# A Bayesian hierarchical analysis of stock–recruit data: quantifying structural and parameter uncertainties

**Catherine G.J. Michielsens and Murdoch K. McAllister**

**Abstract:** Stock–recruit functions are important in fisheries stock assessment, but there is often uncertainty surrounding the appropriate stock–recruit model and its parameter values. Combining different stock–recruit data sets of related species through Bayesian hierarchical analysis can decrease these uncertainties and help to characterize appropriate stock–recruit forms and ranges of plausible parameter values. Two different stock–recruit functions (Beverton–Holt and Ricker) have been parameterized in terms of the steepness, which is a parameter that is comparable between populations. In the hierarchical analysis, the prior probability distribution of parameters for the cross-population variation in steepness is determined through a concise model structure. By calculating the Bayes' posteriors for alternative model forms, model uncertainty is accounted for. This methodology has been applied to Atlantic salmon (*Salmo salar*) stock–recruit data to provide predictions for the steepness of the stock–recruit function for Baltic salmon for which no stock–recruit data exist.

**Résumé :** Les fonctions stock–recrutement sont de grande importance pour l'évaluation des stocks des pêches commerciales, mais il y a souvent de l'incertitude au sujet du choix d'un modèle approprié et des valeurs de ses paramètres. La combinaison de plusieurs séries de données de stock–recrutement d'espèces apparentées dans une analyse hiérarchique bayésienne peut réduire ces incertitudes, aider à identifier les relations stock–recrutement appropriées et déterminer les étendues plausibles des valeurs des paramètres. Nous avons caractérisé les paramètres de deux fonctions stock–recrutement (Beverton–Holt et Ricker) en ce qui concerne l'inclinaison de la pente, qui est un paramètre comparable entre les populations. Dans l'analyse hiérarchique, la distribution de probabilité a priori des paramètres en ce qui a trait à la variation de l'inclinaison d'une population à une autre est déterminée par une structure de modèle concis. Le calcul des distributions bayésiennes a posteriori pour les différentes formes de modèles permet de tenir compte de l'incertitude. Nous avons appliqué cette méthodologie à des données de stock–recrutement du saumon de l'Atlantique (*Salmo salar*) afin de pouvoir prédire l'inclinaison de la fonction stock–recrutement du saumon de la Baltique pour lequel il n'existe pas de données sur la relation stock–recrutement.

[Traduit par la Rédaction]

## Introduction

The parameters and the functional form of the stock–recruit function are among the most important model specifications in fisheries stock assessments. This is because the parameter values and functional forms determine the predicted impacts of changes in the fish stock on future fish recruitment. Quantitative–empirical knowledge of the stock–recruit function for a fish stock can thus improve the ability of managers to make appropriate policy decisions. However, stock–recruit data sets are often short and noisy (Myers et al. 1995), which increases the uncertainty about the underlying stock–recruit relationships. Combining different stock–recruit data sets of related species within an hierarchical model can decrease that uncertainty (Myers 2001). Several such hierarchical analyses have been undertaken for stock–recruit data (Liermann and Hilborn 1997; Myers et al. 1999; Dorn 2002).

This paper provides a general framework for the analysis of stock–recruit data through a Bayesian hierarchical analysis whereby both model form and parameter uncertainties are taken into account. The paper reformulates a set of methodologies to be used for the construction and validation of Bayesian hierarchical models (Gelman et al. 1995). It presents an Atlantic salmon (*Salmo salar*) case study to which the methodology is applied and the stock–recruit data used in the analysis. The models are run using these data to obtain the posterior probability density functions for the steepness of the different stock–recruit functions and to predict the steepness of the stock–recruit function of Baltic salmon

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for which no stock–recruit data have been available. The credibility of the stock–recruit functions is examined by computing the marginal posterior probabilities of the different models.

## Methodology

This paper advocates the use of hierarchical models for the analysis of a group of related stock–recruit data sets. Hierarchical modelling is a statistical technique that allows the modelling of the dependence among parameters that are related or connected through the use of a hierarchical model structure (Gelman et al. 1995). Hierarchical models can be used to combine data from several independent sources (Liermann and Hilborn 1997). In contrast with nonhierarchical models, hierarchical models can estimate parameters simultaneously at the population level and at the metapopulation level. In doing so, hierarchical models also allow the prediction of parameters of a population for which no data are observed, based on the estimates for the metapopulation and the similarities between individual stocks. Furthermore, by structuring some dependence among parameters, we can avoid the problem of overfitting the data, i.e., producing models that fit the data very well but provide inferior predictions for new data (Su et al. 2001).

To allow different stock–recruit data to be used together in the same meta-analysis, stock–recruit functions can be parameterized in terms of steepness (Mace and Doonan 1988; Punt and Hilborn 1997). The steepness of a stock–recruit function is the proportion of the long-term unfished recruitment obtained when the stock abundance is reduced to 20% of the virgin level. The advantage of this parameterization is that the steepness parameter is transportable or comparable between stocks (Hilborn and Liermann 1998). Because of this advantage, this parameterization is a common feature of hierarchical analyses of stock–recruit data (Liermann and Hilborn 1997; Myers et al. 1999; Dorn 2002). The parameterization in terms of steepness was originally derived for the Beverton–Holt stock–recruit function (Beverton and Holt 1957), but a similar parameterization in terms of steepness can be derived for other stock–recruit functions such as the Ricker stock–recruit function (Ricker 1954).

The steepness parameterization permits comparison of estimates of the same parameter between fits of different stock–recruit functions to the same data. If different steepness estimates are found between different models, this may require an evaluation of the goodness-of-fit of the different models to the data to facilitate model selection. However, comparing the fit of the different stock–recruit functions to the data is, by itself, insufficient. Instead, the model uncertainty should be assessed probabilistically to allow it to be incorporated in stock assessments and decision analysis (McAllister and Kirchner 2002).

A Bayesian hierarchical analysis (Gelman et al. 1995) offers a natural way to incorporate both model and parameter uncertainty regarding stock–recruit relationships. The prior probability density function (pdf) of the steepness values for the different stocks used in the hierarchical analysis is determined through the model structure. This is achieved through the use of a mean steepness for the combined set of populations and a cross-population variance in the steepness, which is made to depend on the mean. By calculating the Bayes' posteriors for each stock–recruit model, the model uncertainty can be formally incorporated in fisheries stock assessments and decision analyses. This paper, however, is restricted to the stock–recruit analysis.

The Bayesian hierarchical analysis within this paper has been implemented using a Gibbs sampler to sample from the posterior distribution. Such a method can be executed using WinBUGS (Bayesian inference Using Gibbs Sampling) software (available from http://mrc-bsu.cam.ac.uk/bugs) (Meyer and Millar 1999). As with any Markov Chain Monte Carlo simulation, the Gibbs sampler requires an evaluation to determine if it is reasonable to believe that the samples are representative of the underlying stationary distribution, i.e., if the Markov Chain has converged. To examine convergence, a convergence diagnosis and output analysis software for Gibbs sampling output (CODA) is used (Best et al. 1995). All of the modelling results described in this paper have undergone tests to remove the "burn-in" and to assess convergence and it is assumed that the reported distributions obtained through Gibbs sampling are representative of the underlying stationary distributions.

The hierarchical analysis developed for this paper has been thoroughly tested using a variety of different model forms and data distributional assumptions. The posterior probability distribution for model parameters is determined by the product of the prior pdf of the parameters and a likelihood function of the data given these parameters. Bayesian methodology has been criticized because of the subjective choices of the prior pdf and the likelihood function. Therefore, it is important to assess the sensitivity of the posterior probability distribution to reasonable changes in the choices for the prior probabilities and likelihood functions (Clarke and Gustafson 1998).

To assess the fit of the stock–recruit models to the data, the data can be compared with the posterior predictive distribution of the model, i.e., the distribution of data simulated from the model (Gelman et al. 1995). This will allow us to assess whether the observed data look plausible under the posterior predictive distribution. Systematic differences between the simulations and the data indicate potential failings of the model. We define $R^{\mathrm{rep}}$ as the replicated data point on recruitment that could have been observed as the data if we were to replicate the recruitment data using the model and the observed stock abundance data. Simulation of potential data given the observed data and the joint posterior for θ is easily obtained using WinBUGS. The distribution of $R^{\mathrm{rep}}$ is called the posterior predictive distribution:

$$(1) \qquad p(R^{\mathrm{rep}}|\underline{R}^{\mathrm{obs}}) = \int p(R^{\mathrm{rep}}|\theta)p(\theta|\underline{R}^{\mathrm{obs}})\mathrm{d}\theta$$

The underlined symbols represent vectors of either data or parameters. For example $\underline{R}^{\mathrm{obs}}$ represents the vector of observed recruitment data. We can thereafter compare the observed data with the posterior predictive distribution. The results of this comparison can be expressed in terms of a Bayesian $p$-value (Meng 1994; Gelman et al. 1995, 1996). Bayesian $p$-values can be defined as the probability that the replicated data could be as extreme or more extreme than the observed data (Meng 1994):

$$(2) \qquad \text{Bayesian } p\text{-value} = p(R^{\mathrm{rep}}|\theta) \geq R^{\mathrm{obs}}$$

We can also measure the discrepancy between the model and the data using test quantities or discrepancy measures, $T(R, \theta)$. A discrepancy measure is a scaler summary of parameters and data that is used as a standard when comparing data with predictive simulations. One test quantity useful for routine checks of goodness-of-fit is the $\chi^2$ discrepancy measure (Gelman et al. 1995):

$$\text{(3)} \qquad \chi^2 \text{ discrepancy: } T(R,\theta) = \sum_i \frac{(R_i - E(R_i|\theta))^2}{\mathrm{var}(R_i|\theta)}$$

It is therefore possible to compare the realized discrepancy $T(R, \theta)$ with the discrepancy under the posterior predictive distribution $T(R^{\text{rep}}, \theta)$. To do this, we take a random sample from the posterior distribution for the full set of parameters in the model, $\theta$. For each set of parameter values $\theta_j$, we can simulate a new recruitment data set, $R^{\text{rep}}$, and we can then plot $T(R^{\text{rep}}, \theta_j)$ against $T(R, \theta_j)$. The estimated Bayesian *p*-value is the proportion of times that $T(R^{\text{rep}}, \theta_j)$ is greater than $T(R, \theta_j)$ (Brooks et al. 2002). It is recommended that both the graphical summary and Bayesian *p*-value be used, since it is possible for the distributions of $T(R^{\text{rep}}, \theta_j)$ and $T(R, \theta_j)$ to differ even though a *p*-value of 0.5 is obtained (Brooks et al. 2000).

