} \left\{ \text{dNorm}(y_{it}; \alpha_i - \beta_i S_{it}, \sigma^2_i) \times \text{dLN}(\alpha_i, \beta_i, \sigma^2_\alpha, \sigma^2_\beta, \rho) \right\} \]

The within-population variance \( \sigma^2_i \) in eq. 6 are estimated from the S-R data from population \( i \) to reduce parameters (summarized in Table 2). This marginal likelihood function involves two-dimensional integration to \( \alpha_i \) and \( \beta_i \). To simplify this likelihood function, an analytical integration to \( \alpha_i \) can be performed from eq. 5 as

\[ \int \text{dNorm}(y_{it}; \alpha_i - \beta_i S_{it}, \sigma^2_i) \times \text{dNorm}(\alpha_i, \beta_i, \sigma^2_\alpha, \sigma^2_\beta, \rho) \]
tion or exploration of alternative prior distributions. To some extent, this practice is understandable because analytical solutions for many plausible prior distributions are not available. For example, it is easy to show that an analytical form for eq. 8 can be easily obtained in the case of a bivariate normal prior distribution. If the prior distribution is really normally distributed, a comprehensive theory for Bayesian analysis can be found from Gelman et al. (1995) and Carlin and Louis (1998). Chen et al. (1999) have developed an empirical Bayesian estimator and also a shrinkage estimator with application to such multivariate situations. Pella et al. (1998) used the same approach in forecasting salmon abundance.

However, Rivot et al. (2001) warn that in S–R analysis the Bayesian posterior inferences can be very sensitive to the choice of the prior distributions. Consequently, we began our analysis by estimating the Ricker parameters for each population within the two MUs to provide reasonable regional prior distributions. We found that the regional prior distribution for the two parameters of the Ricker model was bi-

Table 2. Summary of the Ricker models fit to the individual populations within northern British Columbia (NBC) and southern British Columbia (SBC).

<table>
<thead>
<tr>
<th>Region</th>
<th>Parameter</th>
<th>$\alpha_i$</th>
<th>$\beta_i$</th>
<th>$\log(\beta_i)$</th>
<th>$\sigma^2_\alpha$</th>
<th>$\rho_{\text{model}}$</th>
<th>$\rho_{\text{residuals}}$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NBC</td>
<td>Minimum</td>
<td>0.54</td>
<td>2.41 $\times 10^{-4}$</td>
<td>-8.33</td>
<td>0.06</td>
<td>4.28 $\times 10^{-8}$</td>
<td>1.79 $\times 10^{-3}$</td>
<td>8.18 $\times 10^{-3}$</td>
</tr>
<tr>
<td></td>
<td>Median</td>
<td>1.76</td>
<td>6.82 $\times 10^{-3}$</td>
<td>-4.99</td>
<td>0.95</td>
<td>4.85 $\times 10^{-2}$</td>
<td>3.94 $\times 10^{-1}$</td>
<td>4.11 $\times 10^{-1}$</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>1.80</td>
<td>9.56 $\times 10^{-3}$</td>
<td>-5.14</td>
<td>1.00</td>
<td>3.15 $\times 10^{-3}$</td>
<td>5.00 $\times 10^{-1}$</td>
<td>4.10 $\times 10^{-1}$</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>3.41</td>
<td>3.95 $\times 10^{-2}$</td>
<td>-3.23</td>
<td>2.64</td>
<td>7.13 $\times 10^{-1}$</td>
<td>5.00 $\times 10^{-1}$</td>
<td>9.08 $\times 10^{-1}$</td>
</tr>
<tr>
<td>SBC</td>
<td>Minimum</td>
<td>1.07</td>
<td>1.09 $\times 10^{-3}$</td>
<td>-2.96</td>
<td>0.12</td>
<td>2.17 $\times 10^{-4}$</td>
<td>4.55 $\times 10^{-3}$</td>
<td>2.52 $\times 10^{-2}$</td>
</tr>
<tr>
<td></td>
<td>Median</td>
<td>2.02</td>
<td>1.80 $\times 10^{-2}$</td>
<td>-1.74</td>
<td>0.48</td>
<td>6.48 $\times 10^{-2}$</td>
<td>5.00 $\times 10^{-1}$</td>
<td>2.54 $\times 10^{-1}$</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>2.02</td>
<td>4.64 $\times 10^{-2}$</td>
<td>-1.69</td>
<td>0.54</td>
<td>1.44 $\times 10^{-1}$</td>
<td>4.48 $\times 10^{-1}$</td>
<td>2.90 $\times 10^{-1}$</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>3.14</td>
<td>2.71 $\times 10^{-1}$</td>
<td>-0.57</td>
<td>1.64</td>
<td>7.64 $\times 10^{-1}$</td>
<td>5.00 $\times 10^{-1}$</td>
<td>7.87 $\times 10^{-1}$</td>
</tr>
</tbody>
</table>

