

Updated 1978-2001 abundance estimates and their correlations for the Bering-Chukchi-Beaufort Seas stock of bowhead whales

JUDITH E. ZEH* AND ANDRÉ E. PUNT†

Contact e-mail: zeh@stat.washington.edu

ABSTRACT

The method of Cooke (1996) and Punt and Butterworth (1999) for computing abundance estimates for bowhead whales of the Bering-Chukchi-Beaufort Seas stock is reviewed. These abundance estimates are computed from estimates N_4 of the number of whales that passed within the 4km visual range of the observation ‘perch’ from which the whales are counted, the estimated proportions P_4 of the whales that passed within this range and the estimated standard errors (SE) of N_4 and P_4 . Errors discovered while assembling the data used in developing previous estimates were corrected, and new estimated detection probabilities, N_4 and P_4 values and SEs were computed using the corrected data. The method of Cooke (1996) and Punt and Butterworth (1999) was then applied. The resulting 2001 abundance estimate was 10,545 (95% confidence interval 8,200 to 13,500), extremely close to the 2001 N_4/P_4 abundance estimate of 10,470 (95% confidence interval 8,100 to 13,500) (George *et al.*, 2004). The estimated rate of increase of this population from 1978 to 2001 was 3.4% per year (95% confidence interval 1.7% to 5%).

KEYWORDS: BOWHEAD WHALE; ABUNDANCE ESTIMATE; SURVEY-SHORE-BASED; ACOUSTICS; SURVEY-AERIAL; TRENDS

INTRODUCTION

Most estimates of abundance for the Bering-Chukchi-Beaufort Seas (BCB) stock of bowhead whales, *Balaena mysticetus*, have been based on data collected during ice-based visual ‘census’ studies conducted off Point Barrow, Alaska, during the spring migration of these whales from the Bering to the Beaufort Sea. From 1978 to 1988 counts were conducted annually, although in 1979 and 1984 they did not produce enough data to support an abundance estimate because of adverse environmental conditions. The primary documents describing the studies, including two successful studies conducted subsequently in 1993 and 2001, are listed in Table 1.

It was recognised fairly early in the period covered by these studies that visual detection of whales passing more than 4km offshore from the observers was extremely

unlikely. Aerial transect surveys and acoustic monitoring were used to estimate the proportions of whales that passed within and beyond the 4km visual range (Table 1). Aerial surveys were conducted in 1979, 1981, 1984, 1985 and 1986 and acoustic monitoring in 1982, 1984, 1985, 1986, 1988, 1993 and 2001. Although both aerial transect survey and acoustic monitoring took place in 1984, the distributions obtained were not considered useful for assessing offshore distribution because heavy ice in the nearshore lead caused the visual census to fail and may also have affected the offshore distribution of the whales (Zeh *et al.*, 1993).

George *et al.* (2003; 2004) provide a brief summary of the history and methods of the studies. They also review the methods used to estimate abundance from the data. An estimate, N_4 , of the number of whales that passed within the 4km visual range of the observation ‘perch’ from which the whales are counted is computed using methods developed

Table 1
Studies providing data for bowhead abundance estimation.

Year	Visual census	N_4 ?	P_4 ?	No. of perches ³	Acoustic location data	Aerial transect survey
1978	Braham <i>et al.</i> (1979)	Yes	No	2	None	None
1979	Braham <i>et al.</i> (1980)	No ¹	Yes	2	None	Braham <i>et al.</i> (1980)
1980	Johnson <i>et al.</i> (1981)	Yes	No	2	None	None
1981	Marquette <i>et al.</i> (1982)	Yes	Yes	2	None	Marquette <i>et al.</i> (1982)
1982	Dronenburg <i>et al.</i> (1983)	Yes	Yes	2	Cummings <i>et al.</i> (1983), Cummings and Holliday (1985), Dronenburg <i>et al.</i> (1983)	None
1983	Dronenburg <i>et al.</i> (1984)	Yes	No	2	None	None
1984	Dronenburg <i>et al.</i> (1986)	No ²	No ²	1	Clark <i>et al.</i> (1986)	Nerini and Rugh (1986)
1985	Krogman <i>et al.</i> (1986)	Yes	Yes	2	Clark <i>et al.</i> (1986), Clark and Ellison (1988)	Nerini and Rugh (1986)
1986	George <i>et al.</i> (1987)	Yes	Yes	1	Clark and Ellison (1989)	Withrow and Goebel-Diaz (1989)
1987	George <i>et al.</i> (1988)	Yes	No	1	None	None
1988	George <i>et al.</i> (1990)	Yes	Yes	1	George <i>et al.</i> (1990)	None
1993	George <i>et al.</i> (1995)	Yes	Yes	1	Clark <i>et al.</i> (1996), Clark and Ellison (2000)	None
2001	George <i>et al.</i> (2003, 2004)	Yes	Yes	1	Clark <i>et al.</i> (2003)	None

¹No counts were made 25 April-8 May because the lead in front of the perches was closed by ice or after 24 May because of weather. Thus too much of the season was missed to permit an abundance estimate.

