How robust are Bayesian posterior inferences based on a Ricker model with regards to measurement errors and prior assumptions about parameters?

E. Rivot, E. Prévost, and E. Parent

Abstract: We present a Bayesian approach of a Ricker stock–recruitment (*S*/*R*) analysis accounting for measurement errors on *S*/*R* data. We assess the sensitivity of posterior inferences to (*i*) the choice of Ricker model parameterizations, with special regards to management-related ones, and (*ii*) prior parameter distributions. Closed forms for Ricker parameter posterior distributions exist given *S*/*R* data known without error. We use this property to develop a procedure based on the Rao–Blackwell formula. This procedure achieves integration of measurement errors by averaging these closed forms over possible *S*/*R* data sets sampled from distributions derived from a stochastic model relating field data to the *S* and *R* variables. High-quality Bayesian estimates are obtained. The analysis of the influence of different parameterizations and of the priors is made easier. We illustrate our methodological approach by a case study of Atlantic salmon (*Salmo salar*). Posterior distributions for *S* and *R* are computed from a mark–recapture stochastic model. Ignoring measurement errors underestimates parameter uncertainty and overestimates both stock productivity and density dependence. We warn against using management-related parameterizations because it makes the strong prior assumption of long-term sustainability of stocks. Posterior inferences are sensitive to the choice of prior. The use of informative priors as a remedy is discussed.

Résumé : Nous présentons une analyse Bayesienne d'un modèle stock–recrutement (*S*/*R*) de Ricker qui intègre les erreurs de mesure sur les données *S*/*R*. Nous étudions la sensibilité des inférences a posteriori (*i*) à différentes paramétrisations du modèle de Ricker, notamment à celles reliées à la gestion, et (*ii*) aux distributions a priori sur les paramètres. Conditionnellement à une série *S*/*R* connue sans erreur, les distributions a posteriori des paramètres peuvent s'exprimer analytiquement. Nous développons une procédure de Rao–Blackwell qui s'appuie sur cette propriété. Les erreurs de mesure sont intégrées en moyennant ces formes analytiques sur un échantillon de séries *S*/*R* tirées dans leur distribution a posteriori issue d'un modèle stochastique reliant les données de terrain aux variables *S* et *R*. Les estimateurs bayesiens obtenus sont de grande qualité et l'étude de sensibilité aux choix des différentes paramétrisations et des priors est facilitée. Nous illustrons notre approche méthodologique par un cas d'étude sur le Saumon atlantique (*Salmo salar*). Les distributions a posteriori de *S* et *R* sont issues d'un modèle probabiliste de capture–recapture. Ignorer les erreurs de mesure sous-estime l'incertitude et surestime la productivité du stock et la densité dépendance. Nous ne recommandons pas l'utilisation systématique des paramètres reliés à la gestion car cela nécessite l'hypothèse a priori que le stock peut se renouveler seul. Les inférences a posteriori sont sensibles au choix des priors. L'utilisation de priors informatifs pourrait permettre d'y remédier.

Introduction

The analysis of the relationship between stock (*S*) and recruitment (*R*) (*S*/*R* relationship) is critical for setting biological or management reference points, especially for semelparous species such as salmon (Kennedy and Crozier 1993; Chaput et al. 1998; Schnute et al. 2000). Hilborn and Walters (1992) listed various sources of uncertainty and statistical pitfalls that preclude reliable estimation of *S*/*R* model parameters. These problems have been dealt with in more detail by several authors and statistical remedies can be proposed for most of them. Walters (1985) addresses the bias induced by

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nonrepresentative sampling in the *S* variable. An analysis of nonstationarity of the *S*/*R* relationship is provided by Walters (1987). Temporal autocorrelation in the *S*/*R* series has also been analyzed (Walters 1990; Korman et al. 1995). Theoretical studies have shown that measurement errors in both *S* and *R* (observation errors) may induce strong bias in parameter estimates (Walters and Ludwig 1981). This bias possibly entails mistaken *S*/*R* adjustments, which may in turn lead to disastrous stock assessment and management (Ludwig and Walters 1981; Hilborn and Walters 1992; Schnute 1993).

In the present paper, we address three main issues concerning *S*/*R* analysis based on the Ricker model (Hilborn and Walters 1992) using a Bayesian approach. First, we propose an original method to assess the effect of measurement errors on *S*/*R* parameter uncertainty when measurement errors are described by a probability distribution function (PDF). We advocate and demonstrate the use of posterior PDFs conditioned by field data, even though our method can be applied regardless of how measurement error PDFs are obtained. Posterior PDFs advantageously replace restrictive and sometimes unfortunate hypotheses on the form of measurement errors that usually occur. Next, we highlight the ins and outs of expressing the Ricker model directly in terms of management-related parameters. Lastly, we discuss a point that few studies have addressed, that is, how prior hypotheses, including a "noninformative prior" on nuisance parameters that are integrated out (Walters and Ludwig 1994), may influence posterior inferences. For each issue, the implications for statistical estimation of *S*/*R*-related parameters and for management advice are emphasized. We adopt the Bayesian setting because it offers conceptual rigor for quantitatively describing uncertainties in the states of nature (Ellison 1996; Hilborn and Mangel 1997; Punt and Hilborn 1997). The Bayesian framework is also naturally linked with decision and risk analysis (Francis and Shotton 1997; McAllister and Kirkwood 1998; Robb and Peterman 1998).

The Ricker model is widely used in *S*/*R* analysis, especially for salmonids (Kennedy and Crozier 1993; Hill and Pyper 1998). Although other density-dependent relationships are also commonly utilized (e.g., Beverton–Holt or Schnute–Deriso models), we focused our attention on the Ricker model for three reasons. First, in real case studies, it is most often illusive to choose among different *S*/*R* models in the light of the data (Walters and Korman 2001). Indeed, (*i*) the *S*/*R* curves are surrounded by a large amount of residual variability (Hilborn and Walters 1992), and (*ii*) the shape of the *S*/*R* curves differ mainly at high *S* levels for which there are often very few observations (Kennedy and Crozier 1993; Chaput et al. 1998). Second, adjusted curves often exhibit very similar form in the range that determines management and biological reference points (Schnute and Kronlund 1996). Third, the Ricker model offers the advantage of being easily linearized. We seize this opportunity to propose a simple and efficient procedure to account for measurement errors and to address our two additional main issues within a rigorous mathematical framework.

For a *S*/*R* data set known without error, treating the Ricker model as a linear one allows the derivation of an analytic expression for the parameter posterior PDFs. We take full advantage of this mathematical convenience offered by the Ricker model in terms of closed-form calculation and develop a two-step Bayesian procedure for *S*/*R* parameter estimations that clearly distinguishes both sources of uncertainty, measurement errors, and process errors (i.e., "natural" variations of the recruitment process). The first step consists in quantifying measurement errors on *S* and *R* via probability distributions conditioned on yearly field data. In the second step, we introduce the measurement errors via a Rao–Blackwell formula, while simultaneously accounting for process errors. We show how the Rao–Blackwell formula uses a tricky combination between simple averaging over a sample in the posterior distribution of *S* and *R* and the analytic expression of the posterior parameter distribution, available when treating the Ricker model as a linear one. The Rao–Blackwell procedure is more specific than general Monte Carlo Markov Chain (MCMC) simulation methods that may be used with other "nonlinear" *S/R* relationships. However, it has two main advantages. First, it provides very high quality estimators for Bayesian posterior PDFs with modest computational effort. Second, it is based on closed-form expressions in which the influence of the priors and of different parameterizations appears analytically, thus allowing the evaluation of the consequences of implicit hypotheses made in Bayesian *S/R* analysis.

We again take advantage of the easy manipulation of the Ricker model to compare the standard expression of the Ricker function $R = Se^{a-bS}$, with formulations inspired from Schnute and Kronlund (1996) involving parameters directly related to management, for instance the stock S^* producing maximum sustainable yield C^*. These authors advocated management-related parameterization of *S/R* models because it reduces statistical bias and is more robust to the choice of the deterministic *S/R* function. We extend their study by examining whether it makes sense to systematically replace the natural Ricker parameterization (a,b) by a management-related one. We discuss this point from a Bayesian point of view, studying the consequences of switching parameterization in terms of prior parameter specification. We extend the sensitivity analysis to the influence of prior specification of the nuisance parameter. The analysis of the influence of prior assumptions is highly facilitated by the use of the Rao–Blackwell formula, which allows us to separate the prior and the likelihood in the analysis and to work with nonstandard and improper prior PDFs.

We illustrate our methodological work by applying the tools that we developed to a case study on the 13-year *S*/*R* data set of the River Oir (Lower Normandy, France) Atlantic salmon (*Salmo salar*) population. Posterior distributions of *S* (spawning adults) and *R* (measured as young fish or "smolts" migrating to the sea) are obtained by means of a model working from capture–mark–recapture data. Our case study has no pretence to provide a systematical analysis of measurement error bias; rather, we point out how our approach of measurement errors could be transposed to any situation, provided that a sample from the PDFs describing observation errors is available, without restriction on the form of these distributions. Indeed, probability distributions quite often can be set for observations, at worst from expert judgment and at best from field data through the statistical procedures used to estimate stock and recruitment. The derivation of the measurement error PDFs is not central to our purpose. Hence, to stay focused on the three main issues previously mentioned, in this paper we do not detail the observation error model that leads to posterior PDFs for S and R in our case study. The interested reader can refer to Rivot (1998) for a detailed description of this model.

