Estimating Bowhead Whale, *Balaena mysticetus*, Population Size and Rate of Increase from the 1993 Census

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Abstract

Estimating the population size and rate of increase of bowhead whales, *Balaena mysticetus*, is important because bowheads were the first species of great whale for which commercial whaling stopped and so their status indicates the recovery prospects of other great whales, and also because this information is used by the International Whaling Commission (IWC) to set the aboriginal subsistence whaling quota for Alaskan Eskimos. We describe the 1993 visual and acoustic census off Point Barrow, Alaska, which provides the best data available for estimating these quantities. We outline the definitive version of two statistical methods for estimating the population, the generalized removal method and the Bayes empirical Bayes method.

The two methods give results that are close. The estimate of bowhead population size most recently accepted by the IWC Scientific Committee, 8200 with 95% estimation interval from 7200 to 9400, is based on the Bayes empirical Bayes posterior distribution presented here. The Scientific Committee also accepted our estimate of the annual rate of increase of the population from 1978 to 1993. This estimate, based on the generalized removal method population estimates, is 3.2% with a 95% confidence interval [1.4%, 5.1%]. This shows that bowheads are increasing at a healthy rate, indicating that stocks of great whales that have been decimated by commercial hunting can recover after it ends, even in the presence of limited aboriginal subsistence whaling.

KEY WORDS: Bayes empirical Bayes; Capture recapture; Generalized linear model; Jackknife; Missing data; Negative binomial; Overdispersion; Quadrature; Removal method; Sensitivity analysis.

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1 Introduction

Estimation of the population size and rate of increase of the western Arctic (Bering-Chukchi-Beaufort Seas) stock of bowhead whales, *Balaena mysticetus*, is important for two main reasons. Commercial hunting of bowheads ended before that of the other six protected species of great whale, and so the status of bowheads is a good indicator of whether and how fast these species can recover. The stock was decimated by commercial whalers between 1850 and 1914, and since 1914 there has been almost no commercial whaling.

The second reason is that, in spite of the prohibition of *commercial* whaling, aboriginal subsistence whaling by the Eskimos of the North Slope of Alaska has been permitted on a restricted basis, with quotas set by the International Whaling Commission (IWC). Current population size and rate of increase are among the most important pieces of information used in setting the quota.

There has been a major research effort since 1978 aimed at estimating these quantities. This has involved a large interdisciplinary team of investigators and a great deal of rigorous data collection in harsh conditions, and has led to substantial methodological advances in ice-based visual survey techniques, bioacoustics and statistical analysis. The cumulative fruit of this effort is that current population size and rate of increase are now known with more precision for bowheads than for any other species of whale, except gray whales. In this paper we present the results from the 1993 visual and acoustic census, which was the best one to date, and we outline the definitive version of the statistical methodologies used.

In each of the first six years of the research program, from 1978 to 1983, a visual census was carried out at Point Barrow, Alaska during the spring migration, by ice-based observers on two separate counting stations, called perches. One problem with the visual census was that it could not count animals passing more than about 4 km from the shore. An effort to overcome this was made in 1981 by flying aerial transect surveys, but these gave only limited information (Marquette, Braham, Nerini and Miller 1982). A second problem with the visual census was that it could not count whales swimming under the ice. To overcome these difficulties with the visual census, it was supplemented by acoustic monitoring using underwater hydrophones arrayed along the ice edge in front of the visual census perch, starting in 1984, after earlier pilot studies. This provides the times and approximate locations of recorded bowhead sounds.

Unfortunately, the visual and acoustic census does not provide a direct count of the number of whales for the following reasons:

(1) The whale census collects visual and acoustic locations of whales, and it is often impossible to know whether different locations correspond to different whales or to the same one.

(2) Whales may pass Point Barrow without being located at all, because they neither surface nor vocalize while within range of the census perch.

(3) Whales may be missed even if they do manifest themselves while within range, because their surfacings are not seen and their vocalizations not picked up by the hydrophone array. This is especially likely when visual and acoustic conditions are poor.

(4) Whales may pass Point Barrow too far from the shore to be seen or heard by the census-takers.

(5) Parts of the migration season are not monitored at all, so that no whales passing during these periods are located.

Here we summarize two different statistical methodologies for estimating population size that have been developed in parallel over the past ten years. We present several improvements to them, and give the final estimates based on them for the 1993 census, which was the most successful one to date. The first method, called the generalized removal method, estimates population size from overall counts of visually identified whales, using the removal method with adjustments for environmental conditions, missed time and whales passing beyond 4 km. It uses the jackknife to assess variability. It is straightforward conceptually and computationally, but it depends on several broad assumptions that are hard to verify.

We therefore also developed a second, more refined but also more complex, approach, called the Bayes empirical Bayes method. This uses the individual visual and acoustic locations rather than overall counts, and links them together using a *tracking algorithm.* A stochastic model of whale behavior and of errors made by the tracking algorithm is then used to compute a posterior distribution of population size. The prior distributions used are based on external data.

The two methods gave results for 1993 that were similar, reinforcing confidence in both approaches. The IWC Scientific Committee (IWC 1992, 1995) agreed that the Bayes empirical Bayes approach was the most appropriate one for estimating current population size. IWC (1995) also recommended that rate of increase be estimated from the generalized removal method population estimates. However, only preliminary estimates based on incomplete data were available at the 1994 Scientific Committee meeting. An augmented and refined acoustic data set was subsequently analyzed to produce the estimates reported in this paper; these were accepted by the Scientific Committee at its 1995 meeting.

In Section 2 we describe the 1993 census and give the data it yielded in summary form. In Section 3 we describe the generalized removal method, and in Section 4 we outline the Bayes empirical Bayes approach. In Section 5 we give the population size and rate of increase results.

2 Data

George *et al.* (1995) described the 1993 visual census methods and results. There was one counting station, which moved between two different perches, called Carolyn and Spamalot, with Carolyn accounting for most of the monitored hours and whales seen. Locations of whales that are seen are computed from theodolite readings recorded in the visual census data base. We show the visual locations from the 1993 census in Fig. 1(a).

Locations of whales detected acoustically must also be computed before the acoustic and visual data can be combined. Clark, Mitchell and Charif (1995) describe the current procedures for identifying bowhead sounds on the audio tapes recorded during the census and computing locations from data on the arrival times of the sounds at three or more different hydrophones. The hydrophones are arrayed approximately linearly along the ice edge. Sounds received on three hydrophones and within the 120° sector defined by the hydrophone array are candidates for location analysis. Sounds outside the 120° sector (i.e. within 30° of the array axis) are not processed because ranges to such sounds cannot be determined reliably. The effect of the 120° sector can be seen in Fig. 1(b), which shows the 1993 acoustic locations. Because the process of identifying bowhead sounds and computing locations from them is time-consuming, only a sample of the audio tapes was analyzed.

The 1993 census season was divided into 75 monitored and 3 unmonitored periods, shown in Tables 1 and 2. The monitored time, i.e. the time covered by watches from a visual census perch or by acoustic locations obtained from a hydrophone array in operation during the period, or both, was divided so that the level of visual and acoustic effort and the environmental conditions were roughly constant within a period. There were fewer unmonitored hours, 26, than in any previous combined acoustic and visual census. The census season lasted for 1,041 hours, from April 17 to May 30, 1993.