Apart from the models themselves, the data used in these hierarchical models need to be tested on certain assumptions. For a hierarchical analysis, the different data sets need to be exchangeable, i.e., the differences among the data sets should not have predictable effects on the results of the analysis (Gelman et al. 1995). To examine the exchangeability of the data sets, the hierarchical analysis can be run excluding one data set each time. The marginal probability distributions for the steepness parameter of the stock–recruit function obtained from the remaining data sets can be compared to assess the exchangeability of the data sets. If the different data sets are exchangeable in terms of the steepness parameter, the exclusion of one data set should not substantially alter the marginal posterior predictive distribution for the steepness. These different tests on model and data assumptions will be applied within this paper.

Bayesian analyses also allow us to compare the probability of the different models given the stock–recruit data. The posterior probability distribution of model *i* given the observed data is given by the equation

$$\text{(4)} \qquad P(M_i|\,\text{data}) = \frac{P(\text{data}|\,M_i)P(M_i)}{P(\text{data})}$$

or

$$\text{(5)} \qquad P(M_i|\,\text{data}) \propto P(M_i)\int_{\theta_i} P(\text{data}|\,\theta_i, M_i)P(\theta_i|\,M_i)\mathrm{d}\theta_i$$

Kass and Raftery (1995) have proposed a method to approximate the Bayes' posterior using the harmonic mean of the likelihood function

$$\text{(6)} \qquad P(\text{data}|M_i) \approx \frac{m}{\sum_{k=1}^{m} \frac{1}{P(\text{data}|\,\theta_i^k, M_i)}}$$

where $\theta^k$ is the *k*th set of draws from the different model parameters and *m* is the number of Markov Chain Monte Carlo iterations. The harmonic mean of the likelihood values converges to the correct value as the number of samples *m* approaches infinity (Newton and Raftery 1994). However, the harmonic mean of the likelihood value does not satisfy the Gaussian central limit theorem. The occasional occurrence of a value of $\theta^k$ with a small likelihood, resulting in large values for the harmonic mean, makes the harmonic mean unstable (Kass and Raftery 1995). The harmonic mean cannot be obtained directly from WinBUGS. Instead, WinBUGS will calculate the deviance (–2 × log likelihood). Using these output values, the harmonic mean and the Bayes' posterior can be derived.

## Case study: Atlantic salmon

The proposed methodology can be applied to any species, and in this paper, Atlantic salmon stocks are taken as an example. Stock–recruit data exist for some Atlantic salmon stocks and not for others. For example, in the Baltic Sea area, no stock–recruit data have been compiled and no information exists about the stock–recruit function of Baltic salmon stocks. Potentially, we could assume that nothing is known about the stock–recruit function and its parameters in the Baltic Sea area, but this would be ignoring all of the Atlantic salmon stock–recruit data from outside this area (Myers et al. 1999; Barrowman and Myers 2000; Prévost et al. 2001). Because each Baltic salmon stock could be considered as one of the many different Atlantic salmon stocks, the stock–recruit functions obtained by analysing stock–recruit data of Atlantic salmon index rivers can be extrapolated to salmon stocks in the Baltic Sea area. Three components are involved in the extrapolation: a functional form, a scale component, and a population dynamics component (Prévost et al. 2001). Although functional forms could vary among stocks, it is generally accepted that owing to similarities in biology, life history, and ecology among populations of the same species, the functional form is the same. The scale component, irrespective of the functional form, is related to the concept of carrying capacity and can be obtained through an evaluation of habitat quality and (or) availability (Uusitalo 2001). The third component is the population dynamics component, i.e., the steepness parameter, which is comparable between stocks and which can be obtained through a hierarchical analysis of stock–recruit data. The concept of steepness also holds across different functional forms. Bayesian hierarchical analyses therefore allow an extrapolation of the stock–recruit functions of sampled Atlantic salmon stocks to unsampled salmon stocks such as those in the Baltic Sea area (Prévost et al. 2001).

### Stock–recruit data

The stock–recruit data of Atlantic salmon used in the hierarchical analysis are obtained through a search of both published and grey literature. The number of stock–recruit data sets is small and limited compared with the number of Atlantic salmon stocks present. Therefore, it is crucial to make sure that the data set is representative for the entire Atlantic salmon population and that no bias is introduced when selecting the data sets (Myers and Mertz 1998; Prévost et al.

**Table 1.** Description of the different Atlantic salmon stock–recruit data sets found in the literature according to the river and country of occurrence, data format, number of data points collected, form and language in which they have been published, and the publication reference.

| River | Country | Data format | Data points | Publication | Language | Reference(s) |
|---|---|---|---|---|---|---|
| Little Codroy River | Canada | Eggs–smolts | 7 | Journal | English | Chadwick 1982 |
| Margaree River | Canada | Eggs–adults | 36 | Research document | English | Chaput and Jones 1992 |
| Pollett River | Canada | Eggs–smolts | 8 | Journal | English | Elson 1975; Myers et al. 1995 |
| Trinite River | Canada | Eggs–smolts | 8 | Research document | French | Caron 1992; Myers et al. 1995 |
| Western Arm Brook | Canada | Eggs–smolts | 15 | Research document | English | Chaput et al. 1992 |
| River Bush | United Kingdom | Eggs–smolts | 17 | Journal | English | Crozier and Kennedy 1995 |
| River Ellidaar | Iceland | Eggs–adults | 37 | Journal | English | Mundy et al. 1978 |
| River Oir | France | Eggs–smolts | 10 | Journal | French | Prévost et al. 1996 |
| River Bec-Scie | Canada | Eggs–smolts | 5 | Research document | French | Caron 1992 |

2001). The selected stock–recruit data sets needed to be transformed to express the relationship between eggs and smolts. Eggs–adults data were transformed by applying an approximation of the survival rate from smolts to adults (10%). This transformation does not account for any uncertainty in the value for the survival rate from smolts to adults. The assumed survival rate from smolts to adults will affect the estimated steepness parameters of the stocks in question, but sensitivity analyses demonstrate that the impact of the assumed survival rate on the predicted steepness parameter for the Baltic salmon stocks is relatively small owing to the large amount of uncertainty surrounding these estimates. Eggs–parr data, on the other hand, were not transformed and used because of the possible density-dependent relationship between the parr and smolt stage.

In total, nine different stock–recruit data sets (consisting of 143 data points in total) were found covering both sides of the Atlantic Ocean (Table 1). The data sets were found in journal articles and research documents and were all independent of each other. Although searched for, no publications of stock–recruit data were encountered in languages other than English or French.

### Description of stock–recruit functions and their parameterization

In order for a stock–recruit model to be useful, it should adequately represent the biological processes of the stock, fit well to the stock–recruit data and behave sensibly in probabilistic projections (Needle 2002). For Salmonids, the most commonly used stock–recruit functions are the Ricker and the Beverton–Holt stock–recruit functions (Hilborn and Walters 1992). These stock–recruit functions are governed by the following equations (eq. 7, Beverton and Holt 1957; eq. 8, Ricker 1954):

$$(7) \qquad R = \frac{S}{\alpha + \beta S}$$

$$(8) \qquad R = aSe^{-bS}$$

where $S$ is a measure of the spawning stock size and $R$ is the number of recruits. These two functions can be parameterized in terms of river specific parameters: steepness ($z$), recruitment at equilibrium ($R_0$), and spawner biomass per recruit ($\tilde{S}$). The definition for steepness is illustrated for the Beverton–Holt curve through the following equation (Liermann and Hilborn 1997):

$$(9) \qquad zR_0 = \frac{0.2S_0}{\alpha + 0.2\beta S_0}$$

The following equations convert steepness ($z$), recruitment at equilibrium ($R_0$), and spawner biomass per recruit ($\tilde{S}$) into the alpha and beta parameters of the Beverton–Holt stock–recruit function:

$$(10) \qquad \alpha = \frac{(1-z)}{4z} \cdot \frac{S_0}{R_0} = \frac{(1-z)}{4z} \cdot \tilde{S}$$

$$\beta = \frac{5z-1}{4zR_0}$$

Similarly, the $a$ and $b$ parameter of the Ricker stock–recruit function can be expressed in terms of steepness ($z$), recruitment at equilibrium ($R_0$), and spawner biomass per recruit ($\tilde{S}$):