Note: In this table “$\rho_{\text{model}}$” is the $p$ value for the model $F$ test and “$\rho_{\text{residuals}}$” is the $p$ value for the Kolmogorov–Smirnov test.

Table 3. Estimates of the regional Ricker parameter from the empirical Bayes compared with the simple averages of estimates from model fits to individual populations within northern British Columbia (NBC) and southern British Columbia (SBC).

<table>
<thead>
<tr>
<th>Region</th>
<th>Method</th>
<th>$\alpha_R$</th>
<th>$\sigma^2_\alpha$</th>
<th>$\beta_R$</th>
<th>$\sigma^2_\beta$</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NBC</td>
<td>Simple average</td>
<td>1.790</td>
<td>0.219</td>
<td>-5.135</td>
<td>1.222</td>
<td>0.677</td>
</tr>
<tr>
<td></td>
<td>Empirical Bayes</td>
<td>1.357</td>
<td>0.138</td>
<td>-6.332</td>
<td>0.530</td>
<td>0.643</td>
</tr>
<tr>
<td>SBC</td>
<td>Simple average</td>
<td>2.020</td>
<td>0.183</td>
<td>-3.886</td>
<td>1.820</td>
<td>0.802</td>
</tr>
<tr>
<td></td>
<td>Empirical Bayes</td>
<td>1.855</td>
<td>0.165</td>
<td>-4.275</td>
<td>1.548</td>
<td>0.370</td>
</tr>
</tbody>
</table>

Fig. 6. Contour plots for the joint distribution of regional Ricker $\alpha$ and $\beta$ for (a) northern British Columbia and (b) southern British Columbia. The lines with numeric values represent the contour lines of the resultant NLN (normal–lognormal) density.
variate NLN with a high degree of correlation between the two Ricker parameters, a distribution that had not previously been formally described. We would strongly recommend that the selection of the prior distribution should be based on some real data analysis, and if that is not possible, a comprehensive sensitivity analysis should be conducted for different specifications of prior distributions to insure a robust result. In this sense, the approach developed in this paper to derive the regional NLN distribution and the NLN distribution itself can serve as a departure for future Bayesian analysis.

The NLN regional distribution has not been fully developed in the literature. Conceptually, this distribution, which results from applying a log transformation to the second component of a bivariate normal distribution, is one of the distributions in Johnson’s translation system (Johnson 1987). To the best of our knowledge, this distribution has not been formally developed; therefore, to pursue our meta-model, we formulated the probability density for the NLN distribution and the NLN distribution itself can serve as a departure for future Bayesian analysis.