Material and methods

Problem formulation: Bayesian conditional reasoning allows splitting measurement and process errors

The key point of our modeling strategy is the assembling of two models in which the series of stock–recruitment pairs $\{S_i,R_i\}$, $i = 1$ to n (hereafter denoted $\{S,R\}$), are alternatively considered as unknown parameters and as observed variables. These two different statuses for S/R series are combined to compute the parameter posterior PDF. On one hand, in a first stochastic model describing measurement errors, series of nonobserved S and R pairs $\{S,R\}$ are considered unknown multidimensional random variables with a posterior PDF conditioned by all field data available, denoted $P(\{S,R\}|\text{Data})$ (the notation $P(X|Y)$ denotes the conditional probability distribution of the variable X given Y). More precise considerations about this posterior distribution will be given when presenting the case study. On the other hand, in a second model accounting for process errors, $\{S,R\}$ are considered as observed variables. The Ricker model in its natural form (eq. 1) describes the recruitment process:

$$(1)\qquad R_i = S_i\exp(a - bS_i + w_i),\ i = 1 \text{ to } n$$

where S_i is the stock for year i, R_i is the subsequent recruitment, $\theta = \begin{pmatrix} a \\ b \end{pmatrix}$ denotes the two-dimensional Ricker parameter vector, and a and b belong to $]-\infty,+\infty[$. Although the case $b < 0$ leading to an exponential growth of the population is highly improbable, we do not reject it a priori. Multiplicative log-normal process errors e^{w_i}, where the w_i are independent random variables normally distributed with mean 0 and standard deviation σ, represent the stochasticity of recruitment process. We deliberately ignored interannual dependence between S and R to simplify the problem formulation and stay focused on our main issue, the treatment of measurement errors (see Korman et al. (1995) or Meyer and Millar (2000) for more recent work about this problem). The lognormality of process errors has been justified on theoretical grounds (Peterman 1981; Hilborn and Walters 1992; Shelton 1992) and has been shown to be consistent with observed data for salmonids (Bradford 1995).

The posterior PDF for our model parameters (θ,σ) given the observed data, denoted $P(\theta,\sigma|\text{Data})$, results from the integration over $\{S,R\}$ of the joint posterior of all the unobservables, i.e., the parameters (θ,σ) and the variables $\{S,R\}$. Rewriting the joint PDF $P(\theta,\sigma,\{S,R\}|\text{Data})$ as the product of $P(\theta,\sigma|\{S,R\},\text{Data})$ and $P(\{S,R\}|\text{Data})$ and assuming that, given $\{S,R\}$, the law of (θ,σ) is independent of the data, this PDF reads

$$(2)\quad P(\theta,\sigma|\text{Data}) = \int_{\{S,R\}} [P(\theta,\sigma|\{S,R\})P(\{S,R\}|\text{Data})]\mathrm{d}\{S,R\}$$

As advised by Geiger and Koenings (1991) and Walters and Ludwig (1994), we limit the number of parameters to estimate by treating the standard deviation of process errors σ as a nuisance parameter. Therefore, the posterior $P(\theta,\sigma|\{S,R\})$ in eq. 2 is integrated across all possible values of σ in $]0,+\infty[$. This provides a more accurate assessment of uncertainty around θ than would be obtained by assuming a particular value for the nuisance parameter (Walters and Ludwig 1994). This integration over σ necessitates setting a prior PDF on σ, denoted $p\sigma$. We will show in the following section how an analysis of the sensitivity of the results to the choice of the prior on σ can be easily performed thanks to the linearisation of the Ricker model. The marginal posterior PDF for θ of ultimate interest is

$$(3)\quad P_{p\sigma}(\theta|\text{Data}) = \int_{\{S,R\}} [P_{p\sigma}(\theta|\{S,R\})P(\{S,R\}|\text{Data})]\mathrm{d}\{S,R\}$$

where $P_{p\sigma}(\theta|\{S,R\})$ is the marginal posterior of θ under the prior distribution $p\sigma$. The second factor of the right member of eq. 3 represents uncertainty on $\{S,R\}$ given the field data, i.e., measurement errors. The first one brings the recruitment process uncertainty into the analysis.

It must be noted here that eq. 3 can still be used in any case where a probability distribution $P(\{S,R\}|\underline{K})$ conditional to any knowledge denoted by $\underline{K}$ can be derived. Even if the analyst is left with only a time series of point estimates for S/R data, such a distribution $P(\cdot|\underline{K})$ can always be derived from a formalisation, even the simplest one, of the knowledge that one has about the way in which the observations are collected. In such a general case, the conditional probability of interest (eq. 3) becomes

$$P_{p\sigma}(\theta|\underline{K}) = \int_{\{S,R\}} [P_{p\sigma}(\theta|\{S,R\}P(\{S,R\}|\underline{K})]\,\mathrm{d}\{S,R\}$$

Because the most interesting case is when a posterior PDF of measurement errors can be derived from field data and in order not to multiply notations, in the rest of the text measurement errors PDF will always be denoted $P(\{S,R\}|\text{Data})$.

Several methods exist to get out of this integration over measurement errors in eq. 3. Numerical MCMC techniques are the most commonly applied. However, when using the Ricker model, more efficient (i.e., high precision is attained with low computational effort) posterior estimations can be obtained by combining a Monte Carlo method with an analytical expression. Indeed, when conditional PDFs are available in closed form, additional advantages can be taken from outputs simulated via MCMC techniques through the Rao–Blackwell formula (Gelfand and Smith 1990). We introduce this method with a very simple example. Let us define two random quantities A and B, with joint PDF $P(A,B)$, and suppose that we are interested in the marginal posterior of A. Suppose that we know that the conditional PDF $P(A|B)$ is explicitly known in a closed form and that a sample $\{B^{(g)}, g = 1,\ldots,G\}$ of size G has been generated from the posterior distribution of B. Then, a high-quality estimator for the posterior PDF $P(A)$ can be derived from the sample $B^{(g)}$ by the Monte Carlo integration:

$$(4)\qquad \widehat{P(A)} = \frac{1}{G}\sum_{g=1}^{G}[P(A|B^{(g)})]$$

This procedure is easily applied to our case study. Indeed, conditionally to a S/R data set $\{S,R\}$ supposedly known without error, the Ricker model can be conveniently expressed as a linear one (see Appendix). Therefore, under the hypothesis of a uniform prior on (a,b) and a particular prior $p\sigma$, the first term of the right member of eq. 3 has a closed form, denoted $P_{p\sigma,0}(\theta|\{S,R\})$, as shown in Appendix (the subscripts $p\sigma$ and 0 stand for the prior on σ and the uniform prior on θ, respectively). Then, from the Rao–Blackwell formula, a high-quality estimator for $P_{p\sigma,0}(\theta|\text{Data})$ is computed by approximating the integral (eq. 3) as follows:

$$(5)\qquad P_{p\sigma,0}(\theta|\text{Data}) = \frac{1}{G}\sum_{g=1}^{G}[P_{p\sigma,0}(\theta|\{S,R\}^{(g)})]$$

where the sum is over a "sufficiently large number" G of samples $\{S,R\}^{(g)}$, $g = 1,\ldots,G$, generated from the density $P(\{S,R\}|\text{Data})$. It is straightforward to obtain such a sample from an observation error model via MCMC simulations. By contrast with MCMC sampling in $P(\theta,\{S,R\}|\text{Data})$, from which a histogram would have been computed to estimate the marginal $P(\theta|\text{Data})$, the Rao–Blackwell procedure provides an accurate and precise estimation with generally only a few hundred $\{S,R\}$ simulated sets, because the posterior PDF $P(\theta|\text{Data})$ is estimated at each point θ.

Posterior distributions of management-related parameters

Schnute and Kronlund (1996) suggested that the Ricker function could be rewritten in terms of management-related parameters. We focused on two of these parameter pairs, $\varphi_1^* = (C^*,S^*)$ and $\varphi_2^* = (C^*,h^*)$, defined as follows. Let us consider a sustainable population (i.e., $a > 0$), with a S/R relationship that is stable over time (constant S/R parameters), and submitted each year to a constant exploitation of recruitment equal to C that produces an equilibrium state $R - C = S$, where S and R are expressed in the same unit (adults, eggs,…). There is a single equilibrium state for which captures are maximum, denoted C^*, obtained for a stock S^*, verifying $R^* - C^* = S^*$ (T1.2 in Table 1). For each $\varphi_1^* = (C^*,S^*)$ in $]0,+\infty[\times]0,+\infty[$, a unique pair (a,b) in $]0,+\infty[\times]0,+\infty[$ can be deduced through the closed transformation $(a,b) = g_1(C^*,S^*)$ (T1.3 in Table 1). Similarly, defining the exploitation rate $h^* = C^*/R^*$, each $\varphi_2^* = (C^*,h^*)$ in $]0,+\infty[\times]0,1[$ corresponds to a unique pair (a,b) in $]0,+\infty[\times]0,+\infty[$ through the closed transformation $(a,b) = g_2(C^*,h^*)$ (T1.4 in Table 1). Those transformations are nonlinear and do not admit inverse closed-form expression (see Hilborn (1985) for inverse approximations).

φ_1^* and φ_2^* are reference points for stock assessment and management. Under a constant exploitation rate harvesting strategy, h^* is the harvest rate corresponding to the maximum catch C^* on average long term. Under a fixed escapement strategy, S^* is the spawning escapement that should be reached to maximize the catch on average long term. Thereby, by comparison with Hilborn and Walters (1992) or with Meyer and Millar (2000), who derived posterior PDFs for management parameters from the estimation of natural parameters, reformulating the Ricker model as proposed by Schnute and Kronlund (1996) leads to straightforward inferences on reference points helpful to managers.

