

# Estimating Bowhead Whale Population Size and Rate of Increase From the 1993 Census

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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, 8,200 with 95% estimation interval from 7,200 to 9,400, 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.

## 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 seven 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 cumu-

lative 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 great whale, except gray whales. In this article we present the results from the 1993 visual and acoustic census, which was the best one to date, and 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. Efforts were made to overcome this 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. First, some whales pass Point Barrow without being detected. This can happen because they pass too far from shore to be seen or heard, they pass close enough to shore but neither vocalize nor surface while within range, or they pass during periods in which no visual or acoustic monitoring occurs. Even when monitoring occurs and whales manifest themselves within range, they may be missed because their surfacings are not seen and their vocalizations not recorded. This can happen under good visual and acoustic conditions but is most likely when conditions are poor. Second, even when

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whales are detected, it is not always possible to tell whether the visual and acoustic locations recorded represent several different whales or only one whale.

Here we summarize two different statistical methodologies for estimating population size that have been developed in parallel over the past 10 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. The generalized removal method is straightforward conceptually and computationally, but it depends on several broad assumptions that are hard to verify.

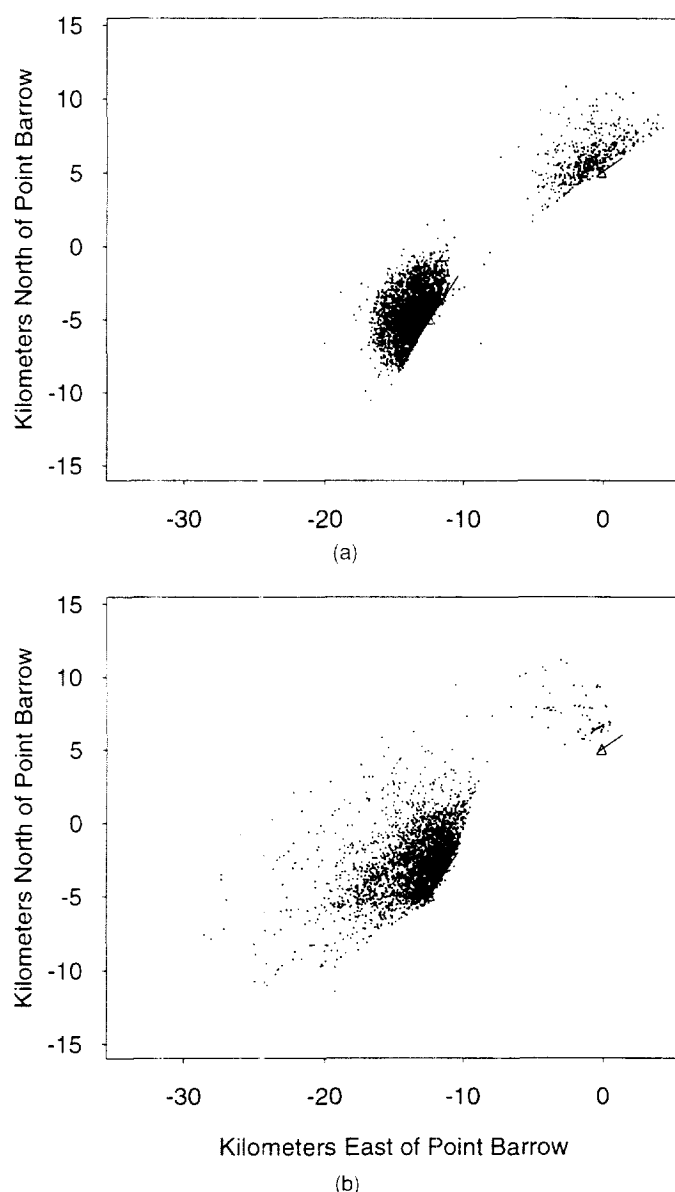


Figure 1. Locations of Bowhead Whales (a) Seen and (b) Heard During the Spring Migration Past Point Barrow, Alaska, in 1993. In each plot two solid lines show the hydrophone arrays during different parts of the migration and two triangles show the corresponding census perches. One unusual acoustic location at  $(-55, -16)$  is omitted from (b).

Thus we 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. The IWC (1995) also recommended that rate of increase be estimated from the generalized removal method population estimates. Only preliminary estimates based on incomplete data were available at the 1994 Scientific Committee meeting. An augmented and refined acoustic dataset was subsequently analyzed to produce the estimates reported herein; 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. Whales are counted from observation sites, called perches, located on ridges of ice near the edge of the channel, called a lead, through which many of the whales migrate. Two perches, each 7–10 m high and within 50 m of the lead edge, were used at different times during the 1993 census. Three observers were on the perch 24 hours a day; one operated a theodolite (used for obtaining whale positions), another recorded the data, and the third watched for whales. Of course, the first two also watched for whales when not occupied with their other assigned tasks. When bowheads surface as they pass the perch, they generally do so several times in rapid succession, so the observer operating the theodolite is able to sight on a standard spot near the blowhole when a whale is seen. Locations of whales computed from theodolite data are accurate; for example, range errors have a standard deviation estimated to be around 2% of range. The visual locations are shown in Figure 1a.

