

Bayesian removal estimation of a population size under unequal catchability

Samu Mäntyniemi, Atso Romakkaniemi, and Elja Arjas

Abstract: We introduce a Bayesian probability model for the estimation of the size of an animal population from removal data. The model is based on the assumption that in the removal sampling, catchability may vary between individuals, which appears to be necessary for a realistic description of many biological populations. Heterogeneous catchability among individuals leads to a situation where the mean catchability in the population gradually decreases as the number of removals increases. Under this assumption, the model can be fitted to any removal data, i.e., there are no limitations regarding the total catch, the number of removals, or the decline of the catch. Using a published data set from removal experiments of a known population size, the model is shown to be able to estimate the population size appropriately in all cases considered. It is also shown that regardless of the statistical approach, a model that assumes equal catchability of individuals generally leads to an underestimation of the population. The example indicates that if there is only vague prior information about the variation of catchability among individuals, a very high number of successive removals may be needed to correctly estimate the population size.

Résumé : Nous utilisons un modèle de probabilité bayésien pour estimer la taille d'une population animale à partir de données de retrait. Le modèle se base sur la présupposition que, dans un échantillonnage par retraits, la capturabilité peut varier d'un individu à un autre, ce qui semble nécessaire pour décrire de façon réaliste de nombreuses populations biologiques. Une capturabilité individuelle hétérogène engendre une situation dans laquelle la capturabilité moyenne de la population décroît graduellement à mesure que le nombre de retraits augmente. Avec cette présupposition, le modèle s'ajuste à n'importe quelle série de données de retrait; il n'y a donc pas de limites en ce qui a trait à la capture totale, au nombre de retraits ou au déclin de la récolte. L'utilisation de données de retrait publiées obtenues sur une population de taille connue montre que le modèle est capable d'estimer la taille de la population de façon adéquate dans tous les cas étudiés. De plus, indépendamment de l'approche statistique utilisée, un modèle qui présuppose une capturabilité individuelle uniforme sous-estime la population. L'exemple montre que, s'il n'existe que des informations préalables vagues sur la capturabilité individuelle, il faudra peut-être un nombre très élevé de retraits successifs pour pouvoir estimer correctement la taille de la population.

[Traduit par la Rédaction]

Introduction

In addition to mark–recapture, removal sampling is commonly used for the estimation of animal population size (Otis et al. 1978; Bohlin et al. 1990; Hammill and Smith 1990). In removal sampling, individuals are removed from the population in successive trials without replacement. Statistical analysis of removal data has traditionally been based on the assumption of equally catchable individuals in the population (Schwarz and Seber 1999). Early methods based on this assumption are not able to deal with nondeclining catches in successive trials (Moran 1951; Zippin 1956; Bohlin et al. 1989). However, this restriction is to some extent relaxed by the method of Carle and Strub (1978).

Most of the statistical methods for removal data are developed in the frequentist framework. The output of the analysis comes then in a form of a value of an estimator and its estimated standard error, the latter describing the variability of the values of the estimator in hypothetical repetitions of the removal sampling. Effectively, these methods provide formal inference about future data under a hypothesis (Pierce 1973). However, usually the goal is the opposite, i.e., to make inferences about particular hypotheses of interest based on the data that we have actually observed. In addition, there may also be relevant background information, which should be properly incorporated into the analysis. The Bayesian approach to statistical inference provides systematic methods for reaching such goals (O'Hagan 1994).

Wyatt (2002) introduced a Bayesian model for removal data, assuming equal catchability of individuals. He also adopted a hierarchical approach to modeling that allows one to gather information about catchabilities and population densities from different sampling sites. In general, this results in an improved precision of the site-specific population estimates.

Electrofishing is widely used as a method for producing removal data. The method is commonly used to estimate the size of an individual fish population, but it has also been applied to assess fish species assemblages and stream inverte-

Received 9 March 2004. Accepted 6 November 2004.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 15 March 2005.
J18018

S. Mäntyniemi¹ and E. Arjas. Department of Mathematics and Statistics, University of Helsinki, P.O. Box 68, FIN-00014 Helsinki, Finland.

A. Romakkaniemi. Finnish Game and Fisheries Research Institute, Tutkijantie 2 A, FIN-90570 Oulu, Finland.

¹Corresponding author (e-mail: shm@rni.helsinki.fi).

brate populations (Hickley 1990; Pusey et al. 1998; Taylor et al. 2001). When electrofishing equipment is used to remove individuals from a fish population, sampling is often found to be size selective (e.g., Borgström and Skaala 1993; Anderson 1995; Dolan and Miranda 2003). Selectivity means that the catchabilities of different individuals are generally not equal. Unequal true catchabilities tend to bias methods based on equal catchabilities downwards and underestimate the true population size (Zippin 1956). Electrofishing experiments with a known population size have revealed that such underestimation occurs in practice when methods assuming equal catchability are applied (Mahon 1980; Bohlin and Cowx 1990; Riley et al. 1993). In most such cases, the removed fraction of the remaining population declines in successive removals, indicating that the catchability declines during the experiment. This has been suggested to arise from unequal but constant catchabilities of individuals (Bohlin and Cowx 1990) or from a change of the equal catchability during the experiment (Libosvářský 1990) or a combination of both. Whatever the reason for the phenomenon may be, it invalidates the use of simple models assuming equal catchability.

Various attempts to formulate statistical models for the case of unequal catchability have been made in the past. A proposition of Schnute (1983) was to assume that there are two catchabilities, one for the first removal and another for later removals. Schnute (1983) also proposed a three-parameter function for the decline of the catchability, and a two-parameter function has been suggested by Scruton and Gibson (1995). In contrast, Otis et al. (1978) and Chao and Chang (1996) discussed a general model where the catchability is assumed to be randomly distributed in the population.

In this paper, we present a Bayesian model for removal data, which is based on the assumption of randomly distributed individual catchabilities in the population. By using a published removal data set of a known population size, we demonstrate that the model provides plausible estimates of the population size, whereas a special case of this model (assuming equal catchability) underestimates the true population size. This work can be seen as an extension of the Bayesian removal model introduced by Wyatt (2002).

