Empirical Bayes estimation of the size of a closed population using photo-identification data

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ABSTRACT

Photo-ID data are broadly used for estimating animal abundance using capture-recapture models. Animals that do not possess either natural or acquired marks sufficient to allow re-identification are called unmarked, and when a substantial part of the population is composed of such individuals, the classical models described in the literature do not apply. In this paper an Empirical Bayes capture-recapture analysis for dealing with the estimation of the capture probabilities and the estimation of abundance N for populations that include unmarked individuals is presented. Using a Gibbs sampling approach, Monte Carlo estimates for the posterior distribution of N were obtained. The Empirical Bayes approach was found to improve precision in the estimation of N compared to the results obtained using other Bayesian methods. Additionally, when the population included a very large number of unmarked individuals, inferences for N obtained using the Empirical Bayes approach were definitely superior to those obtained using any of the vague beta priors tested. The methodology was applied to bowhead whale data for the 1985 and 1986 photo-ID surveys.

KEYWORDS: BOWHEAD WHALE; ABUNDANCE ESTIMATE; PHOTO-ID; EMPIRICAL BAYES; MODELLING; BERING SEA; CHUKCHI SEA; BEAUFORT SEA

INTRODUCTION

The bowhead whale, *Balaena mysticetus*, was once the target of commercial whaling (for oil and baleen) and was severely depleted by commercial whalers up to the beginning of the 20th century (Bockstoce and Burns, 1993); the Bering-Chukchi-Beaufort Seas stock[1] (sometimes referred to as the western Arctic stock) was primarily hunted between 1848 and 1914, after which such activity declined due to the reduction in availability of whales and the advent of petroleum goods (Bockstoce and Botkin, 1983). This species is listed as endangered under the US Endangered Species Act and is protected from commercial whaling by the International Whaling Commission (IWC). Limited whaling for subsistence is allowed by the IWC for native groups in Northern Alaska (USA) and the west coast of Chukotka (Russian Federation) with catch limits being set within sustainable levels determined by the IWC Scientific Committee using the simulation-tested '*Bowhead Strike Limit Algorithm*' (IWC, 2003, pp. 18-23).

Abundance and trend information for the Bering-Chukchi-Beaufort seas stock has been obtained from ice-based censuses carried out during the spring migration past Point Barrow, Alaska (Raftery *et al.*, 1995; Raftery and Zeh, 1998). George *et al.* (2004) used a method that consisted of computing abundance estimates from estimates (*N4*) of the number of whales that passed within the 4km visual range of the observation 'perch' from which the whales are counted, the estimated proportions *P4* of the whales that passed within this range and the estimated standard errors (SE) of *N4* and *P4*. Their 2001 abundance estimate was 10,470 (SE=1,351) with 95% confidence interval of 8,100-13,500. Zeh and Punt (2005) estimated that the annual rate of increase (ROI) of the Western Arctic bowhead whale population from 1978 to 2001 was 3.4% (95% CI 1.7%-5%) indicating a population in steady recovery even with the subsistence harvest.

An independent method of estimating *inter alia* abundance and trend information is the use of mark-recapture data (Hammond *et al.*, 1990). The bowhead whale is totally black, except for white pigmentation on the chin and tail in some animals. Some individuals have natural markings that make their re-identification possible through comparison of photographs taken at different times. Others, besides their natural markings, may have acquired marks (scars) as a result of wounds, attack, etc.

A study by da Silva *et al.* (2000) examined aerial photographs of the bowhead whale suitable for identification of individuals using their natural markings that have been collected in Bering, Chukchi and Beaufort Seas since 1976. Most of the photographs have been collected by LGL Ltd. (LGL), the National Marine Mammal Laboratory (NMML) and the Cascadia Research Collective (CRC). The photos are housed at LGL and NMML.

Capture-recapture methods based on photo-identification data (hereafter photo-ID data) are widely used for estimating abundance of marine mammals and other species. Instead of artificially tagging the captured individuals, the natural and acquired marks of the photographed ones are used to build the matrix of their capture histories that is used in most capture-recapture estimation processes.

Animals whose extent of marks does not allow re-identification are called *unmarked*. Those individuals are *uncatchable* in the sense that they cannot be recognised. This violates a basic assumption of most capture-recapture models which requires that every animal in the population be uniquely identifiable.

In choosing the modelling most adequate for the data in this study, a choice between closed or open capture-recapture models had to be made (e.g. Hammond, 1986).

[1] The most recent review of stock structure and movements can be found in IWC (2007; 2008a; 2008b).