Locations of whales detected acoustically must also be computed before the acoustic and visual data can be combined. Clark, Charif, Mitchell, and Colby (1996) described 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-degree sector defined by the hydrophone array are candidates for location analysis. Sounds outside the 120-degree sector (i.e., within 30 degrees of the array axis) are not processed, be-

cause ranges to such sounds cannot be determined reliably. Within the 120-degree sector, locations are quite accurate. The median of the range errors computed by Clark et al. (1996) for the 1993 acoustic locations was 4% of range. The effect of the 120-degree sector can be seen in Figure 1b, which shows the 6,042 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 census season was divided into blocks of time defined by changes in perch location and visibility conditions. One-half of the blocks in each visibility stratum were randomly chosen initially. All times with acoustic but no visual monitoring were also included in the sample. The final sample also included all possible periods with poor visibility, because many whales are missed by the visual census during such periods; the acoustic data provide most of the information about the number of whales that passed during those periods. Although we did not stratify by acoustic arrays or conditions, all were well represented in the sample.

The 1993 census season was divided into 75 monitored and 3 unmonitored periods, of which some examples are 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.

In 1993, most of the whales passed within visual range, to a greater extent than in previous years. There were about 3.3 whale tracks per hour within visual range. But whales passed the census point at vastly differing rates during the season. One-half of the whales passed during periods totalling only 20% of the season, during which the average number of tracks per hour was 8.25. By contrast, during the least busy 20% of the season, there were only .15 tracks per hour. Thus more than 50 times more whales passed during

the season's busiest quintile than during the least busy quintile.

There was a visual watch during 96% of the season, with watch continuing 24 hours a day (there is virtually continuous daylight at this time of year at Point Barrow). However, visual conditions were not good overall, with median visibility score 2 ("fair") and interquartile range 1.5–2.9 on a scale of 0 ("unacceptable")–5 ("excellent").

We have acoustic data for only 45% of the season, but acoustic conditions were better than visual ones during these times, with a median acoustic condition score of 3 ("good") and a narrow interquartile range of 2.7–3.2. Acoustic data is unavailable for many periods, because the hydrophones had been smashed by the ice and not yet repaired, whereas for other periods the audio tapes have not been analyzed.

In some cases it is impossible to know whether different locations correspond to different whales, but many of the visual locations in 1993 were from whales that were identified as having been seen several times. Also, a subset of acoustic locations provided call tracks (Clark 1989; Clark et al. 1996) of acoustically identified whales. The locations from visually and acoustically identified whales constituted identified tracks 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-

Table 1. Monitored Periods: 1993 Bowhead Whale Visual and Acoustic Census

Period	Monitoring					$\Delta_t$	Locations		Average conditions		New whales	Tracks by zone			Total tracks
	Start		End		Near-shore							Off-shore	Acoustic		
	Day	Time	Day	Time			Visual	Acoustic	Visual	Acoustic					
66	5/23	14:08	5/24	04:00	13.9	44	NE	3.00	0	25	21	0	0	21	
67	5/24	04:00	5/25	00:49	20.8	14	NE	2.18	0	11	9	0	0	9	
68	5/25	00:49	5/25	10:00	9.2	11	0	1.18	2.92	9	8	0	0	8	
69	5/25	10:00	5/26	10:00	24.0	73	22	3.06	2.55	51	40	7	0	47	
70	5/26	10:00	5/26	19:10	9.2	42	27	1.00	2.89	21	22	2	1	25	
71	5/26	19:10	5/27	14:17	19.1	86	105	2.96	2.97	50	42	11	4	57	
72	5/27	14:17	5/28	00:27	10.2	87	22	4.12	2.30	45	32	8	1	41	
73	5/28	00:27	5/29	05:46	29.3	62	37	1.52	2.59	39	35	10	1	46	
74	5/29	05:46	5/30	08:24	26.6	2	NE	3.47	0	1	1	0	0	1	
75	5/30	08:24	5/30	14:00	5.6	0	0	2.24	2.53	0	0	0	0	0	
Total (over the 75 periods)					1,015	5,337	6,042			3,376	2,518	792	196	3,506	

NOTE:  $\Delta_t$  is the number of monitored hours. NE means no effort of the type indicated (usually acoustic) during the time period. Only the last 10 of the 75 periods are shown. The full dataset is available at <<http://www.stat.washington.edu/raftery/Research/Whales/data93>>.

Table 2. Unmonitored Periods, 1993

Start		End		$\Delta_t$
Day	Time	Day	Time	
5/17	06:02	5/17	21:00	15.0
5/18	12:10	5/18	15:51	3.7
5/22	18:02	5/23	01:30	7.5
Total				26

NOTE:  $\Delta_t$  is the number of unmonitored hours.

only bowhead censuses of 1978–1983. In these years, two perches (South and North) were operating simultaneously (unlike in later years, when there was only one perch at a time). Because the whales move from south to north, South Perch 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 Perch, whose mission was to look for whales missed by South Perch.