Through the Rao–Blackwell formula, the posterior of the natural parameters obtained with a uniform prior on θ and a prior $p\sigma$, $P_{p\sigma,0}(\theta|\text{Data})$, can be used as a pivotal quantity to estimate posterior of management-related parameters φ^* for any prior on φ^*. Bayes' rule specifies that the posterior PDF of the management-related parameters φ^* given all of the field data available, denoted $P_{p\sigma}(\varphi^*|\text{Data})$, is proportional to the product of any prior $P(\varphi^*)$ with the likelihood $P_{p\sigma}(\text{Data}|\varphi^*)$. But conditioning upon φ^* or upon θ^* in the likelihood is equivalent when a one-to-one transformation $\theta^* = g(\varphi^*)$ exists. Finally, the likelihood $P_{p\sigma}(\text{Data}|\theta^*)$ is proportional to the posterior PDF $P_{p\sigma,0}(\theta^*|\text{Data})$ obtained with a uniform prior on θ^*, where the proportionality constant depends on Data only. Thus, the posterior of φ^* obtained with any prior $P(\varphi^*)$ is given by eq. 6 where the proportionality constant is the inverse of the integral of the right side of eq. 6 over the vector φ^* and depends on Data only.

$$(6)\quad P_{p\sigma}(\varphi^*|\text{Data}) \propto P(\varphi^*)P_{p\sigma,0}(\theta^*|\text{Data}) \text{ with } \theta^* = g(\varphi^*)$$

We estimate $P_{p\sigma,0}(\theta^*|\text{Data})$, where $\theta^* = g(\varphi^*)$ using the Rao–Blackwell formula (eq. 5). Summarizing, the estimation of the posterior of several parameters of interest φ^* with any prior on φ^* is confined to the Rao–Blackwell estimate of $P_{p\sigma,0}(\theta|\text{Data})$. One can consider $P_{p\sigma,0}(\theta|\text{Data})$ as the likelihood of our data conditioned by our full model hypotheses: the Ricker model featuring the recruitment process and the probabilistic model describing measurement errors from field data.

Sensitivity analysis

This working framework, based on the closed form of parameter posterior distribution $P_{p\sigma,0}(\theta|\{S,R\})$ for the Ricker model used within the Rao–Blackwell procedure, provides a rigorous analysis of sensitivity of posterior inferences to the parameterization and the critical choice of prior PDFs. Whatever the set of parameters used, the simplicity of calculation highlighted in eq. 6 allows us to focus our attention on the influence of their priors.

Table 1. Deterministic Ricker model in terms of natural parameters (a,b) or management-related parameters (C^*,S^*) and (C^*,h^*).

Deterministic Ricker function

(T1.1)
$$R = S\cdot e^{a-bS},\ \theta = \begin{pmatrix} a \\ b \end{pmatrix},\ a \in]-\infty,+\infty[,\ b \in]-\infty,+\infty[$$

Maximization of captures under equilibrium assumption

(T1.2)
$$\begin{cases} S = f_\theta(S) - C & \text{(Equilibrium constraint)} \\ \dfrac{\partial(f_\theta(S) - S)}{\partial S}\Big|_{S^*} = 0 & \text{(Captures maximisation)} \end{cases}$$

Transformation $(a,b) = g_1(C^*,S^*)$

(T1.3)
$$\text{For } C^* > 0 \text{ and } S^* > 0, \begin{cases} a = \ln\left(\dfrac{S^* + C^*}{S^*}\right) + \dfrac{C^*}{S^* + C^*} \\ b = \dfrac{C^*}{S^*[S^* + C^*]} \end{cases}$$

Transformation $(a,b) = g_2(C^*,h^*)$

(T1.4)
$$\text{For } C^* > 0 \text{ and } 0 < h^* < 1, \begin{cases} a = h^* - \ln(1 - h^*) \\ b = \dfrac{h^{*2}}{C^*(1 - h^*)} \end{cases}$$

Jacobians

(T1.5)
$$J_{+1}(C^*,S^*) = +\left|\frac{\partial(a,b)}{\partial(C^*,S^*)}\right| = \frac{C^*(2S^* + C^*)}{S^{*2}\,(S^* + C^*)^3}$$

(T1.6)
$$J_{+2}(C^*,h^*) = +\left|\frac{\partial(a,b)}{\partial(C^*,h^*)}\right| = \frac{h^{*2}\,(2 - h^*)}{(1 - h^*)^2 C^{*2}}$$

(T1.7)
$$J_{+3}(C^*,S^*) = +\left|\frac{\partial(C^*,h^*)}{\partial(C^*,S^*)}\right| = \frac{C^*}{(C^* + S^*)^2}$$

Note: Transformations between (C^*,S^*) or (C^*,h^*) and (a,b) and between (C^*,S^*) and (C^*,h^*) are indicated together with the corresponding Jacobians.

Parameters transformations and choice of prior

Switching from natural to management parameters entails fundamental modifications of model specification. Using management parameters a priori assumes that the stock is capable of self-replacement. Indeed, an equilibrium hypothesis supposes that recruitment exceeds spawning stock over some part of the range of possible stocks, constraining parameter a to be positive. It also assumes that $b > 0$. From a Bayesian point of view, these hidden assumptions have deep implications in terms of prior specification in that using management parameters assigns null prior probability for the range $a < 0$ and $b < 0$. This point should be carefully examined when proceeding to parameter transformation, particularly if the posterior PDF $P_{p\sigma,0}(\theta|\text{Data})$ shows a nonzero probability over the range $a < 0$ and $b < 0$.

Beyond this formulation problem, the choice of priors remains one of the most controversial issues in Bayesian analysis (Box and Tiao 1992; Gelman et al. 1995). Punt and Hilborn (1997) and Hill and Pyper (1998) advocate that noninformative priors are not always a good choice when they ignore available relevant biological information. On the other hand, Walters and Ludwig (1994) and Adikson and Peterman (1996) warn against the use of informative priors because it may result in overly precise posteriors and undue confidence in management decisions arising from the analysis (as in Geiger and Koenings 1991). We then believe that two points should be carefully addressed. First, a transparent approach consists in assessing the sensitivity of the posterior to the choice of the prior. Second, when switching between two parameterizations, it is also fundamental to assess what a prior PDF in one parameter space signifies in the transformed parameter space. For instance, a uniform prior PDF on (a,b) transforms into an odd nonflat prior on (C^*,S^*). For parameters (a,b), we used a noninformative uniform prior $P(a,b)$ over the full range $]-\infty,+\infty[\times]-\infty,+\infty[$ resulting in a posterior PDF primarily determined by the data via the likelihood. To illustrate the influence of the prior of management- related parameters on the posterior, we focused on the (C^*,S^*) parameters. We contrasted four prior assumptions: (1) a uniform PDF in (C^*,S^*) space, (2) a prior in (C^*,S^*) space proportional to $J_{+1}(C^*,S^*)$, the absolute value of the Jacobian of the transformation $(a,b) = g_1(C^*,S^*)$ in T1.5 in Table 1, which corresponds to a uniform PDF in (a,b) space over the restricted range $a > 0$, $b > 0$ (this prior on (C^*,S^*) corresponds to a noninformative prior in the sense of Jeffrey as discussed in Box and Tiao (1992)), (3) a prior in space (C^*,S^*) proportional to $J_{+3}(C^*,S^*)$ in T1.7 in Table 1, which corresponds to a uniform PDF in space (C^*,h^*), (4) a two-dimensional Normal prior for (C^*,S^*) with arbitrary mean (3.5,4.75) and variance matrix $\Sigma = \begin{pmatrix} 4 & 0 \\ 0 & 4 \end{pmatrix}$, indicating that C^* and S^* are a priori noncorrelated with the same variance.

Sensitivity to the choice of prior on σ

Within our methodological framework, an analysis of the sensitivity of the results to the choice of prior on the nuisance parameter σ can also be easily conducted. As shown in the Appendix, we assume a general structure for the prior on σ, $P(\sigma) \propto \sigma^{-q}$, where q is an integer. Under this assumption, $P_{p\sigma,0}(\theta|\text{Data})$ has a closed form depending on q (see Appendix). The prior influence on posterior PDF for parameters (a,b), (C^*,S^*), and (C^*,h^*) can be assessed by making q vary. We tested three different values: q = 0, 1, and 2.

Illustrative case study: Atlantic salmon stock and recruitment on the River Oir

We applied our methodological work to a S/R data set issuing from the wild Atlantic salmon population of the River Oir. The River Oir is a small tributary of the River Sélune, which flows into the Bay of Mont St. Michel (Lower Normandy, France). The studied section is 11.5 km long from the trapping facility downstream to an impassable dam upstream. The trapping facility catches the spawning adults and the smolt migrating out to the sea. No fishery occurs above the trap (Prévost et al. 1996).

Because the River Oir is only a spawning tributary of the River Sélune, there is no precise homing of adult salmon to the Oir (J.L. Baglinière, INRA, UMR-EQHC, Aquatic Ecology Laboratory, Rennes, France, unpublished data). Recruitment cannot be deduced from the adult returns and we therefore estimate it from the smolt outputs. We convert adult spawning stock and smolt recruitment into numbers of eggs. Indeed, for the calculation of management-related parameters, it is necessary to express both variables in the same unit and it is the egg deposition that is ultimately limiting for the size of the upcoming cohort (Prévost et al. 1996; Chaput et al. 1998).

