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# EMPIRICAL BAYES ESTIMATION OF THE SIZE OF A CLOSED POPULATION USING PHOTO-ID DATA

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ABSTRACT
Photo-id data is broadly used for estimating animal abundance using capture-recapture models. The natural and acquired marks of the photographed individuals allow the construction of databases to be used for estimating the size *N* of an animal population. Animals that do not possess natural marks enough to allow re-identification are called *unmarked*. Those individuals are *uncatchable*, 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 we present an empirical Bayes capture-recapture analysis for estimating the size of an animal population including uncatchable individuals. Considering a Gibbs sampling approach we obtain Monte Carlo estimates for the posterior distribution of *N*.

## 1. INTRODUCTION

Capture-recapture methods based on photo-id data are widely used for estimating abundance of marine mammals and other hard to tag species. Instead of artificially tagging the captured individuals, the natural and acquired marks of the photographed ones are used to build a matrix of their capture histories. This kind of data, i.e., the capture histories, are used in most of the 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 recognized. That violates a basic assumption of most capture-recapture models which requires that every animal in the population be uniquely identifiable.

The solution for the problem of estimating animal abundance in the presence of uncatchable individuals has been first attempted by Seber (1982), p. 72. Working with bottlenosed 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 (*Balaena mysticetus*) photo-id data. Their results had a good agreement with those obtained by Raftery and Zeh (1998) and Givens (1993) (personal communication) 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 very same bowhead whale photo-id data used by those authors and obtained bowhead whale population inferences largely in agreement with the ones obtained by them. Working with Western Artic bowhead whales surveyed near Point Barrow, Alaska, 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) reviewed the method of Cooke (1996) and Punt and Butterworth (1999) for computing abundance estimates for bowhead whales of the Bering-Chukchi-Beaufort Seas stock based on N4 and P4. Their 1985 and 1986 abundance estimates are also in agreement with the ones in da Silva *et al*. (2000).

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 (1997), 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 we present an empirical Bayes analysis for estimating the size of an animal population including uncatchable individuals with capture probabilities varying according to the sampling occasions. We consider a Gibbs sampling algorithm 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. We compare the inferences about $N$ obtained with these methods with the ones obtained by da-Silva *et al* (2003). In this last work the authors used the adaptive rejection sampling method (ARS) by Gilks and Wild (1992) for drawing samples from some nonstandard distributions.

In Section 2 we introduce some notation. In Section 3 we restate a conditional likelihood for the problem established by da-Silva *et al*. (2003). In Section 4 we describe a Gibbs sampling algorithm for estimating the size of the whole bowhead whale population, $N$. In Section 5 we propose an empirical Bayes procedure to estimate the hyperparameters of a prior beta distribution. Using bowhead whale simulated data, in Section 6 we compare our inferences for $N$ in a variety of ways. In Section 7 we present an application using actual bowhead data. Finally, in Section 8 we present some concluding remarks.

## 2. 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 are used in the analysis. All good quality photos of the photographed individuals are used. However, only individuals who possess an acceptable extent of natural marks comprise what we call the population of the *"marked individuals"*.

A *capture* means that a good quality photo of a whale was taken and, if a whale presents a non negligible extent of natural marks, it is considered *marked*. We now introduce some notation.

- $N^u$: 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 $j$, $j = 1, \ldots, t$, 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.
- $\omega$ : any subset of $\{1, \ldots, t\}$.
- $u_\omega$: the number of marked whales with history $\omega$. We have that

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

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

## 3. A LIKELIHOOD BASED ON GOOD PHOTOS

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

$$\Delta = \log\left(\frac{N^u}{N^m}\right), \tag{3.1}$$

which represents the log of the unknown fraction of the population sizes of uncatchable to catchable 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 $\Delta$ were estimated using a Bayesian procedure involving a conditional likelihood based on good photos which related a combination of Darroch's model (1958) and a binomial model as follows,

$$\begin{aligned} L(\Delta, p, N^m) &= Pr\left(\{u_\omega\}, \{X_j^m\} | \{X_j\}, \Delta, p, N^m\right) \\ &= Pr\left(\{u_\omega\} | \{X_j^m\}, p, N^m\right) Pr\left(\{X_j^m\} | \{X_j\}, \Delta\right) \\ &\propto \frac{N^m!}{(N^m - r)!} \prod_{j=1}^{t} p_j^{n_j} (1 - p_j)^{N^m - n_j} \\ &\quad \times \left[\frac{1}{1 + e^\Delta}\right]^{\sum_{j=1}^{t} X_j^m} \left[\frac{e^\Delta}{1 + e^\Delta}\right]^{\sum_{j=1}^{t} X_j^u} \end{aligned} \tag{3.2}$$

In expression (3.2), Darroch's model accounts for the marked (catchable) part of the population, while the binomial term incorporates, through the number of good photos of unmarked (uncatchable) individuals, the information about the uncatchable part of the population.