If  $n_1$  is the number of whales seen at South Perch, and  $n_2$  is the number missed at South Perch but seen at North Perch out of  $N$  whales passing in a given time period, then 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 maximum likelihood estimators (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 perch. Zeh, George, Raftery, and Carroll (1991) adapted it to this situation for the 1986–1988 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). Then  $\hat{N} = n_1 / \hat{p}$ , where  $n_1$  is the number of whales seen at the perch and  $\hat{p}$  is the MLE from 1978–1985. 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 acoustic locations directly offshore from the hydrophone array that were within 4 km for this correction. They also 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 that may not hold. It assumes no heterogeneity in sightability among whales, which seems questionable; for example, slower whales may be more likely to be seen. But

this would lead to the estimator  $\hat{N}$  being biased downward, 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). 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

The Bayes empirical Bayes method was developed to avoid the possible oversimplifications of the generalized removal method and to make fuller use of the acoustic data. It has been developed and improved over the past 10 years, with successive iterations 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 data collection. 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; this is further discussed in Section 6. 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:

1. The area offshore from the census perch is divided into three zones: nearshore (within 2 km), offshore (2–4 km), and acoustic (beyond 4 km). Within each period and zone, visual and acoustic locations are linked together to form tracks using a tracking algorithm.
2. 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.
3. The results for different periods and zones are combined to yield an overall posterior distribution for the entire census season.
4. Uncertainty about the tracking algorithm and model parameters is taken into account by rerunning steps 1–3 for a collection of plausible parameter values, and combining

the results in a Bayesian way via approximate numerical integration.

The method overcomes the main difficulties with the generalized removal method. It estimates detection probabilities from the 1993 data themselves, takes heterogeneity in sightability into account explicitly, uses the automated tracking algorithm rather than the observer judgements to obtain the counts of new whales, and models the errors made by the tracking algorithm explicitly. It also assesses uncertainty using a Bayesian posterior distribution rather than the jackknife and makes much fuller use of the acoustic data.

This method is referred to as the Bayes empirical Bayes method because the quantity to be estimated (total population) is viewed as the sum of many components (the numbers of whales passing in each period and zone), each of which itself has to be estimated. These components are viewed as exchangeable a priori, and this is used in estimating them, leading to a parametric empirical Bayes approach (Morris 1983). The common distribution of these components is specified by hyperparameters, and a Bayesian approach is used to incorporate uncertainty and external information about these hyperparameters, making this a fully Bayes empirical Bayes approach (Deely and Lindley 1981).

#### 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 Raftery and Zeh (1993), Sonntag, Ellison, and Corbit (1988), and Zeh, Raftery, and Yang (1990).

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) so that they are likely to be from the same whale. Range and bearing errors for acoustic locations are computed as in Clark et al. (1996), refining methods first developed by Clark, Ellison, and Beeman (1986).

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 range errors and 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/hour. An allowed deviation from the migration direction of  $\pm 22.5$  degrees and a minimum swimming speed of 2.5 km/hour were our central parameter values. We used direction deviations of  $\pm 15$  degrees and  $\pm 30$  degrees and minimum swimming speeds of 1.5 km/hour and 3.5 km/hour 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  $\nu$ ,  $\omega$ , and  $\alpha$  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 passing in each period within each zone are independent Poisson random variables with different means. The mean for a period is proportional to its length. The constants of proportionality for the different periods—rates of passage in whales per hour—are allowed to be different and are assumed to be random variables drawn from a gamma distribution with shape parameter  $\gamma$  and scale parameter  $\phi^\nu$ ,  $\phi^\omega$ , or  $\phi^\alpha$ .

A2. The numbers of surfacings and 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  $\lambda^V$  and  $\lambda^A$ .

A3. Detection probabilities depend on environmental conditions in a log-linear manner. We denote by  $\pi_t^V$  the probability that a whale is located if it surfaces, and by  $\pi_t^A$  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. A similar result holds 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  $\lambda^V$  and  $\pi_t^V$  or  $\lambda^A$  and  $\pi_t^A$  separately. We let

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

where  $x_{1t}^V$  = average visibility in period  $t$  and  $x_{2t} = 1$  for the offshore zone and 0 otherwise. Because no dependence of acoustic detection probability on zone was found in previous years, we let

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

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

A4. The average time,  $\sigma$ , that a whale takes to swim 1 km 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 random, following a uniform distribution in each time period.

We also model errors made by the tracking algorithm. We consider two types of error. The first type is the one that can lead to double counting. If a whale is located twice, then 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  $\rho_2$  the probability that if a whale goes outside its linking area or if it has not previously been located, then it is wrongly linked to another whale. This can vary by period and zone and depends on the number of whales located; estimation of this parameter is discussed in Section 4.5.

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,  $n$ , 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  $\mathbf{w} = (w_0, w_1, \dots)$  has a multinomial distribution with parameters  $n$  and  $\mathbf{q} = (q_0, q_1, \dots)$ . It follows that

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

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 over  $i$  from 0 to infinity unless otherwise specified.

We now derive the  $q_i$ . Let  $\mu$  be the average number of locations of a whale swimming at 1 km/hour. This is  $\lambda^V \pi_t^V \kappa^{z,V}$  for the nearshore or the 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 the offshore zone with both visual watch and acoustic monitoring, and  $\lambda^A \pi_t^A \kappa^{z,A}$  for the nearshore or the 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  $z$  ( $z = \nu, \omega, \text{ or } \alpha$ ) and  $\kappa^{z,A}$  is the corresponding acoustic quantity.

