

Bayesian mark-recapture estimation with an application to a salmonid smolt population

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Abstract: We developed a Bayesian probability model for mark-recapture data. Three alternative versions of the model were applied to two sets of data on the abundance of migrating Atlantic salmon (*Salmo salar*) smolt populations, and the results were then compared with those of two widely used maximum likelihood models (Petersen method and a model using stratified data). Our model follows the basic principles of stochastic models presented for stratified data. In contrast to the earlier models, our model can deal with sparse data. Moreover, even weak dependencies between the studied parameters and the possible factors affecting them can be used to improve the plausibility of the estimates. The assumptions behind our approach are more realistic than those of earlier models, taking into account such factors as overdispersion, which is expected to be present in the mark-recapture data of salmon smolts because of their schooling behavior. Our examples also show that assumptions about the model structure can have a substantial impact on the resulting inferences on the size of the smolt run, especially in terms of the precision of the estimate.

Résumé : Nous avons mis au point un modèle de probabilité bayésien pour étudier des données de marquage et de recapture. Trois versions différentes du modèle ont été appliquées à deux séries de données sur l'abondance de populations de saumoneaux du saumon de l'Atlantique en migration et les résultats ont été comparés à ceux de deux modèles courants de vraisemblance maximale, la méthode de Petersen et un modèle qui utilise des données stratifiées. Contrairement à ces modèles plus anciens, le nôtre peut utiliser des données éparses. De plus, même des liens faibles entre les paramètres étudiés et les facteurs qui les affectent peuvent servir à augmenter la plausibilité des estimations. Les présuppositions sous-jacentes à notre méthodologie sont plus réalistes que celles des modèles précédents, car elles tiennent compte de facteurs tels que la surdispersion que l'on s'attend à trouver dans les données de marquage-recapture de saumoneaux à cause de leur comportement de nage en bancs. Nos exemples montrent aussi que les présuppositions faites au sujet de la structure du modèle peuvent avoir un impact important sur la taille estimée de la population migratrice de saumoneaux, particulièrement en ce qui a trait à la précision de l'estimation.

[Traduit par la Rédaction]

Introduction

Mark-recapture methods are widely used in the assessment of animal abundance (Otis et al. 1978; Seber 1982; Schwarz and Seber 1999). The simplest version of mark-recapture models is the Petersen method (Seber 1982), which assumes a closed population and equal recapture probabilities of all animals during the experiment. The Petersen method is an example of an easy method, but unfortunately it is also too simplistic to be genuinely useful in real applications. Methods with more realistic assumptions are required to analyze complex mark-recapture data. Considerable progress has already been made in developing models that are able to deal with, for example, catchability varying over time (Schwarz and Seber 1999). However, this development has been largely carried out in the context of maximum likelihood estimation. Bayesian mark-recapture models have also been developed (Castledine 1981; Gazey and Staley 1986;

George and Robert 1992), but they too rely on the simplistic assumptions of, for example, independently behaving individuals.

Typical mark-recapture studies on migratory fish species like salmon aim to estimate abundance by partial trapping of either young fish leaving the nursery grounds for the feeding grounds or adult fish assembling in the spawning grounds following the feeding migration. In many such studies, capture probabilities have been reported to vary over the trapping period (Dempson and Stansbury 1991; Schwarz and Dempson 1994; Thedinga et al. 1994). In addition, smolts of Atlantic salmon (*Salmo salar*) have a tendency to school during their downstream migration (Kalleberg 1958; Bakshanskiy et al. 1988; Fängstam et al. 1993), similar to smolts of Pacific salmon species (Burgner 1991; Heard 1991; Salo 1991). Social interaction between smolts has been suggested as the reason behind the schooling behavior (Allen 1944; Hansen and Jonsson 1985; Hvidsten et al. 1995). Schooling

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causes more variation in capture data (overdispersion) than there would be if smolts moved independently. Hvidsten et al. (1995) reported great overdispersion among daily smolt catches in the River Orkla, Norway. To date, implications of schooling behavior have not been taken into account in smolt abundance analyses.

In this paper we present a Bayesian probability model that can be used to derive the posterior probability distribution of the population size from stratified mark–recapture data. We combine the advantages of Bayesian modeling with the detailed statistical model presented by Schwarz and Dempson (1994). By considering the possibility of schooling behavior, a step towards more realistic model assumptions is taken. We also provide an option to incorporate into the model environmental covariates that might influence the values of estimated parameters. We analyze two data sets from Atlantic salmon smolt studies as examples: the Conne River data from Canada, presented and analyzed by Schwarz and Dempson (1994), and similar data from a much larger river in Scandinavia, the River Tornionjoki. Although we apply our model to the abundance estimation of Atlantic salmon, the model could be adapted to apply to any other animal species when using stratified mark–recapture data. The presence of dependent behavior in a form of, for example, spatial aggregation is typical among a wide range of animal species. Similarly, varying capture probability and its crucial role in the estimation of abundance are well recognized in the literature. Thus, our model has the potential to be applied to a wide range of biological problems.

Related study design

The model presented here is tailored to fit a common type of study design in partial smolt trapping. The basic idea is to provide continuous input of marked smolts upstream from the trap. Monitoring the recaptures of marked smolts provides information on the catchability of smolts. By having information on the catchability and knowing the number of unmarked smolts caught, it is possible to make inferences about the total number of smolts that passed the trapping site during the trapping period. It is assumed that there is at least one trapping device used continuously over the migration period. If two devices are available, the upper trap is used for marking and releasing with group-specific or individual marks and the lower “main trap” is used to catch both marked and unmarked smolts. If only one device is used, smolts that are caught are regularly marked and transported upstream and released for possible recapture. Here, the two-trap study design is represented by the Conne River and the one-trap design by the River Tornionjoki data. By assuming that the transportation of marked smolts corresponds to the use of a marking trap, the same model can be used in both cases.

Data from a study design described above is naturally temporally stratified. A proper unit of a stratum is 1 day, which can be easily justified by the commonly observed diurnal periodicity in the migration activity among Atlantic salmon smolts (Österdahl 1969; Hesthagen and Garnas 1986; Fängstam et al. 1993).

The following types of data are collected using the design described above. We release m_i smolts marked by individual

or group-specific marks in day i . In each trapping day j , the number of smolts ($r_{i,j}$) recaptured in day j and released in day i is recorded, as well as the number (c_j) of unmarked smolts captured. Daily measurements of environmental covariates such as water level (WL_j) and water temperature (WT_j) can be recorded and used in the analysis. The notation for data and model parameters is summarized in Table 1.