Materials and methods

Model structure

We consider a population of an unknown size N_0 and attempt to make inferences about N_0 using removal sampling. We assume that the size N_0 of the population does not change during the experiment (i.e., there is no immigration, emigration, reproduction, or mortality). Let us then assume that an individual member ($k = 1, \dots, N_0$) of the population can be characterized by a catchability parameter p_k , which is considered as an independent random draw from a (prior) probability density function $f(p_k | \mu, \sigma)$ with population-specific hyperparameters, mean μ , and standard deviation σ . Now, conditionally on the catchability p_k , let z_k be a Bernoulli-distributed indicator variable that gets value 1 if individual k is captured in the first removal and value 0 otherwise. Then the probability of obtaining z_k given p_k is $p_k^{z_k} (1 - p_k)^{1 - z_k}$. A straightforward computation leads to the following simple

expression for the conditional distribution of z_k given μ and σ :

$$(1) \quad p(z_k | \mu, \sigma) = \int_0^1 p_k^{z_k} (1 - p_k)^{1 - z_k} f(p_k | \mu, \sigma) dp_k \\ = \mu^{z_k} (1 - \mu)^{1 - z_k}$$

Now, all z_k values are assumed to be conditionally independent given the common hyperparameter μ . This reflects the idea that individuals respond independently to the removal. Thus, the number (x_1) of individuals captured in the first removal is binomially distributed given the number of individuals N_0 and the mean catchability μ :

$$(2) \quad x_1 = \sum_{k=1}^{N_0} z_k | N_0, \mu \sim \text{Bin}(N_0, \mu)$$

After the first removal, $N_0 - x_1 = N_1$ individuals still remain in the population. The distribution of catchabilities in the remaining population has also changed from the initial distribution $f(p_k | \mu, \sigma)$ because typically, individuals with the highest catchabilities have been removed. This can be seen by using the results of eq. 1 and employing standard probability calculus (Bayes' formula):

$$(3) \quad f(p_k | z_k = 0, \mu, \sigma) = \frac{P(z_k = 0 | p_k) f(p_k | \mu, \sigma)}{P(z_k = 0 | \mu, \sigma)} \\ = \frac{p_k^0 (1 - p_k)^1 f(p_k | \mu, \sigma)}{1 - \mu} \\ \propto f(p_k | \mu, \sigma) (1 - p_k)$$

Therefore, the probability density of catchability of individuals in the population that remain after the first removal is proportional to $f(p_k | \mu, \sigma) (1 - p_k)$. More generally, the distribution of catchability before the j th removal is proportional to $f(p_k | \mu, \sigma) (1 - p_k)^{j-1}$. It is easy to see from eqs. 1 and 2 that only the expectation of the distribution of catchability is needed to model the number of individuals captured in each removal. By assuming that an individual catchability is initially distributed according to a Beta(α, β) (prior) distribution, it is ensured that, conditionally on parameters α and β , the expectation of the distribution of the catchability p_k for each removal j is always available in a closed form expression. This can be seen from the density function of the Beta(α, β) distribution:

$$(4) \quad f(p_k | \alpha, \beta) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} p_k^{\alpha-1} (1 - p_k)^{\beta-1}$$

for which the mean is $\alpha/(\alpha + \beta)$. Multiplying density (eq. 4) by $(1 - p_k)^{j-1}$ yields a Beta($\alpha, \beta + j - 1$) density function for which the mean is $q_j = \alpha/(\alpha + \beta + j - 1)$.

Unfortunately, the parameterization of a beta distribution in terms of its mean μ and standard deviation σ turns out to be difficult: they cannot be assessed independently because the largest possible value of σ depends on the mean ($\sigma < \sqrt{\mu(1 - \mu)}$). Therefore, we choose a different parameterization by introducing a new parameter $\eta = (\mu(1 - \mu) - \sigma^2)/\sigma^2 = \alpha + \beta$, which then serves as a measure of relative

variation. This parameterization also simplifies the parameter transformation

$$(5) \quad \alpha = \mu\eta$$

$$\beta = (1 - \mu)\eta$$

Thus, by assuming that the catchabilities are a sample from a beta distribution, and knowing that only the mean catchability q_j in the remaining population after $j - 1$ removals is needed to model the successive catches, we can write the model in the form

$$(6) \quad x_j | N_j, q_j \sim \text{Bin}(N_j, q_j)$$

$$N_j = N_{j-1} - x_{j-1}$$

$$q_j = \mu \frac{\eta}{\eta + j - 1}, \quad j = 1, \dots, k$$

$$x_0 = 0$$

It can be seen from eq. 6 that the rate at which the mean catchability declines between consecutive removals depends on the variation of the catchability in the initial population (Fig. 1). A similar kind of change in the distribution of catchability has also been described by Bohlin and Cowx (1990).

From eq. 6, one can see that in this model, there are three parameters ($\Theta = (N_0, \mu, \eta)$) to be assessed. In the Bayesian approach, prior beliefs about these parameters are expressed in terms of prior probability distributions. Assigning a unit probability to a high value of η , say 20 000, yields a model that effectively is equal to the model proposed by Wyatt (2002).

Parameter estimation

In the Bayesian approach, parameter estimation is the process of updating the prior probability distributions of parameters of interest to posterior probability distributions by using observed data. According to the Bayes' theorem, the joint posterior probability density of model parameters ($\Theta = (N_0, \mu, \eta)$), given the observed data ($X = (x_j)$), is obtained as

$$(7) \quad p(\Theta | X) = \frac{P(X|\Theta)p(\Theta)}{\int P(X|\Theta)p(\Theta) d\Theta} \propto p(X|\Theta)p(\Theta)$$

Here, $p(\Theta)$ denotes the prior density of model parameters, and the term $p(X|\Theta)$ denotes the probability density of data given the parameters (the likelihood of data), which we have actually completely defined in eq. 6. In fact, Bayes' theorem was already in use in eq. 3.