How the tracking algorithm affects different manifestations of the same whale produces 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 will not produce an additional track, with probability  $\psi = 1 - (1 - \rho_1)(1 - \rho_2)$ . Also, given  $\sigma$ , the average time the whale takes to swim 1 kilometer, we have

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

and

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

It remains only to find  $\Pr[W = i|k]$ , and this follows directly from the foregoing probabilities. 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 data from Tables 1 and 2, and all other information, viewed as "external" or "prior" information. The latter includes 1988 census results, the 1993 distribution of the whales offshore computed from acoustic locations, and identified tracks from the 1993 census itself. 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; thus there is no double counting of information here.

**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,  $\text{NB}(\gamma, \phi^z \Delta_t)$ , by assumption (A1), where  $\Delta_t$  is the length of period  $t$ , in hours. Estimates of  $\gamma$  and  $\phi^z$  were based on acoustic locations directly offshore from the hydrophone array; that is, in a rectangle with the hydrophone array as one side. This eliminates the effect of the 120-degree sector and makes it reasonable to assume that the number of locations in each zone is proportional to the number of whales passing, and thus is proportional to  $\phi^z$ . We estimated  $\gamma$  by assuming that within each zone, the distribution of the number of these locations in a randomly chosen hour had the same shape parameter  $\gamma$  as the corresponding distribution of the number of whales, but a different mean. This would be the case if the numbers passing in different hours within the same period were independent and identically Poisson distributed random variables, which follows from our assumption (A5). We obtained  $\hat{\gamma} = .114$  by equating the observed and expected means and numbers of zero values (Johnson and Kotz 1969, p. 131).

Having obtained  $\hat{\gamma}$  in this way, we then used it and the 1988 data to obtain the  $\phi^z$ s. Let  $N$  be the total number of whales that passed Point Barrow in spring 1993. Then the prior distribution of  $N$  is that of a sum of independent negative binomial random variables. To estimate the  $\phi^z$ , 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 then obtained  $(\phi^\nu, \phi^\omega, \phi^\alpha) = (44.3, 15.0, 4.1)$ . Although the resulting prior distribution is centered at the 1988 estimate, it is very dispersed relative to the likelihood, and so the final result is relatively insensitive to its precise specification. This statement is based on numerical experiments that are not reported here, but related sensitivity analyses for earlier data and versions of the method have been reported by Raftery, Zeh and Styer (1988) and Raftery et al. (1990).

Fewer than 7% of the whales were outside visual range in 1993, compared to more than 20% in 1988. This difference is probably due to environmental differences between the two years—in particular, differences in distributions of ice and open water along the whales' migration route (George et al. 1995).

**4.4.2 Whale Behavior.** Bowheads pass Point Barrow migrating northeast. George et al. (1995) estimated that 91% of the whales were travelling steadily in the migration direction as they passed the census perch during the 1993 census. The remainder were travelling south or lingering near the perch. These whales are accounted for by the  $\rho_1$  parameter discussed in Section 4.4.4. Although some whales pass too far offshore to be seen, it is reasonable to assume that in most years, including 1993, they are within acoustic range, and we make that assumption. Failure of that assumption to hold would lead to downward bias in our estimates.

Whales are seen when they surface and recorded by the hydrophones when they are beneath the surface. Zeh et al. (1993) reported that the length of time a bowhead spends beneath the surface during a dive ranges from about 1 minute to more than 30 minutes. They are on the surface where they can be seen by observers only about 5.2% of the time. But most whales that pass the perch within viewing range surface at least once, giving observers an opportunity to see them. Many whales vocalize frequently while within range of the hydrophones, but some may pass without vocalizing at all.

Swimming speeds vary considerably between whales, and we approximated the distribution of  $\sigma$  = time to swim 1 km (in hours) 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  $-50$  degrees and  $100$  degrees, where  $0$  degrees is north. The estimated values were  $\hat{a} = 1.19$  and  $\hat{b} = 3.75$ . The mean was  $\hat{a}/\hat{b} = .32$  hours, compared to  $.60$  hours in 1988. Thus whales were traveling on average almost twice as fast in 1993 as in 1988: at about  $3.1$  km/hour in 1993 compared to about  $1.7$  km/hour in 1988. This was due to more northbound currents and fewer southbound currents in 1993 than in 1988, so that whales were more often swimming with the current in 1993.