Statistical methods

In this section, we present three Bayesian models for smolt trapping data. Because the Bayesian approach may be unfamiliar to some of the readers, we briefly explain the basic concepts of Bayesian inference (e.g., O’Hagan 1994) as they appear.

Models

We transfer two models from the frequentist framework to the Bayesian framework by using the original type of model structure, but completing the probability model by assigning prior distributions for model parameters. First, we formulate model M_p , a Bayesian version of the traditional Petersen model. The Petersen model is used here as a simple example to illustrate the notation and basic concepts of Bayesian modeling. The second model, M_{SD} , is based on the mark–recapture model introduced by Schwarz and Dempson (1994). However, the model is also improved by constructing a hierarchical structure for the model parameters. Finally, to allow for dependent behavior of smolts, we introduce model M_S , which accounts for overdispersion.

In each of the three models, it is assumed that (i) all marked and unmarked smolts migrate downstream, (ii) there is no mark loss between release and recapture sites, (iii) there is no mortality between release and recapture sites, (iv) the catchability of a marked smolt does not depend on the time spent in the river after release, and (v) marked and unmarked smolts have equal catchability and equal aggregation patterns.

Model M_p

In addition to assumptions i – v , the Petersen method is based on the assumption that all smolts move independently and are equally catchable throughout the whole trapping period. Thus, the total number of unmarked smolts caught ($C = \sum_{i=1}^M c_i$) is binomially distributed given the size of the unmarked population (U) and the catchability (q). By assumption v , the total number of recaptured smolts ($R = \sum_{i=1}^M \sum_{j=1}^M r_{i,j}$) is also conditionally binomially distributed given the total number of marked smolts released ($T = \sum_{i=1}^M m_i$) and the common catchability (q). Formally, the model specification is

$$(1) \quad C|U, q \sim \text{Bin}(U, q)$$

$$R|T, q \sim \text{Bin}(T, q)$$

This model describes the stochastic relationship between the data and the model parameters and also completely defines the likelihood function of data.

The dependence structure of the model can be illustrated in terms of a directed acyclic graph (DAG; Fig 1a). A DAG

Table 1. List of symbols used in the model specification.

Indices	
M	the number of recapture and release days
i	the day of release $i = 1, \dots, M$
j	the day of recapture $j = i, \dots, M$
Data (X)	
m_i	the number of smolts with group-specific marks released in day i
$r_{i,j}$	the number of smolts with group-specific marks released in day i and recaptured in day j
WT_j	the water temperature in day j
WL_j	the water level or the discharge in day j
c_j	the number of unmarked smolts captured in day j
Parameters (Θ)	
q_j	the catchability of smolts that pass the trapping site in day j
η_j	the mean of logit(catchability) in day j
ν_0, ν_1, ν_2	the intercept and regression coefficients of environmental covariates of logit(catchability)
λ_i	the random effect mean of log(traveling time) of a smolt group released in day i
ϕ_i	the random standard deviation of log(traveling time) of a smolt group released in day i
δ_i	the mean of random effects mean of log(traveling time) of smolts groups released in day i
ψ_0, ψ_1, ψ_2	the intercept and regression coefficients of environmental covariates of δ_i
π	the standard deviation of random means of log(traveling time) of smolt groups
γ_i	the mean of random standard deviations of log(traveling time) of smolt groups released in day i
$\omega_0, \omega_1, \omega_2$	the intercept and regression coefficients of environmental covariates of log(γ_i)
ρ	the standard deviation of random standard deviations
U	the size of the total smolt run
p_j	the probability that a smolt passes the trapping site in day j
u_j	the number of unmarked smolts passing the trapping site in day j
σ	the dispersion parameter of a beta-binomial distribution
ξ	the between-day standard deviation of catchability

is a graphical presentation of a statistical model that facilitates the understanding of the model structure. In a DAG, constants are denoted by rectangles and random variables by ovals. Dependencies between quantities are expressed by arrows: if parameter A follows a distribution with parameter B, there is a solid arrow that points from B to A. If parameter A is a function of parameter B, there is a broken arrow pointing from B to A. Frames or "plates" around a set of parameters are used to represent repetitive parts of the model. More detailed descriptions of DAGs in the context of fisheries science are given by, for example, Meyer and Millar (1999) and Wyatt (2002).

From a Bayesian point of view, the model specification is not yet complete. The idea of Bayesian modeling is to construct a full probability distribution for all quantities in the model, including both data and parameters. Equation 1 already defines the conditional distributions of the data given the parameters. A full probability model is completed by assigning prior probability distributions (priors) for the model parameters, in this case, to the catchability (q) and the total number of unmarked smolts (U). The prior should represent the uncertainty, in the form of probability statements, about the parameter values before obtaining any data. In this regard, the Bayesian approach to inference is very different from the frequentist one. In particular, the frequentist approach does not allow us to make probability statements about parameter values. The prior distributions can be based on previous measurements of the population size and catchability, physical

properties of the area occupied by the population, properties of the sampling design, etc. Thus the prior distribution should always depend on the context. With the notation $U \sim D()$, $q \sim D()$, we express that prior distributions are assigned to these parameters.

Sometimes it may be justified to ignore even strong prior information to see what the value of the data is alone. According to Raftery (1988), a vague prior distribution for the population size in a binomial experiment would be proportional to $1/U$. A vague prior for the catchability is a uniform distribution between 0 and 1.