A detailed description of the field data collected and the model used to derive posterior measurement error PDFs for S/R time series is given in Rivot (1998). We only summarize it briefly here because it is not central to the present paper. For each year between 1984 and 1999, adults (in autumn) and juveniles (smolts, in spring) were caught at the trap. Their number is estimated by capture–mark–recapture experiments. A probabilistic model that mimics the capture–mark–recapture experiments as binomial draws has been developed. A sample of size G = 5000 is generated by MCMC techniques from the posterior distribution of the 1984–1999 time series of the number of spawners and the smolt outputs. From the latter, a size-G sample from the S/R time series $\{S,R\} = \{(S_i,R_i)\}$, $i = 1,\ldots,n$ (n = 13), corresponding to the egg deposition of years 1984 to 1996 and subsequent recruitment expressed in eggs, is deduced via deterministic transformations adult-to-egg (for S) and smolt-to-egg (for R). These calculations use yearly biological characteristics of migrating populations issued from data collected at the trap (river- and sea-age, size, sex ratio, fecundity of females) and are supposedly known without error. Finally, all S_i and R_i are standardized for river size by dividing number of eggs spawned and recruited by the surface area of habitat available for juvenile production, i.e., 25 229 m^2 (Prévost et al. 1996). This sequence of operations leads to a size-G sample generated from $P(\{S,R\}|\text{Data})$ that can be used in the Rao–Blakwell formula (eq. 5) with the data being the number of fish marked and recaptured marked or unmarked.

Technical details

To empirically assess the influence of measurement errors for each couple of parameters (a,b), (C^*,S^*), and (C^*,h^*), we compared the joint and marginal posterior PDFs obtained when accounting for process errors only with those obtained when accounting for both process and measurement errors. The first ones are computed using eqs. A.3 and A.4 (in the Appendix), with S and R set to their most likely values (posterior modes of the MCMC samples). Measurement errors are integrated out using the Rao–Blackwell formula (eq. 5). To focus on the influence of measurement errors only, uniform priors for (a,b), (C^*,S^*), and (C^*,h^*) are used so that posterior PDFs best reflect information provided by the data only. The prior for σ is taken to be noninformative ($P(\sigma) \propto \sigma^{-1}$).

We approximate the joint posterior PDFs as discrete distributions on 300 × 300 two-dimensional grids, linearly spaced for (a,b) and log spaced for (C^*,S^*) and (C^*,h^*) in order to have a thinner grid when approaching 0. The grid ranges are

$$(a,b) \in [-3,+3] \times [-0.2,+0.3]$$

$$(C^*,S^*) \in [1 \times 10^{-5},17] \times [1 \times 10^{-5},18]$$

$$(C^*,h^*) \in [1 \times 10^{-5},17] \times [1 \times 10^{-5},0.99999]$$

The probability in each point of the grid is normalized so that the discrete stairs estimate of the integral over the grid is equal to 1. Closed-form A.4 (Appendix) is used to compute the marginal posterior PDFs for a and b. For C^* (couples (C^*,S^*) and (C^*,h^*)), S^*, and h^*, the marginal PDFs are computed by summation over the corresponding joint dimension of the grid. Posterior modes are interpreted as “most likely values”. x% highest posterior density (HPD) regions (x% HPD regions) or x% intervals (x% HPD intervals), i.e., regions or intervals that contain x% of the probability, are deduced from the approximated PDFs on the grid. As advised by Walters and Ludwig (1994) and Adikson and Peterman (1996), we checked that broadening the grid range and increasing the number of points does not affect results, especially when computing the marginal posterior PDFs for C^*, S^*, and h^*. All calculations were performed using MATLAB 6.0 software (MathWorks, Inc., Natik, Mass.).

Results

Stock and recruitment posterior PDFs

The Oir data set exhibit a high contrast in S, i.e., in eggs deposition (Fig. 1): estimated modes of stock posterior PDFs range from 2.7 eggs·m^{-2} (1991) to 22.1 eggs·m^{-2} (1984). R modal values range from 1.6 eggs·m^{-2} (1989) to 15.6 eggs·m^{-2} (1984). Modal S/R points are scattered between a “high point" with S = 22.1 and R = 15.6 eggs·m^{-2} (1984) and a "low point" with S = 2.7 and R = 2.3 eggs·m^{-2} (1991).

Our estimation of recruitment is more precise than that of stock (Fig. 1). Posterior PDFs of R are relatively homogeneous in dispersion, and almost all are slightly asymmetric with a longer tail towards high values (see the shift between the mode and the median in Fig. 1). By contrast, the dispersion and asymmetry of S posterior PDFs are highly variable between years (Fig. 1). Some distributions have small variance and are relatively symmetric (years 1985, 1996), whereas others are more diffuse and skewed with a long tail toward high values (years 1987, 1994).

Contrary to the common hypothesis of homogeneity in form and variance, our results clearly show that the nature of the measurement error PDFs varies from year to year according to the field data available, because uncertainty of S and R estimations depends on the efficiency of capture–mark–recapture experiments.

Effect of measurement errors on estimation of parameters

The integration of measurement errors as they are estimated by the MCMC sample only slightly increases parameter uncertainty. Posterior PDFs are rather more diffuse when accounting for measurement errors, i.e., by integrating over the posterior PDFs of S and R, than those obtained with the most likely values for S and R (Figs. 2 and 3). However, even with process errors only, uncertainty around all parameters remains large. The effect of accounting for measurement errors on parameter uncertainty is more pronounced for the management-related parameters than for the natural ones (a,b). For the latter, impact of measurement errors on the diffusion of the joint posterior PDF is not obvious. Ninety percent HPD regions cover approximately the same range with measurement errors as with modal S/R values (Fig. 2a). The marginal distribution of a seems to be more sensitive than that of b (Fig. 3). The 95% posterior interval of a is getting wider with measurement errors ([–0.29,1.44] to [–0.71,1.29]), whereas the posterior interval of b remains approximately the same width ([0.022,0.15] and [0.0071,0.13]). With regards to management-related parameters, HPD regions are wider when accounting for the uncertainty in S and R than with fixed modal values, especially toward high values of S^* and C^* (couple (C^*,h^*)) as shown in Figs. 2b–2c. The 95% posterior intervals of C^* and S^* are all broader with measurement errors than with modal values: [1.9,11.8] to [1.8,12.6] for S^* and [0.24,7.7] to [0.17,8.7] for C^* (couple (C^*,S^*)). Both marginal posteriors of S^* and C^* for both couples (C^*,S^*) and (C^*,h^*) are skewed with a long tail toward high values. By contrast, the uncertainty of h^* is not strongly affected by measurement errors (the 95% posterior interval changes from [0.070,0.62] to [0.062,0.61]). Note that the left-hand tail curving upward of the marginal posterior PDFs of h^* (Fig. 3) is not an artifact. The joint posterior P(C^*,h^*|Data) increases when h^* approaches 0, for all values of C^* (owing to the highly nonstandard form of the likelihood in the space (C^*,h^*)). This leads to an accumulation of mass in the neighborhood of h^* = 0.

Parallel to their slight increase in variability, posterior PDFs obtained when taking into account measurement errors differ in location from those obtained when S and R are set to their modal values. Modes for a, b, C^*, and h^* decrease, whereas

Fig. 1. Box and whisker plots for the size-5000 Markov Chain Monte Carlo (MCMC) samples from *(a)* $P(\{S_i\}_{i\,=\,1\text{ to }n}$ |Data) and (*b*) $P(\{R_i\}_{i\,=\,1\text{ to }n}$ |Data). Stock and recruitment are in eggs·m^{-2}. The boxes have lines at the first quartile, the median, and the upper quartile. The broken lines extending from each end of the box show the extent of the 95% posterior intervals. Symbols: ▲, modes; +, 2.5% and 97.5% percentiles. (*c*) Modal values of the MCMC samples for recruitment vs. stock.