²Heavy ice in the lead caused the visual census to fail. The acoustic and aerial survey data were consequently not considered usable for assessing offshore distribution in successful census years.

³Coded as 2 if two perches operated simultaneously to provide data for detection probability estimation, coded as 1 otherwise. The number of different perches used during the season is often a considerably larger number.

* University of Washington, Department of Statistics, Box 354322, Seattle, WA 98195-4322, USA.

† University of Washington, School of Aquatic and Fisheries Sciences, Box 355020, Seattle, WA 98195, USA.

by Zeh *et al.* (1986a; b; 1991). The estimated proportion of the whales that passed within the 4km visual range, P_4 , is obtained from the aerial survey and acoustic data. The estimates N_4 , P_4 and N_4/P_4 were first discussed by Raftery and Zeh (1991; 1993). The International Whaling Commission Scientific Committee (IWC SC) agreed to use the 2001 N_4/P_4 abundance estimate (George *et al.*, 2003) for its 2004 assessment of BCB bowhead whales (IWC, 2004, p.18).

Raftery *et al.* (1995) pointed out that P_4 for years lacking acoustic or aerial survey data could be computed from the years with such data, enabling the rate of increase of the BCB bowhead whales to be estimated from N_4/P_4 for all the years with successful visual censuses. Zeh *et al.* (1995) and Raftery and Zeh (1998) refined the method of Raftery *et al.* (1995) and applied it to the data used by Raftery *et al.* (1995), augmented by aerial survey data from 1981 and additional acoustic data from 1993. These methods were criticised by Cooke (1996) because covariances among the abundance estimates that resulted from using years with P_4 data to obtain the estimates for years without P_4 data were not computed, and the combination of process and observation error in P_4 values was handled in an *ad hoc* fashion. As in IWC (1994, p.75), Cooke (1996) used the term 'process error' to refer to the extent to which the variability of successive estimates exceeds their estimated variability after accounting for any trend over time; 'observation error' refers to the sampling error of the estimates. Process error arises when an estimated variance ignores some components of the true variance, e.g. year-to-year variability in the true proportion of whales that pass within visual range due to differences in ice conditions. Cooke (1996) presented a statistical model that overcame the problems he identified. Punt and Butterworth (1999) (Appendix A) applied the Cooke (1996) model to the N_4 and P_4 data in Zeh *et al.* (1995) and Raftery and Zeh (1998) to obtain the abundance estimates that have been used subsequently by the IWC SC, with coefficients of variation (CVs) and a correlation matrix.

George *et al.* (2003) investigated process error in the number of bowhead whales migrating past Point Barrow and in the proportion within visual range using the approach of Cooke (1996) and including the 2001 data. They found, as Cooke had, that there was no indication of process error in bowhead whale numbers, but considerable process error in the proportion within visual range.

The primary analysis of George *et al.* (2003) treated the N_4/P_4 value they obtained for 2001 as uncorrelated with the earlier abundance estimates in estimating rate of increase. They used the abundance estimates, CVs, and correlations given by Punt and Butterworth (1999) for the years before 2001. However, a careful reading of George *et al.* (2003) and discussions with George (pers. comm.) suggested that the 2001 data could and should be integrated with the earlier data using the Cooke (1996) method. Similarly, the primary references (Table 1) and subsequent discussions with some of the researchers (Cummings, pers. comm.; Ellison, pers. comm.; Rugh, pers. comm.) determined that aerial survey data from 1979, 1985 and 1986 and acoustic location data from 1982 that had not been used previously should be added.

It had been anticipated (IWC, 2004, p.18) that the 2001 N_4/P_4 abundance estimate would not be modified. However, in the process of assembling the data archive, errors were discovered in the visual census data from some of the early years of the census. This necessitated recomputing detection probability and abundance estimates from the archived data,

resulting in small changes to all the N_4 values used previously and their standard errors (SE). Thus the estimates computed from the model of Cooke (1996) also changed.

Most of the corrections involved relatively minor adjustments to perch locations. A more significant set of corrections occurred for 1982, when a number of observers forgot to log out at the ends of their shifts. The correction of those errors resulted in reducing the number of hours in 1982 recorded as having more than two observers. Another significant error was discovered and corrected in the computer program *rawq.f* that extracted data for detection probability estimation. That error had led to incorrect determinations of whether whales were seen within or beyond 2km offshore from the perch. Whales seen and categorised as 'new' (seen for the first time) and 'conditional' (uncertain whether this is a new whale or a subsequent sighting of a whale seen previously) are used in computing N_4 . Of the 20,262 new whales used in our analyses, only two were added as a result of correcting errors. Of the 3,633 conditional whales, only 18 were added.

