Preliminary analyses on identifying yearling bowhead whales (*Balaena mysticetus*) in aerial photographs

W.R. KOSKI[*], J.C. GEORGE[+], J. ZEH[#], AND J.R. BRANDON[**]

[*] *LGL Limited, environmental research associates, 22 Fisher St., P.O. Box 280, King City, Ontario, L7B 1A6, Canada.*
[+] *Department of Wildlife Management, North Slope Borough, Box 69, Barrow, Alaska, 99723, USA.*
[#] *University of Washington, Department of Statistics, Box 354322, Seattle, WA, 98195-4322*
[**] *LGL Limited, environmental research associates, 2418 NW 57th St., Seattle, WA, 98107*

Contact e-mail: bkoski@lgl.com

ABSTRACT

Aerial photographs of bowhead whales taken during the spring of 2004 near Barrow, Alaska, were examined to determine if yearling (10- to 14-month-old) whales could be distinguished from 2-5 year old whales. Variables evaluated included date of passage past Barrow and measurements of body length, snout-to-blowhole distance, fluke width and body width at four standard locations. Preliminary analyses suggest that most of these variables were useful to some degree, but that the most reliable and useful were the ratio of axillary width:body length and migration date. All small whales passing late in the migration (>5 May) appear to be yearlings and measurement from these whales were used to establish measurement ratios that could be used to distinguish yearlings from 2+ year old whales earlier in the migration. During future analyses, the proportion of yearlings in the population in each year will be estimated using the methods of Koski *et al.* (2006; 2008) to correct for biases in sampling and an estimate of calf to yearling survival will be made.

KEYWORDS: SURVEY-AERIAL, PHOTO-ID, BOWHEAD WHALE, ARCTIC, BEAUFORT SEA, NORTHERN HEMISPHERE, MORTALITY, RECRUITMENT

INTRODUCTION

Aerial photography projects conducted from 1981–2004 have provided much of the life history data that are available on the Bering-Chukchi-Beaufort (BCB) stock of the bowhead whale (Angliss *et al.*, 1995; da Silva *et al.*, 2000; da-Silva *et al.*, 2007; Koski *et al.*, 1992; 1993; 2006; 2008; in press; Miller *et al.*, 1992; Nerini *et al.*, 1984; Rugh *et al.*, 1992; Schweder, 2003; Schweder *et al.*, 2010; Zeh *et al.*, 1993; 2002). The photography data are directly relevant to estimates of the underlying demography and productivity of the stock. They therefore have been incorporated into recent stock assessments (e.g., Brandon and Wade, 2006) and have been an underlying component in the testing and selection of the *Bowhead SLA* (IWC, 2003).

Photogrammetry data from 1985-1994 have provided information on the proportions of calves and mature animals in the population (Angliss *et al.*, 1995). More recently, Koski *et al.* (2008) provide an updated and refined index of calf production for eight years during 1985-2004. This index is calculated by taking into account factors (e.g., migration timing, dive times, etc.) that are known to affect the availability and detectability of cow/calf pairs relative to other animals in the population.

The calf index can be used to monitor reproductive rates through time and may be useful in evaluating the effects of environmental variability on population dynamics. Understanding the effects of environmental variability on cetacean population dynamics is an issue that is receiving increased attention in light of anticipated climate change (IWC, 2010). Further, quantifying variability in population dynamics should lead to more accurate estimates of population growth rates and hence more robust catch quotas (IWC, 2009).

Calving rates, or the proportion of calves in a population, have generally been used as an index of recruitment to cetacean populations. It has been suggested, however, that reproductive rates of adult females are expected to remain relatively buffered against environmental variability, whereas survival rates of immature animals are likely to be more sensitive to environmental variability than reproductive rates in populations of large mammals (Eberhardt, 1977). Therefore, the ability to monitor calf-to-yearling survival rates in cetaceans may provide a more powerful indicator of the influence of environmental variability on recruitment than monitoring reproductive rates alone.