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The first option requires that the time span that is considered in the analysis is small enough to prevent the occurrence of substantial demographic changes in the population. In this study closed population models are used.

Recent studies that have used mark-recapture data to estimate bowhead whale abundance (da Silva *et al.*, 2000; Koski *et al.*, 2008) have obtained results that are in accordance with those from the census data referred to above.

Solving the problem of estimating animal abundance in the presence of unmarked individuals was first attempted by Seber (1982, p.72). Working with bottlenose dolphin photo-ID data, Williams *et al.* (1993) used Seber's approach for obtaining an abundance estimate of that population. Da Silva (1999) and da Silva *et al.* (2000) developed frequentist models allowing for heterogeneity in capture probabilities. The inferences were dealt with using parametric bootstrap methods. The methodology was applied to real and simulated bowhead whale photo-ID data. Their results were in good agreement with those obtained by Raftery and Zeh (1998) and Raftery *et al.* (1995), who used bowhead whale ice-based census data. Schweder (2003) developed alternative methodology to that of da Silva (1999) and da Silva *et al.* (2000). He applied his methods to the same bowhead whale photo-ID data used by those authors and obtained bowhead whale population inferences largely in agreement with those obtained by them.

Bayesian estimation of population sizes *(N)* of demographically closed populations often depend upon the estimation of nuisance parameters such as capture probabilities at different occasions. Vague beta priors are usually assigned to those nuisance parameters in order to describe their posterior distributions. Using bowhead whale simulated data, da-Silva *et al.* (2003) observed that some choices of vague beta priors may cause substantial biases in the estimated values of *N*. For a variety of problems the pitfall of using vague priors is, according to Bernardo and Smith (1995, p.298) that 'every prior specification has *some* informative posterior or predictive implications'. One approach to deal with this problem is to estimate the hyperparameters of the prior beta distributions using an Empirical Bayes analysis.

Huggins (2002) proposed an Empirical Bayes analysis for estimating animal abundance for the case of heterogeneous capture probabilities. In this paper, an Empirical Bayes analysis for estimating the size of an animal population including unmarked individuals with capture probabilities varying according to the sampling occasions is presented. A Gibbs sampling algorithm was considered in order to obtain Monte Carlo estimates for the posterior distribution of *N* using both vague and Empirical Bayes defined priors for the nuisance parameters.

NOTATION

The photo-ID data available for capture-recapture estimation of animal abundance consists of the capture histories of the *naturally marked* individuals and some summary statistics related to the photos of an individual taken over the sampling occasions. In order to avoid biases caused by re-identification errors, only good quality photos were used in the analysis. All good quality photos of the photographed individuals were used. However, only individuals who possessed an acceptable extent of natural marks comprise what is termed the population of the '*marked individuals*'. A *capture* means that a good quality photograph of a whale was taken and, if a whale presented a non negligible extent of natural marks, it was considered *marked*. The notation below was used throughout.

N^u : the total number of unmarked whales in the population.

N^m : the total number of marked whales in the population.

$N = N^m + N^u$: the total number of whales.

X_j^m : the number of good photos of marked whales at occasion j, $j = 1, \dots, t$, where good photos are those for which the identification of the whales is possible.

X_j^u : the number of good photos of unmarked whales at occasion j.

The total number of good photos at occasion j: $X_j = X_j^m + X_j^u$.

n_j : the total number of marked whales captured at time j.

r : the number of different marked whales captured over the experiment.

ω : any subset of $\{1, \dots, t\}$.

u_ω : the number of marked whales with history ω.

$$n_j = \sum_{\omega \supset \{j\}} u_\omega \text{ and } r = \sum_{\omega} u_\omega$$

$p = (p_1, \dots, p_t)$ where p_j is the capture probability at time j.

A LIKELIHOOD BASED ON GOOD PHOTOGRAPHS

In da-Silva *et al.* (2003), the relationship between N^m and N^u due to $N = N^m + N^u$ was expressed in terms of

$$\Delta = \log\left(\frac{N^u}{N^m}\right), \tag{1}$$

which represents the log of the unknown fraction of the population sizes of unmarked to marked individuals in the population. Therefore the estimated size of the whole population was given by

$$\hat{N} = \hat{N}^m \left(1 + exp\left(\hat{\Delta}\right)\right).$$

The parameters N^m and Δ were estimated using a Bayesian procedure involving a conditional likelihood of $\theta = (\Delta, p, N^m)$ given the total number of good photos at each of the sampling occasions, $\{X_j\}$. The likelihood consists of a combination of Darroch's model (Darroch, 1958) and a binomial model as follows,