Some of the visual locations in 1993 were from identified whales. Also, a subset of acoustic locations provided call tracks (Clark 1989; Clark, Charif and Colby 1995) of acoustically

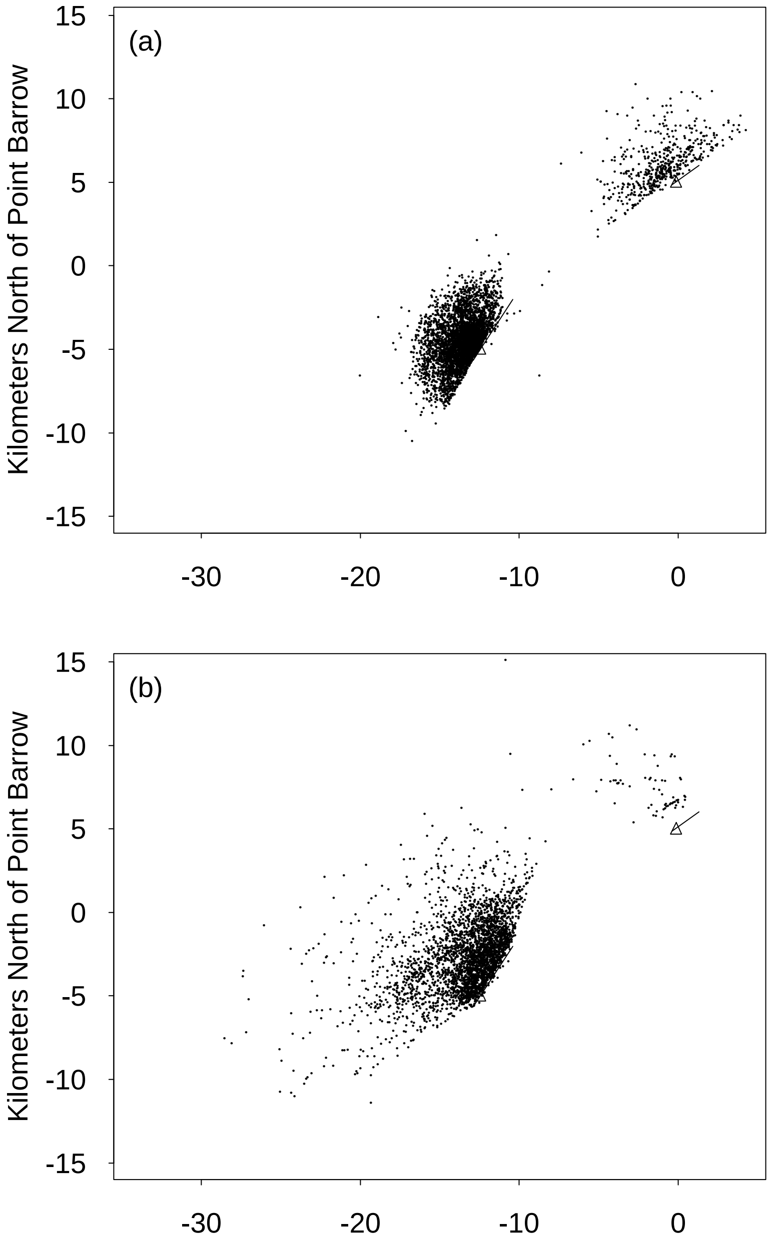

Figure 1: Locations of bowhead whales (a) seen and (b) heard during the spring migration past Point Barrow, Alaska, in 1993. The solid lines in both figures are hydrophone arrays and the triangles are census perches used during different parts of the migration. One unusual acoustic location at $(-55, -16)$ is omitted from (b).

Table 1: Monitored periods: 1993 bowhead whale visual and acoustic census. (Available only in paper version).

Table 2: Unmonitored periods, 1993. (Available only in paper version).

identified whales. The data from visually and acoustically identified whales were used as described in Section 4.4.4 to examine location errors and errors made by the tracking algorithm. In addition, the visual census provides counts of whales, including some that were not located using a theodolite, scored by the visual observers as new (seen for the first time), conditional (may or may not have been seen before), and duplicate (already seen). These counts are used to compute the estimate of the number of whales passing within viewing range that is based on visual census data only, which underlies the generalized removal method described in the next section.

3 The Generalized Removal Method for Estimating Population Size

The removal method (Moran 1951; Zippin 1956) was first adapted to bowhead population estimation by Zeh, Ko, Krogman and Sonntag (1986a,b), for analyzing the visual-only bowhead censuses of 1978–1983. In these years, two counting stations were operating simultaneously, South Camp and North Camp (unlike in later years, when there was only one station at a time). Since the whales move from south to north, South Camp observers generally had the first opportunity to see a whale as it surfaced. They reported their sightings via a one-way radio link to North Camp, whose mission was to look for whales missed by South Camp.

If n_1 is the number of whales seen at South Camp, and n_2 is the number missed at South Camp but seen at North Camp out of N whales passing in a given time period, the removal method models $(n_1, n_2, N - n_1 - n_2)$ as a trinomial random vector with parameters N, p, $p(1-p)$ and $(1-p)^2$, where p is the sighting probability in the absence of prior notification. The MLEs are $\hat{N} = n_1^2/(n_1 - n_2)$ and $\hat{p} = 1 - (n_2/n_1)$ (Seber 1982). Zeh *et al.* (1986a,b) estimated p for each visibility category and combined the estimated whale numbers at different visibilities. They derived simple corrections for time without watch at one or both perches, but they did not attempt to correct for whales that passed too far offshore to be seen. Zeh *et al.* (1986b) derived a jackknife estimate of the variance of the estimator of the number of whales that passed within viewing range.

The removal method cannot be applied directly to the 1993 census because there was only one counting station. Zeh, George, Raftery and Carroll (1991) adapted it to this situation, for the 1984–1988 censuses, by using only the data from the years with two counting stations, 1978–1985, to estimate the sighting probability p (as a function of covariates). They also fit an exponential growth model to the estimated numbers of whales passing within viewing range (N_4) to estimate the rate of increase of the population. Aerial transect survey data and, after 1983, acoustic data were used by IWC (1986) to correct the estimates of Zeh *et al.* (1986a,b) for whales that passed beyond viewing range. Raftery and Zeh (1991, 1993) used the proportion, P_4, of located bowhead sounds straight out from the perch that were within 4 km for this correction, and refined the method of estimating the variance of the resulting population estimator, N_4/P_4.

The removal method is conceptually and computationally straightforward, but it depends on several broad assumptions which may not hold. It assumes that there is no heterogeneity in sightability among whales, which seems questionable: for example, slower whales may be more likely to be seen. However, this would lead to the estimator $\hat{N}$ being biased downwards, which is preferable to upward bias in the present context.

It also assumes that each passing whale is correctly assigned by the ice-based observers to one of the cells of the trinomial distribution, although Zeh *et al.* (1986a) presented a model that accounted for some of the variability due to whales scored as conditional or questionable. This could introduce biases in either the downward or the upward direction.

Perhaps the biggest difficulty is the assumption that sighting probabilities estimated from the 1978–1985 data are valid for the 1993 census. Census methodology and personnel changed substantially from 1985 to 1993, and this could be a source of bias, probably in an upward direction. Finally, it is not known that the jackknife is valid for models of this type. The other assumptions underlying the removal method seem reasonable for the bowhead census, as discussed by Zeh *et al.* (1986a).