Bowhead calves are weaned at 10-11 months of age, and following weaning, they appear to stop growing for a period of several years while they develop their baleen and learn to feed on their own (George, 2009). At weaning, young bowheads are probably at their maximum physical condition, at least until they resume their growth when ~5+ years of age. Thus, it is expected that recently weaned bowheads, which are about 10-14 months old (called yearlings hereafter) during the spring migration past Barrow, would have more stored energy reserves and be fatter than 2-5 year-old whales. Koski *et al*. (2004) suggested that small non-calf whales seen during the latter part of the spring migration may be yearlings, and discussions with subsistence hunters at Barrow supported their premise. The present paper analyses bowhead whale aerial photographs from the 2004 spring migration period to identify features that can be used to reliably distinguish yearlings from 2-5 year old whales and discusses a method to estimate the annual proportions of yearlings in the population during spring. Future analyses can then combine information on the proportion of yearlings with available information on the proportion of calves during the preceding spring to estimate calf-to-yearling survival rates for BCB bowheads.

METHODS

Photographic surveys at Barrow

Aerial photographic surveys that covered most of the spring migration period past Point Barrow, were conducted in 1985, 1986, 1989-1992, 2003 and 2004 (Angliss *et al*., 1995; Koski *et al*., 2006; 2008; in press). The 2004 photographic survey was selected as an appropriate data set for this study because 2003 was a moderate calf production year (Koski *et al*., 2008), and hence, moderate numbers of yearlings would be expected in the 2004 data set. Additional considerations were that the 2004 photographic survey started on 18 April and continued until 6 June with relatively uniform coverage of the migration due to good weather conditions. Further, the 1,975 bowhead whale images obtained during spring of 2004 were the largest number ever obtained during a spring survey.

Measurements from photographs

Standard measurements of body length, snout-to-blowhole distance and fluke width have been taken from bowhead whales during past studies and were available in the bowhead whale database. Methods for obtaining and identifying the quality of these measurements are described in Angliss *et al*. (1995) and Koski *et al*. (1992; 2006). In addition, the widths of whales at up to four locations, the axilla, umbilicus, anus and peduncle (shown on a harvested whale in Fig. 1) were taken as part of this investigation in order to document changes in girth or body condition of whales. The respective width measurements are located at 0.39, 0.56, 0.75 and 0.92 of the body length (George, 2009).

In all analyses presented in this paper, measurements from second and subsequent images of the same whale were included each time that they were measured to avoid biases associated with differential ability to identify whales photographed more than once. Data from harvested whales indicate that during spring whales <10.0m in length potentially could be yearlings (George, 2009) and so analyses were restricted to whales of these sizes.

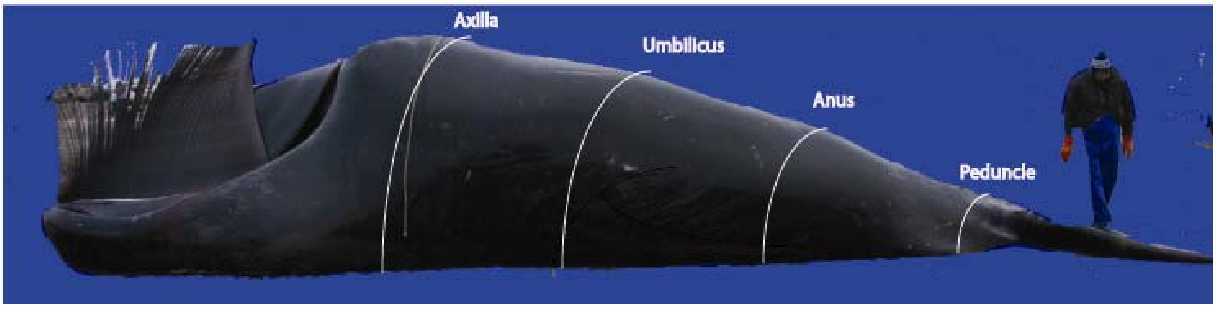

Fig. 1. Locations where width measurements were taken on bowhead whale photographs.

Collecting and processing of images

The 2004 aerial photographic studies were conducted jointly by LGL Limited (LGL), the North Slope Borough Department of Wildlife Management (NSB-DWM) and the Alaska Fisheries Science Center's National Marine Mammal Laboratory (NMML) with support from the Minerals Management Service (MMS). The field and laboratory methods were similar to those of earlier studies (Angliss *et al*., 1995; Koski *et al*., 1992) and are described in Koski *et al.* (2006).