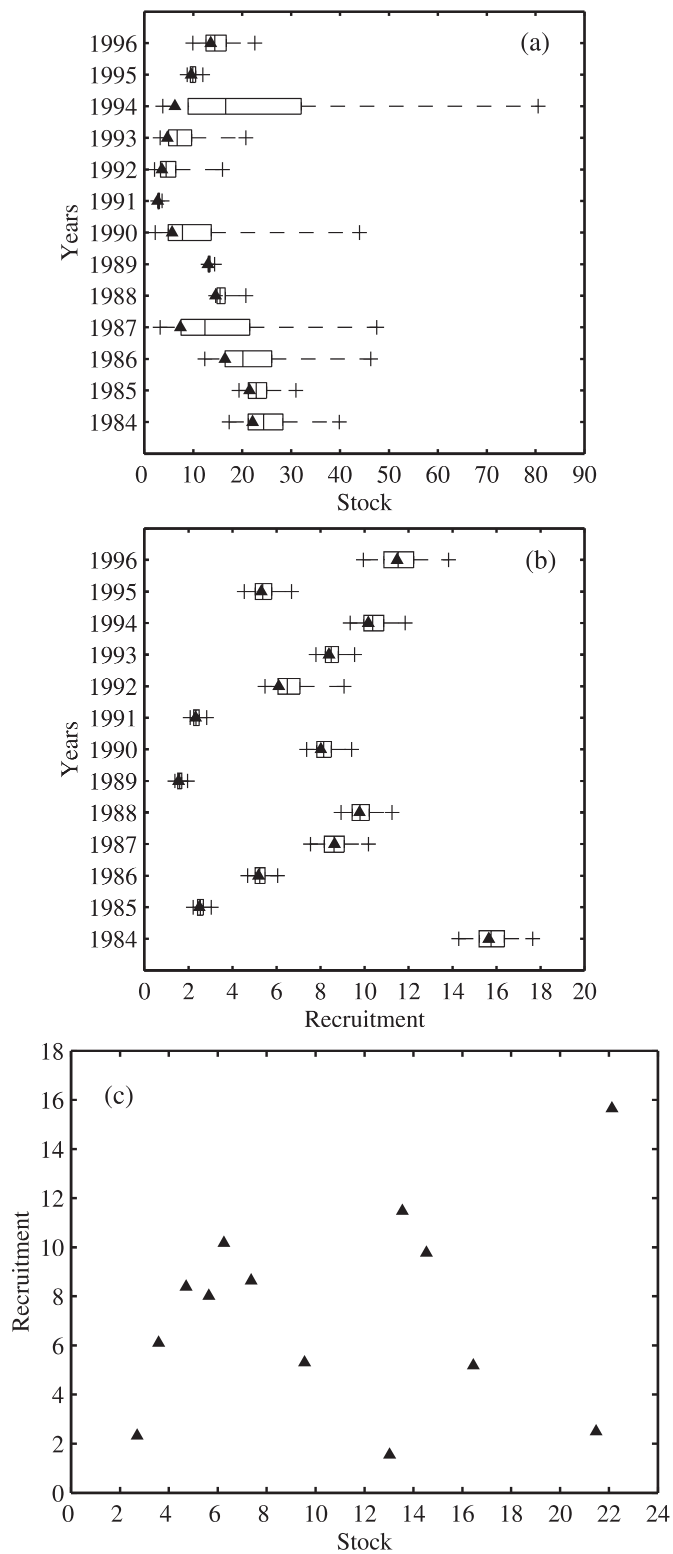
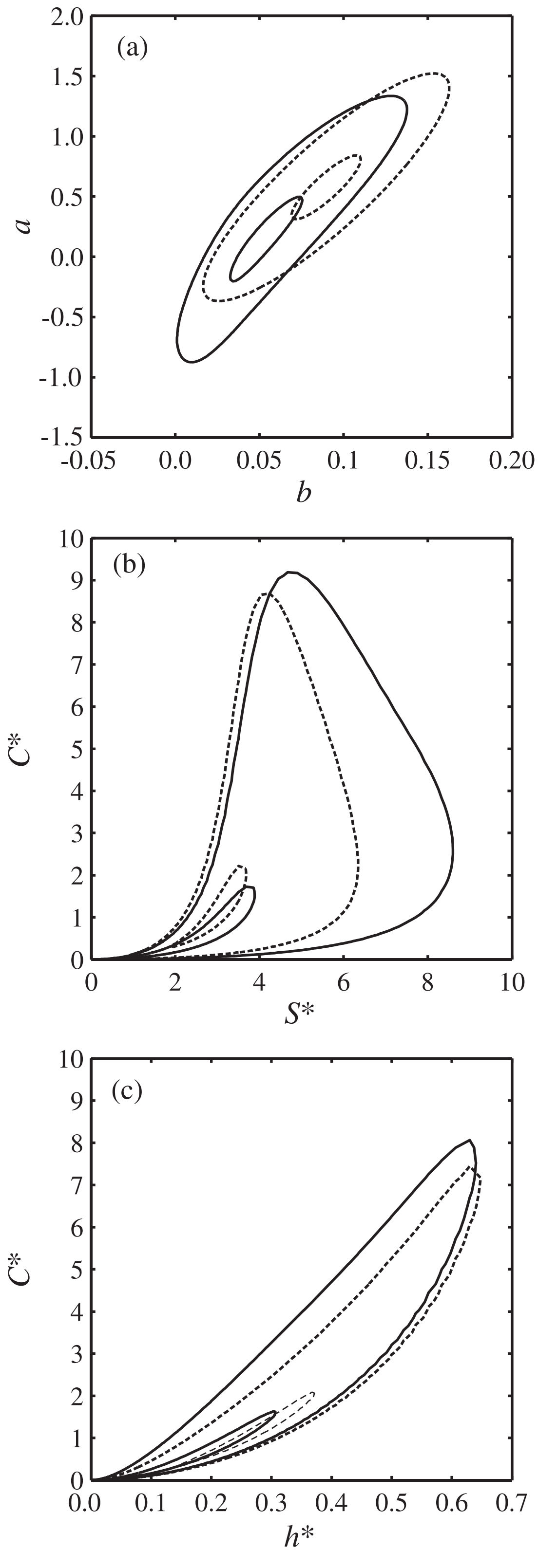


Fig. 2. Contour plots of 20% and 90% highest posterior density regions of (a,b), (C^*,S^*), (C^*,h^*) (*a*, *b*, *c*, respectively) obtained accounting either for process error only, i.e., with *S* and *R* set to their modal values (broken line), or for both process and measurement errors, i.e., *S* and *R* are integrated out (solid line). Uniform priors on the three parameter couples and noninformative prior for σ ($q = 1$) were used.



it increases for S^*. The joint mode for the couple (a,b) changes from (0.57,0.089) to (0.15,0.052) with uncertainty on *S*/*R* data. The modes of the marginal posterior laws (Fig. 3) significantly decrease for *a* (0.57 to 0.23) and *b* (0.089 to 0.050). This results in a probability for $a < 0$ that is approximately 8.3% with *S*/*R* modal values, whereas there is much more chance that $a < 0$ when considering uncertainty in *S* and *R* ($P(a < 0) \approx 0.30$). With regards to management-related parameters and particularly for (C^*,S^*), Fig. 2 highlights that the density is concentrated in the neighborhood of the origin of the grid (small values of parameters). Accounting for errors in *S*/*R* data results in modes of joint distributions for (C^*,S^*) and (C^*,h^*) that drastically shift back towards very small values. The mode of the joint posterior PDF of (C^*,h^*) is located in (1.10,0.27) when *S* and *R* are set to their modes but cannot really be distinguished from the grid origin with *S*/*R* data uncertainty ((0.075,0.060)). The same tendency is observed for the mode of the joint posterior PDF of (C^*,S^*) ((1.15,3.03)) with modal *S*/*R* values vs. (0.10,1.33) with measurement errors). The modes of marginal PDFs for C^* and h^* are different from 0 and slightly decrease when accounting for measurement errors (1.28 to 0.87 for C^* from the couple (C^*,S^*) and 0.35 to 0.30 for h^*), whereas the location of S^* tends to move up from 3.64 to 3.97 eggs·m^{-2} (Fig. 3).

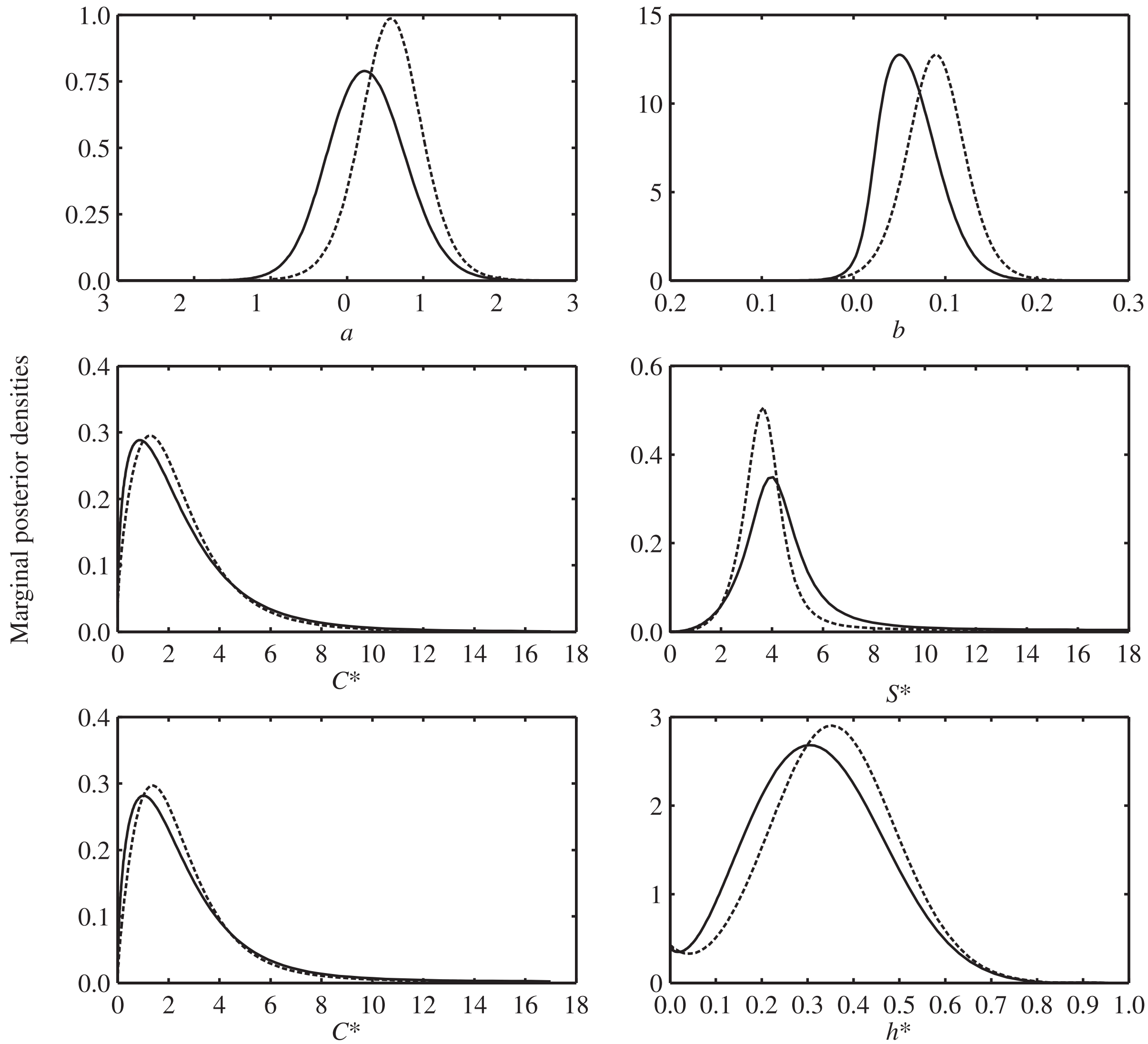
Effect of switching from natural to management-related parameters