$$\begin{aligned}
&L\left(\Delta, p, N^m\right) \\
&= Pr\left(\{u_\omega\}, \{X_j^m\} \mid \{X_j\}, \Delta, p, N^m\right) \\
&= Pr\left(\{u_\omega\} \mid \{X_j^m\}, \{X_j\}, \Delta, p, N^m\right) \\
&\qquad Pr\left(\{X_j^m\} \mid \{X_j\}, \Delta, p, N^m\right) \\
&= Pr\left(\{u_\omega\} \mid p, N^m\right) Pr\left(\{X_j^m\} \mid \{X_j\}, \Delta\right) \\
&\propto \frac{N^m!}{\left(N^m - r\right)!} \prod_{j=1}^{t} p_j^{n_j} \left(1 - p_j\right)^{N^m - n_j} \\
&\qquad \times \left[\frac{1}{1 + e^\Delta}\right]^{\sum_{j=1}^{t} X_j^m} \left[\frac{e^\Delta}{1 + e^\Delta}\right]^{\sum_{j=1}^{t} X_j^u}
\end{aligned} \tag{2}$$

Notice that $Pr(\{u_\omega\} \mid p, N^m)$ accounts for the marked part of the population and is related to Darroch's model, which is completely described in terms of the set of random variables $\{u_\omega\}$ (along with the appropriate parameters p and N^m, only). Thus, the knowledge about $\{X_j\}$ and $\{X^m_j\}$ is irrelevant, justifying them to be dropped. In the expression $Pr(\{X^m_j\} \mid \{X_j\}, \Delta)$, a binomial distribution can be seen, which incorporates, through the number of good photos of unmarked individuals, the information about the unmarked part of the population. The absence of parameters p and N^m, shows that they are clearly not important in describing such a part of the model. Using vague beta priors for the capture probabilities and the adaptive rejection sampling method (ARS) by Gilks and Wild (1992) for drawing values from the full conditional posterior distribution of Δ, da-Silva *et al.* (2003) estimated N for real and simulated bowhead whale data. In that work, the full conditional posterior distributions of N and $\{p_j\}$ were standard, and could be sampled without any difficulty. An alternative way (the Gibbs sampling algorithm) to obtain Monte Carlo estimates of the posterior distribution of N is presented below.

GIBBS SAMPLING FOR ESTIMATING *N*

In this section, alternative methods to the ones proposed by da-Silva *et al.* (2003) are described for drawing samples from the joint posterior distribution of $\theta = (N^m, \{p_j\}, \Delta)$.

The Gibbs sampling is essentially a special case of the Metropolis-Hastings algorithm (Hastings, 1970; Metropolis *et al.*, 1953); which generates a Markov chain by sampling from full conditional distributions. Each iteration cycle of the Gibbs sampler gives an updated vector of the estimated values of θ. Each coordinate of is sampled conditionally to the values of the other components. For a very large number of Gibbs sampling cycles, the sampled values of θ are from the joint posterior distribution. The joint posterior is our target distribution.

Let $\theta = (\theta_1,...,\theta_k)$ be a k dimensional vector of unknowns, D a vector of observed data and $P(\theta \mid D)$ be the corresponding joint posterior distribution. Let $P(\theta_j \mid D, \theta_{-j})$ be the full conditional distribution of θ_j, and θ_{-j} denote the vector θ with θ_j removed. The following scheme illustrates the Gibbs sampling method for generating samples from $P(\theta \mid D)$,

(1) Choose starting values $\theta_1^{(0)},...,\theta_k^{(0)}$;

(2) Sample $\theta_1^{(j+1)}$ from $p\left(\theta_1 \mid \theta_2^{(j)},...,\theta_k^{(j)}, D\right)$;

(3) Sample $\theta_2^{(j+1)}$ from $p\left(\theta_2 \mid \theta_1^{(j+1)}, \theta_3^{(j)} \ldots, \theta_k^{(j)}, D\right)$;

. . .

(4) Sample $\theta_k^{(j+1)}$ from $p\left(\theta_k \mid \theta_1^{(j+1)}, \theta_2^{(j+1)} \ldots, \theta_{k-1}^{(j+1)}, D\right)$;

(5) Repeat step 2 thousands of times.

An extensive discussion of the Gibbs sampler can be found in Gelman *et al.* (1995).