The model and method of Cooke (1996) and Punt and Butterworth (1999) are reviewed here. Revised tables of detection probabilities, N_4 and P_4 values with SEs and N_4/P_4 values with CVs are provided. These are compared with the corresponding data used by Punt and Butterworth (1999). New abundance estimates, CVs and correlation matrix are provided and compared with those given in appendix A of Punt and Butterworth (1999) as well as with previously published estimates of bowhead abundance. The estimated 1978-2001 annual rate of increase for this bowhead population obtained by George *et al.* (2004) using our abundance estimates, CVs and correlation matrix is also reviewed.

METHODS

N_4 and P_4 data used to construct the abundance series

The available N_4 and P_4 data are summarised by year in Table 1. N_4 values (estimated numbers of whales that passed within visual range) were recomputed for the eleven years with adequate data using the corrected data. From 1978 to 1985, two perches were operated as described by George *et al.* (2003; 2004) so that detection probabilities could be estimated as a function of visibility, number of observers and distance of the whales offshore from the primary perch. A generalised linear model (McCullagh and Nelder, 1983) based on the removal method (Seber, 1982) was used (Zeh *et al.*, 1991). In each year with adequate visual effort to support an abundance estimate, counts made from the primary perch under particular conditions each day were corrected by dividing by the corresponding detection probability estimates. A linear combination of the corrected counts, adjusted for time without visual effort under acceptable conditions, provided the estimate for that day (Zeh *et al.*, 1986a; 1991). The daily estimates were summed to obtain the N_4 value for the year, after accounting for missed days using a time series interpolator, and $SE(N_4)$ was estimated by a jackknife that omitted a day at a time (Zeh *et al.*, 1986b).

As described by George *et al.* (2003; 2004), P_4 values were computed as the proportion of acoustic locations directly offshore from the hydrophone array that fall within 4km offshore from the primary perch. Aerial transect survey data from 1979, 1981, 1985 and 1986 give km offshore from the ice edge for each bowhead seen on transect. These data also permit computation of P_4 . At the resolution of the transect surveys, the location of the ice edge is equivalent to

the location of the perch. Rugh (1990) reports that 90% of errors in aerial survey positions are <0.58km in magnitude, although some errors are as large as 1.89km. Only in 1983 (for 13% of the season) and 1986 (9%) were perches more than 0.58km back from the lead edge. Perches were always within 0.3km of the edge except for those years and 2001. They were never more than 1.5km from the edge.

Since there were both acoustic and aerial survey P_4 values for 1985 and 1986, weighted averages (by the inverse of the estimated variance) for those years were calculated. Variances for acoustic P_4 in 1985, 1986, 1988, 1993, and 2001 were obtained via a moving blocks bootstrap (Efron and Tibshirani, 1993) with 3-day blocks because samples of acoustic locations often covered more than a day. Variances for P_4 from the limited acoustic data in 1982 and the aerial transect data were obtained by an ordinary bootstrap that sampled days. In many cases, samples were a day or more apart, and even samples on adjacent days were generally hours apart. It therefore seemed reasonable to assume that samples from different days were independent.

Cooke’s model

Cooke (1996) proposed the following statistical model for the analysis of the N_4 and P_4 data:

$$\begin{aligned} N_{4y} &= N_y p_y e^{\nu_y} & \nu_y &\sim N(0; \sigma_{\nu,y}^2) \\ P_{4y} &= p_y e^{\varepsilon_y} & \varepsilon_y &\sim N(0; \sigma_{\varepsilon,y}^2) \\ p_y &= \pi e^{\eta_y} & \eta_y &\sim N(0; \sigma_{\eta}^2) \end{aligned}$$

where

- N_{4y} is the estimate N_4 for year y ,
- P_{4y} is the estimate P_4 for year y ,
- N_y is the number of whales in the population in year y ,
- p_y is the proportion of the population within visual range in year y ,
- π is the mean proportion of the population within visual range (the actual proportion varies from year to year as a consequence of process error),
- $\sigma_{\nu,y}^2$ is the variance of the logarithm of N_{4y} (reflecting observation error),
- $\sigma_{\varepsilon,y}^2$ is the variance of the logarithm of P_{4y} (reflecting observation error) and
- σ_{η}^2 is the process error variance for the proportion of the population within visual range.