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. For example, to find  $\kappa^{\nu,V}$ , the number of kilometers swum within visual range by a whale in the nearshore zone, we note that the zone midpoint is  $1$  km from the array, and that the limits of visual range are defined by a semicircle centered at the perch with radius  $4$  km and edge on the array. This semicircle has equation  $x^2 + y^2 = 16$  in the coordinate system with origin at the perch and with the array on the  $x$ -axis. Thus the whale swimming parallel to the perch and  $1$  km from it enters and leaves visual range at points  $(\pm\sqrt{15}, 1)$ , so that  $\kappa^{\nu,V} = 2\sqrt{15} = 7.75$ . Similarly,  $\kappa^{\omega,V} = 2\sqrt{7} = 5.29$ ,  $\kappa^{\nu,A} = d_A + 2\sqrt{3} = 7.89$ ,  $\kappa^{\omega,A} = d_A + 6\sqrt{3} = 14.82$ , and  $\kappa^{\alpha,A} = d_A + d_{120^\circ}2\sqrt{3} = 21.75$ , where  $d_A = 4.43$  km is the length of the hydrophone array and  $d_{120^\circ}$  is the distance at which the effect of the  $120$ -degree sector stops, taken to equal  $5$  km (Zeh et al. 1990, p. 415).

**4.4.3 Detection Probabilities.** We estimated the dependence of visual detection probabilities on visibility by considering all of the tracks that 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 dataset where the initial capture consists of acoustic location and the recapture consists of visual location.

Given  $\sigma$  = the average time that the whale takes to swim  $1$  km, the probability that it will be visually detected is

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

where  $V$  is the event that a whale in zone  $z$  ( $z = \nu, \omega$ ) is visually located, by assumption (A3). This is because the number of visual locations is a Poisson random variable with mean  $\lambda^V \pi_t^V \kappa^{z,V} \sigma$ , and a whale is located if and only if this number is not  $0$ ; (5) gives the probability of this. The result for the acoustic detection probability is similar.

The events of visual and acoustic location are assumed here to be statistically independent, conditionally on  $\sigma$  and on the visual and acoustic conditions, given that both visual and acoustic monitoring is taking place. This is supported by the fact that the visual and acoustic monitoring processes are physically independent and separate. Also, empirically, the correlation between the numbers of visual and acoustic locations per track in different periods is small and not significant, at  $-.2$ .

In practice, however, we do not observe  $\sigma$ , and so visual and acoustic detection of the same whales are not *unconditionally* independent. We use the approximation

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

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

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

where  $D_z^V = \log(c \kappa^{z,V} \bar{\sigma})$ . The left side of (7) is the complementary log-log transform of  $p(V|A)$ . The value of  $c$  was estimated by iterating between fitting equation (7) using the GLIM program (Baker and Nelder, 1978) and setting equation (6) equal to the exact value (calculated as in Rafferty and Zeh 1993). The iteration is started by setting  $c = 1$ .

We estimated  $\beta_0^V$ ,  $\beta_1^V$ , and  $\beta_2^V$  using 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  $\hat{c} = 1.27$ ,  $\hat{\beta}_0^V = -1.97$  (.19),  $\hat{\beta}_1^V = .40$  (.08), and  $\hat{\beta}_2^V = -.38$  (.18). Similar analyses of acoustic data yielded  $\hat{\beta}_0^A = -5.44$  (.53) and  $\hat{\beta}_1^A = 1.13$  (.17).

There is substantial over-dispersion in the binomial fit, indicated by the deviance being much larger than the number of degrees of freedom. 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. This overdispersion does not affect what follows, apart from its effect on the uncertainty about  $\beta_0^V, \beta_1^V, \beta_2^V, \beta_0^A$ , and  $\beta_1^A$ .

**4.4.4 Tracking Algorithm Parameters and Error Probabilities.** We estimated  $\rho_1$ , 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 7.5 km/hour. Estimates of  $\rho_1$  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. Figure 2 summarizes the results.

Figure 2a shows  $\rho_1$  computed from visual data as a function of minimum swimming speed ranging from 1 to 4 km/hour. Separate lines are shown for results of just the identified tracks in each zone, and points for results based

on all of the visually identified tracks regardless of zone. Each plotted value is an average of the  $\rho_1$  values obtained for all of the direction deviations considered (10, 15, 20, 22.5, 25, 30, and 35 degrees). Figure 2b is the corresponding plot from the acoustic data. Figures 2c and 2d show  $\rho_1$  as a function of direction deviation, with plotted values averaged over the minimum swimming speeds considered.

Figure 2 provides an informal way of specifying a reasonable range of plausible values of the minimum swimming speed (MSS) and the maximum direction deviation (SMD). Starting at 0,  $\rho_1$  should decline slowly as a function of MSS up to the true value, and thereafter more rapidly. Figure 2 indicates that  $\rho_1$  changes gradually for minimum swimming speeds of 1.5–3.5 km/hour, decreases more quickly at higher speeds, and changes somewhat more slowly at 1–1.5 km/hour. This suggests that MSS should be at most 3.5 km/hour, and that values of 1.5–3.5 km/hour are plausible.