In order to deal with these difficulties, a more refined modeling approach was developed, as described in the next section.

4 The Bayes Empirical Bayes Population Estimation Method

4.1 Overview

We have mentioned five main ways in which the generalized removal method may be unsatisfactory: (a) it assumes that detection probabilities estimated from 1978–1985 data are valid for 1993; (b) it ignores heterogeneity in sightability; (c) it does not take full account of observer errors; (d) the validity of its use of the jackknife has not been established; and (e) it makes only very partial use of the acoustic data.

The Bayes empirical Bayes method was developed to avoid these possible oversimplifications and to make fuller use of the acoustic data. It has been developed and improved over the past ten years: successive iterations are described by Raftery, Turet and Zeh (1988), Raftery, Zeh and Styer (1988), Raftery, Zeh, Yang and Styer (1990), Raftery and Zeh (1991, 1993, 1994), and Zeh, Raftery and Schaffner (1995). The results from earlier versions were used not only to improve the statistical method, but also to improve the data collection design. In particular, the design of the 1993 census, whose results we report here, was influenced by the results from earlier versions of the Bayes empirical Bayes method, and led in turn to improvements in the statistical analysis. Here we report the final version of the statistical methodology, as approved by IWC (1995).

The Bayes empirical Bayes method consists of the following four steps:

(i) The area offshore from the census perch is divided into three zones: nearshore (within 2 km), offshore (between 2 and 4 km), and acoustic (beyond 4 km). Within each period and zone shown in Table 1, visual and acoustic locations are linked together to form tracks using a tracking algorithm.

(ii) A biological and geometric stochastic model of whale behavior and the census process is developed and estimated. This is used to calculate the posterior distribution of the number of whales passing in each period and zone, given the number of tracks and the environmental conditions.

(iii) The results for different periods and zones are combined to yield an overall posterior distribution for the entire census season.

(iv) Uncertainty about the tracking algorithm and model parameters is taken into account by rerunning steps (i)–(iii) for a collection of plausible parameter values, and combining the results in a Bayesian way via approximate numerical integration.

It overcomes the main difficulties with the generalized removal method in that: (a) it estimates detection probabilities from the 1993 data themselves; (b) it takes heterogeneity in sightability into account explicitly; (c) it uses the automated tracking algorithm rather than the observer judgements to obtain the initial counts, and it models the errors made by the tracking algorithm explicitly; (d) it assesses uncertainty using a Bayesian posterior distribution rather than the jackknife; and (e) it makes much fuller use of the acoustic data.

4.2 The Tracking Algorithm

Within each period, visual and acoustic locations were linked together to form tracks, using the tracking algorithm developed by Sonntag, Ellison, Clark, Corbit and Krogman (1986), and refined by Sonntag, Ellison and Corbit (1988), Zeh, Raftery and Yang (1990) and Raftery and Zeh (1993).

The first step is to consolidate locations into a single location if they are close enough in space and time (given their range and bearing errors) that they are likely to be from the same whale. Range and bearing errors for acoustic locations are computed as in Clark, Mitchell and Charif (1995), refining methods first developed by Clark, Ellison and Beeman (1986) and Clark and Ellison (1988).

The second step links the consolidated locations to form tracks. The locations are examined in chronological order to determine which should be linked to others that follow them. Two locations, X and Y, are linked together in the same track if X occurred before Y and if Y could be due to the same whale as X, given the specified minimum and maximum speed and direction parameters. At a given time, the area in which Y could be if it is to be linked to X is called the *linking area* of X at that time. This is roughly a trapezoid.

We used a maximum swimming speed of 7.5 km/hr. An allowed deviation from the migration direction of $\pm 22.5^\circ$ and a minimum swimming speed of 2.5 km/hr were our central parameter values. We used direction deviations of $\pm 15^\circ$ and $\pm 30^\circ$ and minimum swimming speeds of 1.5 km/hr and 3.5 km/hr for the sensitivity study described in Section 4.5. These values were determined by analyses reported in Section 4.4.4.

4.3 Stochastic Model

The assumptions that define our model are as follows, where superscripts ν, ω and α refer to the nearshore, offshore and acoustic zones, and superscripts V and A refer to visually and acoustically detectable whale behaviors.

(A1) The numbers of whales migrating past Point Barrow in each period within each zone are independent Poisson random variables with different means. The mean for a period is proportional to the length of the period. The constants of proportionality for the different periods, or rates of passage (in whales per hour), are themselves allowed to be different, and are assumed to be random variables drawn from a gamma distribution with shape parameter γ and scale parameter ϕ^{ν}, ϕ^{ω} or ϕ^{α}.

(A2) The number of surfacings and the number of vocalizations of a given whale are independent Poisson random variables with means proportional to the lengths of time it spends within visual/acoustic range of the census perch/hydrophone array. The constants of proportionality are λ^V and λ^A.

(A3) Detection probabilities depend on environmental conditions in a loglinear manner. We denote by π_t^V the probability that a whale is located if it surfaces, and by π_t^A the probability that it is located if it vocalizes. Then the number of visual locations of a given whale has a Poisson distribution with mean equal to $\lambda^V\pi_t^V$ times the number of hours the whale spends within visual range, with a similar result for acoustic locations. Thus it is sufficient to model the products $\lambda^V\pi_t^V$ and $\lambda^A\pi_t^A$; we do not need to estimate λ^V and π_t^V or λ^A and π_t^A separately.

We assume a log-linear form for the dependence of $\lambda^V\pi_t^V$ and $\lambda^A\pi_t^A$ on the environmental factors. Let

$$\begin{aligned}\lambda^V\pi_t^V &= \text{Expected number of visual locations per whale per hour in period } t \\ &= \exp\left(\beta_0^V + \beta_1^V x_{1t}^V + \beta_2^V x_{2t}\right), \qquad (1)\end{aligned}$$

where x_{1t}^V = visibility and $x_{2t} = 1$ for the offshore zone and 0 otherwise. We modeled the dependence of $\lambda^A\pi_t^A$ on acoustic condition in a similar way:

$$\begin{aligned}\lambda^A\pi_t^A &= \text{Expected number of acoustic locations per whale per hour in period } t \\ &= \begin{cases}\exp\left(\beta_0^A + \beta_1^A x_{1t}^A\right) & \text{if } x_{1t}^A > 0 \\ 0 & \text{if } x_{1t}^A = 0,\end{cases} \qquad (2)\end{aligned}$$

where x_{1t}^A = average acoustic condition in period t. Visibility and acoustic condition were assessed on a scale ranging from 0 (unacceptable) to 5 (excellent).

(A4) The average time, σ, that a whale takes to swim one kilometer has a gamma distribution with parameters a and b, namely $p(\sigma) \propto \sigma^{a-1} \exp(-b\sigma)$.

(A5) The times at which whales enter each zone are randomly distributed across each time period according to a uniform distribution.

We also model errors made by the tracking algorithm. We consider two types of error. The first type of error is the one that can lead to double counting. If a whale is located twice, the probability that the second location is outside the linking area of the first location is denoted by $(1 - \rho_1)$. The second type of error is the one that can lead to undercounting. We denote by ρ_2 the probability that if a whale goes outside its linking area, it is wrongly linked to another whale; this can vary by period and zone.