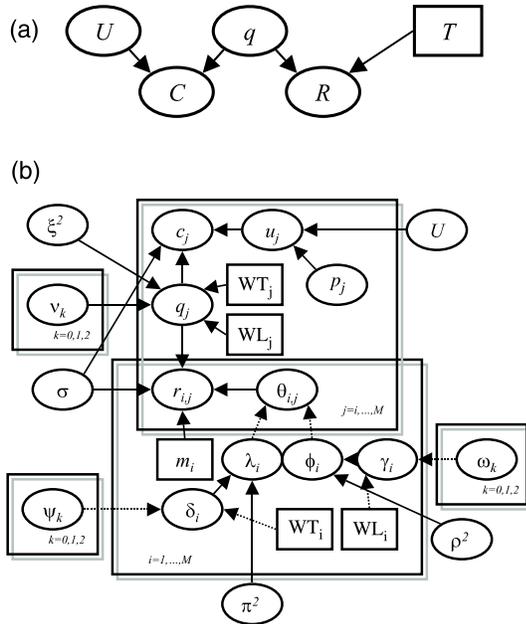
Model M_{SD}

Here we present a Bayesian version of the model introduced by Schwarz and Dempson (1994). In addition to assumptions $i-v$, Schwarz and Dempson (1994) assumed that smolts move independently and that the catchability of smolts remains constant within each day. However, they allowed the catchability to vary between days. The basic idea of their model to allow for variable catchability is to perform Petersen estimations separately for each day. This requires that the movement of each release group be modeled to assess the probability of a marked smolt passing the trap in day j . The distribution for the daily catches is then

$$(2) \quad c_j | u_j, q_j \sim \text{Bin}(u_j, q_j)$$

$$r_{i,j} | q_j, \theta_{i,j}, m_i \sim \text{Bin}(m_i, q_j \theta_{i,j})$$

Fig. 1. Directed acyclic graphs (DAG) for (a) model M_P and (b) model M_S . The DAG for model M_{SD} is similar to that for M_S , but it does not contain parameter σ . Model M_P assumes constant catchability over time and independent behavior of individuals, model M_{SD} assumes temporally varying catchability and independent behavior, and model M_S assumes temporally varying catchability and schooling behavior.



where $\theta_{i,j}$ is the probability that a smolt released on day i will pass the trap on day j . Thus, probabilities $\theta_{i,1}, \dots, \theta_{i,M}$ describe the movement of the group of smolts released on day i . Following the idea of Schwarz and Dempson (1994), the movement of a release group is modeled by a log-normal distribution from which the probabilities $\theta_{i,j}$ are calculated as

$$(3) \quad \theta_{i,j} = \Phi\left(\frac{\log(j-i+0.5) - \lambda_i}{\phi_i}\right) - I_{i,j} \Phi\left(\frac{\log(j-i-0.5) - \lambda_i}{\phi_i}\right)$$

where $I_{i,j} = 1$ if $j > i$ and 0 otherwise, λ_i is the mean of $\log(\text{traveling time})$ of smolts released on day i , ϕ_i is the standard deviation of the $\log(\text{traveling time})$ of smolt group released on day i , and Φ denotes the cumulative density function of the standard normal distribution.

Schwarz and Dempson (1994) assumed that the catchabilities (q_j) were independent, i.e., learning, for example, about the catchability in day $j = 5$ contains no information about the catchability in other days ($q_j, j \neq 5$). Similar assumptions of independence were also made about movement parameters (λ_i, ϕ_i). If such a model seems reasonable, independent prior distributions should be assigned to each catchability and movement parameter.

Our approach is to assume that the daily catchabilities are only conditionally independent, that is, we assume that daily catchabilities vary between days according to a distribution. The parameters of this distribution are not known, but the

data are used to learn about the parameters. Observing data from days $j = 2, \dots, M$, for example, makes it possible to learn about the between-day mean and variance of the catchability. The information can be used to draw inferences about the catchability in day 1 even without using the data observed in that day. This kind of information transfer can be formally built into the model by assuming that daily catchabilities form an independent sample from a distribution of catchabilities, which then has an unknown mean and variance. Modeling parameters of the data by another set of parameters (which are often called hyperparameters) is referred to as hierarchical modeling. Advantages and properties of hierarchical modeling in stock assessment are presented in more detail by Wyatt (2002).

Here we assume that the logit-transformed catchabilities ($\log(q_j/(1 - q_j))$) form an independent sample from the Normal distribution with unknown mean (η_j) and variance (ξ^2):

$$(4) \quad \log(q_j/(1 - q_j)) | \eta_j, \xi^2 \sim N(\eta_j, \xi^2)$$

$$\eta_j = v_0 + v_1 WT_j + v_2 WL_j$$

$$v_0 \sim D(), v_1 \sim D(), v_2 \sim D(), \xi^2 \sim D()$$

The mean is assumed to be a function of environmental covariates with regression coefficients v_0, v_1 , and v_2 . Here, the considered environmental covariates are water temperature (WT_j) and water level or water discharge (WL_j). Hierarchical modeling is useful also when modeling the movement of release groups. It should be reasonable to assume that the mean traveling time (e^{λ_i}) from the release site to the trapping site is not equal for all release groups. However, it is also plausible to think that learning about the mean traveling time from a subset of days would provide us with information about the mean traveling time in the remaining days. A similar reasoning also holds for the standard deviation of the $\log(\text{traveling time})$ (ϕ_i). These ideas can be formally modeled in the same way as the catchability:

$$(5) \quad \log(\phi_i) | \gamma_i, \rho^2 \sim N(\gamma_i, \rho^2)$$

$$\gamma_i = \omega_0 + \omega_1 WT_i + \omega_2 WL_i$$

$$\omega_0 \sim D(), \omega_1 \sim D(), \omega_2 \sim D(), \rho^2 \sim D()$$

$$(6) \quad \lambda_i | \delta_i, \pi^2 \sim N(\delta_i, \pi^2)$$

$$\delta_i = \psi_0 + \psi_1 WT_i + \psi_2 WL_i$$

$$\psi_0 \sim D(), \psi_1 \sim D(), \psi_2 \sim D(), \pi^2 \sim D()$$

Now we have a flexible model for the movement of each release group. Environmental covariates are allowed to influence the expected values of movement parameters, but also the possibility of unexplained random variation is taken into account by measuring the between-day variation by variances ρ^2 and π^2 .

To make the assessment of the prior distributions of daily run sizes (u_j) easier, we construct the prior in two phases. First, a prior distribution is assigned to the total size of the population (U) that passes the trapping site during the M days of trapping. Then the probability (p_j) that a smolt from this population would pass the sampling site in day j should be assessed. Obviously, it is necessary that $\sum_{j=1}^M p_j = 1$.

This condition is satisfied by assigning a Dirichlet prior for

the vector of probabilities. Given that there are U smolts that distribute to M days according to the probabilities (p_1, \dots, p_M) , the daily run sizes (u_1, \dots, u_M) are multinomially distributed:

$$(7) \quad (u_1, \dots, u_M) | U, (p_1, \dots, p_M) \sim \text{Multin}(U, (p_1, \dots, p_M))$$

$$(p_1, \dots, p_M) | (a_1, \dots, a_M) \sim \text{Dirichlet}((a_1, \dots, a_M))$$

$$U \sim D()$$

where (a_1, \dots, a_M) is a vector of constants that must be given by the user to represent prior beliefs about the run curve. The expectation of p_j is $a_j / \sum_{j=1}^M a_j$ and the variance increases as $\sum_{j=1}^M a_j$ decreases. The vector (a_1, \dots, a_M) can also be interpreted to represent a prior experiment with $\sum_{j=1}^M a_j$ individuals from which a_j individuals passed the trapping site in day j .

