# An approach to minimise bias in estimation of the length-frequency distribution of bowhead whales (*Balaena mysticetus*) from aerial photogrammetric data

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ABSTRACT

Past attempts to estimate the length structure of the Bering-Chukchi-Beaufort (B-C-B) stock of bowhead whales have yielded quite different results from one study to the next because of size segregation on the summering areas or because of size segregation during the spring migration combined with inconsistent sampling during the migration period. A new approach is presented to document the length-frequency distribution of the B-C-B stock using length measurements from 3,107 whale images collected during the spring migrations of 1985, 1986, 1989-1992 and 1994. This method provides estimates of the proportion of calves (length <6m), subadults (length 6-<13m) and adults (length ⩾13m). The data from all years are combined by weekly period and a bootstrap sampling procedure is used to construct the length-frequency by week. The distributions for each week are then combined to obtain the overall distribution, with each week's contribution being in proportion to the fraction of the migration estimated from ice-based census studies to pass during that week. Corrections for differential detectability of mother/calf pairs and for calves born after they pass Point Barrow, Alaska, are allowed for in the analysis. This new approach eliminates some of the biases that affected past attempts to estimate the length-frequency distribution for the B-C-B population of bowhead whales. It is robust to inclusion or exclusion of data for any given year and the time interval chosen to define repeat images. The new approach estimates a slightly higher proportion of subadults and lower proportion of adults in the population than most previous studies. The proportion of calves is also lower, but that is suspected to result from our inability to accurately estimate the proportion of the migration late in the season when many of the mother-calf pairs pass Point Barrow. These late season migrants have not been accounted for during past photogrammetry studies or the ice-based census. Although the results do not differ substantially from those of most previous studies, sensitivity analyses indicate that several biases existed in the previous methods, but largely cancelled each other out.

KEYWORDS: BOWHEAD WHALE; ARCTIC; PHOTOGRAMMETRY; PHOTO-IDENTIFICATION; POPULATION PARAMETERS; LENGTH DISTRIBUTION; BERING SEA; CHUKCHI SEA; BEAUFORT SEA

## INTRODUCTION

Several past studies have attempted to establish the length structure of the Bering-Chukchi-Beaufort (B-C-B) stock of the bowhead whale (*Balaena mysticetus*) using aerial photogrammetry. The earliest studies were conducted in 1982 and 1983 by Davis *et al.* (1983) and Cubbage and Calambokidis (1987), respectively, who photographed bowhead whales on their summer feeding grounds in the eastern Beaufort Sea and Amundsen Gulf. These and later studies conducted during the summer were successful at obtaining large numbers of photographs of bowhead whales, but it was difficult to assess whether the photographs were representative of the overall population because of segregation of bowhead whales of different sizes during the summer (Cubbage and Calambokidis, 1987; Koski *et al.*, 1988). During some years, such as 1985, it was clear that the sample was not representative of the overall population because few large whales were photographed even though whales were abundant in the survey area and 1,601 photographs were obtained (Davis *et al.*, 1986).

From 1985-1994, studies attempting to document the length structure of B-C-B bowhead whales were conducted near Point Barrow, Alaska (Withrow and Angliss, 1992; 1994; Angliss *et al.*, 1995), primarily by the National Marine Mammal Laboratory (NMML). Most B-C-B bowhead whales are thought to pass relatively close to Point Barrow during their spring migration from early April to mid-June toward summer feeding areas in the Beaufort Sea (Braham *et al.*, 1980; Braham *et al.*, 1984; Moore and Reeves, 1993). It was thought that photographic surveys at that time of year would provide unbiased estimates of the length structure of the population. However, the length structures obtained during different years differed substantially (Withrow and Angliss, 1992; 1994). The biases associated with the photographic surveys near Point Barrow are discussed by Angliss *et al.* (1995). The two main biases are associated with (1) the differences in behaviour and hence detectability, of the different size classes of bowhead whales; and (2) the fact that the migration is size segregated and sampling has not been constant throughout the period of the migration. The behavioural biases affect collection of photographs throughout the season. Interruptions in surveys due to poor weather, not starting surveys until the migration is well underway, or terminating surveys before the end of the migration result in unequal sampling of different size classes of whales. By analysing data from several years simultaneously, Angliss *et al.* (1995) were able to derive a better estimate of the length structure of the population by averaging biases associated with (2) over several seasons. However, they were not able to directly address bias (1) and that had unknown effects on the population structure that they presented. Additional biases identified by Koski *et al.* (2004) include: (3) mothers and calves linger near Barrow, sometimes for several days, whereas other whales rarely linger, making mothers and calves more likely to be

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photographed; and (4) the surface and dive times of bowhead whales vary with their size and so large whales are less likely to be seen and photographed than small whales or calves.

The purpose of this paper is to present a new method of estimating the length structure of the B-C-B bowhead population that minimises most of the biases that exist in previous methods. It uses the combined data from photographic surveys conducted near Point Barrow during the springs of 1985, 1986, 1989-1992 and 1994. In order to calculate an unbiased length-frequency distribution, data on average rates of passage by weekly interval from the ice-based censuses from 1985 to 2001 (see Zeh *et al.*, 1986a; b; 1991; 1993; George *et al.*, 2003; 2004) are incorporated. Factors to account for biases attributable to differences in the behaviour of mothers and calves relative to other whales (Koski *et al.*, 2004) are also incorporated.

## METHODS

### Field effort

The surveys that contributed to the current analysis were conducted primarily by the NMML and were designed and conducted to cover most of the bowhead migration past Point Barrow. The surveys were conducted from about mid-April to early June in 1985, 1986 and 1989-1992. Less extensive spring surveys by LGL Limited (LGL) were used to supplement the NMML surveys during 1989 and 1991. LGL surveys were the only source of data in 1994.