Note that Punt and Butterworth (1999) used P_y where N_y is used here¹. Except for this change, the notation here matches that of Punt and Butterworth (1999). The parameters of this model to be estimated are N_y and p_y for each of the 11 years which have N_{4y} values, in addition to p_{1979} , π and σ_{η}^2 . Note that p_{1979} is listed separately because 1979 is the only year judged to have usable P_{4y} data but without usable N_{4y} data.

The model assumes that the proportion p_y of the population within visual range varies from year to year around the mean value π . Thus, the natural logarithms of the estimates P_{4y} include two components of error, with only the first reflected in the estimated standard error of P_{4y} : (1) the measurement or observation error ε_y with variance $\sigma_{\varepsilon,y}^2$ and

(2) the process error η_y with variance σ_{η}^2 . For this reason, the estimate of the proportion p_y may differ from P_{4y} in years with P_{4y} data.

Estimation of model parameters

The estimates of the 25 parameters of this model are obtained by restricted maximum likelihood (REML), reviewed by Harville (1977). This involves finding the values for the parameters that minimise the following quantity:

$$0.5[(Y - X\beta)^T V^{-1}(Y - X\beta) + \ln|V| + \ln|X^T V^{-1}X|]$$

where Y is a column vector of length 31, X is the design matrix, β is a vector of length 24 containing the natural logarithms of all the parameters except σ_{η}^2 and V is a diagonal matrix with the first 11 elements on the diagonal the squared CVs of the N_{4y} , the next 8 the squared CVs of the P_{4y} , and the last 12 (corresponding to the years with either N_{4y} , P_{4y} or both) containing σ_{η}^2 . Thus the diagonal elements of V are the variances of the elements of Y . The elements of Y are the natural logarithms of N_{4y} for $y = 1978, 1980, 1981, 1982, 1983, 1985, 1986, 1987, 1988, 1993$ and 2001 ; the natural logarithms of P_{4y} for $y = 1981, 1982, 1985, 1986, 1988, 1993, 2001$ and 1979 ; and 0s for the remaining 12 entries, i.e. a 0 for each year with either N_{4y} or P_{4y} data. According to the third model equation, $\eta_y = \ln(p_y) - \ln(\pi)$, and its expected value $E(\eta_y) = 0$. The only estimate we have for η_y is its expected value. This is the reason for the 0s in Y . Each of the first 11 rows of X consists of 0s except for a 1 to pick out the logarithm of N_y and another 1 to pick out the logarithm of p_y . Each of the next 8 rows has only a single 1 to pick out the logarithm of the correct p_y . Each of the next 12 rows represents η_y for one of the y , so each has a 1 to pick out the logarithm of p_y and -1 in the last column for the logarithm of π . The maximum likelihood estimate of π also provides an estimate of p_y for years in which P_{4y} data are not available.

RESULTS AND DISCUSSION

The revised estimates of detection probability $\hat{p} \pm SE$ obtained from the 1978-1985 data are given in Table 2. Note that previous discussions and tabulations of detection probability data (Zeh *et al.*, 1986a; b; 1991; 1993) were in terms of the probability $\hat{q} = 1 - \hat{p}$ of failing to detect a whale. For comparison purposes, the detection probability estimates obtained by Zeh *et al.* (1991) are given in Table A.1 of Appendix A. The values in Table A.1 were used by Raftery and Zeh (1991; 1993; 1998) and Zeh *et al.* (1995) to compute N_4 .

Table 2

Detection probability estimates $\hat{p} \pm SE$ obtained as described by Zeh *et al.* (1991). These estimates are functions of distance of the whales offshore from the census perch, number of observers and visibility.

Offshore distance	Number of observers	Visibility		
		Excellent to very good	Good	Fair
≤ 2km	> 2	0.72 ± 0.06	0.65 ± 0.07	0.60 ± 0.08
	≤ 2	0.71 ± 0.03	0.63 ± 0.03	0.58 ± 0.05
> 2km	> 2	0.50 ± 0.11	0.40 ± 0.11	0.33 ± 0.12
	≤ 2	0.48 ± 0.08	0.38 ± 0.08	0.31 ± 0.09

¹ N is commonly used to represent number of whales and P to represent a proportion or probability.

Values of \hat{p} in Table 2 are quite similar to those in Table A.1 for the most part. However, Table 2 shows less effect of increasing the number of observers. Detection probabilities in 1982 were apparently high for reasons not captured by these factors, so when observers were correctly counted in that year, \hat{p} was raised for ≤ 2 and lowered for > 2 observers. Table 2 also provides a somewhat clearer indication of the reduction in \hat{p} when whales are more than 2km offshore from the perch. The incorrectly categorised offshore distance data used in estimating the values in Table A.1 blurred the effect.