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The primary objective of this paper was to document a method for describing the distribution of population productivities within a region. The method was illustrated with two examples drawn from coho salmon in British Columbia, and the results are immediately instructive to resource management in several regards. First, the average productivity estimated by averaging estimates from individual populations is higher than the mean of the regional distribution in both MUs. In NBC, the difference in the mean estimated $\mu_{MSY}$ is 0.12, which is the exploitation that would result from a substantial ocean troll fishery or many recreational fisheries. Second, characterization of the distributions of the SR and management parameters within the two MUs will prove essential in exploring the spatial distributions of productivity over the MUs contributing to major mixed-stock fisheries. The same distributions are useful in interpreting the declines in abundance that had been observed. Escapement to the NBC streams has been declining since approximately the 1960s. Over the period 1975 to 1990 and comparing these to the empirical Bayesian approach described in this paper.

We have assumed that the residuals in our $S-R$ models are independently distributed in both space and time. This assumption is a questionable one. Over the spatial scales of the management regions, we consider it is likely that both freshwater and marine survivals of the component populations are correlated (e.g., Bradford et al. (1997) and Mueter et al. (2002), respectively). We are currently investigating a reformulation of model 2 to incorporating these time and spatial structures within the management region.

The estimation procedure in this paper is conducted by reducing the posterior marginal likelihood to a one-dimensional integral. With numerical integration, we estimated the regional Ricker parameters by maximizing the marginal likelihood function. We are currently investigating alternative estimation procedures involving more widely used stochastic methods such as Markov Chain Monte Carlo (Gilks et al. 1996) and nonlinear mixed models (Lindstrom and Bates 1990) and comparing these to the empirical Bayesian approach described in this paper.

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1997, the average exploitation rate is estimated to have been 65%, with a maximum of 81%. That average exploitation rate exceeds the $\mu_{\text{MSY}}$ for approximately 87% of the individual populations within the MU and is sufficient to account for the observed decline in overall abundance. Third, the wide range in productivities exhibited by coho salmon populations within each MU means that inferences drawn from “indicator” streams must be made with care. An indicator stream is one where detailed information about life history and production characteristics is collected. Indicator streams are intended to be representative of other populations in the MU.

The wide range of productivities as reflected by MSY exploitation rates and the highly mixed-stock nature of the fisheries that exploit coho underlies the public policy dilemma facing management agencies attempting to define appropriate exploitation levels for coho salmon and for other anadromous species that have similar population structures. A decision to continue with exploitation rates that are appropriate for the productive populations within a MU would quickly reduce many unproductive populations to low levels. However, the effects of such a harvest policy on within-MU diversity could be unacceptable to those whose perspective is confined to a few component populations. This dilemma is compounded when dealing with numerous co-mingling MUs and extensive enhancement. Even within one MU, the problem is potentially more complex if the spatial pattern of productivity within the MU is such that the low productivity systems are clustered.

The trade-off between production (harvest) and diversity is made more difficult when management units of very different mean productivities co-mingle extensively in ocean fisheries. In this situation, it could be difficult to adequately characterize the trade-offs inherent in a particular exploitation rate. Such a situation exists in northern British Columbia where the distribution of coho from Statistical Area 3 (Nass River and Portland Canal), which contains the most productive populations we encountered in B.C. (Holby et al. 1999), extensively overlaps the distribution of Area 6 (NBC) coho, one of the least productive management units we encountered. The topographies of the two areas are quite different with the streams in Area 6 generally being short and with steep gradients compared with larger and flatter streams in Area 3. Whatever the causes for differing average levels of productivity, the result of that difference has been a geography where coho are slowly becoming rare juxtaposed with an area a scant 100 km away where coho are abundant and becoming more so.

The model developed here enables analyses that can be used to convey to fisheries managers one of the important reasons why extreme contrasts in abundance have developed and, in doing so, encourage more explicit decisions about the setting of exploitation rates in the common fishery that are consistent with desired levels of diversity. The next step in the application of this analysis involves examining in greater detail the spatial and temporal distribution of productivities within and between management unit and the incorporation of environmental information into the model (Chen and Irvine 2001). Wood and Holby (1998) have demonstrated that in coho salmon the levels of neutral gene flow scale linearly with distance between populations. Loss of diversity or local adaptation might therefore be more severe in situations where many adjacent populations are lost compared with the situation where the same total number of nonadjacent populations is lost. The spatial distribution of productivity within an area of generally low productivity, such as Area 6, and the resolve with which resource managers protect spatial elements of diversity will likely underlie the important fisheries management decisions in the near future.