In our case study, the resulting posterior PDFs are not robust to the strong modification of priors induced when switching from the natural parameterization (a,b) to (C^*,S^*) or (C^*,h^*). Working with management-related parameters a priori puts 0 probability on $a < 0$. Based on the marginal posterior PDF of *a* in Fig. 3, the posterior probability that $a < 0$, calculated with a uniform prior on (a,b) and accounting for measurement errors, is about 30%. C^* and h^* are by definition positive, which implies that *a* is also positive. Thus, the 30% probability for $a < 0$ obtained with natural (a,b) parameters is erased when switching to management-related parameterization. However, the information "$P(a < 0) \neq 0$" has not totally vanished. Indeed, HPD regions for (C^*,S^*) and (C^*,h^*) are both concentrated close to the origin of the grid (Fig. 2). In addition, marginal posterior densities for C^* and h^* do not tend towards 0 when C^* and h^* approach 0 in the grid (Fig. 3). This suggests that although we a priori excluded null value for C^* and h^*, the state of nature $a < 0$ remains likely in light of the data. In others words, prior information introduced by the use of management-related parameters seems to be contradictory with the data.

Sensitivity of posterior parameter PDFs to the prior PDFs

Posterior parameter PDFs are highly sensitive to the prior PDFs. For instance, the marginal posterior PDFs for C^* and S^* can differ markedly according to the different priors tested, as well for location and dispersion (Fig. 4). Considering a uniform prior in the (a,b) space and a uniform prior in the (C^*,S^*) space leads to drastically different results. The uniform prior on (a,b) amounts to putting a very high weight on small values of C^* through the Jacobian $J_{+1}(C^*,S^*)$. This is still noticeable in the posterior PDF of

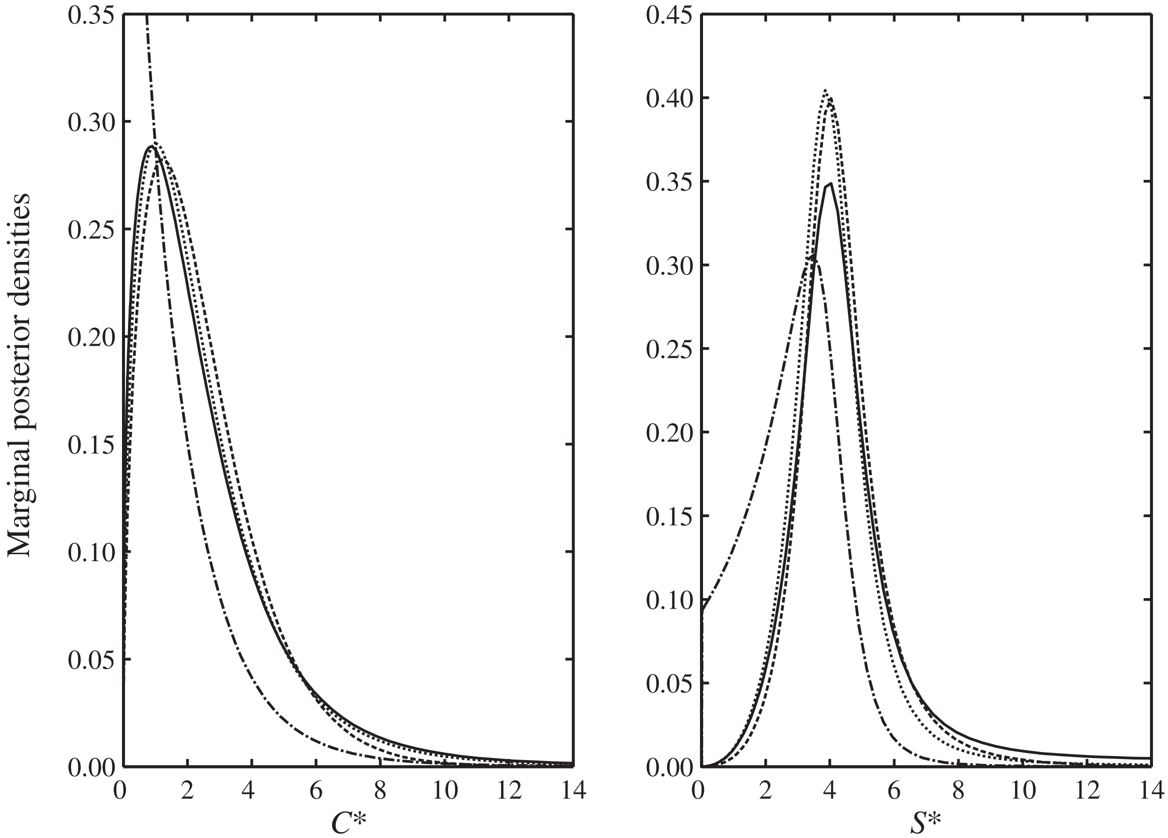
Fig. 3. Marginal posterior density profiles corresponding to joint posterior density of (a,b) (top), (C^*,S^*) (middle), and (C^*,h^*) (bottom) obtained accounting for process errors only (broken line) or for both process and measurement errors (solid line). All are obtained with uniform priors on the three parameter couples and with a noninformative prior for σ (q = 1).



(C^*,S^*) once the information carried by the data has been used to update the prior. The marginal posterior PDF of C^* looks like an inverse function and has a narrower 95% interval compared with other prior PDFs tested. The marginal posterior density of S^* is nonnull when S^* approaches zero, its mode decreases and the width of its 95% posterior interval is reduced compared with posterior PDFs obtained with the other priors. By contrast, similar marginal PDFs are obtained with a uniform prior in the space (C^*,S^*) or in the space (C^*,h^*) and with a prior equal to a two-dimensional normal PDF. Locations remain nearly the same. Differences are more noticeable regarding posterior 95% credibility intervals. The marginal PDFs change slightly when modifying parameters of the two-dimensional normal prior (results not shown here). A larger variance (taking 6 in Σ) leads to posterior marginal PDFs very similar to those obtained with the initial Σ. Decreasing the variance of the prior (replacing 4 by 2 in Σ) reduces dispersion of the posterior and makes both C^* and S^* posterior modes move towards the prior mean (3.5,4.75). By contrast, changing the mean of the normal prior (we tried (5,6.25) and (2,2.25)) has no real influence on posterior parameter PDFs.

For natural parameters as well as for management-related ones, the analysis is not robust to the choice of the prior for σ. Decreasing parameter q from 2 to 0 in the prior $P(\sigma) \propto \sigma^{-q}$ dramatically increases the dispersion of the joint parameter posterior PDFs. Ninety percent HPD regions for joint posterior PDFs (Figs. 5*a*–5*c*) and 95% posterior intervals for marginal posterior densities (results not shown) get drastically wider with decreasing q. On the other hand, changing q has practically no influence on the location of posterior PDFs. This strong effect of q on parameter uncertainty is directly related to the fact that q plays a similar role as the number of observations n in the degrees of freedom $\nu = n - 2 + 2(q - 1)$ for the multidimensional distribution A.3 (in the Appendix). Consequently, the greater the q value, the higher the degrees of freedom and logically the smaller the diffusion of the posterior PDFs. This effect is especially marked in our case

Fig. 4. Marginal posterior density profiles for C^* and S^* obtained with different priors on parameters. Line styles indicate the four priors investigated: solid line, uniform on the space (C^*,S^*); dashed–dotted line, uniform on the space (a,b) then proportional to $J_{+1}(C^*,S^*)$; dotted line, uniform on (C^*,h^*) then proportional to $J_{+2}(C^*,S^*)$; dashed line, two-dimensional normal $N((3.5,4.75), \Sigma = \begin{pmatrix} 4 & 0 \\ 0 & 4 \end{pmatrix})$ on the space (C^*,S^*). Noninformative prior for σ (q = 1) was used and measurement errors are integrated out.



study in which $2(q - 1)$ is not negligible compared with $n - 2$ (n = 13).

Discussion

Advantages and specificity of the Rao–Blackwell procedure

Our Rao–Blackwell procedure (eq. 5) requires random generation of measurement errors and a closed form for the likelihood (and also for the posterior PDF) of the parameters of interest when the observations are assumed known without errors. This restricts its range of application, especially the second condition, but it is compensated for by several advantages.