Because the integral in the denominator of eq. 7 is analytically intractable, numerical integration methods are needed. Our computational approach is to use the Markov chain Monte Carlo simulation (Gilks et al. 1995) to draw samples from the posterior distributions of model parameters by implementing the simulation in WinBUGS software (Spiegelhalter et al. 2003). The use of this software in the context of fisheries science has been demonstrated and discussed, for example, by Meyer and Millar (1999) and Millar and Meyer (2000), and especially in the context of removal sampling by Wyatt (2003).

Example

To demonstrate the performance of our model, we apply it to a data set with a known population size. To illustrate the influence of different model assumptions, we also fit a restricted version of the model, assuming equal catchability of individuals. The model allowing unequal catchability is denoted by M_u and the model allowing only equal catchability by M_e .

Bohlin and Sundström (1977) stocked 150 juvenile brown trout (*Salmo trutta*) to three closed stream sections and conducted up to 20 removals at each sampling site i (Table 1). A detailed description of the study design is provided in their article. The large number of removals gives us an opportunity to study how increasing the number of removals affects the posterior distributions of the population size $N_{0,i}$ and parameters μ_i and η_i . Because Bohlin and Sundström (1977) did not mention the possibility that there could be mortality and (or) emigration, we simply assume that no mortality and (or) emigration took place. Total catches of each site after 20 removals were 141, 144, and 146, indicating that mortality and (or) emigration during the experiment were very low, if not zero.

We assign the following prior distributions for the parameters used in model M_u :

$$(8) \quad \log(N_{0,i}) \sim \text{Unif}(0,10)$$

$$\log(\eta_i) \sim \text{Unif}(0,10)$$

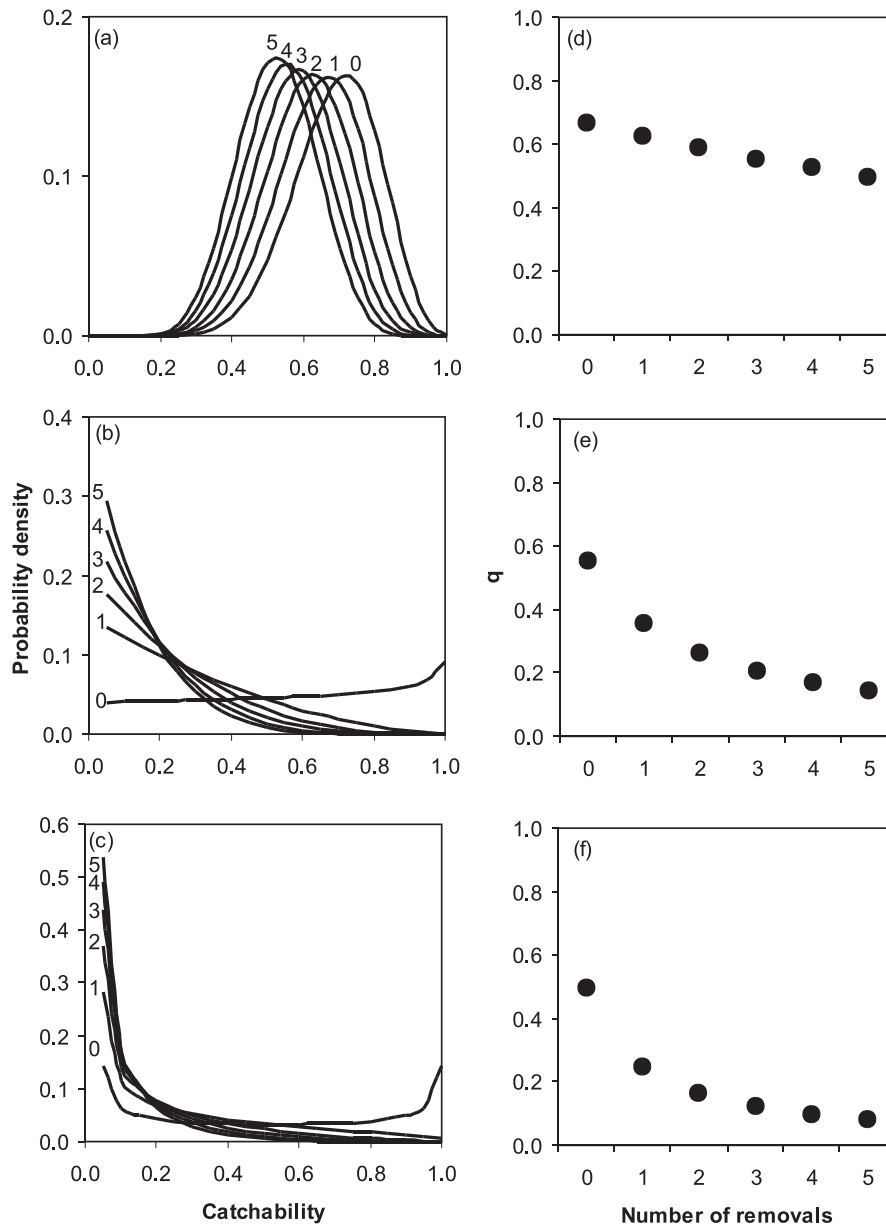
$$\mu_i \sim \text{Beta}(1.1,1.1)$$

These priors are vague, effectively saying that we have little prior information about the model parameters and that we pretend not to know the true population size. Similar prior distributions are also used in model M_e , except that the value of $\log(\eta)$ is assumed to be 10, i.e., it is assumed that there is negligible variation in catchability between different individuals in the population. Thus, models M_u and M_e reflect different prior beliefs about the variation in catchability: model M_u represents the view that the catchability can be highly variable with $\log(\eta)$ being anywhere between 0 and 10, whereas model M_e reflects the idea that we are sure that the catchability is equal (unit probability on $\log(\eta) = 10$).

Posterior distributions for the model parameters were calculated by using both models five times with the observations from the first 4, 8, 12, 16, and 20 removals, respectively. To see how well models M_u and M_e can estimate the differences in the population sizes between sampling sites, we calculated posterior distributions for all pairwise differences. WinBUGS code used for the implementation of the Markov chain Monte Carlo simulation can be found in Appendix A.