$$(11) \qquad a = \frac{(5z)^{5/4}}{\tilde{S}}$$

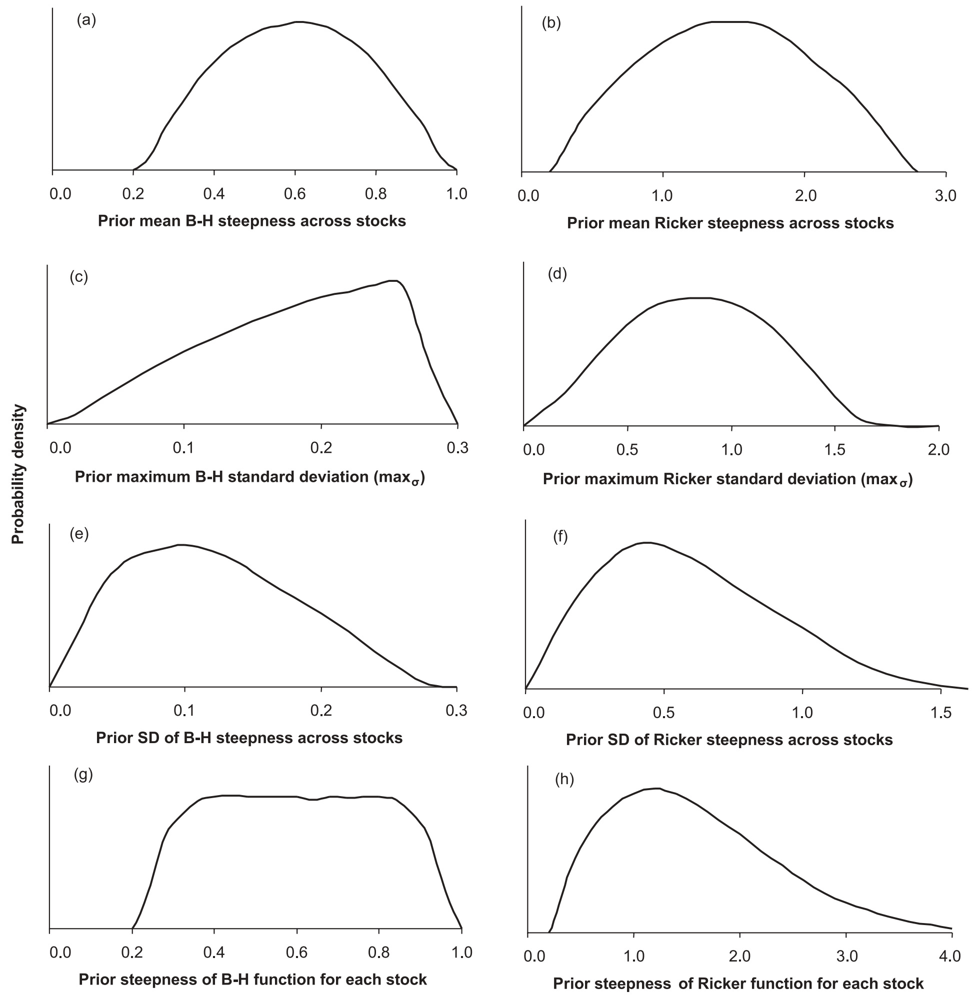
$$b = \frac{5}{R_0\tilde{S}} \cdot \log(5z)$$

The similar parameterization of the Beverton–Holt and the Ricker models allows us to estimate the steepness of the different stock–recruit models within similar overall model structures.

### Description of the prior pdfs

According to Liermann and Hilborn (1997), the most difficult part of using hierarchical models is the construction of prior probability distributions. Some prior information about the model parameters will be present based on their definitions and the structural limitations of the models in which they are placed. By definition, the steepness parameter for the Beverton–Holt stock–recruit function can only have values between 0.2 and 1. Therefore, the mean steepness ($\mu_z$) across salmon stocks will lie between those boundaries. A flat distribution for the mean steepness would be inappropriate, since a mean steepness of 0.2 or 1 would imply zero variation around the mean, i.e., all stocks would have a

**Fig. 1.** Prior probability density functions of (*a* and *b*) mean steepness across Atlantic salmon stocks, (*c* and *d*) maximum standard deviation around the mean steepness, (*e* and *f*) cross-population standard deviation in steepness, and (*g* and *h*) steepness for each of the different Atlantic salmon stocks assuming a Beverton–Holt (B–H) or Ricker stock–recruit function.




steepness of exactly 0.2 or 1, which is a highly unlikely event considering previous steepness estimates (Myers et al. 1999). The pdf of the mean steepness is therefore assumed to follow a beta distribution Beta(2,2) rescaled to lie between 0.2 and 1 and with unlikely outer values. The prior pdf for the mean steepness is shown in Fig. 1*a*.

Apart from a cross-population mean steepness, we also need to define a cross-population variance in steepness. The maximum possible variance $\max(\sigma_z^2)$ given a particular value for mean steepness, a symmetrical uniform distribution for $z$ under the maximum possible variance, and the 0.2–1 boundaries can be calculated using equation (Evans et al. 2000)

$$(12)\qquad \max(\sigma_z^2) = [\max(z) - \min(z)]^2/12$$

where $\max(\sigma_z^2)$ is the maximum possible variance in steepness $z$, $\max(z)$ is the upper limit of the range of steepness $z$, and $\min(z)$ is the lower limit of the range of steepness $z$. Practically speaking, if, for example, one particular draw from the prior distribution for the mean steepness is 0.8, then the upper limit of the range for steepness would be 1 and the minimum would be 0.6. The corresponding maximum possible standard deviation in steepness in this example is therefore 0.12. The prior pdf for the maximum standard deviation in steepness $\max(\sigma_z)$ is also shown in Fig. 1*c*. It is assumed that the maximum standard deviation is the most likely value for the cross-stock standard deviation with a linear relationship expressing the reduction in probability

**Table 2.** Median and 95% probability interval of the prior probability distributions for the spawner biomass (eggs) per recruit (smolts) (SBPR) parameter of the different Atlantic salmon stocks.

| River | Median SBPR | 95% probability interval |
|---|---|---|
| Little Codroy River | 308 | 81–613 |
| Margaree River | 367 | 95–762 |
| Pollett River | 368 | 95–759 |
| Trinite River | 360 | 93–749 |
| Western Arm Brook | 294 | 73–593 |
| River Bush | 210 | 54–410 |
| River Ellidaar | 282 | 73–555 |
| River Oir | 388 | 101–806 |
| River Bec-Scie | 409 | 106–859 |
| Baltic salmon rivers | 500 | 127–1000 |

**Table 3.** Summary of model parameters and their description and WinBUGS representation.

| Model parameter | Description | WinBUGS representation |
|---|---|---|
| $\underline{z}$ | Steepness of the Beverton–Holt stock–recruit function for stock *j* | z[j] |
| $\underline{zt}$ | Steepness of the Beverton–Holt stock–recruit function for stock *j* scaled to lie between 0 and 1 | zt[j] |
| $\alpha_{zt}$ | First shape parameter of the beta distribution for scaled steepness | alpha_zt |
| $\beta_{zt}$ | Second shape parameter of the beta distribution for scaled steepness | beta_zt |
| $\mu_{zt}$ | Mean of the steepness across stocks scaled to lie between 0 and 1 | mu_zt |
| $\mu_z$ | Mean steepness across stocks | mu_z |
| $\sigma_{zt}$ | Cross-stock standard deviation in the scaled steepness | sd_zt |
| $\sigma_{ztt}$ | Cross-stock relative standard deviation in the scaled steepness | sd_ztt |
| $\max(\sigma_{zt})$ | Maximum cross-stock standard deviation in the scaled steepness | max_sd_zt |
| $\underline{\tilde{S}}$ | River-specific spawner biomass per recruit | SBPR[j] |
| $\underline{R}$ | River-specific recruitment potential | R[j] |
| $\mu_R$ | Mean recruitment potential across stocks | mu_R |
| $\tau_R$ | Cross-stock precision of recruitment potential | tau_R |
| $\underline{\alpha}$ | Alpha parameter of the Beverton–Holt stock–recruit function for stock *j*, where 1/α is the maximum recruitment per spawner as spawner abundance approaches 0 | alpha[j] |
| $\underline{\beta}$ | Beta parameter of the Beverton–Holt stock–recruit function for stock *j*, where 1/β is the maximum number of recruits | beta[j] |
| $\underline{\theta}$ | Vector of parameters that are treated as random variables | exp_Smolts[i] |
| $\underline{\text{Eggs}}$ | Observed number of eggs counted in sample *i* | Eggs[i] |
| $\underline{\text{smolts}}^{\text{obs}}$ | Observed number of smolts resulting from eggs of sample *i* | obs_Smolts[i] |
| $\underline{\text{smolts}}^{\text{exp}}$ | Mean number of smolts expected from eggs of sample *i* | exp_Smolts[i] |
| $\underline{\text{smolts}}^{\text{rep}}$ | Replicated number of smolts that could have been observed using the model | rep_Smolts[i] |
| $\tau_{\text{smolts}}$ | Precision of the number of smolts expected | tau_Smolts |

as the cross-stock standard deviation approaches 0 (Beta(2, 1)). The resulting prior for the cross-stock standard deviation ($\sigma_z$) is also shown (Fig. 1*e*). The prior pdf of the mean steepness of the meta-population, $\mu_z$, and of the standard deviation of steepness of the meta-population, $\sigma_z$, are used to define the marginal prior pdf of the steepness for each population or stock ($\underline{z}$) (Fig. 1*g*).