First, it allows the assessment of the effect of measurement errors grounded on any kind of information that can be formalized as PDFs. It uses a random sample of possible observation values that can be constructed in many different ways, for instance using MCMC, bootstrapping, or jackknifing techniques. Our recommended approach is to derive such a sample from posterior measurement error PDFs by means of a probability model linking the S and R variables to the field data as in our illustrative case study. By comparison with the error-in-variable models of Ludwig and Walters (1981) or with the more recent state–space model of Meyer and Millar (2000), simulating measurement errors from posterior PDFs frees the modeler from making hypotheses about the structure of measurement errors. Most often, such hypotheses are almost impossible to justify whether theoretically or by some checking against data. For instance, Walters and Ludwig (1981) need to fix the value of the ratio of the variances of measurement and process errors to be able to provide estimates of S/R-related parameters by means of total least-squares techniques. Owing to a Bayesian treatment of their state–space model, Meyer and Millar (2000) relax the previous hypothesis but still assume that the form of the measurement error distribution is the same for all years (log-normal in their case study). More realistic distributions of measurement errors can be specified from field data. In our case study, we account for the variability from year to year in the form and dispersion of the probability distributions for S and R observations. Had we assumed log-normal errors with the same variance for all years, much information coming from the field data would have been discarded and replaced by a strong prior hypothesis. The posterior PDFs of parameters conditioned by the information brought by the capture–mark–recapture experiments provide a more objective assessment of the uncertainty.

Second, our method offers computational convenience to perform the analysis of the influence of prior easily and rigorously. Closed-form distributions provide an analytical basis to discuss prior hypotheses that underlie parameterization change and the choice of prior for process error variance σ^2. The analysis with prior distributions as $P(C^*,S^*) \propto J_{+1}(C^*,S^*)$ would also be difficult to perform via more general MCMC sampling methods, which would hardly run with such non-standard prior distributions.

Lastly, our method produces smooth estimates of parameter posterior PDFs with modest computational effort. This results from the fact that the posterior probability is calculated by averaging a closed form over a sample from the posterior PDF of the *S*/*R* variables (eq. 5). Smooth estimates are not only esthetic. In our case study, marginal posterior densities for C^* or h^* do not tend towards 0 when C^* or h^* approach 0. The Rao–Blackwell procedure provides precise estimators for the densities over these limit domains that are critical for management considerations.

Owing to the above advantages, we advocate that Rao–Blackwell procedures similar to ours should be preferred to full treatment of the model by MCMC techniques whenever possible. Full treatment by MCMC sampling would be used to estimate $P(\theta|\text{Data})$ when no closed form for the likelihood is available.

Effect of measurement errors on parameter uncertainty

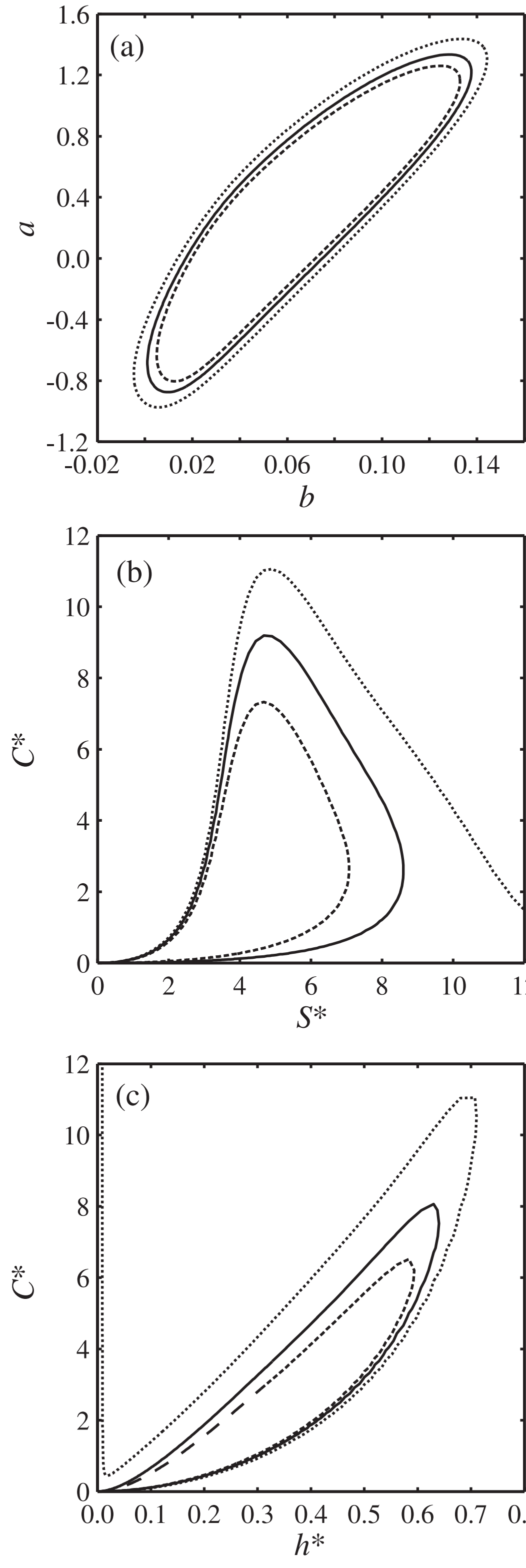
In our case study, the effect of measurement errors on parameter uncertainty remains moderate. This interestingly contrasts with the potentially disruptive effect of measurement errors in *S*/*R* analysis reported by Walters and Ludwig (1981) or Hilborn and Walters (1992). Still, ignoring measurement errors in *S* and *R* observations leads to overestimating the information available concerning the recruitment process. Including measurement errors blurs the information coming from *S*/*R* data, resulting in a looser fit of *S*/*R* curve and a less precise assessment of parameters.

Our results, demonstrating that measurement errors are not always a major concern for the estimation of *S*/*R*- related parameters, should be interpreted and generalized with caution because they may be due to specific features of our case study. Indeed, our data set is characterized by a high contrast in *S* values. This is favorable to the robustness of parameter estimates to measurement errors. By contrast with common situations where *S*/*R* observations are clustered in a small portion of the potential range for *S* (Hilborn and Walters 1992; Adikson and Peterman 1996), in our study the smallest *S* value is less than a tenth of the largest. Our estimation of recruitment is also relatively accurate and less affected by measurement errors than that of stock. Measurement errors for *R* comparable with those of *S* would certainly lead to more uncertain parameter estimates. However, we may have overestimated the precision of our *R* estimates in terms of eggs because we ignore the uncertainty related to the transition between the smolt stage and the subsequent eggs deposition. Indeed, we used a fixed average ratio of eggs produced per smolt for the conversion of the number of smolts into eggs.

Stock status considerations

Ignoring measurement errors gives an overly optimistic view of the stock productive potential and underestimates the risk associated with misspecification of biological reference points. Accounting for measurement errors leads to smaller values for estimated parameters *a* and *b* than those

Fig. 5. Contour plots of 90% highest posterior density regions of (a,b), (C^*,S^*), and (C^*,h^*) (*a*, *b*, and *c*, respectively) obtained with different priors for the standard deviation of the process errors σ. The generic form of the prior is proportional to σ^{-q}. Line style defines different values for *q* as follows: dotted line, $q = 0$; solid line, $q = 1$; dashed line, $q = 2$. Posterior distributions are performed integrating out measurement errors. Uniform distributions are used for the three parameter couples.



obtained with S and R set to their modal values. This in turn yields a best-fit Ricker curve that ascends less rapidly at low stock values (smaller a) and shows less evidence of declining recruitment at large stock size (smaller b, i.e., lower density-dependence effect). For the management-related parameters, ignoring observation uncertainty by setting S and R to their most likely values leads to an overestimation of C^* and h^* (related to stock productivity) while underestimating S^*. Not only the best estimates of parameters are affected, but also the probability that C^* or h^* is under and that S^* is above a certain threshold increases. As a consequence, in a management-advice perspective, the S/R analysis without measurement error could promote overexploitation.

These assessments of the measurement error bias remain empirical. Indeed, because we do not know what the true values of the parameters are, we cannot prove that accounting for measurement errors results in more accurate parameter estimation. The results above cannot be generalized because they depend on the measurement errors that we estimated in our particular case study. However, they are consistent with more theoretical studies dealing with the effect of measurement errors on the estimation of S/R-related parameters (Walters and Ludwig 1981; Hilborn and Walters 1992).

Sensitivity of posterior PDFs to prior inputs

The present work reveals that specification of priors remains of primary importance. In agreement with Adikson and Peterman (1996), we contend that any Bayesian approach to determine S/R-related parameters should examine in detail the prior implementation process. Prior inputs in the analysis, as parameterization (e.g., natural vs. management related) or prior PDFs of the parameters of direct interest or treated as nuisance can have a major influence on the results when facing little informative data such as S/R series (few data points highly scattered by measurement and process stochastic errors).

Choice of parameters

We warn against systematically ignoring natural parameters (a,b), especially in cases where the stock productivity is low as in the Oir salmon population. Management-related parameterizations do not allow us to check for the long-term sustainability of populations. Schnute and Kronlund (1996) advocated that management-related parameters should have priority over natural ones (a,b) because they have direct relevance to management. We agree in the sense that these parameters provide more direct links between population dynamic and regulation of the exploitation. For instance, for the Atlantic salmon populations of Brittany, S^* is used as a spawning target and C^* is used to set total allowable catch (TACs) on a river-by-river basis. However, switching from parameters (a,b) to (C^*,S^*) or (C^*,h^*) dramatically changes the model specification. It amounts to the strong prior assumption that the population is able to at least replace itself in the absence of exploitation, i.e., $P(a < 0)$ is null. In our case study, this assumption is contradictory with the posterior information provided by the analysis with (a,b) using a noninformative uniform prior which states that $a < 0$ and $a > 0$ are almost equally likely events. Then, it would be highly probable that the Oir salmon population is not able to replace itself. This important diagnosis, consistent with the pressure exerted by human activities on the Oir environment (Prévost et al. 1996), is a priori discarded when using management-related parameters. As a cautionary approach, we strongly recommend first performing the analysis with natural parameters (a,b) before eventually switching to management-related parameterization, especially for low productivity stocks suspected to be depleted.