According to model M_u , the posterior distributions for each sampling site obtained by using four removals favored population sizes smaller than the true value (Fig. 2). A similar pattern can also be seen after eight removals, but now, higher probabilities are assigned to values close to the true population size. After 12 or more removals, the locations of posterior distributions did not change markedly, only the precision of the distribution increased as well as the probability assigned to the true population size. All posterior distributions of pairwise differences in abundance between

Fig. 1. (a–c) Evolution of the distribution of catchability in the remaining population after different numbers of removals (the number of removals is marked next to the corresponding probability density) and (d–f) the decline of the mean catchability (q) as a function of the number of removals taken. In all cases, the initial distribution of catchability is a beta distribution. The parameter values $\mu = 0.66$ and $\eta = 15$ are used in Figs. 1a and 1d, $\mu = 0.55$ and $\eta = 1.8$ in Figs. 1b and 1e, and $\mu = 0.5$ and $\eta = 1$ in Figs. 1c and 1f. Parameter μ is the mean catchability in the initial population (no removals taken) and η describes the relative precision of the distribution.



sampling sites also included the true value in their 95% posterior probability intervals (Fig. 3).

The reason for the apparent underestimation of the population size when using a small number of removals and model M_u can be seen from the posterior distributions of $\log(\eta)$ and μ . After four removals, the posterior distributions of $\log(\eta)$ were quite close to their prior distributions, which gave relatively high probabilities to large values of $\log(\eta)$, thus favoring only a small decline in mean catchability between consecutive removals. In other words, data from four removals contained so little information that the prior distribution of $\log(\eta)$ still had a dominant influence on the posterior distributions. As the number of removals used in the

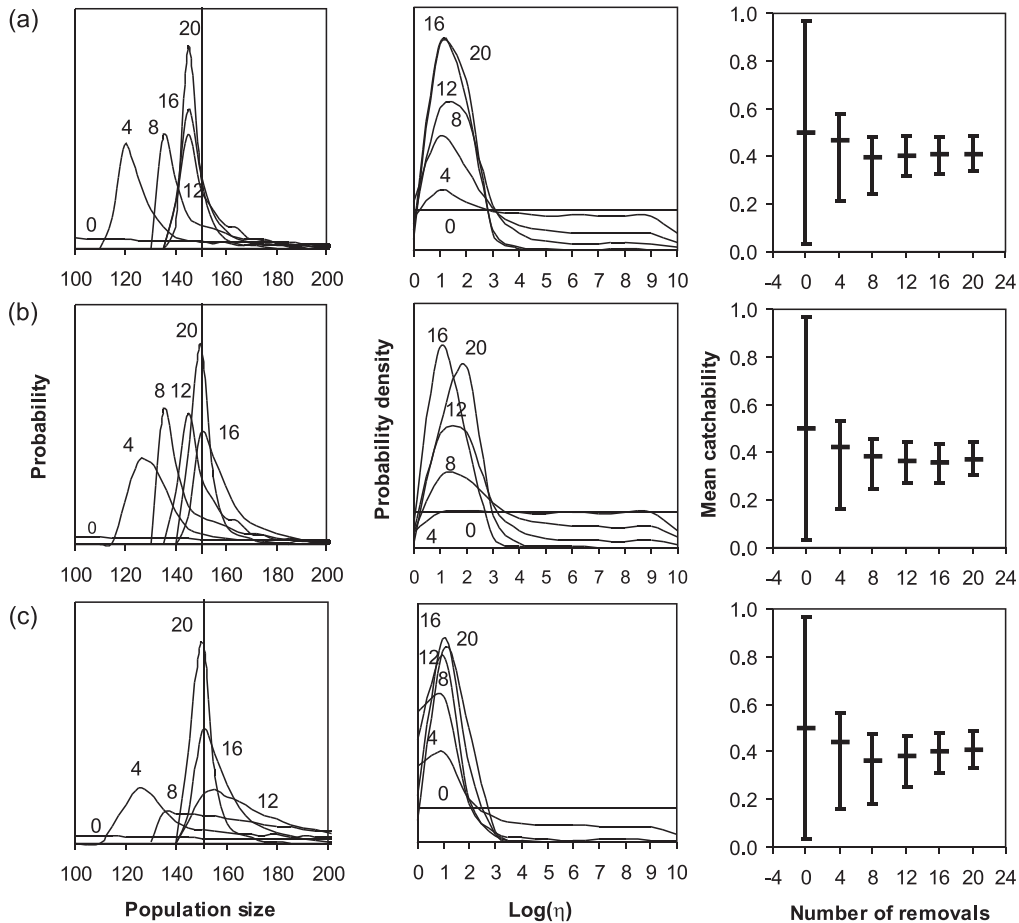
analysis increased, the influence of the prior distribution decreased.

Because the inference about population size appears to be quite sensitive to the choice of the prior distribution for $\log(\eta)$ when only a few removals are conducted, we wanted to study how much information about $\log(\eta)$ was contained in the complete data. For this purpose, we calculated the posterior distribution of $\log(\eta)$ not only by using the observed data from all 20 removals but also by using the information of the true population size (simply by treating the true population size as an observation instead of having prior distribution for N). As would be expected, these posterior distributions (Table 2) are quite similar to the posterior dis-

Table 1. Removal data from the experiment of Bohlin and Sundström (1977) (modified from their article).

Site	Successive catches																			
a	62	26	17	8	9	6	4	1	2	1	1	1	1	1	0	1	0	0	1	0
b	57	28	22	8	3	10	2	3	5	2	0	1	2	0	2	1	0	0	0	0
c	66	25	13	12	9	5	4	3	2	2	2	1	1	0	1	0	1	0	0	0

Fig. 2. Posterior distributions of population size N and dispersion parameter $\log(\eta)$ and quantiles (2.5%, 50%, and 97.5%) of the posterior distributions of the mean catchability μ in three sampling sites (a (site a), b (site b), and c (site c)) calculated by a model assuming unequal catchabilities of individuals. The number of removals used to calculate each posterior distribution of N and $\log(\eta)$ is indicated next to the corresponding probability distribution. Probabilities and probability densities are presented in relative scale.



tributions calculated using only the 20 removals (Fig. 2) but are more precise.