Photographic surveys were carried out in twin-engine (for safety), high-wing (for visibility) aircraft (Twin Otters), with large bubble windows on the sides and a photographic port in the floor, either open or covered with optical quality glass. Flight altitudes for photography were generally 122-152m (400-500ft) above sea level as measured by a radar altimeter and airspeed was usually about 185km $hr^{-1}$ (100kt). During the whales' spring migration past Point Barrow (April to early June), the search efforts were conducted over sea ice and leads but were focused along open water areas, especially near the land-fast ice edge. After finding bowhead whales, a series of aerial passes was made to obtain vertical photographs through the port in the floor of the aircraft. Medium format cameras (70mm) were used for photogrammetry in all years. Fixed focal length lenses were used and all lenses were calibrated to determine their true focal length. Cameras were either hand-held or rigidly mounted. Each year, calibration targets were set up and photographed to permit scaling of radar altimeter altitudes recorded during photography to actual altitudes. For more information on field methods, see Rugh (1990), Koski *et al.* (1992), Withrow and Angliss (1992; 1994) and Angliss *et al.* (1995).

### Photo review

After processing and cataloguing, useable whale images were custom-cropped and printed to nearly fill 12.7cm × 17.8cm (5in × 7in) colour prints (Rugh *et al.*, 1992). The images were assigned quality and identifiability scores for each of four dorsal areas on each photograph of each whale: rostrum; mid-back; lower back; and fluke (Rugh *et al.*, 1998). All images within five days of each other were compared to each other to identify both repeat and duplicate photographs, so that a number of images for that individual could be used to calculate a best estimate of length (see below). Repeat photographs were those taken <60s apart and were treated as a single record during analyses. Duplicate photographs were those taken ≥60s apart during the same study and were included as separate records during analyses. Although past studies have created length-frequency distributions after eliminating repeat and duplicate images from the database, this study uses lengths from all measured images in the analysis in order to minimise biases associated with the ability to reidentify whales of different sizes. Five days was the maximum interval examined for duplicates because that was the maximum resighting interval detected by Rugh (1990). He examined 488 identifiable bowhead whales photographed near Barrow in the springs of 1984-87 for resightings at a later date. Fourteen whales were resighted on a subsequent date; eight, four, one and one were resighted after one, two, three and five days, respectively.

### Measurements of whales

Whales were measured directly from the film using a stereomicroscope (LGL), a dissecting microscope and digitising pad (NMML) or computer image analysis software (NMML). At least three measurements by one person (LGL) or two measurements each by a different person (NMML) were made of each whale image and the measurements were averaged. If individual measurements differed by more than 1% (LGL) or 3% (NMML) the image was remeasured. If the measurements did not converge, the measurements were discarded or downgraded so that they were not used for photogrammetric purposes. The quality of each measurement was evaluated based on the clarity of the end points and the straightness of the whale. The criteria used by each organisation were similar, but with slightly different cut points and are described in Appendix 1. Equivalent grades of measurements (GRL) and the criteria for inclusion in the category are given in Table 1. More details of the measurement techniques and evaluations can be found in Koski *et al.* (1992) for LGL data and Angliss *et al.* (1995) for NMML data.

Table 1

Equivalent quality ratings for length measurements of bowhead whales as documented in various studies. Measurement qualities for each organisation are defined in Appendix 1. (Cascadia data were not used in this study.)

| Measurement quality | LGL | NMML and Cascadia 1985 to present | Cascadia 1983 |
|---|---|---|---|
| Good | 1, 2, and 3 | 1 and 2 | 1 to 6 |
| Fair | 4, 5, and 6 | 3 and 4 | 7 |
| Approximate | 8 and 9 | none | None |
| Negatively biased (oblique) | 7 | 5 | 8 |

### Criteria for analyses of lengths

Previous studies have shown that the major source of between-image variation in the calculation of whale lengths is error in radar altimeter output, with lesser contributions from the posture of the whale or the quality of the photograph (Koski *et al.*, 1992; Angliss *et al.*, 1995). The mean CV of a single length measurement of good or fair quality is ~2.1% (unpublished data). Table 2 shows the mean CV and mean SE of the 'best estimate' of length (BESTLEN in Appendix 1) of whales in this study according to a subjective rating (GRLEN). The better the quality of GRLEN, the more precise the length measurement. Therefore BESTLEN is used for each whale image regardless of the actual measurement made from that image. All good and fair length measurements for each whale in a given year, categorised as shown in Table 1, were averaged to calculate best length. The quality rating for the best length (GRLEN) takes account of the number of measurements and the quality of the original measurements that make up the best length as described in Appendix 1. Although the best length may be available for a particular image, it was not included in the length-frequency analysis if the image itself did not have a measurement rated as good or fair (GRL) as described in Table 1 and Appendix 1.

Table 2
Mean BESTLENs, mean CVs of each BESTLEN and mean SEs of each BESTLEN of whales photographed near Point Barrow, Alaska, during spring 1985-86, 1989-92 and 1994.

| | Mean | | | |
|---|---|---|---|---|
| BESTLEN quality (GRLEN) | BESTLEN | CVs (%) of each BESTLEN | SEs of each BESTLEN | *n* |
| 1 | 10.48 | 1.25 | 0.1206 | 23 |
| 2 | 12.77 | 1.62 | 0.1852 | 97 |
| 3 | 12.23 | 1.81 | 0.2027 | 164 |
| 4 | 11.87 | 1.89 | 0.2037 | 77 |
| 5 | 11.76 | NA* | NA* | 641 |
| 6 | 11.29 | NA* | NA* | 816 |

*Not available – only one measurement is available for each whale.

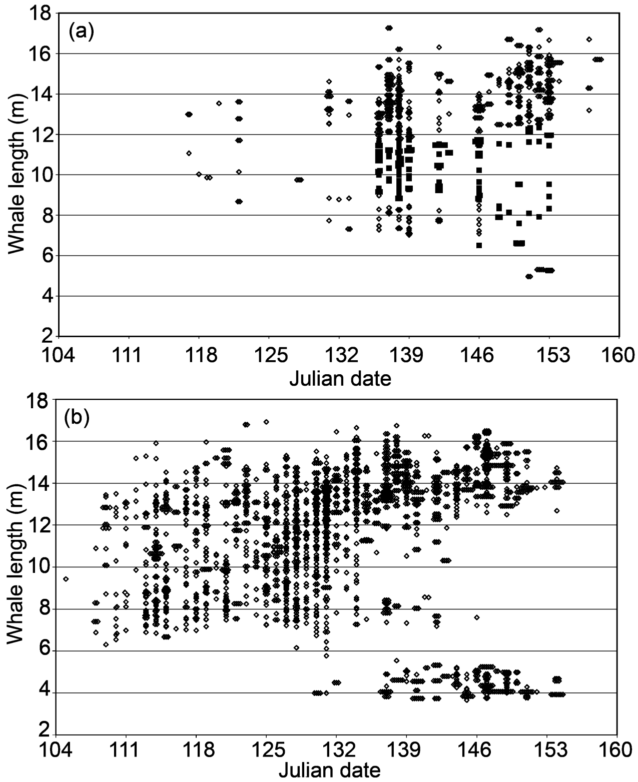


Fig. 1. Lengths of bowhead whales photographed in spring of (a) 1985 and (b) 1986, 1989-92 and 1994. The solid squares in panel (a) are whale sizes that were not seen during that same time period (i.e. were seen earlier) during 1986, 1989-92 and 1994.