These assumptions allow us to find the likelihood, $p(y|n)$, of the observed number of tracks, y, in a specified period and zone, given the number of whales present. Let W be the number of tracks generated by a whale chosen at random among the n whales passing, let $q_i = \Pr[W = i]$ and let w_i be the number of whales that generate i tracks. Thus, if $W = 0$, the whale is not counted, if $W = 1$ it generates just one track, and so on. Then $\mathbf{w} = (w_0, w_1, \ldots)$ has a multinomial distribution with parameters n and $\mathbf{q} = (q_0, q_1, \ldots)$. It follows that

$$p(y|n) = \sum_{\mathbf{w} \in \mathcal{W}} \frac{n!}{\prod(w_i!)} \prod q_i^{w_i}, \tag{3}$$

where $\mathcal{W} = \{\mathbf{w} : \text{each } w_i \text{ is a nonnegative integer}, \sum i w_i = y \text{ and } \sum w_i = n\}$, with the sums and products being from zero to infinity unless otherwise specified.

We now derive the q_i. Let μ be the average number of locations of an individual whale if it is swimming at 1 km/hr. This is $\lambda^V \pi_t^V \kappa^{z,V}$ for the nearshore or offshore zone with no acoustic monitoring, $\lambda^V \pi_t^V \kappa^{z,V} + \lambda^A \pi_t^A \kappa^{z,A}$ for the nearshore or offshore zone with both visual watch and acoustic monitoring, and $\lambda^A \pi_t^A \kappa^{z,A}$ for the nearshore or offshore zone with no visual watch, and for the acoustic zone, where $\kappa^{z,V}$ is the number of kilometers swum within visual range by a whale in zone z ($z = \nu, \omega, \alpha$), and $\kappa^{z,A}$ is the corresponding acoustic quantity.

What the tracking algorithm does to different manifestations of the same whale are independent events. The first manifestation will be in no existing linking area, and hence will produce a new track, with probability $1 - \rho_2$. Each subsequent manifestation will be in an existing linking area (the whale's own or that of another whale), and hence not produce an additional track, with probability $\psi = 1 - (1 - \rho_1)(1 - \rho_2)$. Also, given σ, the average time the whale takes to swim one kilometer, we have:

$$k = \text{number of manifestations of a whale taken at random} \sim \text{Poisson}(\mu\sigma),$$

and

$$q_i = \Pr[W = i] = \int_0^\infty \sum_{k=0}^\infty \Pr[W = i|k] p(k|\sigma) p(\sigma) d\sigma. \tag{4}$$

It remains only to find $\Pr[W = i|k]$, and this follows directly from the probabilities above. For example, $\Pr[W = 0|k] = 1$ if $k = 0$ and $\rho_2\psi^{k-1}$ if $k \geq 1$. These values are substituted into equation (4), and the resulting integrals and infinite sums have analytic forms.

4.4 Prior Distributions and Estimates of Model Parameters

We make a distinction between the "data" that go into the likelihood, which consist only of the contents of Table 1 and 2, and all other information, viewed as "external" or "prior" information. The latter includes censuses from years other than 1993, and a relatively small number of "identified tracks" from the 1993 census itself, made up either of visual locations which the visual observers were almost certain were of the same whale, or of acoustic locations identified as being from the same whale on the basis of spectrogram analysis (Clark 1989). The identified tracks are viewed as external information, because they are based on information that the tracking algorithm does not use, and are used only to set parameter values.

4.4.1 Prior Distribution of Whale Numbers

The prior distribution of n_t^z, the number of whales passing through zone z $(z = \nu, \omega, \alpha)$ in period t, is the negative binomial distribution, $NB(\gamma, \phi^z\Delta_t)$, by assumption (A1). Using the numbers of consolidated acoustic locations straight out from the hydrophone array in each hour of the season and for each zone, we estimated $\hat{\gamma} = 0.114$; for details of the method used see Raftery and Zeh (1993). To estimate the ϕ^z we note that if $E[N]$ is the prior mean of N, then $E[N] = \gamma(\phi^\nu + \phi^\omega + \phi^\alpha)\sum\Delta_t$, where $\sum\Delta_t = 1,041$ is the length of the census season in hours. We set $E[N]$ equal to the IWC estimate based on the previous census in 1988, namely 7,500 (IWC, 1992). We took ϕ^z to be proportional to the number of consolidated acoustic locations in zone z $(z = \nu, \omega, \alpha)$. Only locations in the rectangle with the hydrophone array as one side are counted; this eliminates the effect of the hydrophone geometry. We obtained $(\phi^\nu, \phi^\omega, \phi^\alpha) = (44.3, 15.0, 4.1)$. Fewer than 7% of the whales were outside visual range in 1993, as against over 20% in 1988.

4.4.2 Whale behavior

Swimming speeds vary considerably between whales, and we approximated the distribution of σ = time to swim 1 km, by a gamma distribution, namely $p(\sigma) \propto \sigma^{a-1}\exp\{-b\sigma\}$. The parameters a and b were estimated by the method of moments from the empirical distribution of the speeds of the 213 whales identified at least twice by visual observers and swimming in directions between $-50°$ N and $100°$ N. The estimated values were $\hat{a} = 1.19$ and $\hat{b} = 3.75$. The mean was $\hat{a}/\hat{b} = 0.32$, as against 0.60 in 1988. Thus whales were traveling on average almost twice as fast in 1993 as in 1988: at about 3.1 km/hr in 1993 as against about 1.7 km/hr in 1988. This was due to strong northbound currents in 1993 and strong southbound currents in 1988, so that whales were swimming with the currents in 1993 and against them in 1988.

The number of kilometers swum by a whale while within visual or acoustic range is determined by the geometry of the census. This is calculated for a whale swimming parallel to the hydrophone array at the zone midpoint. Thus we find that $\kappa^{\nu,V} = 2\sqrt{15} = 7.75$, $\kappa^{\omega,V} = 2\sqrt{7} = 5.29$, $\kappa^{\nu,A} = d_A + 2\sqrt{3} = 7.89$, $\kappa^{\omega,A} = d_A + 6\sqrt{3} = 14.82$, and $\kappa^{\alpha,A} = d_A + d_{120°}\, 2\sqrt{3} = 21.75$, where $d_A = 4.43$ km is the length of the hydrophone array, and $d_{120°}$ is the distance at which the effect of the 120° sector stops, taken to be equal to 5 km.

4.4.3 Detection Probabilities

We estimated the dependence of visual detection probabilities on visibility by considering all the tracks which included acoustic locations, and, for each of these, recording whether or not the track also contained at least one visual location. This constitutes, approximately, a capture-recapture data set where the initial capture consists of acoustic location, and the recapture consists of visual location.

Given σ = the average time that the whale takes to swim one kilometer, the probability that it will be visually detected is

$$p(V \mid A, \sigma) = 1 - \exp(-\lambda^V \pi_t^V \kappa^{z,V} \sigma), \tag{5}$$

where V is the event that a whale in zone z ($z = \nu, \omega$) is visually located. The result for the acoustic detection probability is similar.