Equations 2–7 now define the full probability model for the mark–recapture data and model parameters. The model has more parameters than there are data points. However, the structural assumptions made about the dependencies between parameters makes it possible to obtain information about parameter values from data.

Model M_S

In model M_{SD} , the assumption of independently moving smolts gave rise to the assumption that the catches $(c_j, r_{i,j})$ of smolts would be binomially distributed given the movement parameters, catchability, and population size (eq. 2). However, when smolts migrate in schools, they clearly are not behaving independently. Because of this, binomial distribution may be too tightly concentrated to properly describe the behavior of the catches. It is more appropriate to use a distribution that is overdispersed with respect to the binomial distribution, because when smolts move in groups, it is more likely to observe higher or lower catches than predicted by a binomial distribution (Fig. 2). Our choice is to substitute the binomial distribution by one of its overdispersed alternatives, the beta-binomial distribution (Gelman et al. 1995). Thus, to modify the model M_{SD} to model M_S , which allows for overdispersion in catches, we substitute eq. 2 by the specification

$$(8) \quad c_j | u_j, q_j, \sigma \sim \text{Beta-bin}(u_j, q_j, \sigma)$$

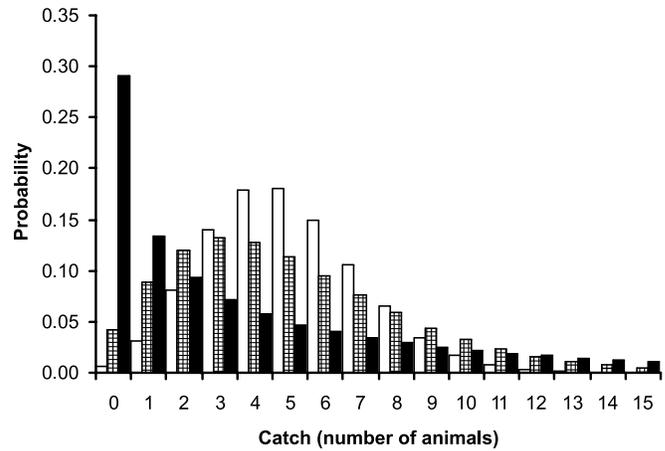
$$r_{i,j} | m_i, q_j, \theta_{i,j}, \sigma_r \sim \text{Beta-bin}(m_i, q_j \theta_{i,j}, \sigma_r),$$

$$\sigma_r = (\sigma + 1) \frac{(1 - q_j \theta_{i,j})}{\theta_{i,j}(1 - q_j)} - 1$$

where σ is the dispersion parameter, assumed to be equal over the whole trapping period and equal for all smolt groups. The role of σ is to adjust the dispersion of the distribution of the catches. If σ is close to 0, there is very much overdispersion, and when σ approaches infinity, the limiting distribution is binomial (Fig. 2). We use a beta-binomial density of the form

$$(9) \quad p(r | q, \sigma, u) = \frac{\Gamma(u + 1)}{\Gamma(r + 1)\Gamma(u - r + 1)}$$

Fig. 2. Probability distributions of recaptures in three situations where the number of released animals (u) is 100 and the catchability (q) is 0.05. Independent behavior corresponds to binomial distribution (open bars), and the effect of schooling behavior is represented by beta-binomial distributions with dispersion parameters $\sigma = 10$ (solid bars) and $\sigma = 70$ (hatched bars).



$$\times \frac{\Gamma(q\sigma + r)\Gamma(u + (1 - q)\sigma - r)}{\Gamma(\sigma + u)}$$

$$\times \frac{\Gamma(\sigma)}{\Gamma(\sigma q)\Gamma(\sigma(1 - q))}$$

where Γ denotes the Gamma function. After a positive-valued prior distribution is selected for σ , model M_S (eqs. 3–8) is completely defined.

Parameter estimation

In the Bayesian approach, parameter estimation is a procedure of updating the prior distribution $p(\Theta)$ of parameters Θ , which describes the uncertainty about the parameter values prior to seeing the data, to the posterior distribution $p(\Theta | X)$, which describes the uncertainty about the parameter values after seeing the data. This is accomplished by an application of Bayes’ theorem, which combines the information contained in the data via the likelihood function $p(X | \Theta)$ with the prior $p(\Theta)$.

$$(10) \quad p(\Theta | X) = \frac{p(X | \Theta)p(\Theta)}{\int p(X | \Theta)p(\Theta)d\Theta}$$

$$\propto p(X | \Theta)p(\Theta)$$

The formula of the posterior distribution is often so complex that analytical calculations are impossible in practice. However, samples from the posterior distribution can usually be obtained by using Markov chain Monte Carlo (MCMC) simulation (Gilks et al. 1995). After obtaining a very large sample from the posterior distribution, the histogram of samples is used as an approximation.

WinBUGS (Spiegelhalter et al. 1995) is a software package that makes the implementation of MCMC simulation easy. WinBUGS requires the model specification in a form of conditional distributions written in WinBUGS language. The use of WinBUGS and MCMC in the context of fisheries

science have been discussed in more detail by Meyer and Millar (1999) and Millar and Meyer (2000).

Examples

To compare our approach with earlier methods and to illustrate the effects of different assumptions on the resulting posterior distributions, we analyzed two data sets as examples of model fitting. We reanalyzed the data provided by Schwarz and Dempson (1994) describing an Atlantic salmon smolt population in the Conne River, Newfoundland, Canada. Our second source of data is the trapping of Atlantic salmon smolts in the River Tornionjoki in northern Scandinavia.

We fitted four models to both data sets. Models M_P , M_{SD} , and M_S were fitted as they appear in the previous section. In addition, we fitted a restricted version of M_S that did not utilize any environmental covariates ($v_1 = v_2 = \omega_1 = \omega_2 = \psi_1 = \psi_2 = 0$). This model is denoted by M_S^r .