**Creation of the length-frequency distribution**

Data from nine surveys conducted from 1985 to 1994 (six by NMML and three by LGL) were used to construct length-frequency distributions of the BCB bowhead whale population. The six NMML surveys were selected because each of them includes a sampling of most or all of the spring migration in the Point Barrow area. Results from two overlapping surveys (one each by NMML and LGL) are available for each of 1989 and 1991, while results from a single survey are available for each of 1994 (LGL), 1985, 1986, 1990 and 1992 (NMML). Earlier studies have shown that the techniques used by the two organisations provide results that are comparable (Koski *et al.*, 1992).

Initially, whale length was plotted against the date on which the photograph was taken for each year and for all years combined. These plots showed that although there were gaps in coverage of 1-7 days during individual years, the combined dataset provided length data for each day during the main part of the migration (Fig. 1b). They also confirmed that migration timing in 1985 was unusual (Fig. 1a). The 1985 migration appears to have been 5-11 days late based on ice-based census data and on photogrammetry data that provide passage dates of whales of a given size in other years (Fig. 1b). A marker for this shift is the end of the migration of small whales, excluding yearlings and young-of-the-year calves (see Koski *et al.*, 2004). Many small whales were present near Point Barrow on day 146 (26 May) in 1985 (Fig. 1a); whereas, in other years, all but a few small whales had passed by day 135 (Fig. 1b). Because 1985 provided the largest number of measured whales, we did not want to exclude it from the analysis. Shifts of 5-11 days were examined to see which best matched the other years' photogrammetry distributions in terms of quartiles of length distributions by week; number of measured whales by week; and % calves, subadults and adults by week. By all criteria, a 9-day shift in the 1985 timing resulted in the best match with other years' data. Thus length data from 1985 were combined with data from other years that were collected nine days earlier as indicated in Table 3.

The procedure used to construct length-frequencies involved first developing a database of 'useable' images (and their associated lengths and quality codes) based on the following criteria.

(1) Any photographs from 71-72°N and from 153-157°30'W were included. This area was chosen because it was surveyed regularly during the selected studies. It would be traversed by a typical whale in about 1-2 days of migration.
(2) Images that did not have a good or fair measurement quality as defined in Table 1 were deleted. The 'best length' for each animal was used rather than the measurement obtained from an individual photograph when more than one photograph of that whale was available. The 'best length' was determined using the approach outlined in Appendix 1 and was taken to be the same for all photographs of each animal in the same year.
(3) Any repeat photographs (i.e. photographs of the same whale taken at the same time) were deleted. 'Same time' was defined as <60s apart. Sensitivity was explored by, alternatively, defining repeats as photographs taken 0 seconds apart (i.e. at the same time) and <5min apart.
(4) During the length sampling, lone calves were discarded and mother/calf pairs were treated as a unit because lone calves often cannot be matched with themselves or with their mothers. When a record indicated that a whale was a mother, but the calf was not measured, the length of the calf was selected at random from the lengths of lone calves.

The length-frequency was computed using a bootstrap process with 10,000 samples being drawn during each bootstrap. This bootstrap process replicated the distribution

Table 3

Dates used to combine length data into 'weekly periods' for years except 1985 (1986, 1989-1992 and 1994) and 1985. Weeks 1 and 7 are longer than 7 days.

| | Weekly period | | | | | | |
|---|---|---|---|---|---|---|---|
| Year | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Except 1985 | <23 Apr | 23-29 Apr | 30 Apr-6 May | 7-13 May | 14-20 May | 21-27 May | >27 May |
| 1985 | <2 May | 2-8 May | 9-15 May | 16-22 May | 23-29 May | 30 May-5 Jun | >5 Jun |

of photographs across the season, accounted for disproportionate sampling at certain times during the season (the number of photographs taken during a week was not necessarily proportional to the number of animals that are estimated to pass Point Barrow during that period) and accounted for over-sampling of mother-calf pairs. This over-sampling occurs because mother/calf pairs are much more likely to be photographed than other whales during their spring migration past Point Barrow (Koski *et al.*, 2004). The surfacing and dive behaviour and swimming speeds of mothers and calves are noticeably different from those of other whales. These biases are described in detail in the section on 'Bias corrections'.

Each bootstrap replicate involved the following steps for each 'week', *w*, of the season.

(1) Determine the number of 'useable' photographs, $N_w$, for 'week' *w* and the proportion of the migration, $R_w$, that passes Point Barrow during this 'week' as determined from the ice-based census data (see 'Proportion of migration by week').
(2) Sample photographs (with replacement) from the 'useable' photographs for the week, discarding photographs of mother-calf pairs with a probability that accounts for 'over-sampling' of mother-calf pairs (a probability of inclusion of 0.406 for the baseline calculations – see 'Bias corrections' below), until the total number of sampled (but not discarded) photographs for the week is $N_w$.
(3) After the length-frequency for 'week' *w* is created, divide the number of calves in that week by 0.89 to account for calves that are born after they pass Point Barrow (see 'Bias corrections' below for the rationale for the choice of 0.89 for this correction factor).
(4) Add the length-frequency for week *w* to the total length-frequency weighting it by $R_w$.

**Bias corrections**

A systematic bias was found in the 1986 NMML length data, based on comparisons of individual whales photographed in two or more years (Koski *et al.*, 1992, p.494). The source of the error could not be identified but it probably was either related to an error in the calibration of the radar altimeter output or an adjustment to the radar altimeter after calibration. Of 19 whales measured both during 1986 and in other years, all were larger (mean 1.066 ±SE 0.012 times) than expected in 1986 after adjusting for expected growth between years (*t*-test, $P<0.001$). Therefore, it appears that a consistent upward bias of 6.6% was present in the original length calculations for 1986. This bias was not allowed for in previous publications based on the photogrammetry database but has been accounted for here by dividing the original 'best lengths' from the 1986 spring study by 1.066.