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**References**


Department of Fisheries and Oceans (DFO). 2000. The six principles of the Wild Salmon Policy. Fisheries and Oceans Canada.


Appendix A

Bivariate NLN distribution

Definition of NLN distribution

We sought a bivariate distribution for (X, Y) with two requirements: (i) the marginal distribution for X is normally distributed, i.e., X ~ N(µX, σ2X) and the marginal distribution for Y is lognormally distributed, i.e., Y ~ LN(µY, σ2Y); and (ii) X and Y are correlated with the correlation coefficient ρ. If X and Y were independent, then the joint distribution would be the product of the normal density function and lognormal density function. However, it was necessary to incorporate the correlation of X and Y into this joint distribution, because in our meta-model, X (the Ricker productivity parameter α) and Y (the Ricker density-dependent parameter β) are correlated. Conceptually, by applying a log transformation to the second component of a bivariate normal distribution, the desired distribution would be one of the distributions in the Johnson’s translation system (Johnson 1987). However, to the best of our knowledge, this distribution has not been fully formulated. Therefore, to pursue our meta-model, we formulated the probability density for this bivariate NLN distribution and proved some of its properties. We have named this distribution the joint bivariate normal–lognormal (NLN) distribution with density function for (X, Y) as
(A.1) \[ f_{X,Y}(x,y;\mu_X,\mu_Y,\sigma_X,\sigma_Y,\rho) = \frac{1}{2\pi\sigma_X\sigma_Y\sqrt{1-\rho^2}} \exp\left\{-\frac{1}{2(1-\rho^2)} \left[ \frac{x-\mu_X}{\sigma_X} \right]^2 - 2\rho \frac{x-\mu_X}{\sigma_X} \frac{\ln y - \mu_Y}{\sigma_Y} + \left( \frac{\ln y - \mu_Y}{\sigma_Y} \right)^2 \right\} \]

where \(-\infty < x < \infty, 0 < y < \infty, \sigma_X \text{ and } \sigma_Y > 0, \rho \in (-\infty, \infty), \text{ and } \mu_X < \infty).\) The additional parameter \(\rho\) is related to the correlation coefficient \(\rho_c\) as
\[ \rho_c = \frac{\rho \exp(\sigma_Y^2)}{\sigma_Y} \]
to make eq. A.1 easy to read.

**Properties for the NLN distribution**

For brevity, we have simply listed the pertinent properties of the NLN distribution without analytical derivations. The detailed mathematical derivation is available on request.

(A.2) \[ \mu_X = E(X), \quad \sigma_X^2 = \text{Var}(X), \quad \mu_Y = E(\ln Y), \quad \sigma_Y^2 = \text{Var}(\ln Y), \quad \text{and } \rho = \frac{\text{Cov}(X,Y)}{\sqrt{\text{Var}(X)\text{Var}(Y)}} \]

(A.3) Marginal distributions:
\[ X \sim N(\mu_X, \sigma_X^2) \text{ and } Y \sim LN(\mu_Y, \sigma_Y^2) \]

(A.4) Conditional distributions:
\[ X|Y = y \sim N\left(x, \mu_X + \rho_x \frac{\sigma_x}{\sigma_y} (\ln y - \mu_Y), \sigma_y^2(1-\rho^2)\right) \]
\[ Y|X = x \sim LN\left(y, \mu_Y + \rho_y \frac{\sigma_y}{\sigma_x} (x - \mu_X), \sigma_x^2(1-\rho^2)\right) \]

(A.5) Covariance of \(X\) and \(Y\):
\[ \text{Cov}(X,Y) = \rho_x \sigma_x \sigma_y \exp\left(\mu_y + \frac{\sigma_y^2}{2}\right) \]