Preliminary Criteria for Categorisation

To establish ranges of values for the various measurements for yearling and 2+ year old whales, it was assumed that all whales 6.0-10m photographed after 5 May were yearlings and all such whales photographed before 24 April were 2+ years old (Fig. 2). Preliminary investigation of the data indicated that this was a reasonable assumption for the purposes of these preliminary analyses. In addition to date, several other criteria were used for categorisation: the presence of a putative mother closely associated with a small whale, total body length, snout-to-blowhole distance:body length, fluke width:body length and width:body length ratios at the four locations shown in Fig.1.

The categorisation criteria for each of these variables were based on an assessment of the limits of each variable that would allow for unambiguous categorisation; that is, limits were chosen so that there was no overlap between values of that variable for yearlings and older animals. All individuals that fell between the limits were categorised as "unknown" age-class using that criterion, but usually those individuals could be successfully classified using a different variable. The classification criteria are listed in Table 1. The numerical limits were based on the assumption that yearlings were temporally segregated from older whales. Differences in the morphological variables for assumed yearlings seen after 5 May versus 2+ year old whales seen before 24 April that are listed in Table 1 are shown in the figures below.

In addition to the above analyses, photographs of yearlings and their putative mothers were investigated to determine if there was sufficient information from those photographs to identify the physical characteristics of yearlings.

Table 1.

Steps used to classify whales as yearlings, unknown or 2+ year old whales. The numeric ranges used to categorise individual whales are based on a combination of bowhead life history information, local and traditional knowledge and emergent patterns in the variables measured from assumed yearlings and assumed older whales. Values may change when more years of data are analysed.

Characteristic	Yearling	Unknown	2+ yr old
Total whales <10.0m	No	Yes	No
Presence of mother	Yes	No	No
Date after 5 May	Yes	No	No
Date before 24 April without mom	No	No	Yes
Length <6.9m	Yes	No	No
Length >9.5m	No	No	Yes
Axillary width:length >0.249	Yes	No	No
Axillary width:length <0.231	No	No	Yes
Umbillicus width:length >0.229	Yes	No	No
Umbillicus width:length <0.211	No	No	Yes
Anus width:length >0.129	Yes	No	No
Anus width:length <0.110	No	No	Yes
Snout-to-blowhole distance:length <0.200	Yes	No	No
Snout-to-blowhole distance:length >0.220	No	No	Yes
Fluke width:length <0.300	Yes	No	No
Fluke width:length >0.330	No	No	Yes

RESULTS

Length and date information for 10- to 14-mo-old bowheads photographed with their putative mothers are summarized in Table 2. Yearlings were distinguished from calves based on the criteria in Koski *et al.* (1990), which include differences in size, colouration and morphology of the head. There are 347 different measured calves in the bowhead whale photography database but only eight different measured yearlings were accompanied by their mother. Thus, there are too few yearlings accompanied by mothers in the database to define the physical characteristics of yearlings.

Table 2.

Lengths of yearling bowhead whales photographed with their mothers.

Whale number			Length (m)	
Yearling	Mother	Date photographed	Yearling	Mother
5040	5039	3 Aug 1985	7.46	13.44
7978	7977	11 May 1986	5.77	12.29
8164	8622	19 May 1986	7.33	13.94
10472	10473	7 May 1991	7.45	14.77
12918	12917	29 Apr 2004	8.37	14.07
12984	12983	12 May 2004	7.48	16.08
13252	13251	23 Apr 2004	7.27	14.10
14214	14213	17 Apr 2003	7.54	13.39

A total of 1,587 bowhead whale images were measured from photographs taken during the spring of 2004; 252 were non-calves smaller than 10m. The sizes of all measurable bowhead images in photographs taken during spring 2004 are shown in Fig. 2. Whales 3.7-5.2m that were photographed from 11 May to 6 June were all confirmed to be calves based on the criteria in Koski *et al*. (1990). Based on the hypothesis of Koski *et al*. (2004), the small whales (7.0-9.0m long) photographed from 6-31 May in Fig. 2 may be yearlings. The appearance of these small whales followed a period of seven days when no small whales were photographed. In addition, no whales between 9.0 and 10.8m were photographed after 29 April in 2004. This observation, combined with the local and traditional knowledge that yearling bowheads arrive at Barrow near the end of the spring migration, supports the supposition that small whales photographed after 5 May were recently-weaned yearlings.