Analyses by Koski *et al.* (2004) indicate that mother/calf pairs (in spring, calves are <5.5m long) are photographed more often than other whales. Thus adjustments were needed to allow for the greater number of photographs of mother/calf pairs compared to other whales. Three biases have been described that contribute to the additional photographs of mothers and calves.

(1) The surfacing, respiration and dive cycles of calves are such that they are at or near the surface and therefore available to be photographed 1.69 times more frequently than other whales (Koski *et al.*, 2004).
(2) Both LGL and NMML made extra passes over mothers and calves to increase the probability of obtaining high quality images of the mother because of interest in documenting calving intervals. Two biases resulted: (a) a higher proportion of mothers than other whales that were encountered had at least one useable length measurement; and (b) more photographs were obtained of individual mothers and calves than of other whales. As a results of these two effects, there are 1.71 measured images (GRL≥1 and GRL≤6) of each mother and only 1.17 measured images of other whales.
(3) The average swimming speed of mother/calf pairs is much slower than that of other whales during their migration past Point Barrow in spring. As a result, mother/calf pairs sometimes remain in the survey area for more than one day and, unlike other whales, could be first photographed on their second or subsequent days in the area. This bias has not been quantified, but results in the proportion of mother/calf pairs in the length-frequency distribution being over-estimated (Koski *et al.*, 2004). Note that step 2 adjusts for mother/calf pairs that are photographed on more than one day but not for those that would not have been photographed if they travelled as fast as other whales.

The first two biases increase the probability that a given mother/calf pair will be sampled by a factor of about 2.46 ($1.69 \times 1.71/1.17$). Accordingly, during the bootstrapping process, images of mother/calf pairs were ignored with probability 0.594 (1-1/2.46) when constructing the length-frequencies. As has been the case for previous analyses of the length-frequency distribution of the B-C-B bowhead whale, it was not possible to account for the third bias.

Estimates of the annual calving rate based on data from the Point Barrow area during spring migration also need to include a factor for pregnant whales that deliver a calf after passing through the study area. An estimate can be made from the number of images with mother/calf pairs by assuming that 11% of calves are born east of Point Barrow, i.e. by dividing the observed number of calves by 0.89 (see Koski *et al.*, 1993). It is assumed that the mothers of these late-born calves are included in the sample of adults for the respective season.

**Proportion of migration by week**

The proportion of the migration that passed Point Barrow during each weekly period was estimated from data from the census years 1985, 1986, 1988, 1993 and 2001. Zeh and Punt (2005) summarise the data and methods used to determine abundance. Data for 1985 were shifted 9 days earlier because of the unusual migration timing, discussed above and 1987 was excluded because the ice-based census started late and ended early that year. Daily estimates of whales passing within visual range were obtained as described by George *et al.* (2004) and were summed for each week. The first and last weeks' estimates were scaled up to account for days before the census started and after the census ended when whales were known to have passed Point Barrow based on ice-based and aerial survey observations (Clark and Ellison, 1988; George *et al.*, 1987; 1990; 1995; 2003). This procedure may underestimate the numbers passing early and especially late in the season because the actual start and end dates of the migration in each year are unknown. Each weekly visual estimate was corrected by dividing by the proportion of whales estimated from acoustic and aerial transect survey data to have passed within visual range during the week. This provided an estimate of the total number of whales that passed each week. The weekly total estimates were divided by their sum for each year to estimate the proportion of the migration for that year represented by each week. Finally, the proportions for each week were averaged over the five census years.

The migration was divided into one week (7 day) bins starting with 23 April and ending on 27 May (Table 3). The proportions of the migration before 23 April and after 27 May each included >7 days because photographic effort during these periods was low and the early and late stages of the migration extended well beyond 7 days earlier and later than these dates.

## RESULTS

A total of 4,828 whale images were obtained within the study area during 1985, 1986, 1989-1992 and 1994. Fig. 2 shows the locations where these images were obtained during April, early-to-mid May and late May to early June. Numbers of whale images with reliable lengths during each year by weekly period are shown in Table 4. Reliable length measurements (GRLEN=1-6 in Appendix 1) are available for 3,107 images or 64% of the available images. Of these measurements, 41% (1,288) are based on more than one measurement (GRLEN=1-4 in Appendix 1C) and 59% (1,819) are based on a single measurement that is precise enough to be used to determine life-history information (GRLEN=5 or 6). Some other whales (109) were measured but were not included in the analysis because they were negatively biased or imprecise because (1) the radar altimeter was unstable, (2) they were estimated from a measurement of a part of the whale or (3) the photograph was not vertical to the water surface.

**Revised length-frequency distribution**

The approach to estimating the length-frequency distribution of the population given here assumes that migration timing is similar from year to year, unless, as in 1985, the migration was delayed for a prolonged length of time. Over- and under-sampling during parts of the migration is accounted for by weighting the size distribution for each week based on the proportion of the migration that passes during that week in an average year. The impact of excluding the 1985 data, which were adjusted for the unusual migration timing, is examined in one of the tests of sensitivity described below.

The total number of whale images within the study area and the number of useable lengths after each exclusion are given in Table 5. The numbers of images in the right-most column of Table 5 are those that were used to create the length-frequency distributions. The proportion of the migration that passed Point Barrow during each of the seven periods and the proportion of useable images are shown in Table 6. The periods through 6 May tended to have fewer length measurements and the later periods more than should have been obtained if sampling were proportional to the migration. Fig. 3 shows the length-frequency distributions generated from the weekly samplings. Primarily subadult animals were photographed before 29 April and the sizes of whales gradually increased throughout the migration period with few small whales and primarily large whales during the 14-20 May period. The small whales on the left side of the 14-20 May plot represent calves and yearlings (see Koski *et al.*, 2004). After 27 May, only mothers with calves and large whales were seen. The overall length-frequency distribution generated using these data is shown in Fig. 4.