Similarly, the distribution of (absolute) deviations from the main migration direction would resemble a mixture of a zero-mean symmetric distribution truncated at 0, and a roughly uniform distribution. The first component of the

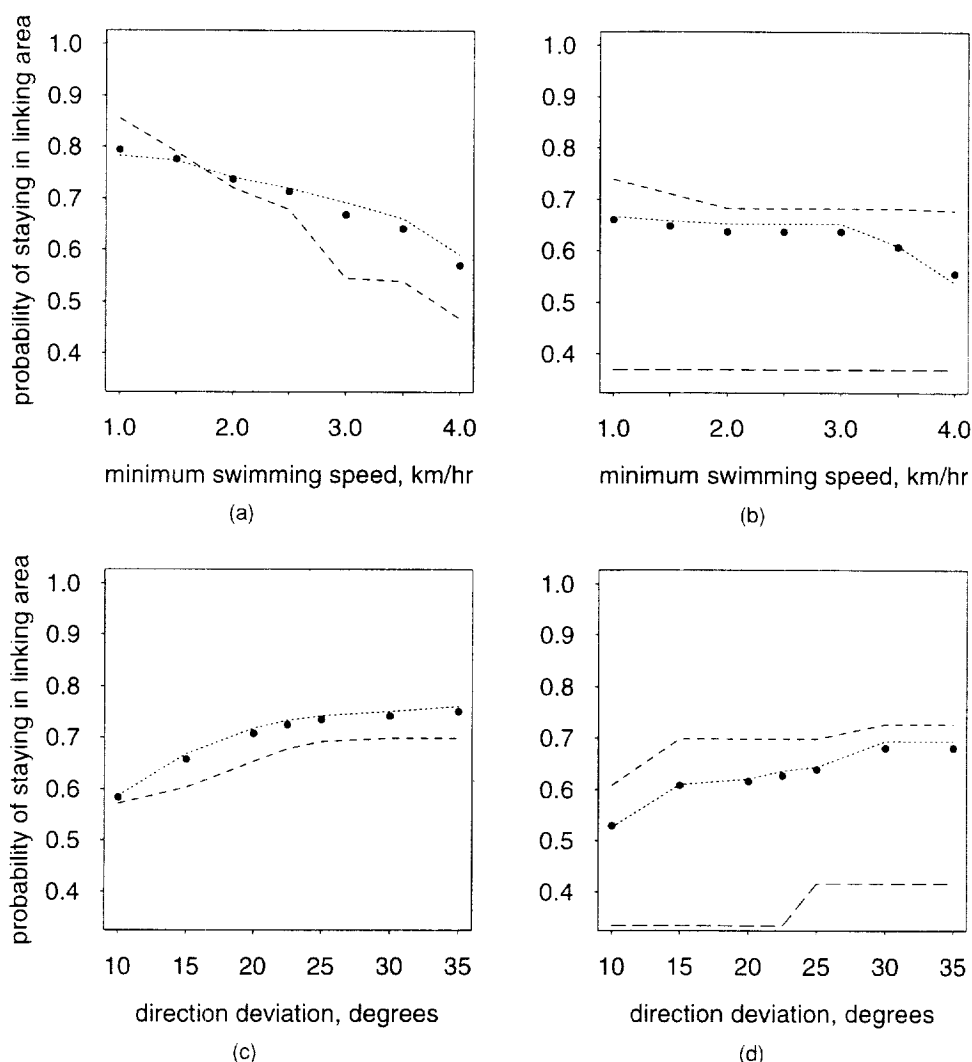


Figure 2. Variation in  $\rho_1$  as a Function of Minimum Speed and Direction Deviation.  $\cdots$ , Nearshore;  $---$ , offshore;  $-.-$ , acoustic; and  $\bullet$ , all zones. The values in (a; visual data) and (b; acoustic data) are averages of the  $\rho_1$  values for all the direction deviations considered. The values in (c; visual data) and (d; acoustic data) 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 tracks.



mixture corresponds to migrating whales, and the second component corresponds to whales that are resting, feeding, or playing, and thus moving (if at all) in an unpredictable direction. One thus would expect the plot of  $\rho_1$  as a function of SMd to increase rapidly from SMd = 0 up to the true value and much more slowly thereafter. Figure 2 shows that  $\rho_1$  increases rapidly for values of SMd below 15 degrees. It increases gradually with direction deviation from 15–30 degrees and more slowly from 30 degrees on. Thus the value of SMd at which  $\rho_1$  ceases to increase rapidly seems to be somewhere between 15 and 30 degrees. (For similar but more detailed analyses of earlier data along these lines see Zeh et al. 1990.)

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 1.5–3.5 km/hour and direction deviations in the range 15–30 degrees. The central values in these ranges (minimum speed 2.5 km/hour and direction deviation 22.5 degrees) were given the most weight in calculating the posterior distributions, as described in Section 4.5. The overall value of  $\rho_1$  obtained using the central minimum speed and direction deviation tracking parameters for combined 1993 visual and acoustic data was .72.

We now consider estimating  $\rho_2$ . We assume that if a whale goes outside of its own linking area, and if  $h$  other whales were located in the previous 1.5 hours, then it is wrongly linked to another whale with probability  $\rho_{2h}^{z,e}$  if it is in zone  $z$  ( $z = \nu, \omega$ , or  $\alpha$ ) and the monitoring effort is  $e$ . Effort  $e$  can take the values VO (visual only), AO (acoustic only), and VA (both visual and acoustic).