For the analyses, we assigned vague priors for the model parameters. To obtain a uniform prior density for catchabilities q_j , the prior distributions of the coefficients v_0 , v_1 , and v_2 of the regression model (eq. 4) were set to be $N(0,0.5)$ and the inverse of the random variance ξ^2 was assigned a Gamma(1,1) prior density. Diffuse prior distributions were assigned to the other hyperparameters of the models. The prior density of the size of the total smolt run U was assumed to be proportional to $1/U$ in the range between 1 and 5 000 000 smolts for both rivers. WinBUGS 1.3 MCMC software (Spiegelhalter et al. 1995) was used to draw large samples from the posterior distributions of model parameters (WinBUGS code is available from authors upon request). MCMC simulation was carried out until Monte Carlo (MC) errors of all parameters were less than 5% of the posterior standard deviation. MC error is the standard error of the mean of the MCMC samples (Gilks et al. 1995), and it can be made arbitrarily small by increasing the number of samples from the posterior distribution.

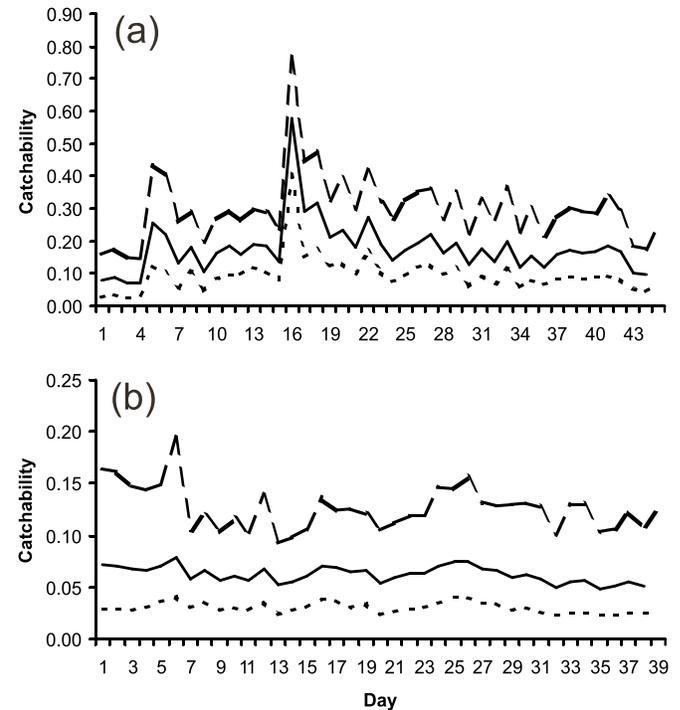
Conne River

The Conne River is 193 km long with a drainage area of 602 km² (Dempson and Stansbury 1991). Salmon smolts were caught in 1987 by two counting fences and were marked with streamer-tags at the upper trap to be recaptured at the lower trap. The study area, study design, and trapping methodology have been described in detail by Dempson and Stansbury (1991) and Schwarz and Dempson (1994).

The random variation in movement parameters between release groups was lower in model M_S than in model M_{SD} : the posterior means of ρ^2 and π^2 were reduced from 0.20 and 0.14 (M_{SD}), respectively, to 0.18 and 0.10 (M_S). The posterior mean of between-day variation in the catchability (ξ^2) was also reduced from 0.78 (M_{SD}) to 0.28 (M_S). This suggests that when overdispersion of catches is not allowed, the model explains the extra variation in catches by random variation in the movement parameters and by between-day variation in the catchability.

According to the model M_S , the data suggest that there are associations between environmental covariates and model parameters: the catchability was positively associated with

Fig. 3. Trajectories of 2.5% (dotted line), 50% (solid line), and 97.5% (broken line) percentiles of the posterior distributions of the catchability (q) in (a) the Conne River and (b) the River Tornionjoki from model M_S . Model M_S assumes temporally varying catchability and schooling behavior.

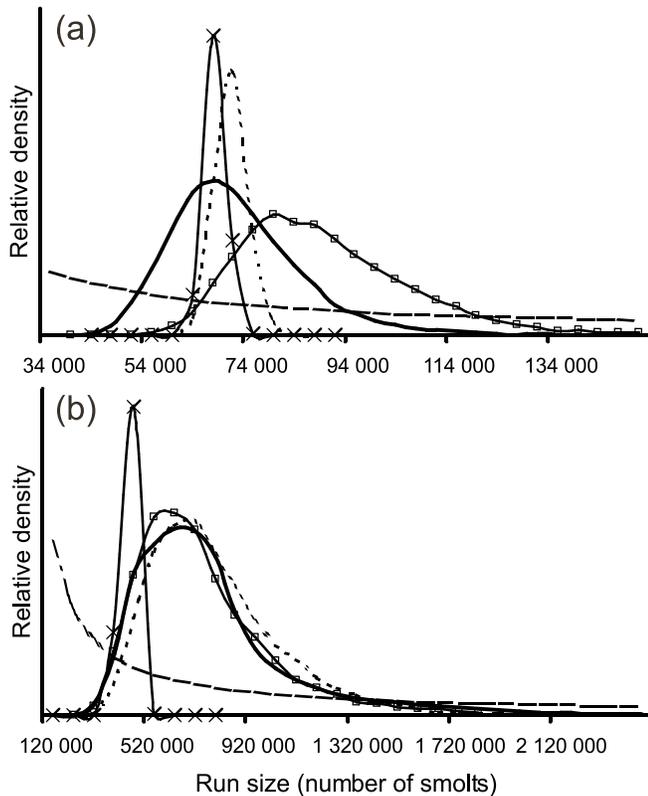


water discharge ($P(v_1 > 0) \approx 1.00$) and water temperature ($P(v_2 > 0) \approx 1.00$). The mean of the traveling time distribution was not very clearly related to the discharge ($P(\psi_1 > 0) \approx 0.48$) but was negatively associated with the water temperature ($P(\psi_2 < 0) \approx 0.99$). The standard deviations of the traveling time distributions were not clearly related to environmental covariates ($P(\omega_1 > 0) \approx 0.75$, $P(\omega_2 > 0) \approx 0.70$).

Including environmental covariates seemed to reduce the between-day random variation in the model parameters and also the amount of overdispersion. The clearest reduction (from 0.19 in model M_S^r to 0.10 in model M_S) took place in the posterior mean of π^2 , which describes the random variation in mean traveling times between release groups. Correspondingly, the posterior mean of ξ^2 was reduced from 0.37 to 0.28. The amount of overdispersion also decreased when environmental covariates were used. This can be seen from the posterior means of σ from models M_S (22.12) and M_S^r (11.84) of which model M_S^r does not use environmental covariates. According to model M_S , the posterior median of the catchability varies from 0.1 to 0.6 because of random variation and environmental covariates (Fig. 3a).