Table 4

Numbers of reliable (GRLEN=1-6) whale measurements obtained in the study area by week during each study. For the 1985 NMML study, raw numbers for the weeks shown in the column headings and adjusted numbers for the 1985 weeks in Table 3 are presented.

| | Weekly period | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Study | <23 Apr | 23-29 Apr | 30 Apr-6 May | 7-13 May | 14-20 May | 21-27 May | >27 May | Total |
| 1985 - raw | 0 | 8 | 9 | 28 | 299 | 117 | 274 | **735** |
| 1985 - adjusted | 8 | 12 | 25 | 336 | 117 | 229 | 8 | **735** |
| 1986 - NMML | 0 | 0 | 93 | 121 | 57 | 139 | 65 | **475** |
| 1989 - NMML | 53 | 66 | 70 | 14 | 59 | 26 | 27 | **315** |
| 1989 - LGL | 0 | 0 | 2 | 0 | 17 | 36 | 32 | **87** |
| 1990 - NMML | 4 | 54 | 1 | 178 | 66 | 24 | 42 | **369** |
| 1991 - NMML | 2 | 37 | 54 | 120 | 41 | 55 | 12 | **321** |
| 1991 - LGL | 0 | 1 | 24 | 12 | 68 | 65 | 0 | **170** |
| 1992 - NMML | 20 | 151 | 36 | 84 | 80 | 45 | 49 | **465** |
| 1994 - LGL | 0 | 0 | 20 | 94 | 53 | 3 | 0 | **170** |
| **Total*** | **87** | **321** | **325** | **959** | **558** | **622** | **235** | **3,107** |

*Totals are based on adjusted numbers for 1985.

The examination of the sensitivity of the results to the various corrections and selection criteria is based on how the proportions of calves, subadults and adults changes (Table 7). The greatest sensitivity is associated with excluding lengths with GRLEN=6; the proportion of subadults declined from 0.569 to 0.483 and the proportion of adults increased from 0.398 to 0.448. None of the other sensitivity cases had a major influence on the proportions of subadults and adults. The proportion of calves was, however, sensitive to the mother/calf corrections; this proportion increased from 0.034 to 0.049 when the correction for diving behaviour was ignored and to 0.063 when all corrections were ignored. Excluding the 1985 data increased the overall proportion of calves slightly.

Table 5

The number of 'useable' whale measurements for the base-case analysis by week after each of the exclusions.

| | | Number of images remaining after exclusion of | | | |
|---|---|---|---|---|---|
| Week | Number of images | GRLEN <1 or >6 | Lengths assigned to images without good lengths | Repeat images | Calves |
| All | 4,828 | 3,107 | 2,433 | 2,235 | 2,069 |
| 1 | 210 | 87 | 73 | 71 | 71 |
| 2 | 543 | 321 | 289 | 266 | 266 |
| 3 | 690 | 325 | 258 | 246 | 246 |
| 4 | 1,588 | 959 | 832 | 778 | 774 |
| 5 | 773 | 558 | 400 | 357 | 322 |
| 6 | 721 | 622 | 439 | 393 | 311 |
| 7 | 303 | 235 | 142 | 124 | 79 |