Returning to the whale problem, since N is expressed as a function of Δ and N^m, its full conditional posterior distribution is estimated through the estimated values of those quantities. Expression (2) can be rewritten in terms of

$$\varphi = \frac{1}{1+e^{\Delta}}$$

Such reparameterisation allows an easy to sample full conditional posterior distribution to be described for φ. Since

$$\Delta = \log\left(\frac{1-\varphi}{\varphi}\right),$$

for each updated value of φ the corresponding updated value of Δ can be obtained.

The following prior distributions are considered:

$p_j \sim beta(a,b)$, $j=1,\ldots,t$;

$\phi \sim beta(c,d)$;

$\pi(N^m) \propto 1/N^m$, i.e. the Jeffreys' prior (see Gelman *et al.*, 1995).

The values a, b, c and d are hyperparameters are discussed later.

Considering prior independence among the parameters, the joint prior distribution is described by

$$\pi(\theta) = \pi(N^m, p, \varphi) = \pi(N^m)\pi(p)\pi(\varphi).$$

Thus, the corresponding joint posterior distribution of

$\theta = (N^m, p, \varphi)$ is

$$\pi\left(\varphi, \mathrm{p}, N^m \mid \{u_\omega\}, \{X^m_j\}, \{X_j\}\right) \propto L\left(\varphi, p, N^m\right) \pi(\varphi)\pi(p)\pi(N^m) \quad (3)$$

The Gibbs procedure for generating samples from the joint posterior distribution of

$\theta = (N^m, \{p_j\}, \phi)$

consists of drawing the θ values through the following sequence of draws:

$$\varphi \mid \{X^m_j\},\{X_j\} \sim Beta\left(\sum_{j=1}^{t} X^m_j + c; \sum_{j=1}^{t} X_j - X^m_j + d\right); \quad (4)$$

$$N^m \mid p, r \sim Negative-Binomial\left(r, 1-\prod_{j=1}^{t}\left(1-p_j\right)\right); \quad (5)$$

$$p_j \mid N^m, n_j \sim Beta\left(n_j + a, N^m - n_j + b\right). \quad (6)$$

Expressions (4) to (6) represent the full posterior distributions of ϕ, N^m and p_j, respectively. The distributions in (4) and (6) are easily obtained. Expression (5) is obtained when, in expression (3), we consider only the terms involving N^m:

$$\pi(N^m \mid p, r) \propto \frac{N^m!}{(N^m-r)!}\prod_{j=1}^{t} p_j^{n_j}(1-p_j)^{N^m-n_j} \times \frac{1}{N^m}$$

$$\propto \frac{(N^m-1)!}{(N^m-r)!}\prod_{j=1}^{t} p_j^{n_j}(1-p_j)^{N^m-n_j} \propto \frac{(N^m-1)!}{(N^m-r)!}\prod_{j=1}^{t}(1-p_j)^{N^m} = \frac{(N^m-1)!}{(N^m-r)!}\left[\prod_{j=1}^{t}(1-p_j)\right]^{N^m}$$

$$\propto \frac{(N^m-1)!(r-1)!}{((N^m-1)-(r-1))!(r-1)!}\phi^{N^m} \propto \binom{N^m-1}{r-1}\phi^{N^m}$$

$$\propto \binom{N^m-1}{r-1}(1-\phi)^r\phi^{N^m-r} = \binom{N^m-1}{r-1}\eta^r(1-\eta)^{N^m-r}$$

where $\phi = \left[\prod_{j=1}^{t}(1-p_j)\right]$ and $\eta = 1-\prod_{j=1}^{t}(1-p_j)$.

Therefore, the full conditional of N^m is Negative-binomial with parameters r and η.

The values *a, b, c* and *d* of the hyperparameters are either fixed in order to define vague priors for the $\{p_j\}$ and φ, or estimated using an Empirical Bayes approach. This is discussed below.

AN EMPIRICAL BAYES APPROACH

In da-Silva *et al.* (2003), the vague priors *beta*(0, 0), *beta*(0.5, 0.5), and *beta*(1, 1) for the capture probabilities were considered in a simulation study aiming to assess the sensitivity of the inferences for N to the choices of the beta hyperparameters (a, b).

For inferences about N, the authors concluded that beta prior (0,0) causes positive bias while beta prior (1,1) causes negative bias. Vague beta prior (0.5, 0.5) seemed to be the best choice for the bowhead whale data.

Inferences for N can possibly be improved with better choices of (a, b). In that sense consider an iterative Empirical Bayes approach which consists of describing a marginal distribution of a given random variable which is parameterised by a and b so that estimation of these two parameters is possible.