Results obtained by model M_e show that the precision of the posterior distributions is very high, but the estimation of the true population size is not successful even when using 20 removals because the posterior distributions are systematically concentrated on values that are too low (Fig. 4). With all 20 removals, model M_e produces very tight posterior distributions between sampling sites (Fig. 3). But even then, two out of three 95% probability intervals failed to include the true value.

The results obtained by Bohlin and Sundström (1977) are not directly comparable with ours because of their fundamentally different approach to statistical inference. However, their frequentist approach assumes constant catchability among individuals, as, in effect, does our model M_e . From

the 95% confidence intervals based on two, three, and four removals, only one included the true population size (site b, three removals) and the remaining eight intervals suggested values lower than the true population size (Bohlin and Sundström 1977).

Discussion

Properties of the model

A Bayesian model for the estimation of population size from removal data and assuming equal catchability was recently developed by Wyatt (2002). Here, we have taken a step further towards more realistic model assumptions and developed a Bayesian model (M_u) that allows heterogeneity in catchability in the population. Our example demonstrated how model M_u can provide reasonable estimates of the true

Fig. 3. Quantiles (2.5%, 50%, and 97.5%) of the posterior distributions of the difference between population sizes in three sampling sites (a, b, and c) calculated by a model assuming (a) unequal capture probabilities and (b) equal capture probabilities. The true value for the difference between all sites is zero.

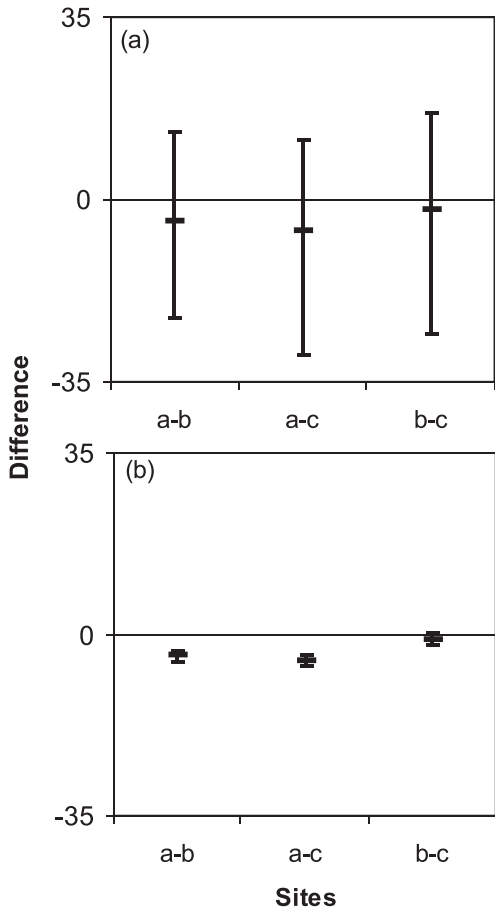


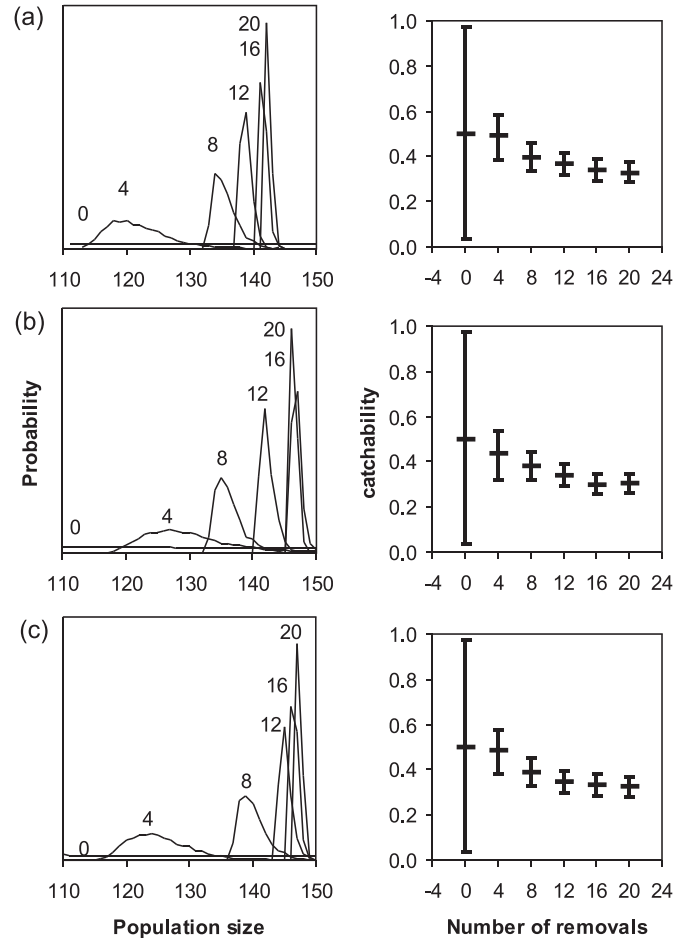
Table 2. Statistics of posterior distributions of dispersion parameter $\log(\eta)$ obtained by using 20 removals (Table 1) and also the known population size of 150 from three sampling sites as observed data.

Site	$\log(\eta)$				
	Mean	SD	2.5%	50%	97.5%
a	1.124	0.2645	0.6475	1.108	1.685
b	1.702	0.3491	1.094	1.682	2.484
c	1.561	0.3491	0.9223	1.543	2.301

population size in cases in which the models assuming equal catchability fail.

The Bayesian model M_u and its special case M_e are suitable for a probabilistic assessment of the uncertainty about the population size when based on observed removal data and background information. They can also tolerate all kinds of catch vectors, that is, catches in the successive removals do not need to decline, as in many earlier removal methods. The number of removals conducted can vary from one to any attainable number, and also, the catch per removal can vary from zero to thousands, without violating the mathematical structure of the model or ruining the numerical com-

Fig. 4. Posterior distributions of the population size N (left panels) and posterior quantiles (2.5%, 50%, and 97.5%) of the catchability μ (right panels) in three sampling sites (a (site a), b (site b), and c (site c)) calculated by a model assuming equal catchability of individuals. The number of removals used to calculate each posterior distribution of N is indicated next to the corresponding probability distribution. Posterior probabilities are presented in relative scale.



putations needed in the estimation. The model proposed by Wyatt (2002) has these same advantages over corresponding frequentist removal methods but does not allow for unequal catchability.