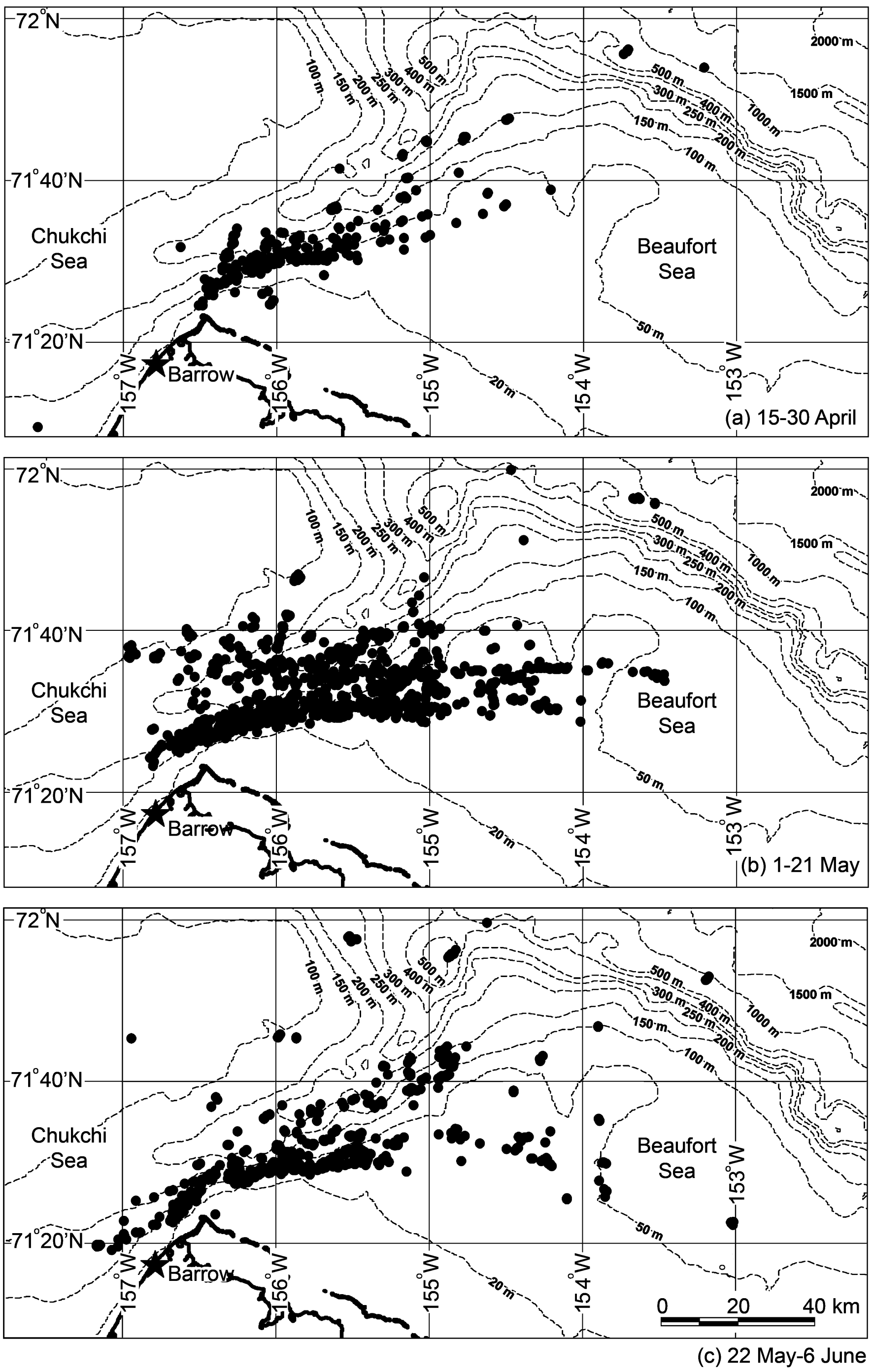


Fig. 2. Locations of measured bowhead whales photographed near Point Barrow, Alaska during photographic studies, 1985, 1986, 1989-1992 and 1994. The top, middle and lower panels show images obtained 15-30 April, 1-21 May and 22 May-6 June, respectively.

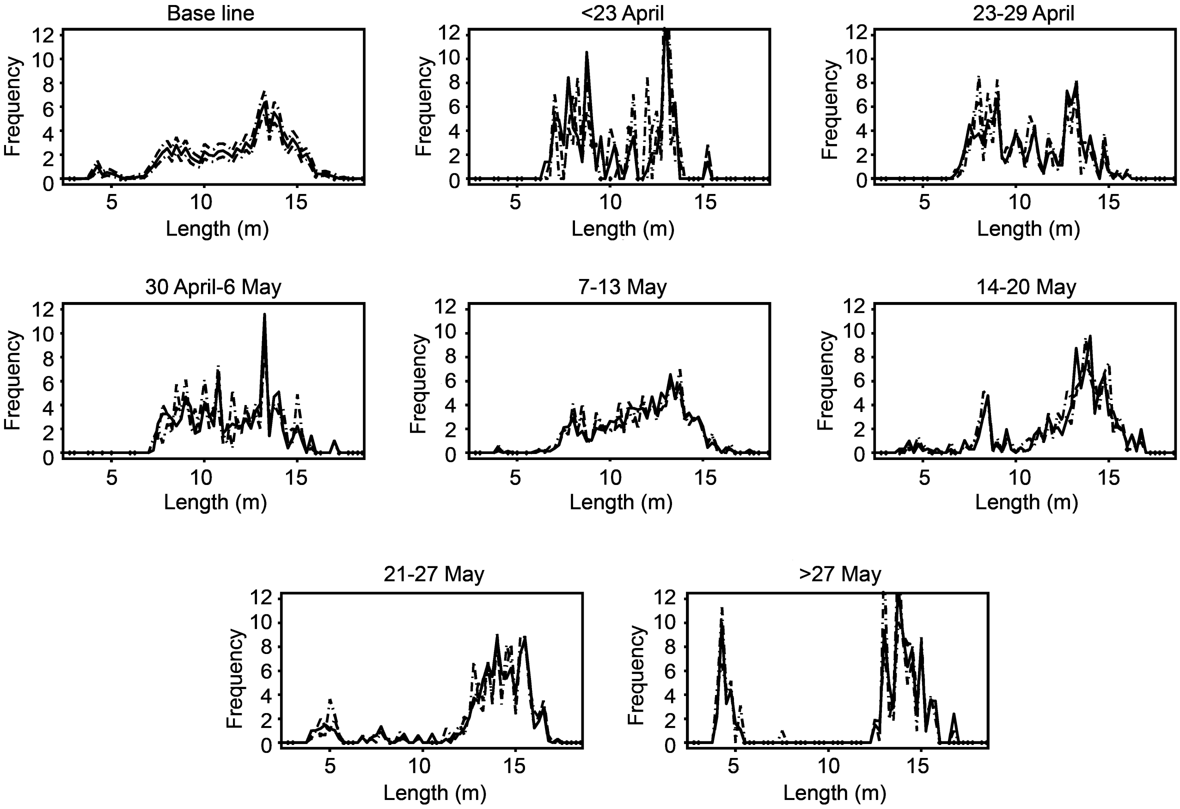


Fig. 3. The weekly length-frequency distributions generated from length measurements obtained during each weekly period 1985, 1986, 1989-1992 and 1994. The solid line is the median from the bootstrap procedure and the dotted lines are bootstrap 95% confidence intervals.

Table 6

The numbers and proportions of 'useable' images obtained in the study area by week after all exclusions and the relative proportions of the bowhead migrations passing Barrow, Alaska, by weekly period. The proportion of images is based on shifting the 1985 images 9 days earlier (1985 – adjusted) in Table 4. The proportion of the migration by week is estimated from ice-based census data from 1985, 1986, 1988, 1993 and 2001.

| | <23 Apr. | 23-29 Apr. | 30 Apr.-6 May | 7-13 May | 14-20 May | 21-27 May | >27 May |
|---|---|---|---|---|---|---|---|
| 'Useable' images | 71 | 266 | 246 | 774 | 322 | 311 | 79 |
| Proportion of images | 0.034 | 0.129 | 0.119 | 0.374 | 0.156 | 0.150 | 0.038 |
| Proportion of migration | 0.0613 | 0.1168 | 0.2087 | 0.3235 | 0.1508 | 0.0787 | 0.0602 |

Table 7

Proportions of calves (≤6m), subadults (6-<13m) and adults (≥13m) for each of the 13 cases. The base case includes: length data from all study years, both m/c corrections, measurements with GRLEN=1-6 and photographs of the same whale taken <60 seconds apart are considered repeats and are only included once.