The models M_{SD} , M_S , and M_S^r produced substantially different posterior distributions for the size of the total smolt run (Fig. 4a). From these, model M_{SD} produced the most concentrated posterior distribution. The Bayesian Petersen model (M_P) produced an even more concentrated posterior distribution than model M_{SD} (Table 2). Although frequentist confidence intervals and Bayesian posterior probability intervals are conceptually very different, their comparison is

Fig. 4. Posterior distributions of the total run size in (a) the Conne River 1987 and (b) the River Tornionjoki 2001 from the models M_S (solid line), M_{SD} (dotted line), M_S^E (solid line with open squares), and M_P (solid line with crosses). Broken line represents the prior distribution. Densities have different scales for the sake of illustration. Model M_P assumes constant catchability over time and independent behavior of individuals, model M_{SD} assumes temporally varying catchability and independent behavior, and model M_S assumes temporally varying catchability and schooling behavior. Model M_S^E is extracted from model M_S by excluding the use of environmental covariates.



nevertheless interesting. The Bayesian version of the model developed by Schwarz and Dempson (1994) yielded a narrower interval than the original maximum likelihood model. There is also the difference that the original analysis of Schwarz and Dempson (1994) used the Petersen method for the first and for the last part of the run, whereas the Bayesian version (M_{SD}) used the same model for the whole data set.

The choice of the model seems to play a major role in the inference about the smolt run in the Conne River in 1987. Because there is firm evidence that smolts form schools during their migration and because we believe that environmental conditions can affect the behavior of smolts and the trapping success, we consider model M_S to be the most plausible from among the models presented here for the Conne River smolt trapping.

In addition, model M_S provided some information about the behavior of smolts: when water temperature rose, marked smolts tended to speed up their migration. They were also easier to catch when the water was warm and the discharge was high. However, these associations may not be causal, because there may be latent factors affecting such observed

phenomena. The use of environmental covariates reduced the amount of overdispersion, and thus the coefficient of variation (CV) of the posterior of the total smolt run was reduced by about 10% from model M_S^E to model M_S .

River Tornionjoki

The River Tornionjoki, which flows into the northern end of the Baltic Sea, and its headwaters form a 500 km long border between northern Finland and Sweden. It is the largest, with a drainage area of approximately 40 000 km², and most productive of the Baltic salmon rivers. The annual mean discharge is about 380 m³·s⁻¹, and during the spring flood (May – early July), when smolts migrate out from the river, the discharge is commonly 1000–2000 m³·s⁻¹ at the trapping site near the river mouth.

In the River Tornionjoki, only a single large trap was used because of logistical problems. Usually the smolt trap was emptied once a day, but during the peak run, this was done more frequently. Daily, smolts were marked by streamer-tags and were immediately transported upstream to a release site. The smolt trapping data (Table 3) from the summer of 2001 is clearly more sparse than the data used by Schwarz and Dempson (1994).

According to the results from model M_S , environmental covariates and model parameters had some associations. The mean traveling time was clearly negatively related to water temperature ($P(\psi_2 < 0) \approx 1$) and positively related to water level ($P(\psi_1 > 0) \approx 0.98$). The other model parameters were not that clearly associated with environmental covariates ($P(v_1 > 0) \approx 0.69$, $P(v_2 > 0) \approx 0.36$, $P(\omega_1 > 0) \approx 0.21$, and $P(\omega_2 > 0) \approx 0.21$). Catchability did not seem to vary very much during the trapping period (Fig. 3b). Model M_S yielded a posterior mode at 650 000 smolts and a standard deviation of 363 000. The posterior distributions from models M_{SD} and M_S^E were very close to that obtained from model M_S . However, their standard deviations were slightly smaller, apparently because of the heavier tail of the posterior distribution obtained from model M_S (Fig. 4b).

Again, from a biological perspective, we consider model M_S to be the most plausible of these four alternatives. However, in the case of the River Tornionjoki in 2001, the selection between models M_S , M_S^E , and M_{SD} does not substantially change the inferences that can be made about the size of the smolt run. In contrast to these, model M_P yields posterior mode at 418 000 smolts and a standard deviation of 22 700.

Discussion

Properties of the models

Using the idea of hierarchical modeling removes the problem of small sample size often faced in the frequentist framework. For example, Schwarz and Dempson (1994) did not include the first and the last days of the smolt trapping period in their detailed analysis because of sparse data. They also assumed that the daily catchabilities were independent and that movement parameters of each release group of smolts are independent of the movement parameters of the other release groups. Our approach utilizes the hierarchical structure in model parameters, which makes it possible to apply the model over the entire trapping period, with days borrowing information from each other. This is a general feature of hi-

Table 2. Run size estimates for the Conne River smolt population in 1987 produced by different models together with the maximum likelihood (ML) estimates provided by Schwarz and Dempson (1994).

Bayesian models	Mean	Mode	SD	2.5%	97.5%	CV
M^r_S	88 700	78 000	18 000	63 000	130 000	0.20
M_S	70 500	67 000	12 800	50 400	101 000	0.18
M_{SD}	69 500	69 000	3 000	63 700	75 800	0.04
M_P	66 500	66 500	1 930	62 900	70 500	0.03
ML models		MLE	SE	95% confidence interval		
Schwarz and Dempson		69 609	3 565	62 500 – 76 740		
Petersen		67 250	2 159	62 942 – 71 578		

Note: CV, coefficient of variation; SD, standard deviation; SE, standard error.

erarchical Bayes models, known as “shrinkage” (O’Hagan 1994): parameter estimates from days with sparse data are pulled towards the common mean. As a consequence, there will be no need to judge afterwards which parameter estimates are to be used in the calculations or to use interpolation to find “better” estimates.

Uncertainty included in the posterior distribution of population size is heavily dependent on assumptions made about the behavior of animals. Salmon smolts in natural conditions are typically not independent because of their tendency to form schools during migration. Hence, methods that assume independent behavior appear far too optimistic about the precision of the estimation procedure. Our models M_S and M^r_S take into account this additional uncertainty by allowing for overdispersion in recapture data. They also take into account other possible latent factors affecting catchability by allowing for random variation in the daily catchabilities.