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 $\Delta$, 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 $\{p_i\}$ were standard ones, that could be sampled without any difficulty.

We realize that, for ecologists working with photo-id data, the ARS method described in da-Silva *et. al*. (2003) for drawing $\Delta$ samples may represent a major barrier to the use of the methodology suggested by those authors for estimating $N$. Therefore, in the next section we present an alternative way (the Gibbs sampling algorithm) for obtaining Monte Carlo estimates of the posterior distribution of $N$. This alternative is is both computationally friendlier and easier to grasp than the ARS.

## 4. GIBBS SAMPLING FOR ESTIMATING *N*

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

The Gibbs sampling is essentially a special case of the Metropolis-Hastings algorithm Metropolis *et al*. (1953); Hastings (1970)) 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 $\theta$. Each coordinate of $\theta$ is sampled conditionally to the values of the other components. For a very large number of Gibbs sampling cycles, the sampled values of $\theta$ are from the joint posterior distribution. The joint posterior is our target distribution.

Let $\theta = \left(\theta_1, \ldots, \theta_k\right)$ 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 $P\left(\theta_j \mid D, \theta_{-j}\right)$ be the full conditional distribution of $\theta_j$, and $\theta_{-j}$ denote the vector $\theta$ with $\theta_j$ removed. The following scheme illustrates the Gibbs sampling method for generating samples from $P(\theta \mid D)$,

1. Choose starting values $\theta_1^{(0)}, \ldots, \theta_k^{(0)}$;
2. Sample $\theta_1^{(j+1)}$ from $p\left(\theta_1 \mid \theta_2^{(j)}, \ldots, \theta_k^{(j)}, D\right)$;
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 about the Gibbs sampler can be found in Gelman *et al*. (1998).

Returning to the whale problem, since *N* is expressed as a function of $\Delta$ and $N^m$, its full conditional posterior distribution is estimated through the estimated values of those quantities. Expression (3.2) can be rewritten in terms of $\phi = \dfrac{1}{1+e^{\Delta}}$. Such reparametrization allows to describe an easy to sample full conditional posterior distribution for $\phi$.

Since $\Delta = \log\left(\dfrac{1-\phi}{\phi}\right)$, for each updated value of $\phi$ we can get the corresponding updated value of $\Delta$. The Gibbs procedure for generating samples from the joint posterior distribution of $\theta = \left(N^m, \left\{p_i\right\}, \phi\right)$ consists on drawing the $\theta$ values through the following sequence of draws:

$$\phi \mid \left\{X_j^m\right\}, \left\{X_j\right\} \sim Beta\left(\sum_{j=1}^{t} X_j^m + c; \sum_{j=1}^{t} X_j - X_j^m + d\right); \quad (4.1)$$

$$N^m - r \mid p, \left\{X_j^m\right\}, \left\{X_j\right\} \sim Neg-Bin\left(r, 1 - \prod_{j=1}^{t}\left(1 - p_j\right)\right); \quad (4.2)$$

$$p_j \mid N^m, \left\{X_j^m\right\}, \left\{X_j\right\}, n_j \sim Beta\left(n_j + a, N^m - n_j + b\right) \quad (4.3)$$

In expression (4.3) independence is assumed. The values *a, b, c* and d are hyperparameters that will be either fixed in order to define vague priors for the $\left\{p_i\right\}$ and $\phi$, or estimated using an empirical Bayes approach that will be discussed in the next section.