| Case | Description | No. Images | Calves | | Subadults | | Adults | |
|---|---|---|---|---|---|---|---|---|
| | | | Estimate | SD | Estimate | SD | Estimate | SD |
| 1 | Base-case | 2,069 | 0.0339 | 0.0040 | 0.5686 | 0.0105 | 0.3975 | 0.0100 |
| 2 | No m/c corrections | 2,069 | 0.0627 | 0.0045 | 0.5440 | 0.0103 | 0.3933 | 0.0095 |
| 3 | No 1.69 correction | 2,069 | 0.0493 | 0.0044 | 0.5556 | 0.0103 | 0.3951 | 0.0097 |
| 4 | GRLEN ≤5 | 1,290 | 0.0691 | 0.0051 | 0.4825 | 0.0138 | 0.4484 | 0.0132 |
| 5 | Repeats = 0 sec | 2,247 | 0.0337 | 0.0037 | 0.5622 | 0.0101 | 0.4041 | 0.0096 |
| 6 | Repeats <5 mins | 1,898 | 0.0341 | 0.0044 | 0.5711 | 0.0108 | 0.3948 | 0.0103 |
| 7 | Without 1985 data | 1,544 | 0.0436 | 0.0052 | 0.5623 | 0.0128 | 0.3941 | 0.0120 |
| 8 | Without 1986 data | 1,819 | 0.0326 | 0.0052 | 0.5937 | 0.0183 | 0.3737 | 0.0174 |
| 9 | Without 1989 data | 1,839 | 0.0281 | 0.0046 | 0.5727 | 0.0141 | 0.3992 | 0.0135 |
| 10 | Without 1990 data | 1,805 | 0.0297 | 0.0045 | 0.5708 | 0.0119 | 0.3995 | 0.0115 |
| 11 | Without 1991 data | 1,750 | 0.0302 | 0.0043 | 0.5774 | 0.0125 | 0.3925 | 0.0121 |
| 12 | Without 1992 data | 1,751 | 0.0369 | 0.0046 | 0.5683 | 0.0125 | 0.3947 | 0.0120 |
| 13 | Without 1994 data | 1,906 | 0.0363 | 0.0042 | 0.5513 | 0.0113 | 0.4124 | 0.0108 |

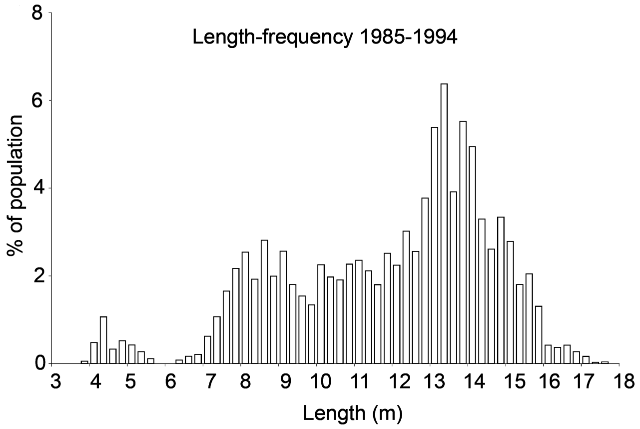


Fig. 4. Length-frequency distribution of the Bering-Chukchi-Beaufort stock of bowhead whales based on measurements from photogrammetric studies conducted in spring 1985, 1986, 1989-1992 and 1994.

## DISCUSSION

The length-frequency distribution of the BCB bowhead whales presented here accounts for most of the potential biases associated with the collection of the length data. However, three biases could not be addressed: (1) mother/calf pairs move more slowly past Point Barrow than do other whales (Koski *et al.*, 2004) and the effect of this slower travel on the probability of photographing a mother/calf pair has not been quantified; (2) mortality among new-born calves has not been quantified and may be significant; and (3) some of the migration passes Point Barrow before the census starts and after the census ends. Although the fraction of the migration after the census ends is small, it may have significant impacts on the estimate of the proportion of calves in the population because mothers and calves make up about half of the whales during the last sampling period (Fig. 3).

The robustness of the method is confirmed by the minor changes in the proportions of each age class during the sensitivity runs. No noticeable change in the proportion of each age class was found when any of the years was excluded from the analysis, although those proportions are highly variable among years (Table 8). Similarly, the results were insensitive to whether 0s, <60s or <5min between photos was selected to designate when images are repeats (i.e. those images treated as a single photograph for sampling purposes).

Corrections to the proportions of mother/calf pairs during the bootstrapping procedure had the greatest effect on the proportions of calves in the population, but exclusion of the mother/calf corrections had little effect on the proportions of adults and subadults other than the obvious effect of slightly decreasing the proportions of subadults and adults as the proportion of calves increased. Studies by Withrow and Angliss (1992; 1994) and Angliss *et al.* (1995) attempted to account for increased effort to photograph mothers and calves by including only one photograph of each whale when constructing their distribution (i.e. they removed known repeat and duplicate measurements). However, their method causes overestimation of small, unmarked whales in the length-frequency distribution because duplicates of small whales are less likely to be recognised and eliminated as duplicates. Our method samples all measured whales, whether or not they are duplicates (except for repeats which are multiple simultaneous or nearly simultaneous images of the same whale which are treated as a single image) and so does not rely on accurate re-identification of whales to obtain an unbiased sample. The procedure of Withrow and Angliss (1992; 1994) and Angliss *et al.* (1995) also assumes that mother/calf pairs are no more likely to be detected and photographed than other whales. Analyses conducted by Koski *et al.* (2004) show that mother/calf pairs are about 1.69 times more likely to be detected than other whales because dives of small calves are much shorter than those of other whales.

Table 8

Percentages of calves, subadults and adults estimated during different analyses.

| | Calves | Subadults | Adults |
|---|---|---|---|
| **Withrow and Angliss (1994)** | | | |
| 1985 | 1.0 | 56.9 | 42.1 |
| 1989 | 6.6 | 48.7 | 44.7 |
| 1990 | 8.1 | 53.4 | 38.6 |
| 1991 | 4.0 | 64.1 | 31.8 |
| 1992 | 0.7 | 65.5 | 33.7 |
| Weighted average | 3.3 | 57.5 | 39.2 |
| **Angliss *et al.* (1995)** | | | |
| 1985-86, 1989-92 | 5.2 | 53.7 | 41.1 |
| **This study** | | | |
| 1985-86, 1989-92, 1994 | 3.4 | 56.9 | 39.7 |

Previous analyses have found that small whales are more difficult to measure and that the quality of measurements of small whales tends to be poorer than that of large whales (see Davis *et al.*, 1983, table 8). For that reason, all measurements with quality considered suitable for life-history studies were used (GRLEN = 1-6, Appendix 1). Sensitivity analysis that restricted the calculation of the length-frequency to higher quality measurements (Table 7 – case 4) resulted in a 103% increase in the proportion of calves (from 0.034 to 0.069), a 13% increase in adults and a 15% decrease in subadults. These results are consistent with the finding of the previous study by Davis *et al.* (1983) and was the only sensitivity analysis that had a noticeable impact on the proportions of subadults and adults.