It has been emphasized in many previous papers about removal sampling that models assuming unequal catchabilities can be used only if a large number of removals are conducted (e.g., Schnute 1983; Wyatt 2002, 2003). This idea probably has its roots in the theory of maximum likelihood estimation, where identifiability of parameters is an important issue, whereas this is less central in Bayesian inference. According to the Bayesian approach, the assumption about the catchability should be based on expert knowledge about the behavior of animals and on knowledge about the sampling method, assessed before obtaining removal data and before knowing the number of removals.

If there is uncertainty about the equality of individual catchabilities, this uncertainty should be brought into the Bayesian analysis in the form of prior probabilities. Ob-

served data will then update the beliefs about the equality of the catchability. The prior that we gave for $\log(\eta)$ in the model M_u serves as an example of a high degree of prior uncertainty in this respect, i.e., all parameter values from highly variable individual catchabilities to very equal catchabilities were regarded as being possible. It was partly due to this high prior uncertainty that we pretended to have in our example that many data (many removals) were needed to produce firm posterior beliefs. However, in the case of electrofishing in rivers, for example, there is firm evidence in the literature that the catchabilities are not equal, and thus, unless some case-specific background information justifies an assumption of equal catchabilities, very low prior probabilities should be assigned to high values of $\log(\eta)$.

Even though model M_e is a special case of model M_u , there might be situations in which regarding model M_e as an alternative to model M_u might have some particular value. For example, if catchabilities really were practically equal, model M_u would waste the information contained in the data and use it for dragging the posterior distribution of $\log(\eta)$ to support values close to 10. In such a case, more precise and accurate estimates would be obtained by using model M_e . However, it is difficult to know exactly which model to use. Such an uncertainty can be accounted for by adopting an approach termed Bayesian model averaging (Hoeting et al. 1999). In Bayesian model averaging, all alternative models are assigned prior probabilities, and observed data are used to come up with posterior probabilities for all models. Posterior distribution from Bayesian model averaging is a weighted mixture of posterior distributions from individual models in which posterior probabilities of the models are used as weights. Bayesian model averaging can be implemented within the Markov chain Monte Carlo simulation by using the method of Carlin and Chib (1995), for example.

Violating the assumptions of model M_u

Although derived from a specific assumption, model M_u can also be expected to provide reasonable estimates in other cases in which the mean catchability declines between removals. The mean catchability will decline under the following circumstances. (i) Each individual has its own catchability, which remains constant between removals. For example, individuals with different physical properties and (or) habitats keep their positions and do not learn how to avoid removal. This is the underlying assumption of model M_u . (ii) All individuals in the population have equal catchability, which decreases between removals. For example, individuals not caught in one removal learn how to avoid being caught in the next removal. (iii) Each individual has its own catchability, which decreases between removals. For example, individuals have different habitats or physical properties and they learn how to avoid removal. (iv) Each individual has its own mean catchability around which the catchability varies randomly between removals. For example, individuals with different physical properties change their habitats between removals. (v) Each individual has its own mean catchability around which the catchability varies randomly between removals and the mean catchability decreases between removals. For example, individuals with dif-

ferent physical properties change their habitats between removals and learn how to avoid removal.

We have included above the possibility that individuals may learn to avoid removal (or otherwise change their behavior with similar effect on catchability) because several authors have suggested that this might be the case in electrofishing (Cross and Stott 1975; Bohlin and Sundström 1977; Libosvářský 1990). It should be noted that if all individuals in the population have the same mean catchability around which their catchabilities vary between removals, then model M_e can be used because the mean catchability does not decline between removals.

Our model is based on the assumption that individuals behave independently during the removal process. This assumption is violated if individuals are schooling. Schooling behavior increases the probabilities of high and low catches compared with the binomial distribution, thus invalidating the use of models using binomial distribution (also see Bohlin et al. (1989) and Wang and Loneragan (1996)). Catches of schooling species can be modeled more realistically by, for example, using the beta-binomial distribution (Mäntyniemi and Romakkaniemi 2002). Another common social interaction is territorial behavior. This form of dependence between individuals is unlikely to harmfully influence the performance of our model, unless it leads to an increase in the mean catchability during the removal process.

A further assumption in our model, made for mathematical convenience, was that the catchability is beta-distributed in the initial population. The beta distribution is very flexible and can represent various uni- and bi-modal shapes. Bimodal distributions that can be presented by a beta distribution have modes at 0 and 1. Other types of multimodality cannot be well captured by a beta distribution.

If the catchability is multimodally distributed in the initial population, model M_u may not be able to describe the decline in the mean catchability well enough. To avoid multimodal distributions of catchability, the population to be estimated should be divided to subgroups that are believed to have unimodally distributed catchabilities. In the case of electrofishing in streams, fish in the same sampling site should be classified according to their species and separable size groups. Because larger individuals should be generally easier to catch by electrofishing than smaller ones (Dolan and Miranda 2003), the mean catchabilities could be ordered according to size groups within a sampling site.

The performance of model M_u under various violations of its assumptions could be studied further by using simulated data. Simulated data could also be used to explore the effects of increasing or decreasing the number of removals under different conditions and to conduct cost efficiency analysis for choosing the best sampling design. Such an analysis could also compare removal methods with alternative ways of measuring the population size, like mark-recapture. However, only methods based on similar assumptions should be compared. Our removal method presented could be compared with a Bayesian mark-recapture model assuming heterogeneous catchability and having comparable prior distributions, but so far, such methods have not been developed. However, a frequentist literature for unequal catchability within mark-recapture design does exist (e.g., Lee and Chao 1994; Anderson 1995; Coull and Agresti 1999).