For the Ricker stock–recruit function, the steepness parameter cannot be smaller than 0.2 but it can be larger than 1. Applying the same prior probability distribution for the steepness parameter as for the Beverton–Holt stock–recruit model would result in an underestimation of the steepness of the Ricker curve. Instead, a new prior needs to be constructed for the steepness parameter of the Ricker model. The main problem when constructing such a prior is to define the upper limit for the prior mean steepness across populations. This prior knowledge has been based on the results of Myers et al. (1999) who have estimated the slope at the origin for many different stocks. Based on their results obtained for Salmonidae (transformed into steepness values for the Ricker model using eq. 11), it is unlikely that the mean steepness across stocks will be larger than 2.8. This prior knowledge can be translated into a prior probability distribution for the mean steepness across stocks defined by a beta distribution Beta(2, 2) rescaled between 0.2 and 2.8 (Fig. 1*b*).

Using the same rules as for the steepness-related priors of the Beverton–Holt function, it is possible to derive the corresponding prior probability distributions for the maximum standard deviation around the mean steepness, the cross-standard deviation in steepness, and the steepness of the Ricker stock–recruit function for each stock (Figs. 1*d*, 1*f*, and 1*h*). Compared with the prior for the Beverton–Holt function, the maximum standard deviation around the mean steepness only has a lower boundary but no upper boundary when assuming a symmetrical distribution for $\sigma_z$.

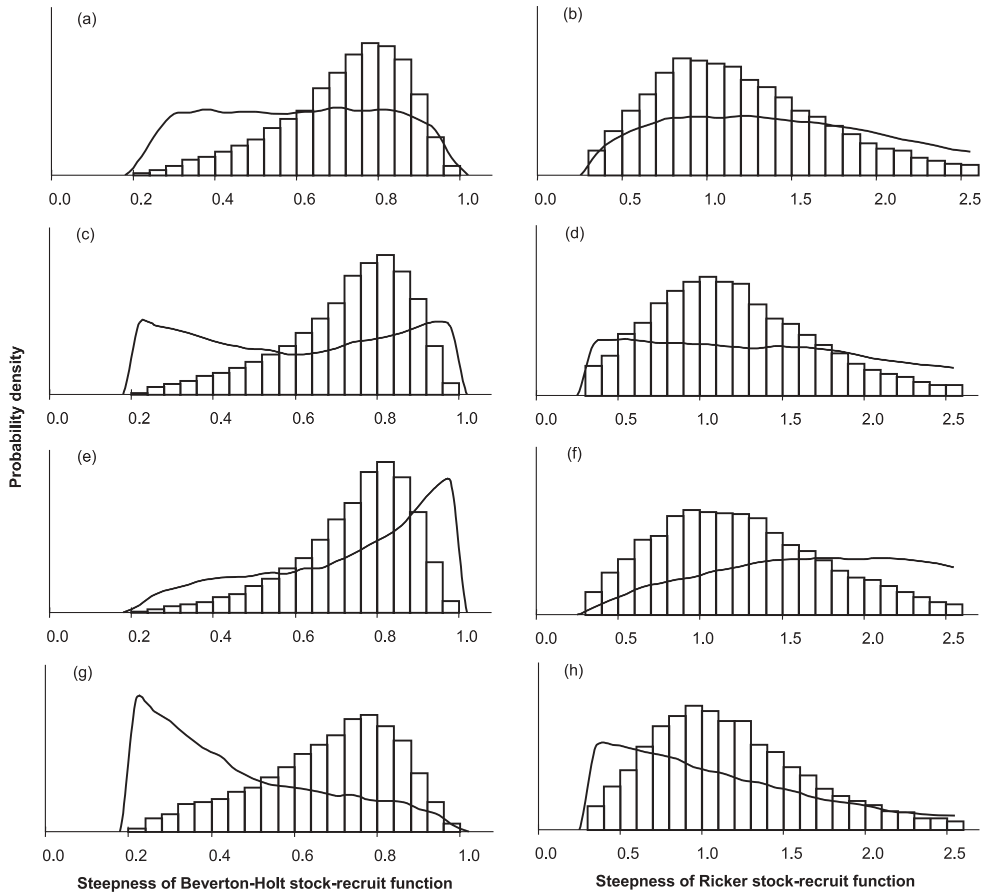
The prior probability distributions for the smolt production capacity are assumed to be lognormally distributed. The log-transformed mean smolt production capacity across Atlantic salmon stocks is given an uninformative normal distribution $N(0, 1000^2)$. The cross-stock deviance around that mean capacity is defined in terms of precision (precision = 1/variance) and given an uninformative gamma distribution $G(0.001, 0.001)$.

The spawner biomass per recruit parameter is given stock-specific informative priors. The spawner biomass per recruit can be calculated through the following equation:

$$(13)\qquad \tilde{S} = HF\sum_{k=1\text{SW}}^{3\text{SW}} p_k s_k W_k$$

where $H$ is the smolt to grilse survival rate from natural mortality (expressed as a proportion), $p$ is the relative proportion given natural mortality and homing rates of one-sea-winter (1SW), 2SW, or 3SW salmon, $s$ is the proportion of females, $W$ is the weight of the fish, and $F$ is the relative fecundity of female salmon (eggs per kilogram). Different Atlantic salmon stocks may have a different productivity depending on the relative proportion of female salmon in different age groups. River-specific estimates for the relative proportion of 1SW, 2SW, and 3SW salmon and the propor-

**Fig. 2.** Prior and marginal posterior predictive probability distribution of the steepness for (*a*, *c*, *e*, and *g*) Beverton–Holt and (*b*, *d*, *f*, and *h*) Ricker stock–recruit functions for Baltic salmon when using different prior probability distributions for the mean steepness across Atlantic salmon stocks: (*a* and *b*) Beta(2, 2); (*c* and *d*) *U*(0,1); (*e* and *f*) Beta(1, 2); (*g* and *h*) Beta(2, 1).




tion of females have been obtained from Hutchings and Jones (1998) and the International Council for the Exploration of the Sea (2003). Where river specific estimates were missing, as for example for the Rivers Pollet and Bec-Scie, region-specific estimates have been chosen (Hutchings and Jones 1998). Hutchings and Jones (1998) also provided estimates for the smolt to grilse survival (1.3–17.4%). This has been translated into a probability distribution for $H$ in eq. 13 ($N(0.1, 0.05^2)I(0.013, 0.17)$, meaning that the normal distribution has been truncated at 0.013 and 0.17). The weight of a grilse is assumed to be between 1.5 and 3 kg ($N(2.25, 0.38^2)I(1.5, 3)$), while the weight of a 2SW and 3SW salmon is assumed to vary between 3 and 7 kg ($N(5, 1.2^2)I(3,7)$) and between 6 and 14 kg ($N(10, 2.24^2)I(6, 14)$), respectively. The relative fecundity is given a uniform distribution between 1600 and 1800 eggs per kilogram female salmon ($U(1600, 1800)$) (Bardonnet and Bagliniere 2000). The resulting statistics for the prior probability distributions of the spawner biomass per recruit parameter for the different rivers are presented in Table 2.

## Description of the hierarchical model

The joint posterior density function of the hierarchical model parameters is given by the equation

$$(14)\quad p(\theta|\underline{\text{smolts}}^{\text{obs}}) = p(\mu_z)p(\sigma_z)p(\mu_R)p(\tau_R)p(\tau_{\text{smolts}}) \times p(\underline{\tilde{S}})p(\underline{z}|\mu_z,\sigma_z)p(\underline{R}|\mu_R,\tau_R)p(\underline{\text{smolts}}^{\text{obs}}|\underline{z},\underline{\tilde{S}},\underline{R})$$

where θ represents all parameters treated as random variables in the model, namely

$$(15)\quad \theta = \underline{z}, \mu_z, \sigma_z, \underline{\tilde{S}}, \underline{R}, \mu_R, \tau_R, \tau_{\text{smolts}}$$

We give an overview of all the model parameters and their description in Table 3. We also present part of the WinBUGS code for the hierarchical model for the Beverton–Holt stock–recruit function of different Atlantic salmon stocks (Appendix A). The model assumes a lognormal likelihood function. The WinBUGS code for the Ricker model is similar to this code except for the stock–recruit function. In the model, the river-specific values of $\tilde{S}$ are to be obtained from eq. 13.

In this model, we are mainly interested in the marginal posterior distribution of the steepness for some unsampled stock, which is determined by the mean and standard deviation in steepness across stocks. The joint posterior distribution for the mean and standard deviation in steepness is governed by the equation

**Fig. 3.** Prior and marginal posterior predictive probability distribution of the steepness for (*a*, *c*, and *e*) Beverton–Holt and (*b*, *d*, and *f*) Ricker stock–recruit functions for Baltic salmon when using different prior probability distributions for the precision of the likelihood function: (*a* and *b*) $G(0.001, 0.001)$; (*c* and *d*) $G(0.1, 0.001)$; (*e* and *f*) $G(10, 10)$.