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

$$\rho_{2h}^{\nu,VO} = 1 - \exp[-.252h^{.308}].$$

We then calculated  $\rho_{2h}^{\hat{z},e}$  for other tracking parameters, zones, and efforts as described by 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  $z$  ( $t = 1, \dots, 75$ ;  $z = \nu, \omega$ , or  $\alpha$ ), is derived from the likelihood  $p(y|n)$  given by equation (3) and the negative binomial prior distribution. The likelihood (3) is conditional on  $\rho_2$ , but the number of tracks,  $y$ , itself provides information about the value of  $\rho_2$  for that zone and period. We use the approximation (dropping period and zone superscripts and subscripts)

$$\begin{aligned} p(n|y) &= \int p(n|\rho_2, y) p(\rho_2|y) d\rho_2 \\ &\approx p(n|y, \hat{\rho}_2) \\ &\propto p(y|n, \hat{\rho}_2) p(n), \end{aligned}$$

where  $\hat{\rho}_2$  is an estimate of  $\rho_2$  for period  $t$  and zone  $z$ . We use the estimate

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

where  $\rho_{2h}$  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 ( $h = 1, \dots, y$ ).

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 were 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 MSS and SMd in the tracking algorithm and the vector parameters governing the detection probabilities,  $\beta^V = (\beta_0^V, \beta_1^V)$  and  $\beta^A = (\beta_0^A, \beta_1^A)$  (Raftery et al. 1988, 1990; Sonntag et al. 1988). The posterior distribution of  $U$  is sensitive only to the prior mean of  $N$ .

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 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  $\beta^V$ , 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 overdispersion. The parameter  $\beta^A$  was also varied 1.73 standard errors in each direction. The upper and lower values for MSS and SMd were based on the data analyses in Section 4.4.4.

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. For the unmonitored periods, we obtained  $p(U|\nu)$  by simulation, where  $\nu$  is the prior mean of  $N$ . We are uncertain about  $\nu$ , and we need to incorporate that uncertainty into our final posterior distribution of  $U$  using the fact that  $p(U) = \int p(U|\nu)p(\nu) d\nu$ . We evaluate this, as before, using the three-point Gauss-Hermite quadrature formula, namely

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

where  $\nu_1$ ,  $\nu_2$ , and  $\nu_3$  are the 4%, 50%, and 96% quantiles of the distribution of  $\nu$ . 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  $U$ .

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; that is,  $P_4 = .93$ . 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 [6,800, 8,900].

5.2 The Bayes Empirical Bayes Estimate

We carried out the sensitivity analysis designed as in Section 4.5 and Table 3. The results are insensitive to changes in  $\beta^A$ , unlike the results from previous censuses. This is because most of the whales passed within visual range in

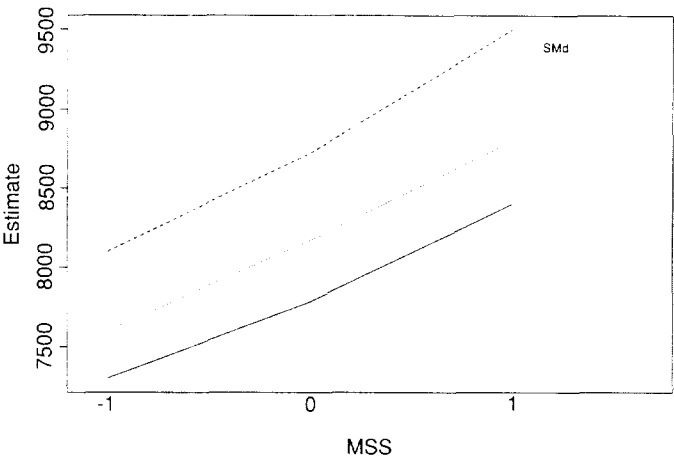


Figure 3. Interaction Plot of the Effects of MSS and SMd on  $\hat{N}$ . The values -1 (---), 0 (···), and 1 (—) correspond to the low, main, and high values in Table 3.

1993, unlike in previous years, and so the results were less dependent on the estimated acoustic detection probabilities.

The results are sensitive to changes in the other three parameters. Changing MSS from its main value to the high or low value in Table 3 changes the estimate by about 600 on average, with corresponding values of 470 and 135 for SMd and  $\beta^V$ . Analysis of variance shows that the only interaction is between MSS and SMd and that this is relatively small, as the interaction plot in Figure 3 shows. Overall, most of the sensitivity is attributable to the tracking algorithm parameters.

We obtained the posterior distribution of 1993 population size shown in Figure 4. 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.

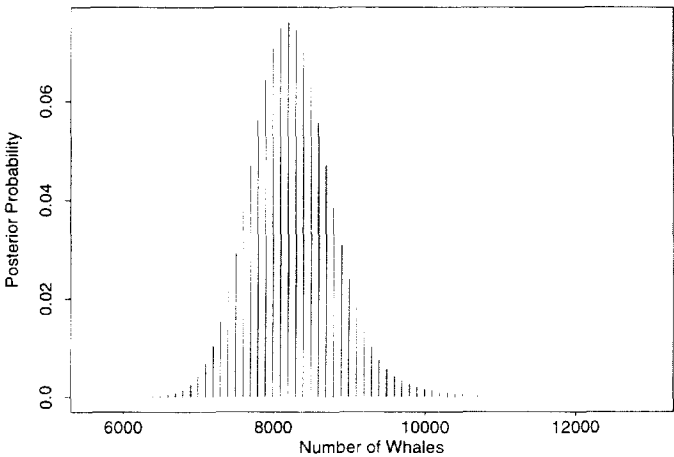


Figure 4. Posterior Distribution of the Number of Whales for 1993.