Revised estimates N_4 and P_4 obtained from the archived data are given in Table 3. The CVs used in the first 19 elements on the diagonal of V are obtained by dividing Table 3 N_4 and P_4 standard errors (SE) by the corresponding estimates. Table 3 also lists the N_4/P_4 abundance estimates obtained by dividing N_4 by P_4 for years for which both N_4 and P_4 are available. Although the N_4/P_4 values in Table 3 are not used when computing abundance estimates using the method of Cooke (1996) and Punt and Butterworth (1999), they are of interest for comparison purposes. They are sometimes cited, e.g. for 2001 by George *et al.* (2004), because they are computed directly from the data obtained during a particular survey and the Table 2 detection probabilities.

Table A.2 gives the corresponding estimates used by Punt and Butterworth (1999). Comparing the values of N_4 in Table 3 with those in Table A.2, we can see the effects of the changes in the detection probability estimates. There were few hours with more than two observers in the early years of

the census, so they show few changes related to the reduced effect of >2 observers except for 1982. From 1986 on, there were usually three observers. The effect of the additional observer in Tables A.1 and A.2 was to raise estimated detection probabilities and hence lower values of the estimate N_4 . Because the estimated effect of the additional observer is less in Table 2 than in Table A.1, N_4 values from 1986 on tend to be greater in Table 3 than in Table A.2. Lower estimated detection probabilities when whales were farther offshore also contribute to increased N_4 values in Table 3 for years like 1983 when many whales were seen more than 2km offshore from the perch. This effect was exacerbated in 1983 because corrections to perch locations resulted in an increase in the number of whales >2 km offshore compared to the 1983 data used in previous analyses.

The abundance estimates, \hat{N}_y , obtained using the method of Cooke (1996) and Punt and Butterworth (1999) are shown in Table 4, along with their CVs and correlation matrix. The mean proportion π within visual range was estimated to be 0.701, and the process error standard deviation σ_η was estimated to be 0.270.

Not surprisingly, the abundance estimates in Table 4 differ most from the N_4/P_4 values in Table 3 when P_4 has a large SE and/or differs quite markedly from the estimate of π (0.701). The abundance estimates for 1988, 1993 and 2001 have considerably lower CVs than the estimates for the earlier years and are not highly correlated with them. These estimates do not differ greatly from the corresponding N_4/P_4 values because acoustic monitoring was more

Table 3

Data used in the construction of the abundance estimates \hat{N}_y for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Table 4). N_4/P_4 is shown for comparison with the estimates in Table 4.

Year	N_4/P_4		N_4		Acoustic P_4		Aerial survey P_4		Weighted average P_4	
	Estimate	CV	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1978			3,338	295	NA		NA		NA	
1979			NA		NA		0.850	0.090	NA	
1980			2,722	491	NA		NA		NA	
1981	4,348	0.310	3,261	689	NA		0.750	0.166	NA	
1982	8,388	0.382	4,756	814	0.567	0.191	NA		NA	
1983			4,605	848	NA		NA		NA	
1985	6,547	0.271	3,136	583	0.500	0.131	0.457	0.132	0.479	0.093
1986	10,272	0.217	4,160	600	0.515	0.080	0.194	0.111	0.405	0.065
1987			3,712	544	NA		NA		NA	
1988	6,895	0.123	5,102	456	0.740	0.062	NA		NA	
1993	8,160	0.071	7,613	531	0.933	0.014	NA		NA	
2001	10,470	0.129	9,025	1,068	0.862	0.044	NA		NA	

NA = not available.

Table 4

Abundance estimates \hat{N}_y , CVs (actually standard errors of the logarithms) and the correlation matrix for the logarithms of the abundance estimates for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the estimation procedure described above.

Year	Estimate	CV	Correlation matrix														
1978	4,765	0.305	1.000														
1980	3,885	0.343	0.118	1.000													
1981	4,467	0.273	0.056	0.050	1.000												
1982	7,395	0.281	0.094	0.084	0.035	1.000											
1983	6,573	0.345	0.117	0.104	0.049	0.084	1.000										
1985	5,762	0.253	0.070	0.062	0.020	0.078	0.062	1.000									
1986	8,917	0.215	0.072	0.064	0.017	0.092	0.064	0.113	1.000								
1987	5,298	0.327	0.124	0.110	0.052	0.088	0.110	0.065	0.067	1.000							
1988	6,928	0.120	0.028	0.025	0.013	0.017	0.024	0.009	0.007	0.026	1.000						
1993	8,167	0.071	0.001	0.001	0.001	0.000	0.001	-0.001	-0.002	0.001	0.000	1.000					
2001	10,545	0.128	0.008	0.007	0.005	0.001	0.007	-0.004	-0.008	0.008	0.003	0.000	1.000				

comprehensive during those years than during other years and provided relatively precise P_4 values. The addition of P_4 data for 1979 and 1982 in Table 3, compared to Table A.2, also contributes to lower between-year correlations in Table 4, compared to those in appendix A of Punt and Butterworth (1999) (their table A.1, our Table A.3).