The approach used in this consisted of: (1) finding the joint distribution of $(\{n_j\} \mid N^m,a,b)$; (2) given initial guesses for a and b, obtaining a temporary estimate of N^m using a Bayesian procedure; (3) given such an estimated value of N^m, estimating a and b via maximum likelihood; (4) repeating steps (2) and (3) until convergence of the estimates of a and b; and (5) using the final estimated values of a and b, running, one more time, the Bayesian procedure in order to estimate N^m, ϕ (and then Δ) and N, using the expression $\hat{N} = \hat{N}^m\left(1+exp\left(\hat{\Delta}\right)\right)$.

FINDING THE JOINT DISTRIBUTION OF $\left(\{n_j\} \mid N^m, a, b\right)$

Consider a population with N_* individuals and a model where capture probabilities vary only due to temporal effects. For the bowhead whales, let $N_* = N^m$. Also, let p_j be the capture probability at sampling occasion j for individual i, $i = 1,..., N_*$ and $j = 1,..., t$, and let n_j be the sample size at sampling occasion j, with

$n_j \mid N_*, p_j,a,b \sim binomial\left(N_*, p_j\right)$;

$p_j \mid a,b \sim beta\left(a,b\right)$.

In order to find a distribution for n_j given N_*, a and b, i.e., $P\left(n_j \mid N_*, a, b\right)$, $P\left(n_j, p_j \mid N_*, a, b\right)$, is integrated with respect to p_j:

$$P\left(n_j \mid N_*, a, b\right) = \int_0^1 p\left(n_j, p_j \mid N_*, a, b\right) dp_j = \int_0^1 P\left(n_j,p_j \mid N_*, a, b\right) \mathrm{P}\left(p_j \mid a, b\right) dp_j$$

$$= \binom{N_*}{n_j}\frac{\Gamma(a+b)}{\Gamma(a)\Gamma(b)}\frac{\Gamma(N_*+b-n_j)\Gamma(n_j+a)}{\Gamma(N_*+a+b)}$$

$$= \binom{N_*}{n_j}\frac{B(n_j+a, N_*-n_j+b)}{B(a,b)} \tag{7}$$

The right-hand side of expression (7) describes the parametric form of a binomial-beta distribution with parameters a, b and N_* for variable n_j (see Bernardo and Smith, 1995, p.117). Let $\Psi = \left(N_*, a, b\right)$ and $L\left(\Psi\right)$ be the likelihood associated to Ψ. Note that the n_js are independent and N_* fixed, so that

$$L(\Psi) = \prod_{j=1}^{t} P(n_j \mid N_*, a, b)$$

$$= \prod_{j=1}^{t}\int_0^1 p(n_j, p_j \mid N_*, a, b)\, dp_j$$

$$= \prod_{j=1}^{t}\binom{N_*}{n_j}\frac{B(n_j+a, N_*-n_j+b)}{B(a,b)} \tag{8}$$

ITERATIVE APPROACH TO ESTIMATE *a* AND *b*

(1) Initially consider $a^{(o)} = a$ and $b^{(o)} = b$, where a and b are the parameters of a vague beta prior.

(2) Using $a^{(k-1)}$ and $b^{(k-1)}$ and the Gibbs sampling discussed earlier, obtain $\hat{N}_*^{(k)}$, for the estimated value of N_*. Here we use a point estimate for N_* represented by the average of the MCMC draws from the conditional posterior distribution N_*.

(3) Replace $\hat{N}_*^{(k)}$ in equation (8) and obtain the maximum likelihood estimates $\hat{a}^{(k)}$, and $\hat{b}^{(k)}$.

(4) For k = 1,... return to step 2 until convergence of a and b.

Below some analyses resulting from the application of the methods discussed in the previous sections to simulated data are presented.

SENSITIVITY OF THE INFERENCES FOR *N*

The sensitivity of the inferences for N to choices of the beta priors is described in this section. The same bowhead whale simulated datasets analysed by da-Silva *et al.* (2003) were used.

Da Silva *et al.* (2000) generated bowhead whale data considering a total of four sampling occasions in the simulation and two intra-year occasions (spring and summer) in 1985 and 1986. For the intra-year occasions the population was considered closed. However, inter-year additions and deletions were allowed for. The authors worked with five scenarios (cases) for varying values of total population size, capture probabilities and population size of unmarked individuals. For each of the cases the authors generated 500 four occasion capture-recapture samples, in order to make possible to evaluate bias and uncertainty in the estimated values produced by the models they proposed.