## 5. 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 empirical Bayes approach which consists of describing a marginal distribution of a given random variable which is parametrized by *a* and *b* so that estimation of these parameters is possible. Thus consider a population with $N_*$ individuals and a model where capture probabilities vary only due to temporal effects. Again, 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*;
- $n_j \mid N_*, p_j, a, b \sim binomial\left(N_*, p_j\right)$;
- $p_j \mid a,b \sim beta(a,b)$;
- $\pi\left(N_*\right) = \frac{1}{N_*}, N_* = 1,2,...$

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

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

$$= \frac{1}{n_j} \sum_{N_*-n_j=0}^{\infty} \frac{\Gamma(a+b)}{\Gamma(a)\Gamma(b)} \Gamma\left(a+n_j\right) \binom{n_j + \left(N_* - n_j\right) - 1}{n_j - 1}$$

$$\times \frac{\Gamma\left(b + \left(N_* - n_j\right)\right)}{\Gamma\left(a + b + \left(N_* - n_j\right) + n_j\right)}. \qquad (5.1)$$

In expression (5.1) the integrand represents a negative beta-binomial distribution with parameters *a*, *b* and $n_j$ for variable $N_* - n_j$ (See Bernardo and Smith (1997), p. 118). Therefore,

$$P\left(n_j \mid a,b\right) = \frac{1}{n_j}, n_j = 1, 2 ... \qquad (5.2)$$

However, $P\left(n_j \mid a,b\right)$ does not depend on *a* and *b*. Therefore, we considered instead an iterative procedure to estimate *a* and *b* that we describe below.

Let $\psi = \left(N_*, a, b\right)$ and $L(\psi)$, the likelihood associated to $\Psi$. Also consider that the $n_j^{'}s$ are iid and $N_*$ fixed so that

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

$$= \prod_{j=1}^{t} \binom{N_*}{n_j} \frac{B\left(n_j + a, N_* - n_j + b\right)}{B(a,b)} \qquad (5.3)$$

**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 in Section 4, obtain $\hat{N}_*^{(k)}$, for the estimated value of $N_*$. Here we use a point estimate for $N_*$ represented by the mean over the conditional posterior distribution.
3. Replace $\hat{N}_*^{(k)}$ in equation (5.3) and obtain the maximum likelihood estimates $\hat{a}^{(k)}$, and $\hat{b}^{(k)}$;
4. For $k=1,\ldots$ return to step 2 until convergence of *a* and *b*.

In the next section we present some analyses resulting from the application of the methods discussed in the previous sections to simulated data.

## 6. SENSITIVITY OF THE INFERENCES FOR N

In this section we are interested in studying the sensitivity of the inferences for $N$ to choices of the beta priors.

We worked with the same bowhead whale simulated datasets analysed by da-Silva *et al.* (2003).

da Silva *et al.* (2000) generated bowhead whale data considering 5 scenarios (Cases) and 500 four occasion capture-recapture samples each.

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 low or high.

For brevity consider the events:

$C$ = closed population, $S$ = small capture probabilities, $U$ = High number of 8 unmarked individuals in the population, where the complementary event of $E$ is $\overline{E}$.

The five cases are the following:
$Case\ 0 = \left(C, S, \overline{U}\right)$, $Case\ 1 = \left(\overline{C}, S, \overline{U}\right)$, $Case\ 2 = \left(C, \overline{S}, \overline{U}\right)$, $Case\ 3 = \left(C, \overline{S}, U\right)$, $Case\ 4 = \left(C, S, U\right)$.

Case 2 represents the most optimistic scenario where capture probabilities are high and the number of unmarked individuals is moderate.

**Table 1:** Summary statistics for estimated values of $N$ based on 500 bowhead whale simulated samples, Gibbs sampling approach and different values of $a$ and $b$. These are the cases with relatively few unmarked individuals.