Although earlier attempts to construct length-frequency distributions yielded relatively similar results to those of this study (Table 8), it was coincidental that negative and positive biases in the earlier methods for determining the length-frequency of the population largely cancelled each other out. Even after combining data from seven spring seasons, photographs from some weekly periods were not proportional to the migration passing during that period (Table 6). There is a tendency to under-sample whales passing early in the season because heavy ice cover makes detection and photography of whales difficult and a tendency to over sample near the end of the migration when open water makes detection and photography relatively easy. However, the adequacy of sampling at the end of the season, when the majority of mothers and calves pass Point Barrow (Fig. 1b), has been variable. In all of the seasons reported here, photography stopped before the migration ended and the end dates were variable among years.

The remaining weakness in the analysis presented here is the inability to accurately estimate the proportion of whales passing after the census ended. This is true for all years, but is more problematic during years when aerial surveys were not conducted after the ice-based census ended. For example, 1993 was a year with large numbers of calves but no census observations or aerial surveys after 4 June. Based on data from other years, the migration may have continued for another week, therefore resulting in a possible underestimate of the proportion passing after 27 May. Based on the available 1993 data, an estimated 3.5% of the migration passed after 27 May, but in 2001, which was a high calf year when survey data were available later in the season, an estimate of 8.6% of the migration passing after 27 May was obtained. This bias causes an underestimate of the proportion of calves in the population.

Krogman (1980) estimated that <4% of the bowhead migration passes Point Barrow after the end of the ice-based census. Here data from ice-based observations, acoustic arrays and aerial surveys were used to estimate the proportion of the population passing Point Barrow before and after the census. While some animals may have passed before the nominal start date or after the nominal end date for the respective years, these numbers were probably small and would not alter the overall length-frequency distribution. However, as noted above, failure to account for small numbers passing at the end of the migration probably led to an underestimate of the proportion of calves in the population.

Data obtained from photography/photogrammetry studies of bowhead whales have made major contributions to our knowledge of the biology and life history of this species. Continuation of these studies will allow us to refine estimates made from past studies and estimate parameters that have not yet been examined. Unlike some other forms of observation, photographs provide permanent records of whales at a point in time.

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## Appendix 1

### (a) Length grades (GRL) as documented by NMML

Definitions of quality ratings assigned to bowhead whale morphometric measurements as documented for NMML (from Table 1 in Angliss *et al.*, 1995).

| Quality | Description |
|---|---|
| **Total length, fluke width and rostral length** | |
| 1 | Good view of measurement points; clear, unambiguous end points. |
| 2 | Fair view of measurement points; edges fuzzy, but discernible endpoints. |
| 3 | Poor view of endpoints; edges hazy; questionable as to where endpoints are; judgement required. |
| 4 | Points estimated or interpolated; one end obscured; tail or snout not visible. |
| 5 | Endpoints not visible. |
| **Flatness** | |
| 1 | Whale is flat relative to the sea surface. |
| 2 | Whale is slightly flexed upward or downward at snout or flukes; slight bow in the back; one end is higher than the other; twist in one plane. |
| 3 | Whale is clearly flexed; foreshortening undisputed. |

### (b) Length grades (GRL) as documented by LGL

| Grade | Description |
|---|---|
| **Total length, fluke width and rostral length** | |
| 1 | The whale was flat, horizontal and straight. The extremities are distinct. |
| 2 | The whale is approximately flat but may be slightly twisted. The extremities are distinct. |
| 3 | The whale is slightly inclined, arched or flexed or severely twisted and horizontal or the extremities are indistinct, but visible. |
| 4 | The whale is arched, flexed or severely twisted and the extremities could be indistinct. If the whale is straight and horizontal the end points may not be visible but nearby areas are visible, such as the trailing edge of the fluke. |
| 5 | Whale is severely arched or flexed. Measured lengths are multiplied by 1.0185 to account for the average underestimate of lengths of this grade of measurement. |
| 6 | The tail is down or the end points are not visible but some feature is available which will permit an estimation of the end points. Also used when the radar altimeter is fluctuating 8-12 feet within a few seconds of the photo. |
| 7 | Measurement is negatively biased because the photograph was oblique or the whale was too severely arched or inclined to measure accurately. |
| 8 & 9 | Adequate calibration data were not available; measurement is approximate. |

### (c) Best length grades and calculations

*Best length (BESTLEN)*

For purposes of most analyses, each whale photographed must be assigned a single length value - the best length. This value is assigned to each duplicate and repeat image of that whale. (That is, within each year, the same length is given to all images of the same whale).

For whales measured once, it is of course the same as the length measurement (LEN). However, in cases where duplicate and repeat images have been obtained, the evaluation of the best estimate of length is somewhat more complicated.

For LGL images with measurement grades 1-6, the average value is the best estimate; for NMML images, the best length is the average of all measurements of grades 1-4. Poorer measurements are not used unless they are the only option.

In addition, lengths derived from regressions based on snout-to-blowhole or fluke width measurements are used if a better measurement is not available.

### Quality of best length (GRLEN)

| | |
|---|---|
| 1 | BESTLEN was obtained from 5 or more measurements of grades 1-6 for LGL or grades 1-4 for NMML. |
| 2 | BESTLEN was obtained from 2 to 4 measurements of grades 1-3 for LGL or grades 1-2 for NMML. |
| 3 | BESTLEN was obtained from 2 to 4 measurements of grades 1-6 for LGL or grades 1-4 for NMML. |
| 4 | BESTLEN was obtained from 2 to 4 measurements of grades 4-6 for LGL or grades 3-4 for NMML. |
| 5 | BESTLEN was obtained from 1 measurement of grades 1-3 for LGL or grades 1-2 for NMML. |
| 6 | BESTLEN was obtained from 1 measurement of grades 4-6 for LGL or grades 3-4 for NMML. |
| 7 | BESTLEN was obtained from lengths derived without rigorous correction factors (i.e. grades 8 and 9 lengths). |
| 8 | BESTLEN was obtained from a snout-to-blowhole or fluke width measurement and regression equation. |
| 9 | BESTLEN was derived from an oblique photograph. |