Lessons to learn from the illustration

Our example illustrates a few important points regarding the use of removal methods with electrofishing. First, it gives further support to the widely shared view that the assumption of equal catchability tends to lead to underestimation of the true population size. It also shows that when the assumption of equal catchability is not tenable, using methods based on such an assumption may not provide reliable indices of abundance. Instead, results obtained by model M_e give the impression that the population sizes in different sampling sites are different with a very high probability. The variation of population density between sampling sites will therefore become overestimated if the assumption of equal catchability does not hold and model M_e is nevertheless used. Also, the temporal changes in population density and species composition will be overestimated in such a situation. These results are not in line with many previous suggestions, according to which estimates from models like M_e could be used to analyze the spatial and temporal changes in the relative population density (e.g., Bohlin et al. 1989; Bohlin 1990; Bohlin and Cowx 1990). These ideas are based on the assumption that the bias would be a constant fraction of the true population size.

However, overestimation of spatial and temporal variation might be reduced to some extent by using a hierarchical model for the site-specific abundances because hierarchical modeling tends to pull the site-specific estimates toward their mean (Wyatt 2002). On the other hand, the amount of such shrinkage may not be substantial because site-specific data are likely to be quite informative when model M_e is used. These issues could be further studied by simulating data from model M_u and by producing estimates by model M_e , with and without hierarchical prior distributions for the model parameters.

A further important issue is the number of removals to be conducted at each sampling site. Electrofishing tends to be a time-consuming and laborious activity (Mitro and Zale 2000), which poses some practical limits on the possible number of removals. Although a minimum of three removals has been the standard practice in some studies (Scruton and Gibson 1995), in practice, only one to three removals are usually used (e.g., Mitro and Zale 2000; Niemelä et al. 2000; Wyatt 2002). Theoretical results from removal experiments have pointed towards the need to perform one to five removals per site (e.g., Bohlin 1990; Riley and Fausch 1992). However, these theoretical results are based on the assumption of equal catchability under which precise estimates can be achieved. Under the conditions of our example, it seems that at least eight removals might be needed when the catchability is assumed to vary between individuals and there is poor prior knowledge about parameter values. Of course, there are many factors that influence such recommended number of removals, like (i) the desired precision of the posterior distribution, (ii) the true population size (not known precisely), (iii) the true mean catchability in the initial population (not known precisely), (iv) the true variation of catchability in the initial population (not known precisely), and (v) the amount of prior uncertainty about the population size and catchability parameters.

Of these, only the desired precision of the estimate and the amount of prior uncertainty can be specified in advance,

and all others are uncertain quantities before and after collecting data. The knowledge about the uncertain parameters is expressed in the form of prior distributions. This means that prior distributions can be used to simulate multiple data sets with a large number of removals taken from the population. Analyzing such simulated data sets by using different numbers of removals can give some clue about the number of removals needed. If the mean catchability is high and the variation in catchability is low and there is much prior knowledge about all parameters, then the number of removals that are needed will be lower and vice versa.

As there are practical limitations regarding the number of removals possible in electrofishing, a parallel strategy to improve the precision of the population density estimates would be to use all feasible sources of information to reduce the prior uncertainty about the population size and catchability parameters. Within the Bayesian framework, this can be done by utilizing the idea of hierarchical modeling, which makes it possible to transfer information between, for example, different sampling sites. Wyatt (2002, 2003) has described the use of hierarchical modeling and the use of Geographic Information System data for improving the estimates of population density from electrofishing in streams. The model presented here could be extended to allow for simultaneous mark-recapture and removal estimation, which would under suitable circumstances improve the information content of data and thus reduce the number of removals needed. For example, individuals caught in the first removal could be marked and released to the population before continuing with further removals, as suggested by Scruton and Gibson (1995).

Because our example indicates that the prior knowledge about the variation in catchability between different individuals ($\log(\eta)$) has a dominant role in the resulting inference, it might be worthwhile to study whether there are parameter values that are inherent for particular species and (or) sampling circumstances. For instance, the posterior distribution of $\log(\eta)$ could serve as a prior distribution of the parameter under conditions believed to be similar to those of Bohlin and Sundström (1977). Finding such a range of commonly applicable values for different situations would then release some of the pressure for conducting unpractically high numbers of successive removals in each sampling. Conducting specially designed removal experiments of a known population size and a large number of removals using different combinations of species and sampling circumstances would provide information about realistic values of $\log(\eta)$ and also about the influential factors in each such situation. In addition to Bohlin and Sundström (1977), Mahon (1980) and Riley et al. (1993) have also published removal data sets with known true population size, which are readily available for examination of $\log(\eta)$. Posterior distributions from these kinds of studies can either be used directly as prior distributions or be used as starting points when eliciting case-specific prior information.

Acknowledgements

We wish to thank Dr. Markku Julkunen (Finnish Game and Fisheries Research Institute) for providing his help in the search of data sets with known population size. This pa-

per has been partly funded by EU project No. 99/064, "Probabilistic modelling of Baltic salmon stocks". The study was also supported by the Graduate School of Computational Biology, Bioinformatics and Biometry (ComBi) and by the Centre of Population Genetic Analyses supported by the Academy of Finland (project No. 53297).