| Case | Parameters | | | | Mean | Bias | Standard |
|---|---|---|---|---|---|---|---|
| | a | b | c | d | | | deviation |
| | | | 0.0 | 0.0 | 6,845 | 113 | 773 |
| 0 | 0.0 | 0.0 | 0.5 | 0.5 | 6,843 | 111 | 772 |
| | | | 1.0 | 1.0 | 6,842 | 110 | 771 |
| | | | 0.0 | 0.0 | 6,695 | -37 | 730 |
| 0 | 0.5 | 0.5 | 0.5 | 0.5 | 6,693 | -40 | 729 |
| | | | 1.0 | 1.0 | 6,691 | -41 | 729 |
| | | | 0.0 | 0.0 | 6,552 | -179 | 693 |
| 0 | 1.0 | 1.0 | 0.5 | 0.5 | 6,550 | -182 | 692 |
| | | | 1.0 | 1.0 | 6,548 | -184 | 692 |
| 0 | 6.1 | 68.8 | 0.0 | 0.0 | 6,761 | 108 | 763 |
| | | | 0.0 | 0.0 | 6,902 | 167 | 848 |
| 1 | 0.0 | 0.0 | 0.5 | 0.5 | 6,901 | 166 | 848 |
| | | | 1.0 | 1.0 | 6,898 | 164 | 848 |
| | | | 0.0 | 0.0 | 6,744 | 10 | 799 |
| 1 | 0.5 | 0.5 | 0.5 | 0.5 | 6,743 | 9 | 800 |
| | | | 1.0 | 1.0 | 6,743 | 8 | 800 |
| | | | 0.0 | 0.0 | 6,596 | -138 | 757 |
| 1 | 1.0 | 1.0 | 0.5 | 0.5 | 6,594 | -141 | 755 |
| | | | 1.0 | 1.0 | 6,592 | -143 | 757 |
| 1 | 5.4 | 62.9 | 0.0 | 0.0 | 6,903 | 169 | 840 |
| | | | 0.0 | 0.0 | 6,746 | 12 | 360 |
| 2 | 0.0 | 0.0 | 0.5 | 0.5 | 6,745 | 11 | 360 |
| | | | 1.0 | 1.0 | 6,745 | 11 | 355 |
| | | | 0.0 | 0.0 | 6,721 | -13 | 356 |
| 2 | 0.5 | 0.5 | 0.5 | 0.5 | 6,720 | -14 | 356 |
| | | | 1.0 | 1.0 | 6,720 | -15 | 352 |
| | | | 0.0 | 0.0 | 6,697 | -37 | 352 |
| 2 | 1.0 | 1.0 | 0.5 | 0.5 | 6,696 | -38 | 352 |
| | | | 1.0 | 1.0 | 6,695 | -39 | 353 |
| 2 | 5.5 | 28.4 | 0.0 | 0.0 | 6,744 | 23 | 362 |

For the Gibbs sampling approach for estimating $N$ discussed in Section 4, we defined $\phi = \frac{1}{1+e^{\Delta}}$, with $\phi \sim beta\left(c, d\right)$.

Now 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 9 capture probabilities, but also to choices of the values of $c$ and $d$.

From Tables 1 and 2, we observe that inferences about $N$ are sensitive to the choices of $a$ and $b$. However, the inferences are not sensitive to the choices of $c$ and $d$.

Thus, any choice of the beta priors (beta(0, 0), beta(1, 1) or beta(0.5, 0.5)) for $\phi$ works equally well, i.e., none of them causes any remarkable bias in the estimated values of $N$.

**Table 2:** Continuation of Table 1 - summary statistics for estimated values of $N$ based on 500 bowhead whale simulated samples, Gibbs sampling approach and different values of $a$ and $b$. These are the cases with high numbers of unmarked individuals.

| Case | Parameters | | | | Mean | Bias | Standard |
|---|---|---|---|---|---|---|---|
| | a | b | c | d | | | deviation |
| 3 | 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 |
| 3 | 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 |
| 3 | 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 |
| 3 | 6.1 | 68.6 | 0.0 | 0.0 | 13,392 | 103 | 1,702 |
| 4 | 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 |
| 4 | 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 |
| 4 | 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 |
| 4 | 6.4 | 143.7 | 0.0 | 0.0 | 13,025 | 384 | 3,919 |

For each Case and each of the 500 simulated samples, we estimated the respective values of ($a$, $b$) using the iterative empirical Bayes approach. The *10th* line of each of the Cases in Tables 1 and 2 represents the average of those estimated values of ($a$, $b$). We observe that, for Cases 3 and 4, the inferences for $N$ using the estimated ($a$, $b$) present very small biases. Actually, these biases were smaller than those yielded using vague beta(0.5,0.5). For Case 2, the choice of the values for $a$ and $b$ is not really an issue since the biases were all very close.