The events of visual and acoustic location are statistically independent, conditionally on σ. However, in practice we do not observe σ, and so these events are not *unconditionally* independent. We use the following approximation:

$$p(V \mid A) \approx 1 - \exp(-c\kappa^{z,V}\bar{\sigma}\lambda^{V}\pi_t^{V}), \tag{6}$$

where $\bar{\sigma} = E[\sigma] = a/b$, and c is a constant to be estimated. This is equivalent to

$$\log[-\log\{1 - p(V \mid A)\}] \approx \beta_0^V + \beta_1^V x_{1t}^V + \beta_2^V x_{2t} + D_z^V, \tag{7}$$

where $D_z^V = \log(c\kappa^{z,V}\bar{\sigma})$. The left-hand side of equation (7) is the complementary log-log transform of $p(V \mid A)$. The value of c was estimated by iterating between (a) fitting equation (7) using GLIM; and (b) setting equation (6) equal to the exact value (calculated as in Raftery and Zeh 1993). The iteration is started by setting $c = 1$.

We estimated β_0^V, β_1^V and β_2^V using the GLIM program (Baker and Nelder, 1978) with binomial error, complementary log-log link and offset D_z^V. Each period and zone with both visual and acoustic data constitutes one case in the GLIM estimation procedure, the denominator for the binomial error distribution is the total number of tracks with acoustic locations in the period and zone, and the numerator is the number of these tracks that also contain visual locations. The estimates (with standard errors) were $\hat{c} = 1.27$, $\hat{\beta}_0^V = -1.97(0.19)$, $\hat{\beta}_1^V = 0.40(0.08)$, and $\hat{\beta}_2^V = -0.38(0.18)$. Similar analyses of acoustic data yielded $\hat{\beta}_0^A = -5.44(0.53)$ and $\hat{\beta}_1^A = 1.13(0.17)$.

There is substantial over-dispersion in the binomial fit, indicated by the deviance being much larger than the number of degrees of freedom. This is not surprising given the dependence of the number of locations on the number of whales present, and the highly dispersed distribution of the latter. However, parameter estimation using the binomial log-likelihood remains valid (McCullagh and Nelder, 1989, p. 126). The standard errors have been adjusted to take account of the over-dispersion.

4.4.4 Tracking Algorithm Parameters and Error Probabilities

We estimated ρ_1, the probability that the tracking algorithm puts a second location from a whale on the same track as the first location, from identified tracks, as described by Raftery and Zeh (1993). We set the maximum speed parameter for the tracking algorithm to 7.5km/hr. Estimates of ρ_1 were computed for a number of different minimum speeds and direction deviations in the tracking algorithm to investigate the sensitivity of the first type of tracking algorithm error to these tracking parameters. Fig. 2 summarizes the results.

Fig. 2(a) shows ρ_1 computed from visual data as a function of minimum swimming speed ranging from 1–4km/hr. Separate lines are shown for each zone and points for all taken

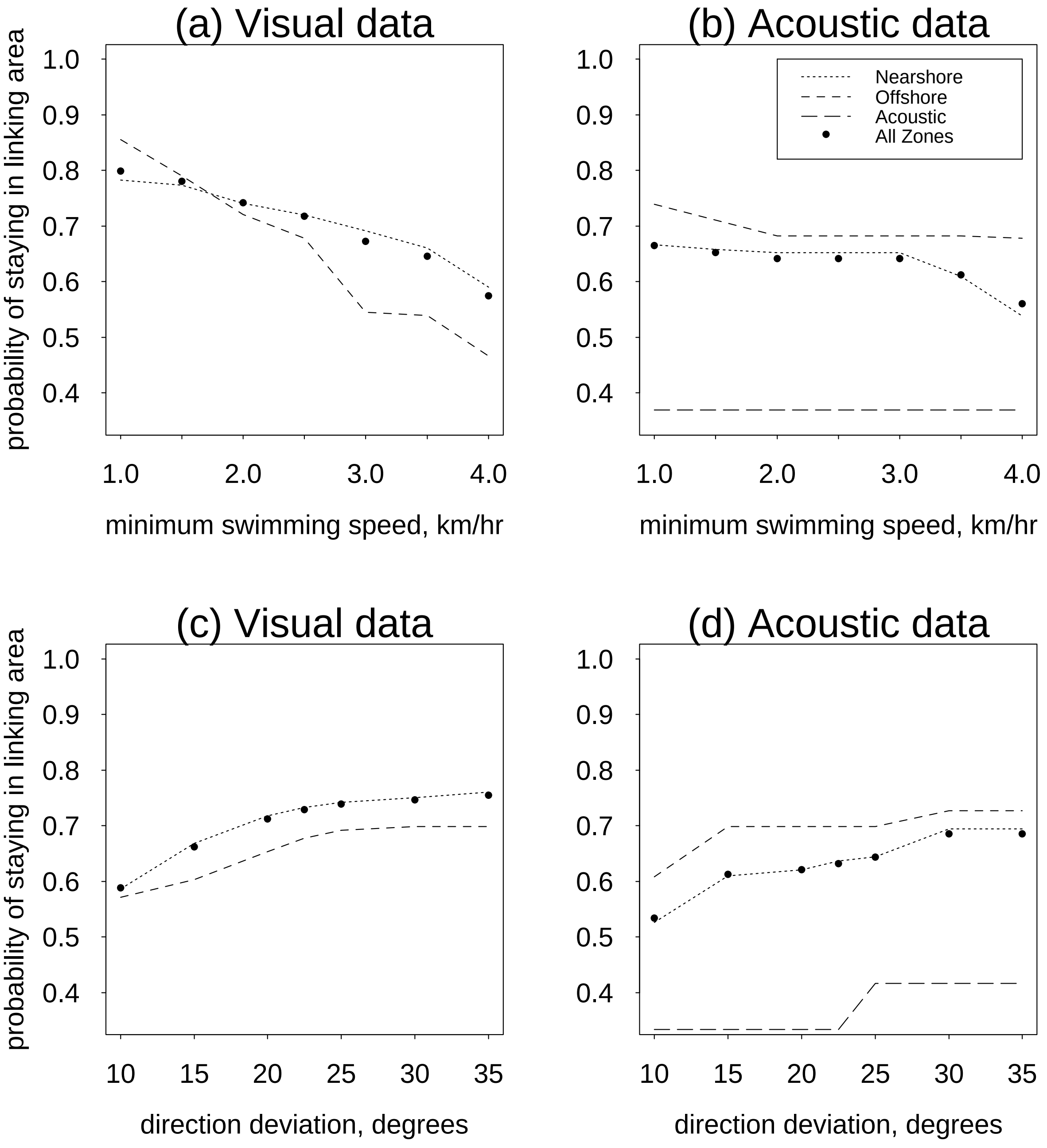

Figure 2: Variation in ρ_1 as a function of minimum speed and direction deviation. The values in (a) and (b) are averages of the ρ_1 values for all the direction deviations considered. The values in (c) and (d) are averages over all the minimum swimming speeds considered. The acoustic results in the offshore and acoustic zones show unusual patterns because they are based on only 25 and 10 acoustically identified whales, respectively.

together. Each plotted value is an average of the ρ_1 values obtained for all the direction deviations considered (10°, 15°, 20°, 22.5°, 25°, 30° and 35°). Fig. 2(b) is the corresponding plot from the acoustic data. Figs. 2(c) and 2(d) show ρ_1 as a function of direction deviation, with plotted values averages over the minimum swimming speeds considered.