References

- Anderson, C. 1995. Measuring and correcting for size selection in electrofishing mark-recapture experiments. *Trans. Am. Fish. Soc.* **124**: 663–676.
- Bohlin, T. 1990. Estimation of population parameters using electric fishing: aspects of the sampling design with emphasis on salmonids in streams. *In Developments in electric fishing. Edited by I. Cowx.* Fishing News Books, London, UK.
- Bohlin, T., and Cowx, I. 1990. Implications of unequal probability of capture by electric fishing on the estimation of population size. *In Developments in electric fishing. Edited by I. Cowx.* Fishing News Books, London, UK.
- Bohlin, T., and Sundström, B. 1977. Influence of unequal catchability on population estimates using the Lincoln index and the removal method applied to electro-fishing. *Oikos*, **28**: 123–129.
- Bohlin, T., Hamrin, S., Heggberget, T., Rasmussen, G., and Saltveit, S. 1989. Electrofishing — theory and practice with special emphasis on salmonids. *Hydrobiologia*, **173**: 9–43.
- Bohlin, T., Heggberget, T., and Strange, C. 1990. Electric fishing for sampling and stock assessment. *In Fishing with electricity. Edited by I. Cowx and P. Lamargue.* Fishing News Books, London, UK.
- Borgström, R., and Skaala, Ø. 1993. Size-dependent catchability of brown trout and Atlantic salmon parr by electrofishing in a low conductivity stream. *Nord. J. Freshw. Res.* **68**: 14–21.
- Carle, F., and Strub, M. 1978. A new method for estimating population size from removal data. *Biometrics*, **34**: 621–630.
- Carlin, B., and Chib, S. 1995. Bayesian model choice via Markov chain Monte Carlo. *J. R. Stat. Soc.* **57**: 473–484.
- Chao, A., and Chang, S.-H. 1996. An estimating function approach to the inference of catch-effort models. *Environ. Ecol. Stat.* **6**: 313–334.
- Coull, B., and Agresti, A. 1999. The use of mixed logit models to reflect heterogeneity in capture-recapture studies. *Biometrics*, **55**: 294–301.
- Cross, D., and Stott, B. 1975. The effect of electric fishing on the subsequent capture of fish. *J. Fish Biol.* **7**: 349–357.
- Dolan, C., and Miranda, L. 2003. Immobilization thresholds of electrofishing relative to fish size. *Trans. Am. Fish. Soc.* **132**: 969–976.
- 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 and Hall, London, UK.
- Hammill, M., and Smith, T. 1990. Application of removal sampling to estimate the density of ringed seals *Phoca hispida* in Barrow Strait, Northwest Territories. *Can. J. Fish. Aquat. Sci.* **47**: 244–250.
- Hickley, P. 1990. Electric fishing in practice. *In Fishing with electricity. Edited by I. Cowx and P. Lamargue.* Fishing News Books, London, UK.
- Hoeting, J., Madigan, D., Raftery, A., and Volinsky, C. 1999. Bayesian model averaging: a tutorial. *Stat. Sci.* **14**: 382–417.
- Lee, S.-M., and Chao, A. 1994. Estimating population size via sample coverage for closed capture-recapture models. *Biometrics*, **50**: 88–97.
- Libosvářský, J. 1990. Notes on electric fishing mainly on the probability of capture. *In Developments in electric fishing. Edited by I. Cowx.* Fishing News Books, London, UK.
- Mahon, R. 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. *Environ. Biol. Fishes*, **5**: 343–363.
- Mäntyniemi, S., and Romakkaniemi, A. 2002. Bayesian mark-recapture estimation with an application to a salmonid smolt population. *Can. J. Fish. Aquat. Sci.* **59**: 1748–1758.
- 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.
- Mitro, M., and Zale, A. 2000. Predicting fish abundance using single-pass removal sampling. *Can. J. Fish. Aquat. Sci.* **57**: 951–961.
- Moran, P. 1951. A mathematical theory of animal trapping. *Biometrics*, **38**: 307–311.
- Niemelä, E., Julkunen, M., and Erkinaro, J. 2000. Quantitative electrofishing for juvenile salmon densities: assessment of the catchability during a long-term monitoring program. *Fish. Res.* **48**: 15–22.
- O'Hagan, A. 1994. Bayesian inference. *In Kendall's advanced theory of statistics. Vol. 2B.* Edward Arnold, Suffolk, UK.
- Otis, D., Burnham, K., White, G., and Anderson, D. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* No. 63.
- Pierce, D. 1973. On some difficulties in a frequency theory of inference. *Ann. Stat.* **1**: 241–250.
- Pusey, B., Kennard, M., Arthur, J., and Arthington, A. 1998. Quantitative sampling of stream fish assemblages: single- vs. multiple-pass electrofishing. *Aust. J. Ecol.* **23**: 365–374.
- Riley, S., and Fausch, K. 1992. Underestimation of trout population size by maximum likelihood removal estimates in small streams. *N. Am. J. Fish. Manag.* **12**: 768–776.
- Riley, S., Haedrich, R., and Gibson, R. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. *J. Freshw. Ecol.* **8**: 97–101.
- Schnute, J. 1983. A new approach to estimating populations by the removal method. *Can. J. Fish. Aquat. Sci.* **40**: 2153–2169.
- Schwarz, C., and Seber, G. 1999. Estimating animal abundance: review III. *Stat. Sci.* **14**: 427–456.
- Scruton, D., and Gibson, R. 1995. Quantitative electrofishing in Newfoundland and Labrador: results of workshops to review current methods and recommend standardization of techniques. *Can. Manuscr. Rep. Fish. Aquat. Sci.* No. 2308.
- Spiegelhalter, D., Thomas, A., Best, N., and Lunn, D. 2003. WinBUGS version 1.4 user manual. MRC Biostatistics Unit, Cambridge, UK.
- Taylor, B., McIntosh, A., and Peckarsky, B. 2001. Sampling stream invertebrates using electroshocking techniques: implications for basic and applied research. *Can. J. Fish. Aquat. Sci.* **58**: 437–445.
- Wang, Y.-G., and Loneragan, N. 1996. An extravariation model for improving confidence intervals of population size estimates from removal data. *Can. J. Fish. Aquat. Sci.* **53**: 2533–2539.
- 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.
- Wyatt, R. 2003. Mapping the abundance of riverine fish populations: integrating hierarchical Bayesian models with a geographic information system (GIS). *Can. J. Fish. Aquat. Sci.* **60**: 997–1006.
- Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics*, **12**: 163–169.

Appendix A

This appendix contains the entire WinBUGS 1.4 program required to implement the example. Note that all text after the character # is comments until the end of the line.

```
model{
  for(j in 1:k){
    x[j]~dbin (q[j], n[j])
    n[j+1] < -n[j] -x[j]
    q[j] < -mu*(eta/ (eta+j-1))
  }
  n[1] < -exp(u)
  u~dunif (0, 10)
  eta < -exp(log.eta)
  log.eta~dunif (0, 10)
  #log.eta < -10 # needed only when restricting M_u to M_e
  mu~dbeta(1.1, 1.1)
}
```