For Cases 1 and 0, the biases for $N$ using the estimated ($a$, $b$) were larger than the biases for $N$ using beta(0.5,0.5). For Case 1, the bias yielded when the empirical Bayes method was applied was the largest one: *bias* = 169. Still, that represents only 2.5% of the true value of $N$. Again, for the Cases where sampling information about $N$ is very imprecise due to unmarked whale excess in the population, the empirical Bayes approach described in Section 5 represented a useful option for minimizing biases in the inferences for $N$. Inferences for N obtained using the presented methods were very similar to those by da-Silva *et al*. (2003).

## 7. ANALYSIS USING REAL BOWHEAD WHALE DATA

The actual data for the bowhead whale 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. That gives an idea of how sparse the bowhead whale data are. For more details about the real bowhead data see da Silva *et al*. (2000).

The result of the application of the methods discussed in the previous sections are summarized in Table 3. For convenience, the inferences for $N$ obtained by da-Silva *et al.* (2003) are also restated. Since in the last section we concluded that inferences for $N$ are not sensitive to the values of the hyperparameters of the beta prior for $\phi$ (see equation (4.1)), we only considered a vague beta prior *beta*(0, 0) for $\phi$ in the Gibbs sampling calculations.

As we can observe from Table 3, there exists a good agreement among the estimated values of $N$ obtained using the two MCMC sampling methods for various choices of vague beta priors for the capture probabilities.

da-Silva *et al*. (2003) estimated that the fraction $N^u / N$ of unmarked individuals in the population was around 0.815, i.e., the majority of the individuals in the bowhead population does not possess any natural marks that could be used to uniquely identify the individuals. Therefore, according to our conclusions at the end of Section 6 for Cases 3 and 4 (representing a large number of unmarked individuals in the population), for the actual bowhead whale data, the best choice for the hyperparameters $a$ and $b$ is obtained when using the empirical Bayes approach discussed in Section 5.

Still considering the inferences for *N* obtained using the empirical Bayes approach, those results compare favorably with the ones obtained by Raftery and Zeh (1998) (6,039 (s.e.=1,915) and 7,734 (s.e.=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 Givens (1993) (personal communication). The Bayesian bowhead whale population size estimates using photo-id data represent independent estimates from those already obtained using ice-based visual and acoustic counts of whales (Raftery and Zeh (1998)).

**Table 3:** Inferences for *N* based on actual bowhead whale data - ARS estimates restated from da-Silva *et al*. (2003). Data from photo-id data in the spring 1985, summer 1985, spring 1986, and summer 1986.

| Method | Parameters $a$ | $b$ | $c$ | $d$ | $\hat{N}$ | Credible Intervals (95%) |
|---|---|---|---|---|---|---|
| ARS | 0.0 | 0.0 | - | - | 7,109 | (4,746; 11,138) |
| | 0.5 | 0.5 | - | - | 6,389 | (4,466; 9,704) |
| | 1.0 | 1.0 | - | - | 5,935 | (3,978; 8,311) |
| Gibbs | 0.0 | 0.0 | 0.0 | 0.0 | 6,690 | (4,360;10,200) |
| | 0.5 | 0.5 | 0.0 | 0.0 | 6,150 | (3,970;9,610) |
| | 1.0 | 1.0 | 0.0 | 0.0 | 5,700 | (3,760;8,500) |
| | 5.9 | 107.7 | 0.0 | 0.0 | 6,340 | (4,544;8,595) |

## 8. CONCLUSION

The present paper considers 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; (3) part of the population is uncatchable. 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. In the MCMC approach proposed by the last authors they used the Adaptive Rejection Sampling (ARS) by Gilks and Wild (11) to generate samples from a non standard distribution. In order to facilitate the whole MCMC process involved in the estimation of *N*, a Gibbs sampling approach was suggested in Section 4. Performance of the proposed methods was evaluated through a simulation study involving bowhead whale data generated under five different scenarios (the same used by da-Silva *et al*. (2003)). An empirical Bayes analysis is 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: (1) the two methods, ARS and Gibbs sampling yielded very similar inferences for *N*. Therefore, considering the computational difficulties involved in the implementation of the discussed methods for estimating *N*, the Gibbs sampling is a good alternative since it is very easy to implement. (2) The use of the empirical Bayes approach proposed in Section 5 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. When the population includes a very large number of uncatchable individuals, inferences for *N* obtained using the empirical Bayes approach are definitely superior to those obtained using any of the vague beta priors.

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