In this study, only 4 of the 5 cases in da Silva *et al.* (2000) are presented. For all the cases a fixed population size of 1,186 marked individuals was considered whereas the size of the unmarked population varied from moderate to high. Capture probabilities were set as low or high. For the simulated data, the population sizes for the years of 1985 and 1986 were fixed as 6,649 and 6,820, respectively. Such values were obtained using the most likely trajectory from the Bayesian synthesis analysis by Raftery *et al.* (1995). The value 1,186 for the population size of marked whales was derived by fixing in about 82% the fraction of the unmarked whales in the hypothetical population when the average population size is 6,734. This percentage matched the fraction of good photographs of unmarked whales to the total number of good photos. For more details about the simulated data see da Silva (1999).

For brevity consider the events: S = small capture probabilities, U = high number of unmarked individuals in the population, where the complementary event of E is $\bar{E}$. The four cases are the following: *Case* 1 = $(S, \bar{U})$, *Case* 2 = $(\bar{S}, \bar{U})$, *Case* 3 = $(\bar{S}, U)$, *Case* 4 = (S, U). Case 2 represents the most optimistic scenario where capture probabilities are high and the number of unmarked individuals is moderate. Case 4 represents the most pessimistic one, with low capture probabilities and high number of unmarked individuals.

For the Gibbs sampling approach for estimating N discussed earlier,

$$\varphi = \frac{1}{1+e^{\Delta}}, \text{ with } \varphi \sim beta\ (c,\ d)$$

was defined. It is important to evaluate whether or not inferences about N are sensitive not only to the choices of the values a and b of the beta prior for the capture probabilities, but also to choices of the values of c and d.

For each capture-recapture sample (data in this study) from a given case, the corresponding Bayesian point estimate of N^m was based on the average value (considering the quadratic loss) of 1,600 MCMC pseudo-independent draws from the full conditional posterior of N^m (see expression (5)), obtained from 20,000 MCMC such draws, having the first 4,000 ones discarded (burn-in period) and using thinning of 10 observations. The convergence of the MCMC procedure was verified by the convergence diagnosis techniques of Gelman and Rubin (1992), Heidelberger and Welch (1983) and Geweke (1992), which is available in the software CODA (*http://www.mrc-bsu.cam.ac.uk/bugs/classic/coda04/readme.shtml*).

Considering the Bayesian approach via Gibbs sampling, for each Case and their corresponding 500 capture-recapture generated samples (the data), the corresponding 500 Bayesian estimates of N^m were obtained. Some descriptive analyses were performed in order to evaluate bias and uncertainty of the inferences using the proposed methodology (see Table 1). As can be observed from Table 1, the inferences about N are sensitive to the choices of the hyperparameters a and b for the p_js, but not to the choices of the hyperparameters c and d for φ. Therefore, any choice of the beta priors (*beta*(0, 0), *beta*(1, 1) or *beta*(0.5, 0.5)) for φ works equally well, i.e. none cause any remarkable bias in the estimated values of N. In general it was noticed that the hyperparameters a=1/2 and b= 1/2 for the p_js, produced smaller biases in the estimation of N.

Considering the Empirical Bayes methodology described earlier, it can be seen from Table 2 (and also Table 1) for Cases 1 and 2, that the Empirical Bayes methodology did not improve the estimates with respect to either bias or uncertainty, compared to the Bayes estimation approach using the Gibbs sampling. For Cases 3 and 4, the Empirical Bayes approach using the estimates for (a,b) yielded small biases (Table 2, lines 3 and 4), whereas the Bayes method (via Gibbs sampling), even for the best choice of vague prior for the p^js, (a,b)= (1/2,1/2) (see second half of Table 1) had negative biases which were greater in magnitude.

ANALYSIS USING BOWHEAD WHALE DATA

The bowhead whale photo-ID data was obtained by aerial surveys off Barrow, Alaska. Such data consists of capture histories for four sampling occasions (spring 1985, summer 1985, spring 1986, and summer 1986).

Of the 1,677 records in the data set, only 229 belong to marked individuals and, of those, only 16 were captured more than once. This gives an idea of how sparse the bowhead whale data are. For more details about the bowhead whale data see da Silva *et al.* (2000). These data were processed (see Table 3) in order to obtain the data needed in models (4) to (6) among others.

Table 1

Summary statistics for estimated values of N based on 500 bowhead whale simulated samples, using the Gibbs sampling approach and different values of a and b and c and d . The events, S = small capture probabilities, U = High number of unmarked individuals in the population (where the complementary event of E is $\bar{E}$) describe the cases. Cases 1 and 2 are the ones with few while Cases 3 and 4 are the ones with high numbers of unmarked individuals.