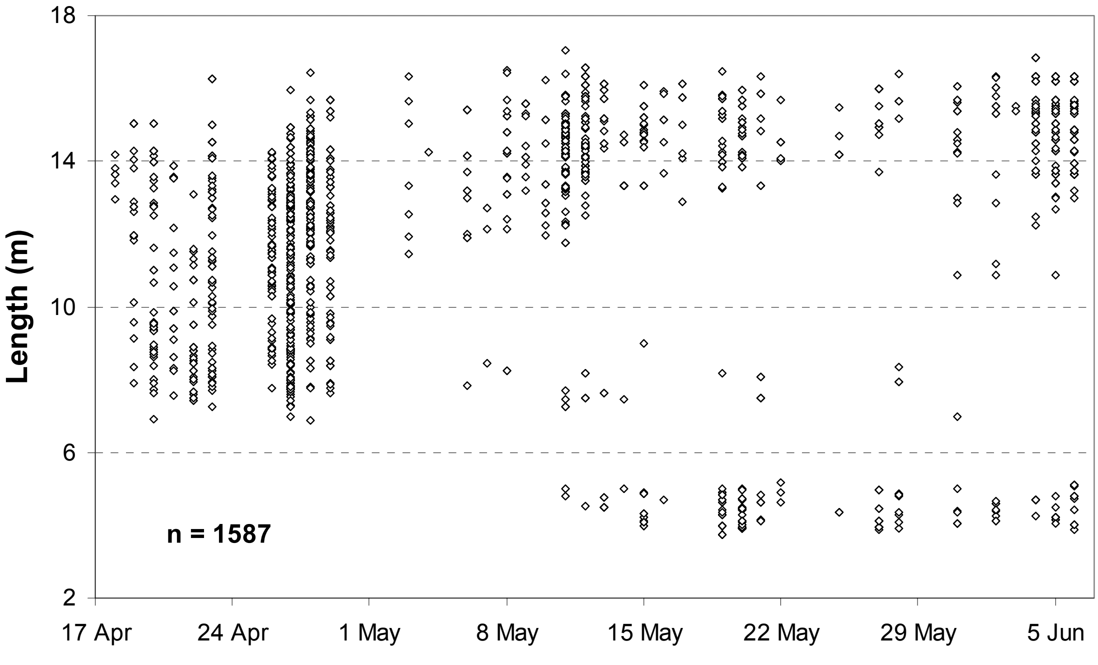

Fig. 2. Lengths of bowhead whales photographed near Barrow, Alaska, 18 April to 6 June 2004. Known duplicate whales are plotted each time they were measured.

Measurements of snout-to-blowhole distance were obtained from 18 whales and fluke width from 30 animals. Width at the axilla, umbillicus, anus, peducle and maximum width were obtained from 161, 161, 154, 117 and 161, respectively, of the 252 images with length measurements.

Fig. 3 shows axillary width plotted versus length for whales 6.0-10.0m long with different symbols shown for whales photographed during the periods 19-23 April, 26-29 April and 6-31 May. Most of the small whales photographed after 5 May were wider than similar sized whales photographed earlier in the season and tended to be wider than larger whales photogaphed earlier in the season. There is a large amount of overlap between lengths of small whales of different ages (George, 2009), so to better show the relationship between the relative fatness among whales of different ages, the ratio of axillary width:length was calculated. Fig. 4 shows the ratio of axillary width:length by date. This plot shows that all but one of the whales photographed after 5 May has an axillary width:length ratio >0.249, which is fatter than those seen earlier in the season. Some whales seen 26-29 April are fatter than the majority seen earlier based on axillary:length ratios >0.249 (Figs 4 and 5) and are probably yearlings. However, the majority of whales photographed during the 26-29 April period appear to be 2+ year old whales. Although the majority of presumed yearlings (i.e., those with axillary width:length ratio >0.249) are 7.0-8.5m long, Fig. 5 suggests that some yearlings may be as long as 9.5m. Fig. 5 also shows that the axillary width:length ratio for whales photographed 18-26 April declines significantly with body length until whales are at least 10m long (P<0.01; r = -0.36, df=63). That strongly suggests that the 9.5m whale with an axillary width:length ratio of 0.27 coded + in Fig. 5 was a yearling.