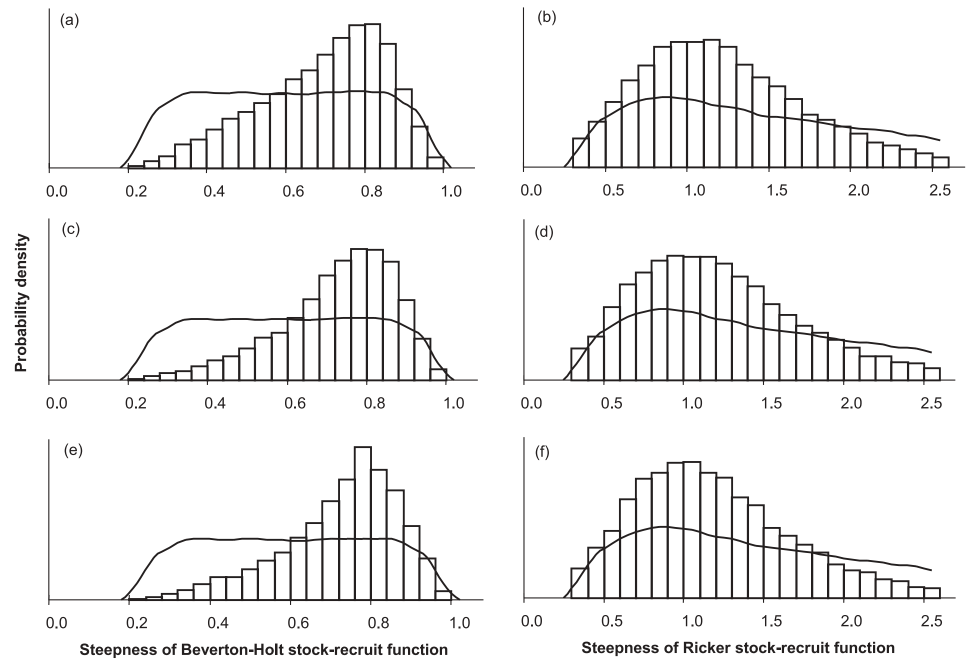
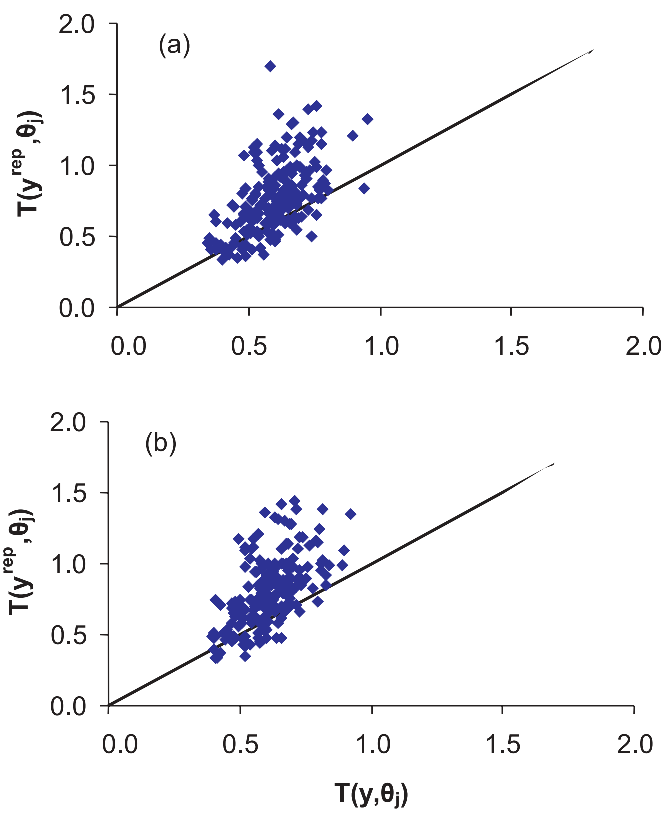



**Fig. 4.** Discrepancy plots between the data and the models using (*a*) Beverton–Holt and (*b*) Ricker stock–recruit functions. The corresponding Bayesian *p*-values, computed as the proportion of points above the line, are 0.78 and 0.8, respectively. Values close to 0.5 represent a good fit to the data.




(16) $$p(\mu_z, \sigma_z \underline{\text{smolts}}^{\text{obs}}) = \int\int\int\int\int\int p(\theta | \underline{\text{smolts}}^{\text{obs}})\, d\mu_R\, d\tau_R\, d\tau_{\text{smolts}}\, d\underline{z}\, d\underline{\tilde{S}}\, d\underline{R}$$

The marginal predictive posterior distribution function of the steepness for some unsampled stock, $z_j$, is given by the equation

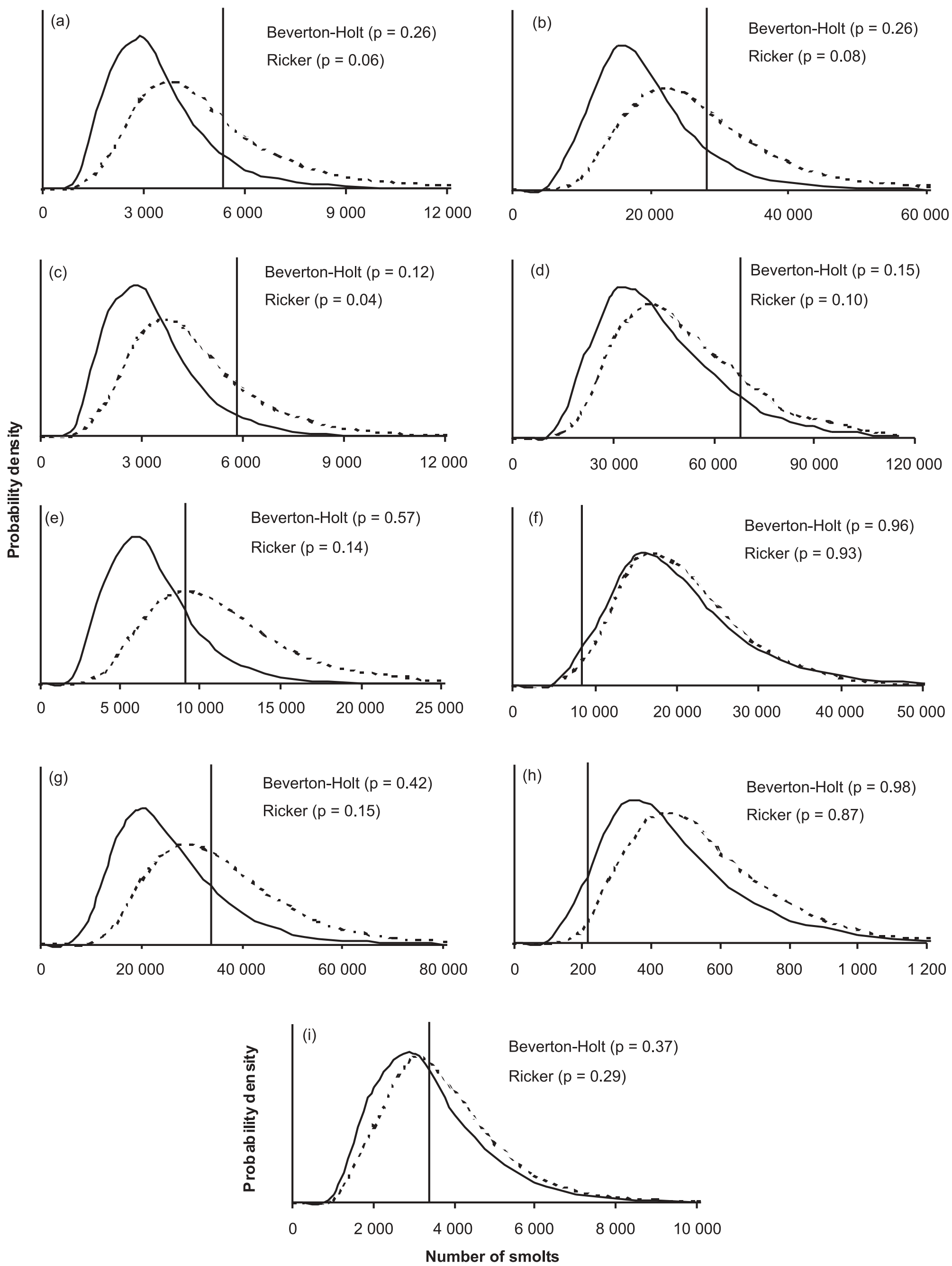
(17) $$p(z_j | \underline{\text{smolts}}^{\text{obs}}) = \int\int p(z_j | \mu_z, \sigma_z)\, p(\mu_z, \sigma_z | \underline{\text{smolts}}^{\text{obs}})\, d\mu_z\, d\tau_z$$

## Results

### Tests concerning model structure and data assumptions

Evaluations of the sensitivity of results to prior pdf specifications for all of the major model parameters have been conducted. However, since the probability distribution for the steepness parameter is of most interest for the current analysis, we present mostly results for changes in the prior for the steepness parameter. We have replaced the dome-shaped prior probability distribution (Beta(2, 2) rescaled to lie between 0.2 and 1 or between 0.2 and 2.8 depending on the stock–recruit function) with distinctly different prior distributions ($U(0, 1)$, Beta(1, 2), and Beta(2 ,1) all rescaled, e.g., to lie between 0.2 and 1) to assess the impacts on the marginal posterior distribution of the steepness parameter for Baltic salmon. The graphs (Fig. 2) show limited differences between the posterior density functions when using different prior density functions. Similar sensitivity analyses have been done for the distribution of the precision parameter of the likelihood function. The graphs show no substantial differences in the marginal posterior probability distribution for

**Fig. 5.** For each data set, the observed smolt abundance at the lowest stock level is compared with the predictive probability distribution. The observed number of smolts (vertical line) is compared with the posterior predictive distribution of the number of smolts using a Beverton–Holt (broken line) or Ricker (solid line) stock–recruit function. The posterior predictive *p*-value is defined as the probability that the replicated data are more extreme than the observed data.




the steepness of the different stock–recruit functions for Baltic salmon (Fig. 3).