The largest changes between the new abundance estimates in Table 4 and those in appendix A of Punt and Butterworth (1999) (their table A.1, our Table A.3) occur for the years for which additional P_4 data were used, particularly 1982 and 1986. In both of these cases, the added data suggested considerably fewer whales within viewing range than the data used previously. Withrow and Goebel-Diaz (1989) expressed concern that the transect distribution in 1986 did not reflect the distribution of whales they observed during photogrammetry flights. Those flights indicated a larger proportion within visual range. However, use of the Cooke (1996) model, as well as averaging P_4 from the transect surveys with P_4 from the acoustic locations, prevented that distribution from having undue influence.

Prior to the 2001 study, the most recent estimate of bowhead population size accepted by the IWC SC was 8,200 with 95% estimation interval from 7,200 to 9,400. This estimate was based on the Bayes empirical Bayes posterior distribution computed from 1993 data by Zeh *et al.* (1995) and Raftery and Zeh (1998). The 1993 estimate of 8,167 (Table 4) presented here is virtually identical to their estimate. The 95% confidence interval, computed as recommended by Buckland (1992), is 7,100 to 9,400. The 2001 estimate of 10,545 presented here has a 95% confidence interval of 8,200 to 13,500. This is almost the same as the corresponding interval based on N_4/P_4 given by George *et al.* (2004) as 8,100 to 13,500. George *et al.* (2004) estimated the annual rate of increase of this bowhead population from the data in our Table 4 by using generalised least squares to fit an exponential growth model. The estimated rate of increase from 1978 to 2001 was 3.4% per year, with a 95% confidence interval of 1.7% to 5%.

ACKNOWLEDGEMENTS

We thank the Alaska Eskimo Whaling Commission (AEWC) for their support of this research. We gratefully acknowledge funding provided by the North Slope Borough Department of Wildlife Management (NSB DWM) and the National Oceanic and Atmospheric Administration (NOAA, through the AEWC). We thank Sharon Hedley (University of St Andrews), Tore Schweder (University of Oslo) and Hans Skaug (Institute of Marine Research, Bergen, Norway) for helpful comments on drafts of this manuscript. We thank all who participated in the difficult and dangerous work of conducting the ice-based visual census, acoustic monitoring and aerial survey flights. We also thank all who helped to assemble the data included in our analyses and to make sure these data were correct. Two people who were instrumental in both the field work that produced the data and the work in assembling the data archives for the 2004 bowhead assessment deserve special mention for their contributions—without Craig George (NSB DWM) and Dave Rugh (NOAA), the data used in this paper could not have been gathered.

REFERENCES

Braham, H., Krogman, B., Leatherwood, S., Marquette, W., Rugh, D., Tillman, M., Johnson, J. and Carroll, G. 1979. Preliminary report of the 1978 spring bowhead whale research program results. *Rep. int. Whal. Commn* 29:291-306.