Fig. 2 indicates that ρ_1 changes gradually for minimum swimming speeds from 1.5 to 3.5km/hr, decreases more quickly at higher speeds, and changes somewhat more slowly between 1 and 1.5 km/hr. It decreases rapidly when direction deviation is decreased below 15°. It increases gradually with direction deviation from 15°–30° and more slowly from 30° on. These results suggest that sensitivity of the Bayes empirical Bayes population estimate to tracking parameters should be assessed for minimum swimming speeds in the range 1.5–3.5km/hr and direction deviations in the range 15°–30°.

The central values in these ranges (minimum speed 2.5km/hr and direction deviation 22.5°) were given the most weight in calculating the posterior distributions, as described in Section 4.5. The overall value of ρ_1 obtained using the central minimum speed and direction deviation tracking parameters for combined 1993 visual and acoustic data was 0.72.

We now consider estimating ρ_2. We assume that if a whale goes outside its own linking area, and if there were h other whales located in the previous 1.5 hours, it is wrongly linked to another whale with probability $\rho_{2h}^{z,e}$ if it is in zone z ($z = \nu, \omega, \alpha$) and the monitoring effort is e. Effort e can take the values VO (visual only), AO (acoustic only), and VA (both).

We estimated $\rho_{2h}^{\nu,VO}$ as described by Raftery and Zeh (1993). We obtained

$$\rho_{2h}^{\nu,VO} \;=\; 1 \;-\; \exp\left[\,-\,0.252\,h^{0.308}\,\right].$$

We then calculated $\rho_{2h}^{z,e}$ for other tracking parameters, zones, and efforts as described in Raftery and Zeh (1993), using the data on zone areas, range errors in locations and times between locations given by Zeh *et al.* (1995).

4.5 The Posterior Distribution of Total Population Size

The posterior distribution of n_t^z, the number of whales passing in period t and in zone z ($t = 1, \ldots, 75$; $z = \nu, \omega, \alpha$), is derived from the likelihood $p(y|n)$ given by equation (3), and the negative binomial prior distribution. The likelihood (3) is conditional on ρ_2, but the number of tracks, y, itself provides information about the value of ρ_2 for that zone and period. We use the approximation (dropping period and zone superscripts and subscripts):

$$p(n|y) \;=\; \int p(n|\rho_2, y)\, p(\rho_2|y)\, d\rho_2$$

$$\begin{aligned} &\approx p(n|y,\hat{\rho}_2) \\ &\propto p(y|n,\hat{\rho}_2)p(n), \end{aligned}$$

where $\hat{\rho}_2$ is an estimate of ρ_2 for period t and zone z. We use the estimate

$$\hat{\rho}_2 = \sum_{h=1}^{y} \rho_{2h} p(h),$$

where ρ_{2h} is calculated as in Section 4.4.4 and $p(h)$ is the probability that h linking areas are open at a random time in the period, given by a Binomial $(y,\ 1.5/\Delta_t)$ distribution $(h = 1, \ldots, y)$.

We now address the problem of combining the posterior distributions from the individual periods and zones into a single posterior distribution for the total number of whales, N. We do this separately for the monitored periods and zones and for the unmonitored periods and zones. Let M be the total number of whales passing in the monitored periods and zones, and let U be the total number passing in the unmonitored periods and zones, so that $N = M + U$. When there was visual watch but no acoustic monitoring, whales passing in the acoustic zone are considered part of U rather than M.

We approximated the posterior distribution of M by a normal distribution, obtained by computing the posterior mean and variance of n_t^z for each period t and zone z, and adding them up. This approximation, motivated by the central limit theorem, is very good, as we verified by simulation and by computing the posterior skewness and kurtosis of M.

U is a sum of negative binomial random variables with long tails, and is *not* well approximated by a normal distribution. We estimated the posterior density of U by simulating from its posterior distribution and then applying nonparametric kernel density estimation, using the maximal smoothing principle of Terrell (1990) to choose the window width.

So far, we have computed the posterior distribution of M and U conditionally on the tracking algorithm and model parameters. Extensive previous sensitivity analyses have shown that the only parameters to which the posterior distribution of M is sensitive are the minimum swimming speed (MSS), the allowed deviation from the migration direction (SMd) in the tracking algorithm, and the parameters governing the detection probabilities, (β_0^V, β_1^V) and (β_0^A, β_1^A) (Raftery *et al.* 1988, 1990; Sonntag *et al.* 1988). The posterior distribution of U is sensitive only to the prior mean of N.

In order to assess the sensitivity of the posterior distribution to changes in the model and tracking algorithm parameters, we carried out a sensitivity analysis by perturbing the parameters and recomputing the results. The values used for the sensitivity analysis are

Table 3: Parameters for sensitivity analysis.

Parameter	Low	Main	High
MSS (km/hr)	1.5	2.5	3.5
SMd (degrees)	15	22.5	30
β_0^V	-1.638	-1.969	-2.301
β_1^V	0.267	0.399	0.531
β_0^A	-4.531	-5.442	-6.353
β_1^A	0.840	1.132	1.427

shown in Table 3. The basic idea is to use approximate upper and lower quantiles of a notional distribution of plausible values. We use the results not only to assess sensitivity, but also to take uncertainty about the parameters into account by integrating over them, the standard Bayesian prescription. To allow us to use the approximate iterated three-point Gauss-Hermite quadrature described in Raftery and Zeh (1993), we used the approximate 4%, 50% and 96% quantiles.

The vector parameter (β_0^V, β_1^V), which specifies visual detection probabilities and how they depend on visibility, was varied 1.73 standard errors in each direction along the principal component of the approximate covariance matrix of its estimator, as provided by GLIM and corrected for over-dispersion. The vector parameter (β_0^A, β_1^A) was also varied 1.73 standard errors in each direction. The upper and lower values for MSS and SMd were based on data analyses similar to those reported in Zeh *et al.* (1990).

The final posterior distribution of M, the number of whales passing in monitored zones during monitored periods, was obtained using approximate iterated three-point Gauss-Hermite quadrature as in Raftery and Zeh (1993). For the unmonitored periods, we have obtained $p(U \mid \nu)$ by simulation, where ν is the prior mean of N. We are uncertain about ν and we need to incorporate that uncertainty into our final posterior distribution of U using the fact that $p(U) = \int p(U \mid \nu) p(\nu) d\nu$. We evaluate this, as before, using the three-point Gauss-Hermite quadrature formula, namely

$$p(U) \;\approx\; \frac{1}{6}(U \mid \nu_1) + \frac{2}{3}(U \mid \nu_2) + \frac{1}{6}(U \mid \nu_3),$$

where ν_1, ν_2 and ν_3 are the 4%, 50% and 96% quantiles of the distribution of ν. We used the corresponding quantiles of the posterior distribution for 1988 adopted by the IWC (1992), namely $\nu_1 = 6{,}500$, $\nu_2 = 7{,}500$ and $\nu_3 = 8{,}900$. Finally, we obtained the posterior distribution of $N = M + U$, the total number of whales, by numerically convolving the distributions of M and U as in Raftery and Zeh (1993).

5 Results

5.1 The Generalized Removal Method Estimate

The visual census estimate N_4 of the number of whales that passed within viewing range in 1993 is 7,250 with a standard error of 500. Based on the acoustic locations, we estimated that 93% of the whales passed within viewing range (4 km) in 1993, i.e. $\hat{P}_4 = 0.93$. The generalized removal method estimate N_4/P_4 is 7,800 with a standard error of 550. A 95% confidence interval, computed as recommended by Buckland (1992), is [6800, 8900].