Table 3. Parameters for Sensitivity Analysis

Parameter	Low	Main	High
MSS (km/hour)	1.5	2.5	3.5
SMd (degrees)	15	22.5	30
$\beta_0^V$	-1.638	-1.969	-2.301
$\beta_1^V$	.267	.399	.531
$\beta_0^A$	-4.531	-5.442	-6.353
$\beta_1^A$	.840	1.132	1.427

The smaller posterior standard deviation and greater symmetry of the posterior distribution in 1993 were due primarily to the smaller amount of unmonitored time (26 hours compared to 71 hours in 1988.) Time with visual but not acoustic monitoring also played a smaller role in 1993, because in 1993 a smaller percentage of the whales passed Point Barrow in the acoustic zone, beyond viewing range, than in 1988. 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 less uncertainty to the final combined posterior distribution in 1993 than in 1988.

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% is due to periods without any monitoring or without monitoring in the acoustic zone, and the remaining 5% is due to uncertainty about whale numbers in the monitored periods conditional on the estimated model parameters. This is in contrast to 1988, when most (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 1988, with 95% confidence interval [1%, 6.2%]. This was the first time it had been shown that the bowhead population was increasing despite the annual take by Eskimo hunters. But the width of the confidence interval and the closeness of its lower bound to 0 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 .674, but with a large standard error based on the interannual variation, namely .189. The data used to estimate the rate of increase are shown in Table 4.

Table 4. Data for the Calculation of the 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	.674	.189	5,019	1,476
1980	2,737	488	.674	.189	4,061	1,365
1981	3,231	716	.750	.108	4,308	1,147
1982	4,612	798	.674	.189	6,843	2,279
1983	4,399	839	.674	.189	6,527	2,241
1985	3,134	583	.519	.131	6,039	1,915
1986	4,006	574	.518	.062	7,734	1,450
1987	3,615	534	.674	.189	5,364	1,714
1988	4,862	436	.739	.053	6,579	757
1993	7,249	505	.933	.013	7,770	552

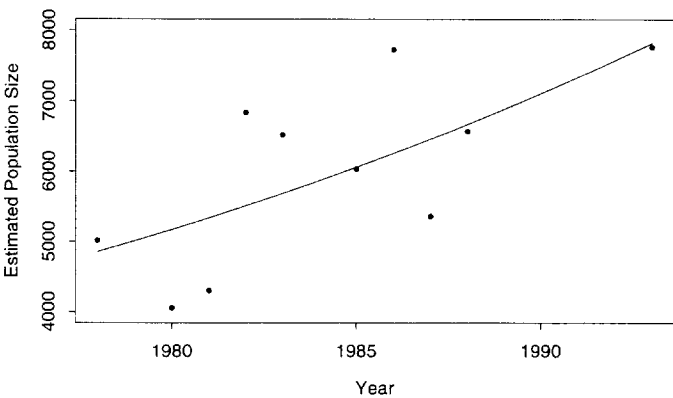


Figure 5. Generalized Removal Method Estimates of Bowhead Population Size, 1978–1993, and the Exponential Growth Curve Fit to Them.

The rate of increase was estimated by a regression of  $\log(N_4/P_4)$  on  $(\text{year} - 1977)$ , 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, along with the population estimates on which it is based, are shown in Figure 5.

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 [6,800, 8,900], whereas the Bayes empirical Bayes method gives the most probable value as 8,200 with 95% of the posterior probability in the range [7,200, 9,400]. 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 the 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 can be combined with biological information and knowledge of the historic catch record to yield an upper bound for the allowable subsistence whaling quota (e.g., Givens, Zeh, and Raftery 1995; Raftery, Givens, and Zeh 1995), 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. It also led to priority being given to increasing the proportion of the audio tapes that were analyzed and the allocation of resources to developing ways of automating this process (Clark et al. 1996).

Also, problems in the estimates of acoustic location errors in the 1988 census uncovered by Zeh et al. (1990) led to the improved location error estimates described by Clark et al. (1996). The combination of our advice, technological advances, 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 fivefold reduction in posterior variance from 1986 to 1993.

The Bayes empirical Bayes method provided a good framework for communicating the statistical results to the other (about 100) members of the International Whaling Commission Scientific Committee, because it is based on biological assumptions and involves a substantial amount of sensitivity analysis. It also provided a way of incorporating the sensitivity analysis into the conclusions, as distinct from the more usual practice of just reporting the sensitivity analysis results. Iterated three-point Gauss–Hermite quadrature is a simple and effective way of doing this. Its use of external (or “prior”) information is a strong point of the Bayes empirical Bayes method. Population size estimation is intrinsically hard, because there is an inherent near nonidentifiability between detection probability and population size, which external information can help to break.

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 use of the tracking algorithm. Because tracking algorithm error probabilities do not need to be estimated, no data from acoustically identified whales are needed. Because 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. Because 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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