	Parameters						
Case	a	b	c	d	Mean	Bias	SD
1 $(S,\bar{U})$	0.0	0.0	0.0	0.0	6,845	113	773
			0.5	0.5	6,843	111	772
			1.0	1.0	6,842	110	771
	0.5	0.5	0.0	0.0	6,695	-37	730
			0.5	0.5	6,693	-40	729
			1.0	1.0	6,691	-41	729
	1.0	1.0	0.0	0.0	6,552	-179	693
			0.5	0.5	6,550	-182	692
			1.0	1.0	6,548	-184	692
2 $(\bar{S},\bar{U})$	0.0	0.0	0.0	0.0	6,746	12	360
			0.5	0.5	6,745	11	360
			1.0	1.0	6,745	11	355
	0.5	0.5	0.0	0.0	6,721	-13	356
			0.5	0.5	6,720	-14	356
			1.0	1.0	6,720	-15	352
	1.0	1.0	0.0	0.0	6,697	-37	352
			0.5	0.5	6,696	-38	352
			1.0	1.0	6,695	-39	353
3 $(\bar{S},U)$	0.0	0.0	0.0	0.0	13,574	106	1,711
			0.5	0.5	13,569	101	1,711
			1.0	1.0	13,563	95	1,711
	0.5	0.5	0.0	0.0	13,276	-192	1,616
			0.5	0.5	13,270	-198	1,617
			1.0	1.0	13,264	-204	1,615
	1.0	1.0	0.0	0.0	12,995	-473	1,530
			0.5	0.5	12,989	-479	1,531
			1.0	1.0	12,981	-487	1,529
4 (S,U)	0.0	0.0	0.0	0.0	14,716	1,248	4,931
			0.5	0.5	14,702	1,234	4,922
			1.0	1.0	14,685	1,217	4,908
	0.5	0.5	0.0	0.0	13,058	-410	3,532
			0.5	0.5	13,046	-422	3,528
			1.0	1.0	13,035	-433	3,529
	1.0	1.0	0.0	0.0	11,817	-1,651	2,736
			0.5	0.5	11,808	-1,660	2,734
			1.0	1.0	11,797	-1,671	2,728

Table 2

Summary statistics (mean and bias) for the estimated values of N based on the empirical Bayes method with 500 bowhead whale 1985 and 1986 surveys simulated data from each Case (and the corresponding $\bar{a}$ and $\bar{b}$ - average values of a and b based on the 500 mentioned data). Each N estimated according to the posterior mean based on 1,600 MCMC draws and different values of a and b. The events, S = small capture probabilities, U = High number of unmarked individuals in the population (where the complementary event of E is $\bar{E}$) describe the cases. Cases 1 and 2 are the ones with few while Cases 3 and 4 are the ones with high numbers of unmarked individuals.

Case	$\bar{a}$	$\bar{b}$	Mean	Bias	SD
1- $(S,\bar{U})$	6.1	68.8	6,761	108	763
2- $(\bar{S},\bar{U})$	5.5	28.4	6,744	23	362
3- $(\bar{S},U)$	6.1	68.6	13,392	103	1,702
4- (S,U)	6.4	143.7	13,025	384	3,919

Table 3

Bowhead whale data from photo-ID surveys in the spring 1985, summer 1985, spring 1986, and summer 1986. The statistics in column 1 are the ones needed for the models in this article.

Occasions	Spring 1985	Summer 1985	Spring 1986	Summer 1986
n_j	87	56	76	26
X_j^m	166	115	126	37
X_j^u	609	704	382	255

Table 4

Inferences for N based on bowhead whale data – Empirical Bayes estimates and Gibbs sampling. Data from photo-ID data in the spring 1985, summer 1985, spring 1986, and summer 1986.

a	*b*	$\hat{N}$	CV	Credible intervals (95%)
Empirical Bayes				
5.9	107.7	6,340	0.162	(4,544; 8,595)
Gibbs sampling				
0.0	0.0	6,690	0.261	(4,360; 10,200)
0.5	0.5	6,150	0.248	(3,970; 9,610)
1.0	1.0	5,700	0.215	(3,760; 8,500)

All images taken in the photographic surveys were submitted to screening and classified using the scoring system developed by Rugh *et al.* (1998). All images were scored on the basis of their *quality* and *identifiability*.

The result of the application of the methods discussed above are summarised in Table 4.