5.2 The Bayes Empirical Bayes Estimate

The results of the sensitivity analysis are shown in Table 4. The results are sensitive to changes in the first three of the four parameters considered, but are far less sensitive to changes in (β_0^A, β_1^A) than were the results from previous censuses. This is because most of the whales passed within visual range in 1993, unlike in previous years, and so the results were less dependent on the estimated acoustic detection probabilities.

We obtained the posterior distribution of 1993 population size shown in Fig. 3. The .025 and .975 quantiles of the posterior distribution are 7,200 and 9,400. The posterior mode (most probable value) is 8,200, and the posterior standard deviation is 560. The posterior distribution is only slightly asymmetric.

In comparison, the 1988 posterior distribution had 95% of its probability between 6,400 and 9,200. The mode of the 1988 distribution was 7,500 and the standard deviation was 700. The posterior variance was about one-third less in 1993 than in 1988, indicating considerable success in reducing uncertainty about the population size.

The larger posterior standard deviation and greater asymmetry of the posterior distribution in 1988 were due primarily to the larger amount of unmonitored time (71 hours, compared to 26 hours in 1993.) Time with visual but not acoustic monitoring also played a larger role in 1988. The reason can be seen by comparing Fig. 1 of the present paper with Fig. 2 of Raftery and Zeh (1993). A larger percentage of the whales passed Point Barrow in

Table 4: Sensitivity analysis results (in hundreds). “1” means that the “low” value of the parameter from Table 3 is used, “2” means that the “main” value is used, and “3” means that the “high” value is used.

MSS	SMd	β^V	β^A	Estimate
2	2	2	2	82
1	2	2	2	76
3	2	2	2	88
2	1	2	2	87
2	3	2	2	78
2	2	1	2	80
2	2	3	2	83
2	2	2	1	82
2	2	2	3	82
1	1	2	2	81
1	3	2	2	73
3	1	2	2	95
3	3	2	2	84
1	2	1	2	75
1	2	3	2	77
3	2	1	2	87
3	2	3	2	89
1	2	2	1	76
1	2	2	3	76
3	2	2	1	88
3	2	2	3	88
2	1	1	2	86
2	1	3	2	89
2	3	1	2	76
2	3	3	2	79
2	1	2	1	87
2	1	2	3	87
2	3	2	1	78
2	3	2	3	78
2	2	1	1	80
2	2	1	3	80
2	2	3	1	83
2	2	3	3	83

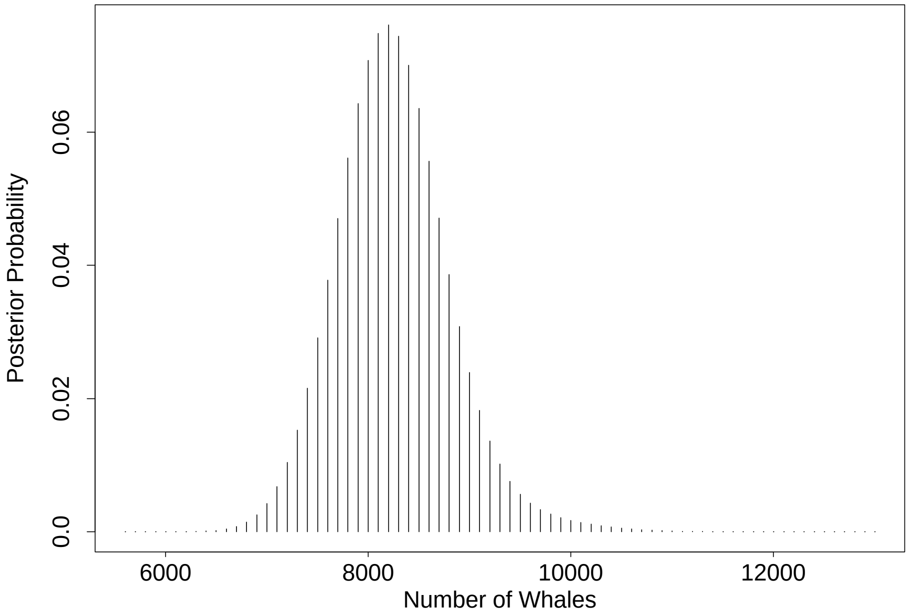

Figure 3: Posterior distribution of the number of whales for 1993.

the acoustic zone, beyond viewing range, in 1988 than in 1993. In periods with visual but not acoustic monitoring, the acoustic zone is treated as unmonitored. The prior distribution for the number of whales that passed in the acoustic zone is used as the posterior distribution for such periods. Thus these periods contributed more uncertainty to the final combined posterior distribution in 1988 than in 1993.

We can find the main sources of uncertainty about whale numbers, as measured by the posterior variance in 1993. We find that 64% of the posterior variance is due to uncertainty about the tracking algorithm parameters and detection probabilities, 31% to periods without any monitoring or without monitoring in the acoustic zone, and the remaining 5% to uncertainty about whale numbers in the monitored periods conditional on the estimated model parameters. This is in contrast to 1988, when the majority (57%) of the posterior variance was due to unmonitored periods.

5.3 Rate of Increase, 1978–1993

Zeh *et al.* (1991) estimated that bowhead population size had been increasing at 3.1% per year between 1978 and 1993, with 95% confidence interval [0.1%, 6.2%]. This was the first time it had been shown that the bowhead population was increasing in spite of the annual

Table 5: Data for the calculation of 1978–1993 rate of population increase.

Year	N_4	SE(N_4)	P_4	SE(P_4)	N_4/P_4	SE
1978	3,383	289	0.674	0.189	5,019	1,476
1980	2,737	488	0.674	0.189	4,061	1,365
1981	3,231	716	0.750	0.108	4,308	1,147
1982	4,612	798	0.674	0.189	6,843	2,279
1983	4,399	839	0.674	0.189	6,527	2,241
1985	3,134	583	0.519	0.131	6,039	1,915
1986	4,006	574	0.518	0.062	7,734	1,450
1987	3,615	534	0.674	0.189	5,364	1,714
1988	4,862	436	0.739	0.053	6,579	757
1993	7,249	505	0.933	0.013	7,770	552

take by Eskimo hunters. However, the width of the confidence interval and the closeness of its lower bound to zero indicate that it was not known, based on the data up to 1988, whether the rate of increase was a healthy one or not.

We updated these results by including the 1993 data, and also by using N_4/P_4 instead of N_4 in the calculation as recommended by IWC (1995). We used the aerial survey data of Marquette *et al.* (1982) to estimate P_4 for the 1981 census. For years in which no acoustic or aerial data were available, we assigned a value of P_4 estimated from the years for which such data were available, namely 0.674, but with a large standard error based on the inter-annual variation, namely 0.189. The data used to estimate the rate of increase are shown in Table 5.

The rate of increase was estimated by a regression of $\log(N_4/P_4)$ on (year − 1977), with an additional variance component for the measurement error, as in Zeh *et al.* (1991). The estimated annual rate of increase from 1978 to 1993 is 3.2%, with 95% confidence interval [1.4%, 5.1%]. The curve representing this increase is shown in Fig. 4, along with the population estimates on which it is based.