The observed data have been compared with the posterior predictive distributions of the data. When looking at the resulting Bayesian *p*-values for all of the data points, 4.9% of the data points fell outside the 95% probability intervals of the predictive probability distribution when using a Beverton–Holt stock–recruit function compared to 2.1% of the data points when assuming a Ricker stock–recruit function. The discrepancy plots indicate that the models fit the data relatively well and that the Beverton–Holt stock–recruit model is performing slightly better than the Ricker stock–recruit model (Fig. 4). Because of the concern of Barrowman and Myers (2000) that at low stock or egg abundance, the Ricker and the Beverton–Holt functions tend to lie above the observed data points, we have selected from each data set the point at the lowest stock level and compared this point with the predictive probability distribution of the data (Fig. 5). We have done this graphical comparison for the two different stock–recruit functions. When comparing the observed value against the predictive probability distribution for each data point at the lowest stock level, there does not seem to be consistent overprediction of smolt recruitment.

To examine the exchangeability of the data sets, the two different stock–recruit models are each run nine times, excluding one data set each time. The graphs (Fig. 6) indicate that none of the data sets substantially alter the outcome of the hierarchical analysis. Therefore, it is concluded that the requirement of exchangeability between data sets has been met.

### Estimating and predicting the steepness of different stock–recruit functions

After having tested the different model and data assumptions, the models have been used to estimate the steepness parameter of the different stocks and to predict the steepness parameter of an unsampled stock such as the salmon stock in the Baltic Sea. The results of the hierarchical analysis for the two stock–recruit functions are presented in Figs. 7 and 8 and Table 4. The posterior probability distributions of steepness are markedly more informative than the prior probability distributions but still reflect considerable uncertainty. The lower percentiles of the posterior probability distributions for the steepness of the Ricker stock–recruit function overlap with the posterior pdfs for the Beverton–Holt function. There does not seem to be a relationship between the origin of the stock–recruit data (Europe or Canada) and the estimated values for steepness. The marginal probability distribution of the steepness parameter for the Beverton–Holt stock–recruit function is much more informative than the marginal pdf for the steepness of the Ricker stock–recruit function. The medians of the marginal probability distributions for steepness of the Beverton–Holt and Ricker stock–recruit functions for Baltic salmon are 0.72 and 1.15, respectively. The probability distributions for steepness can be compared with the steepness calculated by Myers et al. (1999). By using a standard linear mixed model and a Ricker stock–recruit function, Myers et al. (1999) obtained a median steepness of 0.54 for Atlantic salmon with a 60% probability interval between 0.46 and 0.62. The results for the steepness of Atlantic salmon by Myers et al. (1999) are lower and the confidence interval is narrower than the probability intervals obtained in the current study. The reasons for the differences in results will be discussed in the Discussion section.

From the graphs of the fitted stock–recruit functions (Fig. 7), it becomes clear that the Beverton–Holt model consistently estimated a higher slope at the origin than the Ricker model, resulting in a higher predictive value for the slope at the origin for the Baltic salmon population (Table 5). Significant autocorrelation in the stock–recruit data has only been detected for one data set and there was no strong correlation between the steepness parameter and the smolt production capacity.

### Calculating Bayes' posteriors for the different models

The previous section illustrated that depending on the stock–recruit model, the marginal predictive posterior density function for the steepness is very different. It is common to assess the fit of the individual models with the data, continue with the model that fits best, and discard the other models. In WinBUGS, the statistic used for this is the deviance information criterion (DIC), which is a Bayesian measure of model complexity and fit that can be used to compare models of arbitrary structure (Spiegelhalter et al. 2002). It is the sum of the posterior mean of the deviance (defined as –2 times the log likelihood from the Markov chain) and the effective number of parameters (defined as the posterior mean of the deviance minus the deviance of the posterior means). In this case, the DIC for the model with the Beverton–Holt function is 311, while the DIC for the Ricker model is 336. Discarding the Ricker stock–recruit function, however, would be ignoring model uncertainty.

Using the harmonic mean of the likelihood function, it is possible to calculate the Bayes' posterior model probability. The Beverton–Holt model obtains 99.9% probability, while the Ricker model obtains 0.1%, given the current stock–recruit data. This result was obtained consistently from several different chains with different starting values and is therefore reliable. The Beverton–Holt is favoured over the Ricker stock–recruit function, largely because it fits the data better. In addition, the Bayes' posterior, based on the harmonic means, tends to favour models containing less uncertainty whereby the variance of the deviances is smaller and this variance was less for the Beverton–Holt model (Fig. 9). The statistical models using the Beverton–Holt and Ricker stock–recruit functions are practically identical except for the prior for the steepness parameter. This steepness prior pdf is much more informative for the Beverton–Holt stock–recruit function than for the Ricker stock–recruit function owing to the strict boundaries for this parameter when using the Beverton–Holt function. This results in a smaller variance in

**Fig. 6.** Marginal predictive probability distributions of the steepness parameter for two different stock–recruit functions excluding one data set from the analysis at a time.

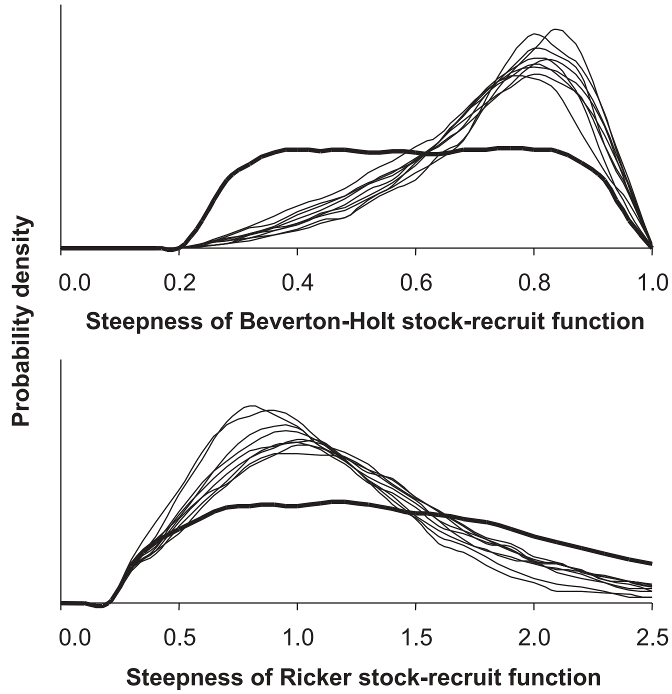
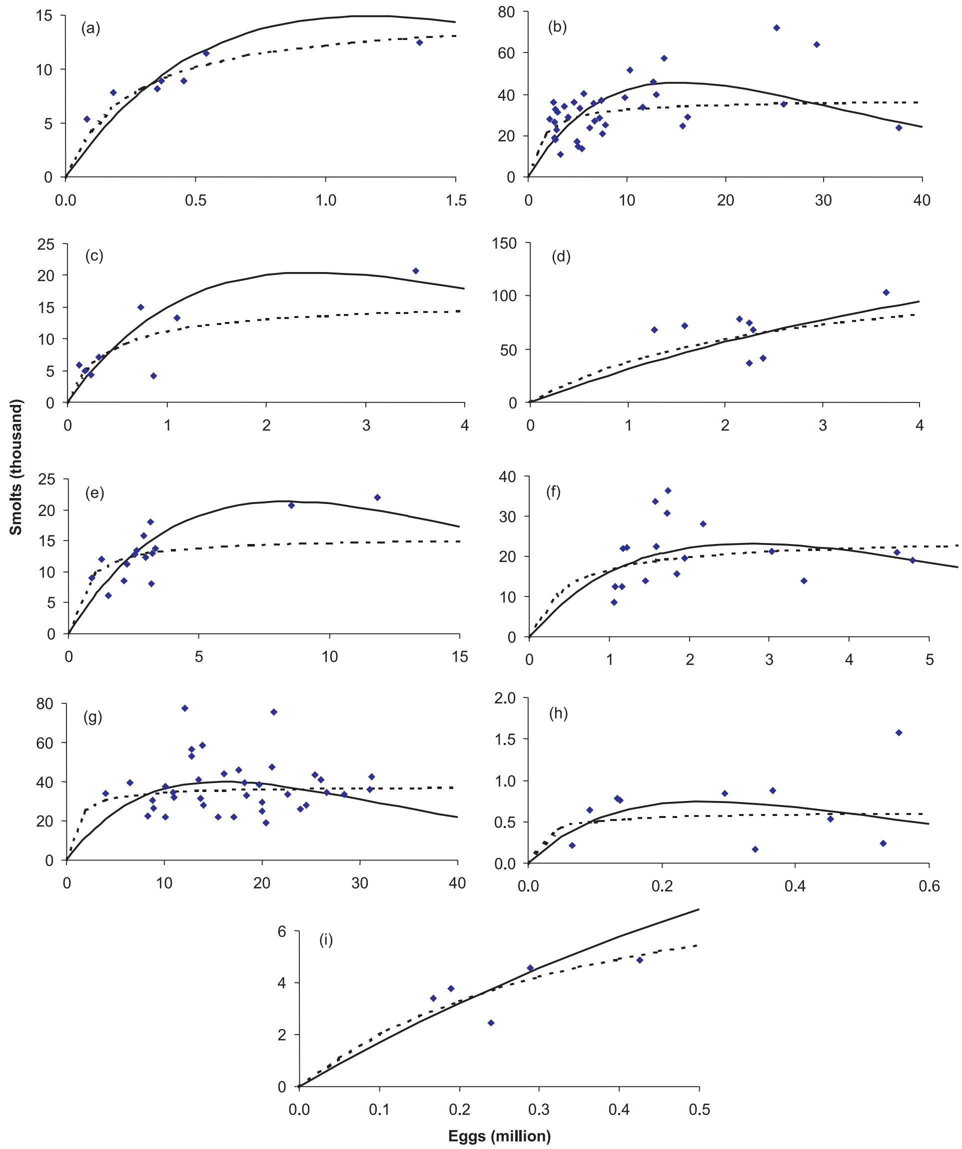