- Braham, H., Krogman, B., Johnson, J., Marquette, W., Rugh, D., Nerini, M., Sonntag, R., Bray, T., Brueggeman, J., Dahlheim, M., Savage, S. and Goebel, C. 1980. Population studies of the bowhead whale (*Balaena mysticetus*): Results of the 1979 spring research season. *Rep. int. Whal. Commn* 30:391-404.
- Buckland, S.T. 1992. Report of the Scientific Committee, Annex H. Proposal for standard presentation of abundance estimates. *Rep. int. Whal. Commn* 42:235.
- Clark, C.W. and Ellison, W.T. 1988. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1985 acoustic study off Pt. Barrow, Alaska. *Rep. int. Whal. Commn* 38:365-70.
- Clark, C.W. and Ellison, W.T. 1989. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1986 acoustic study off Pt. Barrow, Alaska. *Rep. int. Whal. Commn* 39:297-303.
- Clark, C.W. and Ellison, W.T. 2000. Calibration and comparison of the acoustic location methods used during the spring migration of the bowhead whale, *Balaena mysticetus*, off Pt. Barrow, Alaska, 1984-1993. *J. Acoust. Soc. Am.* 107(6):3509-17.
- Clark, C.W., Ellison, W.T. and Beeman, B. 1986. A preliminary account of the acoustic study conducted during the 1985 spring bowhead whale, *Balaena mysticetus*, migration off Point Barrow, Alaska. *Rep. int. Whal. Commn* 36:311-6.
- Clark, C.W., Charif, R., Mitchell, S. and Colby, J. 1996. Distribution and behavior of the bowhead whale, *Balaena mysticetus*, based on analysis of acoustic data collected during the 1993 spring migration off Point Barrow, Alaska. *Rep. int. Whal. Commn* 46:541-52.
- Clark, C.W., Colby, J.A., Cortopassi, K., Ponirakis, D., Fowler, M.C., Tessaglia-Hymes, C., Frstrup, K.M., Dunsmore, K.J. and George, J.C. 2003. Passive acoustic locations and offshore distribution of bowhead whales (*Balaena mysticetus*) during the entire Spring 2001 census off Pt. Barrow, Alaska. Paper SC/55/BRG4 presented to the IWC Scientific Committee, May 2003, Berlin. 10pp. [Paper available from the Office of this Journal].
- Cooke, J.G. 1996. Preliminary investigation of an RMP-based approach to the management of Aboriginal Subsistence Whaling. Paper SC/48/AS5 presented to IWC Scientific Committee, June 1996, Aberdeen (unpublished). 20pp. [Paper available from the Office of this Journal].
- Cummings, W.C. and Holliday, D.V. 1985. Passive acoustic location of bowhead whales in a population census off Point Barrow, Alaska. *J. Acoust. Soc. Am.* 78:1163-9.
- Cummings, W.C., Holliday, D.V., Ellison, W.T. and Graham, B.J. 1983. Technical feasibility of passive acoustic location of bowhead whales in population studies off Point Barrow, Alaska: a report to the North Slope Borough. Tracor Document Number T-83-06-002 (U), Tracor Applied Sciences, Tracor, Inc., 9150 Chesapeake Drive, San Diego, CA 92123, USA (unpublished). 169pp. [Available from the North Slope Borough Department of Wildlife Management, PO Box 69, AK 99723, USA].
- Dronenburg, R.B., Carroll, G.M., Rugh, D.J. and Marquette, W.M. 1983. Report of the 1982 spring bowhead whale census and harvest monitoring including 1981 fall harvest results. *Rep. int. Whal. Commn* 33:525-37.
- Dronenburg, R., Carroll, G.M., George, J.C., Sonntag, R.M., Krogman, B.D. and Zeh, J.E. 1984. Final report of the 1983 spring bowhead whale census and harvest monitoring including the 1982 fall harvest results. *Rep. int. Whal. Commn* 34:433-44.
- Dronenburg, R.B., George, J.C., Krogman, B.D., Sonntag, R.M. and Zeh, J.E. 1986. Report of the 1984 spring bowhead whale (*Balaena mysticetus*) ice-based visual census. *Rep. int. Whal. Commn* 36:293-8.
- Efron, B. and Tibshirani, R.J. 1993. *An Introduction to the Bootstrap*. Chapman & Hall, New York. 436pp.
- George, J.C., Carroll, G.M., Tarpley, R.J., Albert, T.F. and Yackley, R.L. 1987. Report of field activities pertaining to the spring 1986 census of bowhead whales, *Balaena mysticetus*, off Point Barrow, Alaska with observations on the subsistence hunt. *Rep. int. Whal. Commn* 37:301-8.
- George, J.C., Carroll, G.M. and Philo, L.M. 1988. Preliminary report on bowhead whale, *Balaena mysticetus*, census-related field activities during Spring 1987 off Point Barrow, Alaska. *Rep. int. Whal. Commn* 38:393-9.
- George, J.C., Carroll, G.M., Philo, L.M. and Albert, T.F. 1990. Report of field activities of the Spring 1988 census of bowhead whales (*Balaena mysticetus*) off Point Barrow, Alaska with observations on the subsistence hunt. *Rep. int. Whal. Commn* 40:383-91.
- George, J.C., Suydam, R.S., Philo, L.M., Albert, T.F., Zeh, J.E. and Carroll, G.M. 1995. Report of the spring 1993 census of bowhead whales, *Balaena mysticetus*, off Point Barrow, Alaska, with observations on the 1993 subsistence hunt of bowhead whales by Alaska eskimos. *Rep. int. Whal. Commn* 45:371-84.