6 Discussion

We have presented the data from the 1993 visual and acoustic census of bowhead whales, and the final version of the two population estimation methods. The generalized removal method estimate is 7,800 with 95% confidence interval [6800, 8900], while the Bayes empirical Bayes

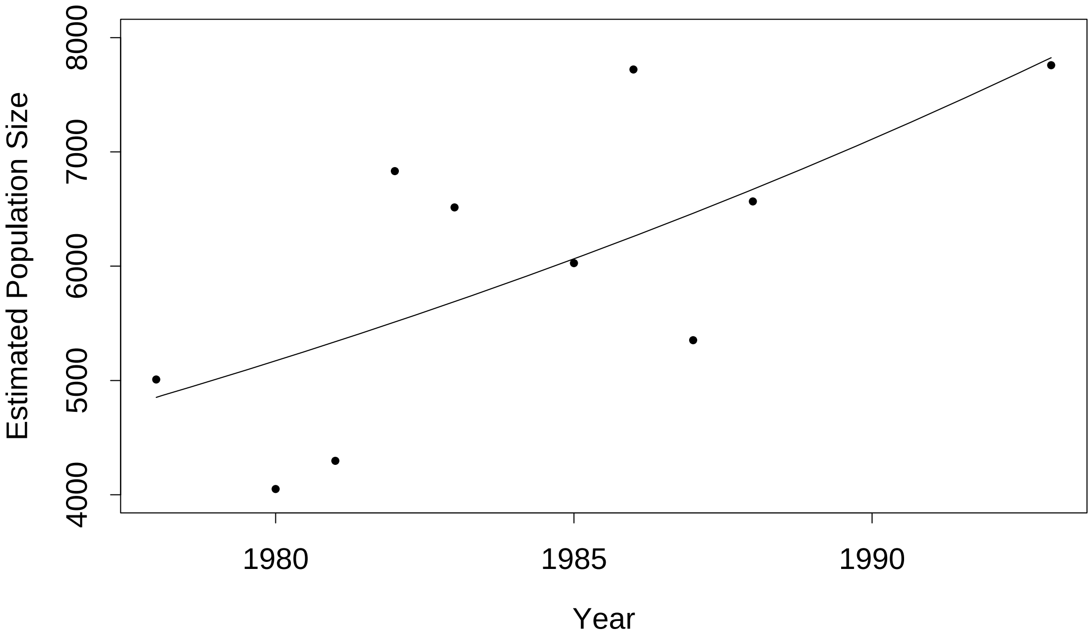

Figure 4: Generalized removal method estimates of bowhead population size, 1978–1993, and exponential growth curve fit to them.

method gives the most probable value as 8,200 with 95% of the posterior probability in the range [7200, 9400]. The two methods give results that are in close agreement, reinforcing confidence in each of them. At its 1995 meeting in Dublin, Ireland, the IWC Scientific Committee accepted an estimate of bowhead whale population size based on the Bayes empirical Bayes posterior distribution.

The Scientific Committee also accepted our estimate of 1978-1993 rate of increase in the population. This is 3.2% with 95% confidence interval [1.4%, 5.1%]. Addition of the 1993 estimate to the time series of generalized removal method estimates allowed us to establish that the bowhead population is increasing at a healthy rate. The bowhead was the first species of great whale of which commercial hunting stopped after greatly reducing the stock, and the fact that it is now recovering shows that great whale populations can recover if they are protected from commercial whaling.

These results were combined with biological information and knowledge of the historic catch record using the Bayesian synthesis method (Raftery, Givens and Zeh 1995; Givens, Zeh and Raftery 1995), to yield an upper bound for the allowable subsistence whaling quota, which would permit the population to continue to recover. The final quota was set by the IWC with reference to subsistence need as well as the biological constraints; it was well below the specified upper bound.

The fact that the simpler generalized removal method and the more refined Bayes empirical Bayes approach gave similar results shows that the overly simple assumptions underlying the simpler method and its very partial use of the acoustic data did not seriously impair its accuracy. Of course, it would have been hard to know this without doing the fuller Bayes empirical Bayes analysis.

The Bayes empirical Bayes approach has provided several other benefits. The most important of these was that it enabled us to partition the uncertainty about N according to its sources, and in this way helped to decide how best to allocate the data collection resources so as to minimize uncertainty. In the 1986 census, unmonitored time was by far the largest source of uncertainty, accounting for 84% of the posterior variance of N. This led us to advise that in designing subsequent censuses, resources be allocated first to reducing the amount of unmonitored time, especially by increasing the number of hydrophones and by replacing them quickly when lost. The combination of our advice and better weather led to a decrease in acoustically unmonitored time from 698 hours in 1986, to 520 hours in 1988, to 295 hours in 1993. The number of hours with neither acoustic nor visual monitoring went down from 244 to 71 to 26 hours. This resulted in a nearly five-fold reduction in posterior variance from 1986 to 1993.

Since inference in the Bayes empirical Bayes approach follows directly from a set of biological assumptions, it provided an effective way of communicating the method and the results to the other (about 100) members of the International Whaling Commission Scientific Committee. This was helped by our sensitivity analysis, which enabled us to answer the many "what if" questions that arose.

Another contribution of Bayesian thinking was to enable us to incorporate the results of the sensitivity analysis into our conclusions. Sensitivity analyses are often just reported and not acted upon: if the results are not sensitive to a particular assumption or input, all is well; if they are sensitive, that fact is recorded and some words of caution are put into the report. The Bayes empirical Bayes approach enables us to take the necessary further step and account for the uncertainty associated with the sensitivity in our final inference. Many sensitivity analyses are based on a 3^k design, where "high", "main" and "low" values are assigned for each input and the model is run for all or some combinations of these. We have shown how, by using a simple modification of iterated three-point Gauss-Hermite quadrature, we can parlay the sensitivity analysis results into a full assessment of uncertainty. The Bayesian approach also yielded a more satisfactory way of assessing the contribution of unmonitored time to the overall uncertainty in the population estimate.

The final main contribution of the Bayesian approach is its ability to incorporate external (or "prior") information. Population size estimation is intrinsically hard because there is often a near non-identifiability between detection probability and population size. External information can be important in breaking this near non-identifiability and should be used whenever available; the Bayesian approach makes it easy to do so. Here we had three data sources that were "external" in the sense of not being used in the estimation proper: the set of visual duplicates, the acoustic call tracks based on spectrogram analysis, and the previous (1988) census. These were all used to develop "prior" distributions for the parameters of the Bayes empirical Bayes model.

On the other hand, the generalized removal method has some advantages over the Bayes empirical Bayes approach because it is simpler. A much smaller sample of acoustic locations is required to produce a reliable estimate, and the removal method estimate has proven to be less sensitive to errors in acoustic locations than the Bayes empirical Bayes estimate. This is because the removal method estimate does not require the use of the tracking algorithm. Since tracking algorithm error probabilities do not need to be estimated, no data from acoustically identified whales are needed. Since tracking algorithm minimum speed and direction deviation parameters do not need to be chosen, variability caused by less than optimal choices of these parameters is eliminated. Since both collection and analysis of census data required by the generalized removal method are easier and cheaper, more frequent censuses can be conducted if the goal is to produce a generalized removal method estimate than if a Bayes empirical Bayes posterior distribution is to be computed.

The software to compute the Bayes empirical Bayes estimate, and the 1993 census data on which it is based, have been lodged with the Secretariat, International Whaling Commission, The Red House, Station Road, Histon, Cambridge CB4 4NP, U.K.

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