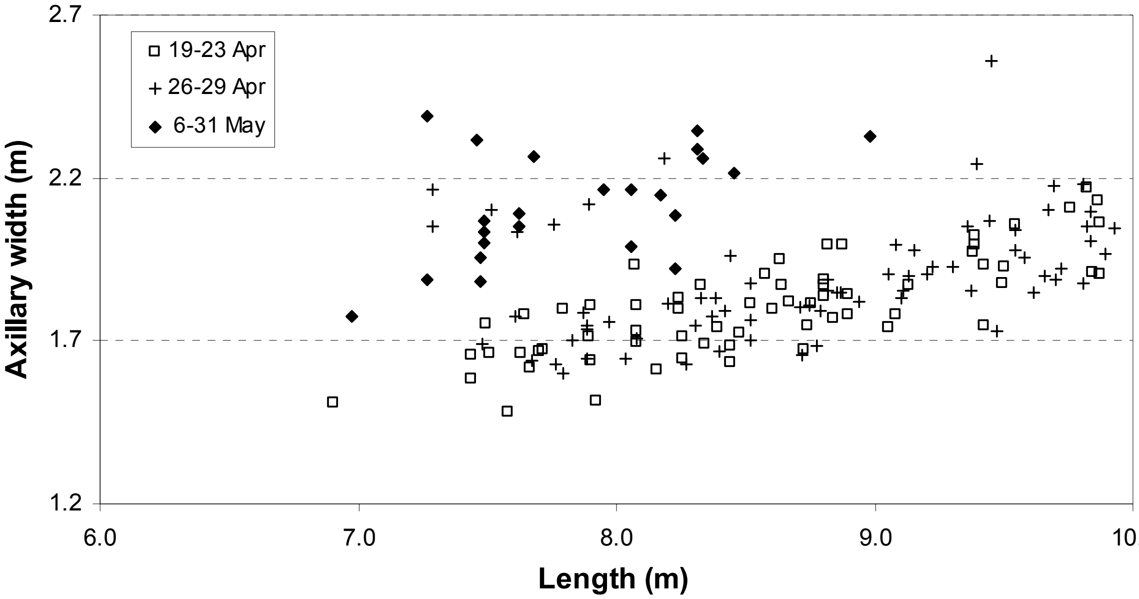

Fig. 3. Axillary width versus length for non-calf bowhead whales <10m photographed during spring 2004.