**Fig. 7.** Median values of the marginal posterior probability distributions for the Beverton–Holt (broken line) and Ricker (solid line) stock–recruit functions for (*a*) Little Codroy River, (*b*) Margaree River, (*c*) Pollett River, (*d*) Trinite River, (*e*) Western Arm Brook, (*f*) River Bush, (*g*) River Ellidaar, (*h*) River Oir, and (*i*) River Bec-Scie.




deviances in the Beverton–Holt model output than in that for the Ricker model and contributes further to the higher weighting for the Beverton–Holt model. This issue is treated in further detail below.

## Discussion

Hierarchical analyses have become standard methods to obtain stock–recruit functions for fisheries stock assessment (Liermann and Hilborn 1997; Myers and Mertz 1998). The Beverton–Holt stock–recruit function is commonly parameterized in terms of the steepness parameter, which is transportable from stock to stock, making it ideal for hierarchical analyses of stock–recruit data. This paper advocates a similar parameterization for other possible stock–recruit functions such as the Ricker function, allowing estimation of the parameters of the stock–recruit function and estimation of the probability of the different stock–recruit functions given the stock–recruit data through the use of Bayes' posterior probabilities.

However, several dangers are connected to the use of a hierarchical analysis of stock–recruit data, which can make the results invalid: publication and selection bias, the use of studies of poor academic quality, and the mixing of dissimilar studies (Arnqvist and Wooster 1995). Furthermore, the different studies used in the hierarchical analysis should be exchangeable (Gelman et al. 1995). Most authors conclude that it is more important to be unbiased than to include every existing study (Englund et al. 1999).

As mentioned before, a steepness parameter is transportable from stock to stock. However, the value of the steepness parameter is not independent of the functional form of the stock–recruit function (e.g., steepness values above 1 can only occur for a Ricker stock–recruit function and not for

**Fig. 8.** Prior (thick broken line) and posterior probability distributions for stock–recruit data sets from Europe (thin solid line) and Canada (thin broken lines) and the corresponding marginal predictive probability distributions for Baltic salmon (thick solid lines) of the steepness parameter for different stock–recruit functions.

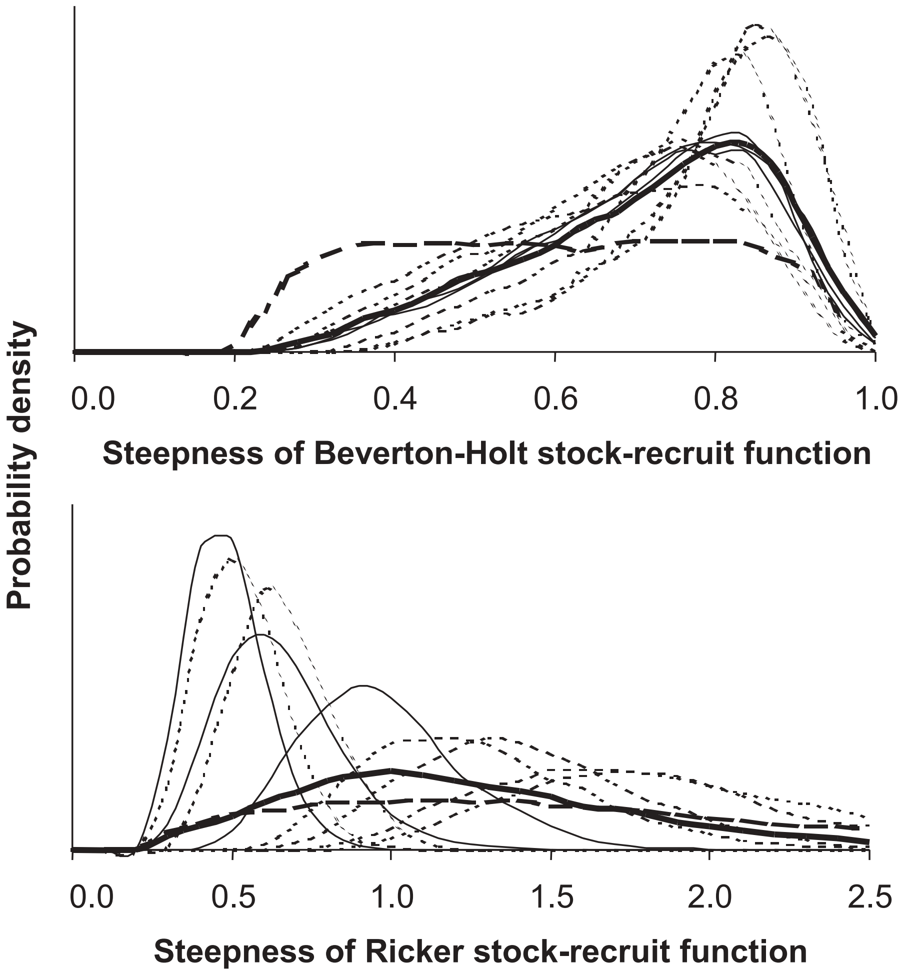



**Table 4.** Estimated mean and CV for the posterior probability distribution of the steepness for the Beverton–Holt and Ricker stock–recruit functions.

| | Beverton–Holt | | Ricker | |
|---|---|---|---|---|
| Parameter | Mean | CV | Mean | CV |
| Little Codroy River | 0.78 | 0.15 | 1.75 | 0.29 |
| Margaree River | 0.65 | 0.22 | 0.61 | 0.25 |
| Pollett River | 0.72 | 0.17 | 1.40 | 0.27 |
| Trinite River | 0.78 | 0.16 | 1.91 | 0.29 |
| Western Arm Brook | 0.63 | 0.26 | 0.48 | 0.27 |
| River Bush | 0.69 | 0.22 | 0.93 | 0.27 |
| River Ellidaar | 0.70 | 0.22 | 0.44 | 0.27 |
| River Oir | 0.69 | 0.22 | 0.60 | 0.32 |
| River Bec-Scie | 0.67 | 0.22 | 1.25 | 0.31 |
| Baltic rivers | 0.70 | 0.23 | 1.24 | 0.48 |

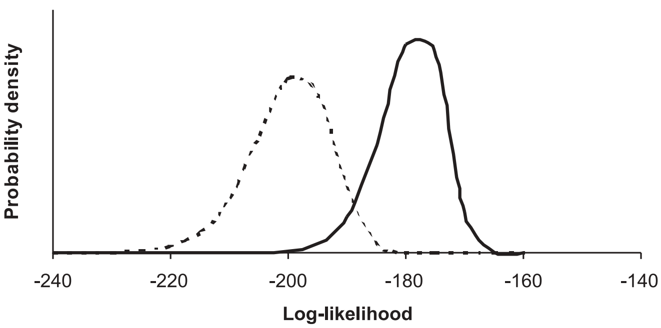
the Beverton–Holt function). Myers et al. (1999) have used a Ricker stock–recruit function within an hierarchical model to estimate the slope at the origin. From these results, they have estimated a steepness value for the Beverton–Holt function based on the assumption that the slope at the origin is the same for the Ricker and Beverton–Holt stock–recruit functions. According to our results (Table 5), the estimates for the slope at the origin can be distinctly different between the two different functions given the same stock–recruit data. By assuming the slopes to be the same and transforming the slope at the origin of a Ricker stock–recruit function to a steepness value for the Beverton–Holt function, Myers et al. (1999) have underestimated the steepness parameter for the Beverton–Holt function. This explains their lower steepness estimates compared with the current analysis.