According to the conclusions above for Cases 3 and 4 (representing a large number of unmarked individuals in the population), the inferences for N using the estimated (a,b) present very small biases. Those biases are even smaller than those obtained using the vague *beta*(0.5,0.5). Da-Silva *et al*. (2003) estimated that the fraction N^u / N of unmarked individuals in the population to be around 0.815, i.e. the majority of the individuals in the population do not possess any natural marks that could be used to uniquely identify the individuals. Therefore, for the actual bowhead whale data, the best choice for the hyperparameters a and b is obtained when using the Empirical Bayes approach.

When compared to the estimates obtained by Raftery and Zeh (1998) - 6,039 (SE=1,915) and 7,734 (SE=1,450) for 1985 and 1986 respectively - and with the 1985 and 1986 estimates of 6,649 and 6,820 (excluding calves) from the Bayesian synthesis analysis of Raftery *et al.* (1995), the inferences for N obtained with the Empirical Bayes approach (see first line of Table 4), yields smaller estimated standard deviation than those other approaches. However, it is not at all clear whether this is because the Empirical Bayes is truly a more precise estimator or because the estimate of SE produced by the Empirical Bayes approach is downwardly biased.

CONCLUSION

The present paper considered Bayesian approaches for estimation of the size N of animal populations considering that: (1) the data are from a photo-ID capture-recapture experiment; (2) capture probabilities vary only due to temporal effects; and (3) part of the population is unmarked. Da-Silva *et al.* (2003) concluded that, for such setting, the corresponding Bayesian analysis for N is sensitive to the choices of vague beta priors for the capture probabilities. A Gibbs sampling approach was suggested for the estimation of N. The objective was to define a quantity that represents the log of the unknown fraction of the population sizes of unmarked to marked individuals. As a function of that it was possible to define the probability of occurrence of a good photograph of a marked individual. Additionally, a reparameterisation of such probability allowed further simplification of the Gibbs sampling procedure.

Performance of the proposed methods was evaluated through a simulation study involving bowhead whale data generated under four different scenarios (the same as used by da-Silva *et al.*, 2003). An Empirical Bayes analysis was proposed as an attempt to diminish the biases in the inferences for N caused by sensitivity to the prior specifications of the capture probabilities. The conclusions are given below.

(1) The use of the Empirical Bayes approach yields either smaller or comparable biases for the estimated values of N compared to the biases observed using the *beta*(0.5,0.5) prior (the one that conducted to the smaller biases for the Bayes estimation via Gibbs sampling).

(2) The Empirical Bayes approach apparently also improves precision in the estimation N as revealed by the comparison of CVs in Table 4 (however, it is possible that such estimated standard deviation are downwardly biased).

(3) When the population includes a very large number of unmarked individuals, inferences for N obtained using the Empirical Bayes approach are definitely superior to the Bayes approach (via Gibbs sampling) using any of the vague beta priors.

Some observations and concerns about possible violations in the model assumptions are addressed below.

(1) *Possible changes in markings*. Only photographs in which the mid-back region of the whales was of good quality, i.e. classified as 2- or better, were used in the analyses so that whales with identifying marks in that region would be recognised when they were photographed on more than one sampling occasion. (*Quality* is scored on a five-point scale (1+, 1-, 2+, 2-, 3) indicating how much of the area is visible: 1+ represents the highest and 3 the lowest quality. A whale must also be at least moderately marked on the mid-back to be treated as marked in the analyses. The scoring system developed by Rugh *et al.* (1998) is stringent enough to ensure that a whale categorised as marked on one occasion will be recognised if photographed again on a subsequent occasion. Miller *et al.* (1992) argues that it is unlikely that large scars disappear. However, small marks may be disguised by new marks, and they are also more likely than large marks or groups of marks to be obscured in a photograph).(*Identifiability* is scored as H+, H-, M+, M-, U+, U-, with highly (H) and moderately (M) and unmarked (U) whales).

(2) *Closed population assumption*. In the analyses performed data were used from two different years (photo-ID data from spring 1985, summer 1985, spring 1986 and summer 1986). The closed population assumption does not strictly apply since whales are born and die between samples. However, bowhead whales have high survival rates (George *et al.*, 1999) and low fecundity rates (Miller *et al.*, 1992), which implies that the population is not expected to suffer considerable demographic changes and the closed population assumption to be reasonably acceptable. George *et al.* (2004) discuss the population trend of Western Arctic bowhead whales from 1978 to 2001. Their estimate of annual rate of increase of the population in such period is 3.4%. So the estimates presented here may be somewhat negatively biased.

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