As shown by the example from the Conne River, allowing for overdispersion may also have an impact on point estimates of the population size. This is likely to happen when catchability is low and the amount of overdispersion is high. By allowing for overdispersion, we allow the probability that large schools of animals pass the trapping without getting caught to increase. If overdispersion gets support from the observed data, the mode of the posterior distribution of the population size will support larger population sizes than in the case of independent behavior. However, assumptions about the temporal variation in catchability also play a role in this comparison, because the posterior distribution of the population size is sensitive to daily variation in catchability during the days with high catches of unmarked animals.

As demonstrated in methodological literature (e.g., O’Hagan 1994; Gelman et al. 1995) and also here, the Bayesian framework allows for explicit incorporation of prior knowledge. In our examples, there may be substantial prior knowledge about behavior and movement of the smolts, size and distribution of the smolt population, and possible effects of environmental factors on sampling or smolt migration.

One more key point in using the Bayesian framework is that the end product of the analysis is a probability distribution of the population size, which is useful when making management decisions under rigorous assessment of uncertainty (McAllister and Kirkwood 1998; Wade 2000).

Model selection

Our view is that the model selection for mark–recapture data should be based primarily on the plausibility of a model. That is, one should make sure that the assumptions of the

model correspond, as well as possible, to substantive biological knowledge about the animal behavior and about the properties of the study design. Formal model selection procedures are useful only when comparing models that are equally plausible from a biological perspective. Formal methods of model selection and model averaging, like the ones proposed by King and Brooks (2001), would be useful when comparing different structural assumptions, for example, whether to use a probit-link function instead of a logit-link one in the regression equation of daily catchability.

The adequacy of the selected model can be assessed by comparing the posterior predictive distributions of the model with the observed data (Gelman et al. 1995). In the case of mark–recapture data, the interpretation of such model-checking results is not straightforward: most of the recaptures are zeros, which are easily predicted by almost any model. Because of the large number of zeros, most of the residuals are also very close to zero, making their interpretation very difficult. For these reasons, we have not included model-checking procedures in this work.

Violations in model assumptions

All mark–recapture models have basic assumptions that should be filled in the real world to achieve some credibility for the analysis. Our model M_S assumes that there is no mark loss or mortality of marked fish. To some extent, these assumptions can be empirically tested by monitoring marked fish in captivity.

Another important assumption made in all mark–recapture models is that marked individuals should have catchability equal to that of unmarked individuals. In the case of aggregating species, marked and unmarked individuals should also show similar aggregation patterns. However, marked individuals are allowed to move at different speeds than unmarked individuals, because only the schooling behavior of fish when passing the trap matters in the estimation of the population size. Violation of the assumption of equal catchability has different consequences depending on whether the marked individuals exhibit trap shyness or trap happiness.

Consequences of violation of model assumptions are basically similar in both the Bayesian and the frequentist frameworks. In the context of mark–recapture of smolts, for example, Dempson and Stansbury (1991) have treated the subject. If there existed knowledge about violation of the model assumptions, the Bayesian framework would allow flexible ways to incorporate quantitative correction of these sources of errors. For instance, one could introduce a parameter representing the difference in the catchability of marked

Table 3. The data from the smolt trapping experiment in the River Tornionjoki, 2001.

Date	Recoveries by number of days following release											c	WT, °C	WL, 0.1 m		
	m	1	2	3	4	7	13	15	17	20	21					
28 May	79				2	1				1				83	6.21	10.00
29 May	26													27	5.96	10.00
30 May	9								1					9	6.48	9.60
31 May	77	1	1		1									83	7.70	8.70
1 June	136	29								1				143	9.00	7.90
2 June	60	3												227	10.40	6.90
3 June	182	9												355	11.23	6.30
4 June	138	4												146	11.52	5.60
5 June	169	11	1											176	11.07	5.00
6 June	33													60	10.74	4.90
7 June	41	9												78	11.81	5.20
8 June	73													285	12.14	5.30
9 June	79	1												169	12.64	5.80
10 June	242	9												708	13.27	5.90
11 June	251	24	1											815	12.98	6.50
12 June	286	7												3 810	12.53	8.00
13 June	152													6 847	12.74	10.40
14 June	393	8												2 212	12.90	11.90
15 June	205													1 345	13.67	13.00
16 June	223	3												413	14.09	13.70
17 June	218	3												324	14.66	13.80
18 June	418	17												571	15.27	13.40
19 June	464	56	1											642	15.41	13.00
20 June	485	36	1											583	15.75	12.80
21 June	177	27												2 061	16.19	12.60
22 June	189	19	1											1 405	16.33	12.05
23 June	137	9												631	17.34	11.10
24 June	0													163	18.18	10.60
25 June	160	15												241	18.91	9.20
26 June	0													255	19.50	8.20
27 June	66													221	20.03	7.50
28 June	0													129	19.92	6.90
29 June	0													56	19.94	6.20
30 June	44													52	19.86	5.70
1 July	20													22	19.88	5.05
2 July	0													7	19.58	4.90
3 July	0													7	18.81	4.45
4 July	0													2	18.75	4.15
5 July	0													10	19.31	4.10
Total	5232													25 373		

314 Streamer-tagged smolts recaptured

Note: Columns with no recaptures are omitted to save space. *m*, number of released smolts; *c*, number of unmarked smolts captured; WT, water temperature; WL, water level; na, not available; no entry, 0.

and unmarked animals and express the knowledge about the difference in the form of a prior probability distribution.

Model modifications and future research

There are many variations and extensions of our model that may be of interest in ecological studies. For example, the population of interest may include distinguishable subgroups of animals, such as wild and hatchery-reared individuals among salmon smolts. Because subgroups with different histories may differ, for instance, in their behavior in relation to sampling procedures, it may be of interest to model the subgroups separately. For example, the means of the catchability and (or) movement distributions could differ across groups, whereas the other model parameters could remain equal.

In models M_{SD} and M_S , we assumed that daily catchabilities vary randomly between days, given that the mean and variance are known. However, it could also be justified to assume that the random deviations in catchabilities in successive days are correlated. This idea could be implemented by using an autoregressive structure in the prior distribution. This kind of assumption may improve the precision of posterior distributions for catchabilities and the precision of the posterior distribution of the total run size.