Choice of priors

In some instances where little is known a priori on parameters values, the Bayesian approach offers the opportunity to define noninformative priors. This choice is appropriate when attempts to define a meaningful informative prior may appear as a desperate quest, as for the standard deviation of the process errors, σ. Our results highlight that although often overlooked, the choice of a prior for this nuisance parameter may be of great significance even if it vanishes from the final interpretation after integrating over it. This should be an incentive to elicit a meaningful prior PDF for σ, but probably too little is still known about the process generating the recruitment variability to do so. The process error has in itself a formal nature with no real experimental grounds to assess relative degrees of belief of different values before proceeding to the S/R analysis. The modeler has little opportunity to propose a realistic variance structure and we recommend a conservative choice of $q = 0$ or $q = 1$ for a less informative prior of the form σ^{-q} (preserving the analytical simplification ensuing from this form).

To summarize, should a noninformative prior be the default choice in any case? The answer is a qualified no. A noninformative prior can become hard to interpret when translated into another parameterization. When proceeding to parameter transformation, careful consideration must be given to the implications in terms of priors. Our approach forces a decision regarding which of the parameter pairs, natural ones (a,b) or management-related ones, should be of primary concern. For Box and Tiao (1992), a noninformative prior should be used as a reference to judge what kind of unprejudiced inference can be drawn from the data. In our case study, a uniform PDF on (a,b) seems to correspond to this definition. It is not only noninformative in the sense of Jeffrey (Box and Tiao 1992), but it also seems to bring little information into the analysis. When changing parameters (a,b) into (C^*,S^*), the prior could be adjusted by transforming the uniform prior on (a,b) into a prior on (C^*,S^*) proportional to $J_{+1}(C^*,S^*)$. We argue that this prior is not noninformative in the space (C^*,S^*) in the sense that the information that it carries, i.e., a huge weight on very small C^* and S^* values (see the high degree of S^* and C^* in the denominator of $J_{+1}(C^*,S^*)$), overcomes information brought by the data. What brings about little information in the space (a,b) becomes informative in the space (C^*,S^*). Hence, we join Box and Tiao (1992) in contending that each parameterization must be considered for its own merits and the form of noninformative prior input depends on the parameterization considered. In other words, as proposed by Schnute and Kronlund (1996) for (C^*,h^*), it is relevant to seek another form of noninformative prior regarding (C^*,S^*), without reference to (a,b).

Towards informative prior elicitation

We agree with Hilborn and Liermann (1998) that one of the most challenging issues in the Bayesian approach to stock and fisheries assessment is the elicitation of informative priors summarizing our previous knowledge. Indeed, the Oir *S*/*R* data set, as in many ecological studies, does not provide enough information to supersede the influence of the prior: posterior parameter PDFs are largely sensitive to the choice of the prior. Consequently, we believe that this forces the analyst to devote much care on prior elicitation so as to introduce relevant prior knowledge. We must look at what is known about the biological process of interest before its specific study. This is of special importance for *S*/*R* analysis in salmonids where the data are most often not very informative, even though salmonids are among the most-studied fish species of the last century. This extensive biological and ecological knowledge cannot be ignored when defining priors. Myers (1997) and Hilborn and Liermann (1998) emphasized the potential of Bayesian meta-analysis to derive meaningful priors. Whatever the method used, prior elicitation might be facilitated by expressing models relative to parameters of ecological significance, which can be directly connected with available knowledge. For instance, the *b* parameter in the Ricker function has no concrete meaning for an ecologist. However, it is closely related to maximum recruitment, directly connected with the concept of carrying capacity of rivers, which has been most studied for juvenile salmonids.

The Bayesian approach potentially allows the incorporation of prior knowledge. We should take full advantage of this possibility and devote more effort to prior elicitation. When not doing so, we are sometimes left with debatable posterior inferences that are significantly influenced by prior assumption and possibly meaningless regarding the ecological process of interest. Still, whatever the interest in using informative priors, it should always be accompanied by a careful analysis of the influence of the prior on the posterior.

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Appendix

A closed form for $P_{p\sigma,0}(\theta|\{S,R\})$: treating the Ricker model as linear

Considering $\{S,R\}$ as observable known without error, we assess $P_{p\sigma,0}(\theta|\{S,R\})$ by using classical results of linear models. The linear form is obtained by rearranging the logarithm of the Ricker relation (eq. 1). Equation A.1 defines a linear model A.2 with a two-dimensional mean parameter $\theta = \begin{pmatrix} a \\ b \end{pmatrix}$. We rigorously need the strong assumption that the $\ln(R_i/S_i)$ are independently distributed with a constant variance. Although this hypothesis is neither supported by theoretical consideration nor verified experimentally because process and measurement errors occur simultaneously, it is commonly used (see Quinn and Deriso (1999) for a discussion). Note that here, we made the hypothesis that $\{S,R\}$ are measured without error, i.e., only recruitment process errors are considered. Under this hypothesis, the least-square procedure provides unbiased estimators $\hat{\theta}$ (Quinn and Deriso 1999). Box and Tiao (1992) provide the analytical expression of the posterior of θ integrated over σ assuming a joint prior for (θ,σ), $P(\theta,\sigma) \propto \sigma^{-1}$. We performed calculation with $P(\theta,\sigma) \propto \sigma^{-q}$, where q is an integer. This corresponds to independent priors for θ and σ, with $P(\theta)$ uniform on $]-\infty;+\infty[\times]-\infty;+\infty[$, that is noninformative for the mean of a linear model and with $P(\sigma) \propto \sigma^{-q}$. $q = 1$ corresponds to a noninformative prior on σ. Under those assumptions the closed form for posterior PDF $P_{p\sigma,0}(\theta|\{S,R\})$ is given by eq. A.3. Marginal PDFs for a and b have closed-form expressions (eq. A.4).

Table A1. Treatment of the Ricker model as linear.

Linear model

(A.1) $$Y_i = \ln(R_i/S_i) \Rightarrow Y_i = a - bS_i + w_i \text{ for } i = 1 \text{ to } n$$

(A.2) $$\begin{pmatrix} Y_1 \\ \vdots \\ Y_n \end{pmatrix} = \begin{bmatrix} 1 & -S_1 \\ \vdots & \vdots \\ 1 & -S_n \end{bmatrix} \cdot \begin{pmatrix} a \\ b \end{pmatrix} + \begin{pmatrix} w_1 \\ \vdots \\ w_n \end{pmatrix}, \text{ that is, } Y = X \cdot \theta + W$$

Notations

$k = 2$, $\nu = n - k + 2(q-1)$, $\theta = \begin{pmatrix} \theta_1 \\ \theta_2 \end{pmatrix}$. $\hat{\theta} = \begin{pmatrix} \hat{\theta}_1 \\ \hat{\theta}_2 \end{pmatrix}$ and s^2 are the maximum likelihood estimates of θ and σ^2, respectively. $T = (X'X)/s^2$ is the approximate precision matrix with partition $T = \begin{bmatrix} T_{11} & T_{12} \\ T_{21} & T_{22} \end{bmatrix}$, $T_1 = (T_{11} - T_{12} \cdot T_{22}^{-1} \cdot T_{21})$.

Posterior PDFs

(A.3) $$P_{p\sigma,0}(\theta|\{S,R\}) = \left[\left(\frac{|T|^{\frac{1}{2}} \cdot \Gamma((\nu + k)/2)}{\Gamma(\nu/2) \cdot ((n-k)\prod)^{\frac{k}{2}}} \right) \right] \cdot \left(1 + \frac{(\theta - \hat{\theta})' \cdot T \cdot (\theta - \hat{\theta})}{(n-k)} \right)^{-\left(\frac{\nu + k}{2}\right)}$$

Table A1 (*concluded*).

(A.4)	$P_{p\sigma,0}(\theta_1 \mid \{S,R\}) = \left[\left(\dfrac{\lvert T_1\rvert^{\frac{1}{2}} \cdot \Gamma((\nu+1)/2)}{\Gamma(\nu/2)\cdot((n-k)\prod)^{\frac{1}{2}}}\right)\right] \cdot \left(1 + \dfrac{(\theta_1 - \hat{\theta}_1)^2 \cdot T_1}{(n-k)}\right)^{-\left(\frac{\nu+1}{2}\right)}$
	(Marginal of b is obtained by permutation of indices 1 to 2)
	Γ is the Gamma function $\Gamma(x) = \int_0^{\infty} y^{x-1} \cdot e^{-y} \cdot dy$

Note: Equations A.3 and A.4 are closed-form expressions of joint posterior and marginal PDFs, under prior assumptions of a uniform prior on (a,b) and $P(\sigma) \propto \sigma^{-q}$ (see Box and Tiao (1992) for more details). Note that when $q = 1$, $P_{p\sigma,0}(\theta \mid \{S,R\})$ is a multivariate t distribution with $\nu = n - 2$ degrees of freedom, location vector $\hat{\theta}$, and precision matrix T. Marginal posterior PDFs of a and b are both Student's distributions with $\nu = n - 2$ degrees of freedom, location vectors $\hat{\theta}_1$ and $\hat{\theta}_2$, and precision T_1 and T_2, respectively.