Within this paper, a different approach has been advocated by implementing the same definition of steepness to both the Beverton–Holt and Ricker stock–recruit functions (i.e., the corresponding proportion of virgin recruitment when reducing the stock biomass to 20% of its virgin level). Using this parameterization, posterior distributions can be obtained for the steepness parameter for each stock–recruit function whereby the steepness parameters are dependent on the functional form of the stock–recruit function. This parameterization has produced plausible results for both the Beverton–Holt and Ricker stock–recruit functions. Potentially, this parameterization could also be expanded to other stock–recruit formulations. For some stock–recruit functions, however, there may be no reduction in recruitment when reducing the stock biomass to 20% of its virgin level. This, for

**Table 5.** Estimated mean and 95% probability interval for the posterior probability distribution of the slope at the origin for the Beverton–Holt and Ricker stock–recruit functions.

| | Beverton–Holt | | Ricker | |
|---|---|---|---|---|
| Parameter | Mean | 95% probability interval | Mean | 95% probability interval |
| Little Codroy River | 0.060 | 0.031–0.207 | 0.035 | 0.022–0.053 |
| Margaree River | 0.025 | 0.013–0.082 | 0.008 | 0.006–0.010 |
| Pollett River | 0.038 | 0.022–0.094 | 0.022 | 0.015–0.032 |
| Trinite River | 0.052 | 0.028–0.235 | 0.034 | 0.023–0.052 |
| Western Arm Brook | 0.026 | 0.009–0.138 | 0.007 | 0.005–0.010 |
| River Bush | 0.051 | 0.022–0.227 | 0.023 | 0.015–0.034 |
| River Ellidaar | 0.040 | 0.015–0.204 | 0.007 | 0.005–0.010 |
| River Oir | 0.027 | 0.010–0.146 | 0.008 | 0.004–0.012 |
| River Bec-Scie | 0.025 | 0.013–0.106 | 0.018 | 0.011–0.030 |
| Baltic rivers | 0.026 | 0.009–0.153 | 0.017 | 0.004–0.039 |

**Fig. 9.** Probability density function of the log-likelihood values for samples of the posterior distributions when fitting the Beverton–Holt (solid line) and Ricker (broken line) stock–recruit functions to Atlantic salmon stock–recruit data.




example, is the case for the hockey stick model, a simple segmented regression line that starts at the origin at a certain slope and whereby the recruitment becomes constant above some level of spawner abundance (Barrowman and Myers 2000). Unless the steepness parameter is actually 1 or the slope parameter is very low and gives a high value for the spawning stock inflection point relative to the carrying capacity, and there are some data available near the origin, this parameterization will not contain the necessary information to estimate the slope at the origin for the hockey stick model.

Within this paper, two different stock–recruit functions have been fitted to stock–recruit data within a Bayesian framework. This requires the selection of appropriate prior probability distributions for the model parameters. The prior for the steepness parameter has traditionally been given distributions between 0.2 and 1 because of the shape of the Beverton–Holt stock–recruit function. When expanding the concept of steepness to other stock–recruit functions, this prior needs to be revised. For the Ricker stock–recruit function, it is, for example, possible to obtain a value for the steepness parameter larger than 1. Therefore, the prior distribution for steepness should be dependent on the functional form of the stock–recruit function. The prior for steepness proposed within this paper is formed by the structure of the model. The mean steepness and standard deviation, which is dependent on the mean, shape the probability distribution of the steepness through a concise model structure.

The steepness parameter is commonly used in population assessments. By parameterizing more than one stock–recruit function in terms of steepness, the uncertainty in the stock–recruit function can be incorporated in the population assessments by running the same assessment models using different stock–recruit functions. The DIC has been developed to compare the fit of hierarchical models to the data (Spiegelhalter et al. 2002). This criterion, however, does not provide a mechanism to compare the overall plausibility of the different model structures given the data.

Within this paper, the computation of marginal Bayes' posterior probabilities for alternative models is advocated because this allows the estimation of the probability (or credibility) of each stock–recruit function given the available stock–recruit data (McAllister and Kirchner 2002). The Bayes' posterior probabilities have been calculated using the harmonic mean of the likelihood (Kass and Raftery 1995). This harmonic mean, however, may be unstable owing to the occasional occurrence of a set of parameters with a very small likelihood. Furthermore, the harmonic mean can be biased towards models with lower prior uncertainty in the parameter values owing to smaller prior variances. Gelman et al. (1995) identified this biasing effect as a potential distraction and suggested an alternative approach to accounting for model uncertainty that instead uses a continuous family of models. If the alternative model structures only differ in the use of the stock–recruit function and are limited to a Beverton–Holt or Ricker stock–recruit function, then the two discrete models could be replaced with a continuous family of models by using a three-parameter model for which the Ricker and Beverton–Holt stock–recruit functions are special cases.

The use of alternative discrete models, however, still has some advantages (McAllister and Kirchner 2002). It is more flexible when it is of interest to explore the probability of a wide variety of different model structures. The use of two two-parameter models as opposed to a single generalized three-parameter model may offer improved statistical performance in parameter estimation, particularly for stock–recruit data that are typically relatively uninformative even for two-parameter models. Instability problems from using the harmonic mean likelihood can be overcome by using other computational methods such as reversible jump or importance sampling (Kass and Raftery 1995; Patterson 1999; McAllister and Kirchner 2002). Moreover, in our calculations, instability was not a problem because Markov chains with different starting points gave the same results. Also, when the harmonic means for the two alternative stock–recruit models were recalculated using deviances with the original mean deviance but constrained to have the same variance in deviances, practically the same results were obtained.

The proposed methodology enables prediction of the steepness of the stock–recruit function for unsampled salmon stocks such as the salmon in the Baltic Sea even though no stock–recruit data have been collected in the region. The means of the marginal probability distributions for steepness of the Beverton–Holt and Ricker stock–recruit functions for Baltic salmon are 0.70 (CV 23%) and 1.24 (CV 48%), respectively. Although by definition, the steepness of the different stock–recruit functions has the same meaning, the estimated value for steepness is dependent on the functional form of the stock–recruit function, thus explaining the different results obtained for the different stock–recruit functions. According to the Bayes' model posteriors, the Beverton–Holt stock–recruit function is more likely than the Ricker stock–recruit function given the current stock–recruit data, although the Ricker model cannot be ruled out. This model uncertainty should be carried along into fisheries stock assessments and decision analyses. To identify plausible stock–recruit functions for a given stock where no stock–recruit data exist, the posterior predictive distribution for steepness obtained through hierarchical modelling can be used in combination with estimates for the carrying capacity of salmon in the Baltic Sea area (Geiger and Koenings 1991; Adkison and Peterman 1996). For example, estimates for the smolt carrying capacity of salmon in the Baltic Sea have been obtained through an evaluation of habitat availability and quality (Uusitalo 2001). When incorporating the stock–recruit functions in fisheries stock assessments, the steepness parameter still needs to be adjusted for region-specific mortality effects. In the Baltic Sea, for example, this should include the juvenile mortality resulting from the M74 syndrome (Karlsson and Karlström 1994). This syndrome occurs only in the Baltic Sea and not in the areas where the stock–recruit data have been collected and should lower the steepness for salmon stocks in this region.

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## Appendix A. WinBUGS code for a Bayesian hierarchical model of the Beverton–Holt stock–recruit function

```
model {
for(j in 1:n) { # for the n samples
   obs_Smolts[j] ~ dlnorm(X[j], tau_Smolts) # Likelihood function
   X[j] <– log(exp_Smolts[j])
   exp_Smolts[j] <– Eggs[j] / (alpha[river[j]] + (beta[river[j]] * Eggs[j])) # B-H function
}
for(j in 1:m) { # for the m Atlantic salmon stocks
   alpha[j] <– ((1 – z[j]) / (4 * z[j])) * SBPR[j] # definition of alpha in terms of steepness
   beta[j] <– ((5 * z[j]) – 1) / (4 * z[j] * R[j]) # definition of beta in terms of steepness
   z[j] <– (0.8 * zt[j]) + 0.2 # transformation to beta distribution between 0.2 and 1
   zt[j] ~ dbeta(alpha_zt, beta_zt) # prior for the transformed steepness
   R[j] ~ dlnorm(mu_R, tau_R)I(0.001, ) # prior for recruitment potential
   SBPR[j] # river specific prior for spawner biomass per recruit
   # the detailed code for the calculation of the river specific SBPR is not shown to avoid cluttering the presentation
}
tau_Smolts <– 1/pow(sigma, 2) # derived prior for precision of predicted smolts
sigma ~ dgamma(0.001, 0.001) # prior for the standard deviation of predicted smolts
mu_R ~ dnorm(0.0, 1.0E-6)I(1.01, 25) # hyperprior for mean of recruitment potential
```

```
tau_R ~ dgamma(0.001, 0.001) # hyperprior of precision of recruitment potential
alpha_zt <– (pow(mean_zt, 2) – pow(mean_zt, 3) – (mean_zt * pow(sd_zt, 2))) / pow(sd_zt, 2)
beta_zt <– ((1 – mean_zt) / pow(sd_zt, 2)) * ((mean_zt * (1 – mean_zt)) – pow(sd_zt, 2))
# reparameterisation from mean and variance to alpha and beta parameters
sd_zt <– sd_ztt * max_sd_zt # defining the distribution of the transformed variance zt
sd_ztt ~ dbeta(2, 1)
mean_zt ~ dbeta(2, 2)
mean_z <– (0.8 * mean_zt) + 0.2 # transformation to beta dist. between 0.2 and 1
k <– step(mean_zt – 0.5) # if mean_zt – 0.5 > 0 then k = 1 else k = 0
   min <– (1 – ((1 – mean_zt) * 2)) * k
   max <– ((1 – (mean_zt * 2)) * k) + (mean_zt * 2)
max_sd_zt <– sqrt(pow((max – min), 2) / 12)} # maximum variance given a mean
```