We assumed that the amount of overdispersion does not change during the experiment. This may not be appropriate in all cases, because animals may change their tendency to aggregate during the experiment. The aggregation pattern may also vary spatially, which is important to take into account when multiple recapture sites are used.

In our examples we used vague prior distributions of model parameters. In practice, prior information about various parameters might well exist. For example, prior information about the smolt run may be obtained from a probabilistic salmon parr population model, which uses the data from sampling of parr. If a mark-recapture experiment is performed according to a constant design in successive years, it is possible to obtain prior information about the relationship between environmental factors and model parameters. For example, the basic level of catchability may vary independently between years, but the regression slopes of environmental covariates might be quite similar each year. Meta-analysis of multiple years could also be used to learn about the shape of the run curve and its relationship with environmental factors like water temperature as a trigger of the smolt run. Hierarchical Bayesian meta-analysis of this kind could also be extended to cover mark-recapture studies in several distinct populations of an animal species. All of these diverse ways to incorporate prior information in the analysis will eventually result in reduced posterior uncertainty about the population size, provided that the prior information is not in strong disagreement with the information contained in the observed data.

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References

- Allen, K. 1944. Studies on the biology of the early stages of the salmon (*Salmo salar*). 4. The smolt migration in the Thurso River in 1938. *J. Anim. Ecol.* **13**: 63–85.
- Bakhtanskiy, E., Nesterov, V., and Neklyodov, M. 1988. Development of schooling behaviour in juvenile Atlantic salmon, *Salmo salar*, during seaward migration. *J. Ichthyol.* **28**: 91–101.
- Burgner, R. 1991. Life history of sockeye salmon. In *Pacific salmon life histories*. Edited by C. Groot and L. Margolis. The University of British Columbia Press, Vancouver, B.C.
- Castledine, B. 1981. A Bayesian analysis of multiple-recapture sampling for a closed population. *Biometrika*, **67**: 197–210.
- Dempson, J., and Stansbury, D. 1991. Using partial counting fences and a two-sample stratified design for mark-recapture estimation of an Atlantic salmon smolt population. *N. Am. J. Fish. Manag.* **11**: 27–37.
- Fängstam, H., Berglund, I., Sjöberg, M., and Lundqvist, H. 1993. Effects of size and early sexual maturity on downstream migration during smolting in Baltic salmon (*Salmo salar*). *J. Fish Biol.* **43**: 517–529.
- Gazey, W., and Staley, M. 1986. Population estimation from mark-recapture experiments using a sequential Bayes algorithm. *Ecology*, **67**: 941–951.
- Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 1995. *Bayesian data analysis*. Chapman & Hall, London.
- George, E., and Robert, C. 1992. Capture-recapture estimation via Gibbs sampling. *Biometrika*, **79**: 677–683.
- Gilks, W., Richardson, S., and Spiegelhalter, D. 1995. Introducing Markov chain Monte Carlo. In *Markov chain Monte Carlo in practice*. Edited by W. Gilks, S. Richardson, and D. Spiegelhalter. Chapman & Hall, London.
- Hansen, L., and Jonsson, B. 1985. Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the River Imsa, Norway. *Aquaculture*, **45**: 237–248.
- Heard, W. 1991. Life history of pink salmon. In *Pacific salmon life histories*. Edited by C. Groot and L. Margolis. The University of British Columbia Press, Vancouver, B.C.
- Hesthagen, T., and Garnas, E. 1986. Migration of Atlantic salmon smolts in River Orkla of central Norway in relation to management of a hydroelectric station. *N. Am. J. Fish. Manag.* **6**: 376–382.
- Hvidsten, N., Jensen, A., Vivås, H., Bakke, Ø., and Heggberget, T. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nord. J. Freshw. Res.* **70**: 38–48.
- Kalleberg, H. 1958. Observations in stream tank of territoriality and competition in juvenile salmon (*Salmo salar* and *Salmo trutta* L.). *Rep. Inst. Freshw. Res Drottningholm*, **39**: 55–98.
- King, R., and Brooks, S. 2001. On the Bayesian analysis of population size. *Biometrika*, **88**: 317–336.
- McAllister, M., and Kirkwood, G. 1998. Bayesian stock assessment: a review and example application using the logistic model. *ICES J. Mar. Sci.* **55**: 1031–1060.
- Meyer, R., and Millar, R. 1999. BUGS in Bayesian stock assessments. *Can. J. Fish. Aquat. Sci.* **56**: 1078–1086.

- Millar, R., and Meyer, R. 2000. Bayesian state-space modeling of age-structured data: fitting the model is just the beginning. *Can. J. Fish. Aquat. Sci.* **57**: 43–50.
- O'Hagan, A. 1994. Bayesian inference. *In* Kendall's advanced theory of statistics. Vol. 2B. Edward Arnold, Suffolk, U.K.
- Österdahl, L. 1969. The smolt run of a small Swedish river. *In* Salmon and trout in streams. *Edited by* T. Northcote and H. MacMillan. Lectures in Fisheries, the University of British Columbia Press, Vancouver, B.C.
- Otis, D., Burnham, K., White, G., and Anderson, D. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* No. 63.
- Raftery, A. 1988. Inference for the binomial N parameter: a hierarchical Bayes approach. *Biometrika*, **75**: 223–228.
- Salo, E. 1991. Life history of chum salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. The University of British Columbia Press, Vancouver, B.C.
- Schwarz, C., and Dempson, J. 1994. Mark-recapture estimation of a salmon smolt population. *Biometrics*, **50**: 98–108.
- Schwarz, C., and Seber, G. 1999. Estimating animal abundance: review III. *Stat. Sci.* **14**: 427–456.
- Seber, G.A.F. 1982. Estimation of animal abundance and related parameters. Griffin, London.
- Spiegelhalter, D., Thomas, A., and Best, N. 1995. WinBUGS version 1.3 user manual. MRC Biostatistics Unit, Cambridge, U.K.
- Thedinga, J., Murphy, M., Johnson, S., Lorenz, J., and Koski, K. 1994. Determination of salmonid smolt yield with rotary-screw traps in the Situk River, Alaska, to predict effects of glacial flooding. *N. Am. J. Fish. Manag.* **14**: 837–851.
- Wade, P. 2000. Bayesian methods in conservation biology. *Conserv. Biol.* **14**: 1308–1316.
- Wyatt, R. 2002. Estimating riverine fish population size from single- and multiple-pass removal sampling using a hierarchical model. *Can. J. Fish. Aquat. Sci.* **59**: 695–706.