- George, J.C., Zeh, J., Suydam, R. and Clark, C. 2003. N_4/P_4 abundance estimate for the Bering-Chukchi-Beaufort Seas stock of bowhead whales, *Balaena mysticetus*, based on the 2001 census off Point Barrow, Alaska. Paper SC/55/BRG7 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 16pp. [Paper available from the Office of this Journal].
- George, J.C., Zeh, J., Suydam, R. and Clark, C. 2004. Abundance and population trend (1978-2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Mar. Mammal Sci.* 20(4):755-73.
- Harville, D.A. 1977. Maximum likelihood approaches to variance component estimation and to related problems. *J. Am. Stat. Assoc.* 72:320-40.
- International Whaling Commission. 1994. Report of the Scientific Committee. *Rep. int. Whal. Commn* 44:41-67.
- International Whaling Commission. 2004. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 6:1-60.
- Johnson, J.H., Braham, H.W., Krogman, B.D., Marquette, W.M., Sonntag, R.M. and Rugh, D.J. 1981. Bowhead whale research: June 1979 to June 1980. *Rep. int. Whal. Commn* 31:461-75.
- Krogman, B.D., George, J.C., Carroll, G., Zeh, J. and Sonntag, R. 1986. Preliminary results of the 1985 spring ice-based census of the bowhead whale, *Balaena mysticetus*, conducted near Point Barrow, Alaska. *Rep. int. Whal. Commn* 36:343-52.
- Marquette, W.M., Braham, H.W., Nerini, M.K. and Miller, R.V. 1982. Bowhead whale studies, autumn 1980 – spring 1981: harvest, biology and distribution. *Rep. int. Whal. Commn* 32:357-70.
- McCullagh, P. and Nelder, J.A. 1983. *Generalized Linear Models*. Chapman and Hall, London. 261pp.
- Nerini, M.K. and Rugh, D.J. 1986. Distribution of bowhead whales in the vicinity of Point Barrow, Alaska: aerial observations 1984 and 1985. *Rep. int. Whal. Commn* 36:359-61.
- Punt, A.E. and Butterworth, D.S. 1999. On assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) using a Bayesian approach. *J. Cetacean Res. Manage.* 1(1):53-71.
- Raftery, A.E. and Zeh, J.E. 1991. Bayes empirical Bayes estimation of bowhead whale population size based on the visual and acoustic census near Barrow, Alaska, in 1986 and 1988. Paper SC/43/PS8 presented to the IWC Scientific Committee, May 1991 (unpublished). 51pp. [Paper available from the Office of this Journal].
- Raftery, A.E. and Zeh, J.E. 1993. Estimation of bowhead whale, *Balaena mysticetus*, population size. pp. 163-240. In: J.S. Hodges, R.E. Kass, C. Gatsonis and N. Singpurwalla (eds.) *Bayesian Statistics in Science and Technology: Case Studies*. Springer-Verlag, New York. 437pp.
- Raftery, A.E. and Zeh, J.E. 1998. Estimating bowhead whale population size and rate of increase from the 1993 census. *J. Am. Stat. Assoc.* 93:451-63.
- Raftery, A., Zeh, J. and Givens, G. 1995. Report of the Scientific Committee, Annex F. Report of the Sub-Committee on Aboriginal Subsistence Whaling. Appendix 6. Revised estimate of bowhead rate of increase. *Rep. int. Whal. Commn* 45:158.
- Rugh, D.J. 1990. Bowhead whales reidentified through aerial photography near Point Barrow, Alaska. *Rep. int. Whal. Commn* (special issue) 12:289-94.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd Edn. Charles Griffin and Company Ltd., London. i-xvii+654pp.
- Withrow, D. and Goebel-Diaz, C. 1989. Distribution of bowhead whales near Point Barrow, Alaska, 1984-1986. *Rep. int. Whal. Commn* 39:305-8.
- Zeh, J.E., Ko, D., Krogman, B.D. and Sonntag, R. 1986a. A multinomial model for estimating the size of a whale population from incomplete census data. *Biometrics* 42:1-14.
- Zeh, J.E., Ko, D., Krogman, B.D. and Sonntag, R. 1986b. Statistical considerations in estimating the number of bowhead whales, *Balaena mysticetus*, from ice-based visual census data. *Rep. int. Whal. Commn* 36:317-23.
- Zeh, J.E., George, J.C., Raftery, A.E. and Carroll, G.M. 1991. Rate of increase 1978-88, of bowhead whales, *Balaena mysticetus*, estimated from ice-based census data. *Mar. Mammal Sci.* 7(2):105-22.
- Zeh, J.E., Clark, C.W., George, J.C., Withrow, D., Carroll, G.M. and Koski, W.R. 1993. Current population size and dynamics. pp. 409-89. In: J.J. Burns, J.J. Montague and C.J. Cowles (eds.) *The Bowhead Whale*. Special Publication No. 2. The Society for Marine Mammalogy, Lawrence, Kansas. 787pp.
- Zeh, J.E., Raftery, A.E. and Schaffner, A.A. 1995. Revised estimates of bowhead population size and rate of increase. Paper SC/47/AS10 presented to the IWC Scientific Committee, May 1995 (unpublished). 28pp. [Paper available from the Office of this Journal].

Date received: August 2005

Date accepted: August 2005