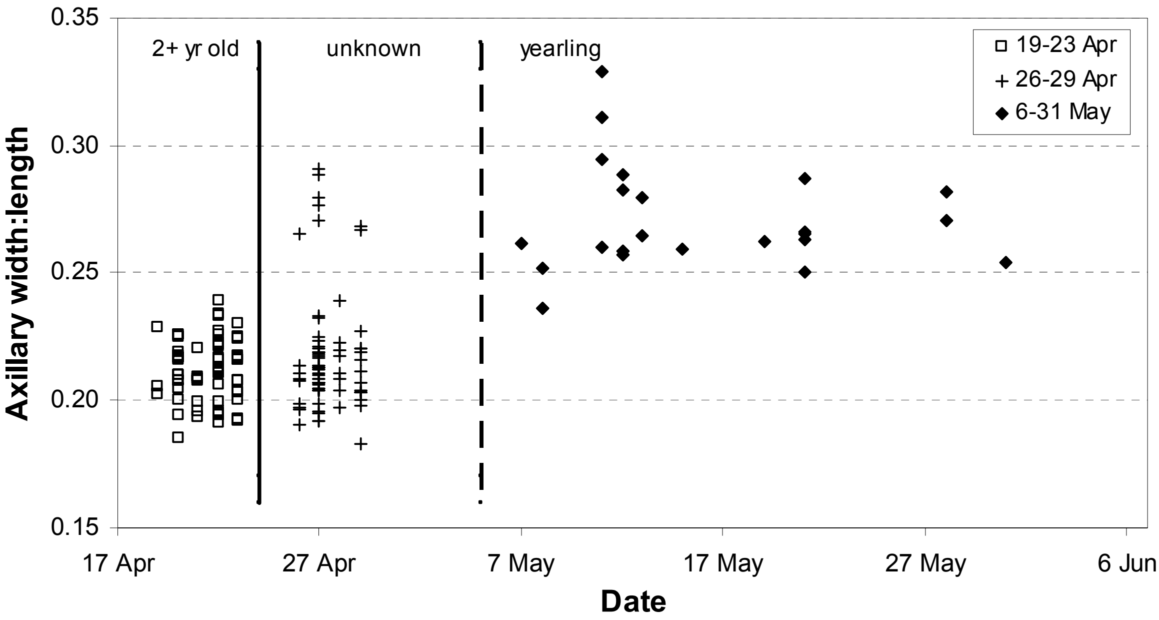

Fig. 4. Axillary width:length versus date for non-calf bowhead whales <10.0m during spring 2004. The vertical lines show the dividing lines between yearlings and unknown (dashed line) and 2+ year old and unknown (solid line) based on date.

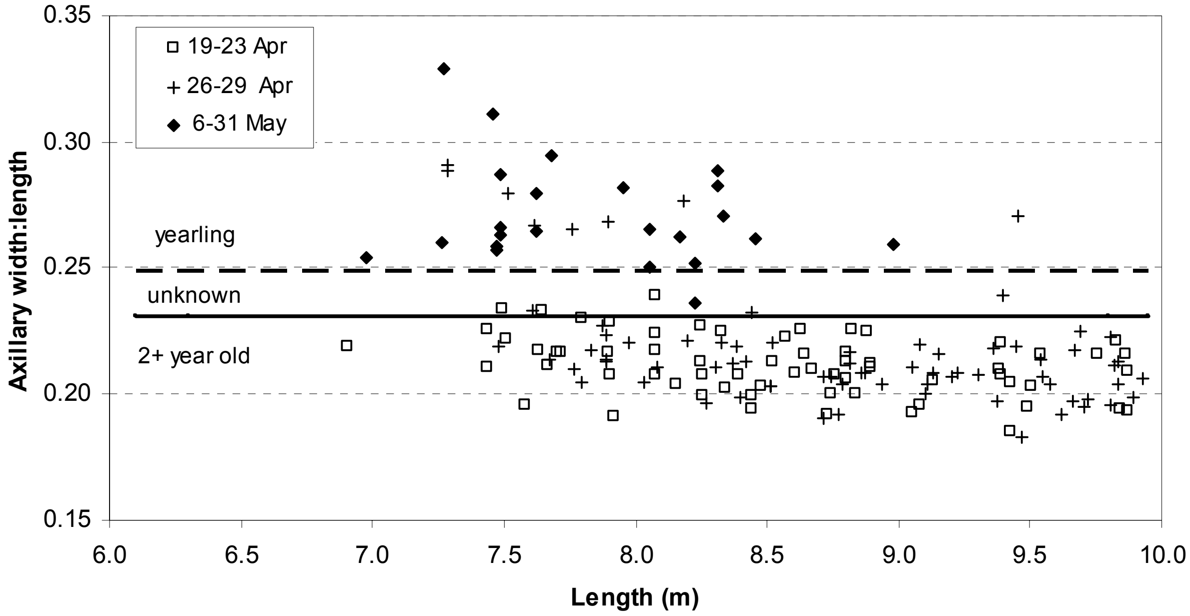

Fig. 5. Axillary width:length versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May. The dashed and solid horizontal lines show the dividing line between yearlings and unknown (dashed line) and unknown and 2+ year old whales (solid line) based on the axillary width:length ratio.

Fig. 6 shows the parallel plot for the ratio of umbillicus width:length that is shown in Fig. 5 for axillary width:length. Umbillicus width has a similar separation between values for yearlings and older whales as the axillary width with a small area of overlapping values around a ratio of 0.22. Width at the anus seems to be more variable than the previous two measurements and has more overlap in values for yearlings and older whales (Fig. 7) and peduncle width has even more overlap, to the point where peduncle width:length does not appear to be a useful measurement for classifying whales as yearlings versus older whales (Fig. 8). The maximum width:length is shown in Fig. 9 and is very similar to the axillary width:length because the maximum width is often at or near the location of the axillary measurement.

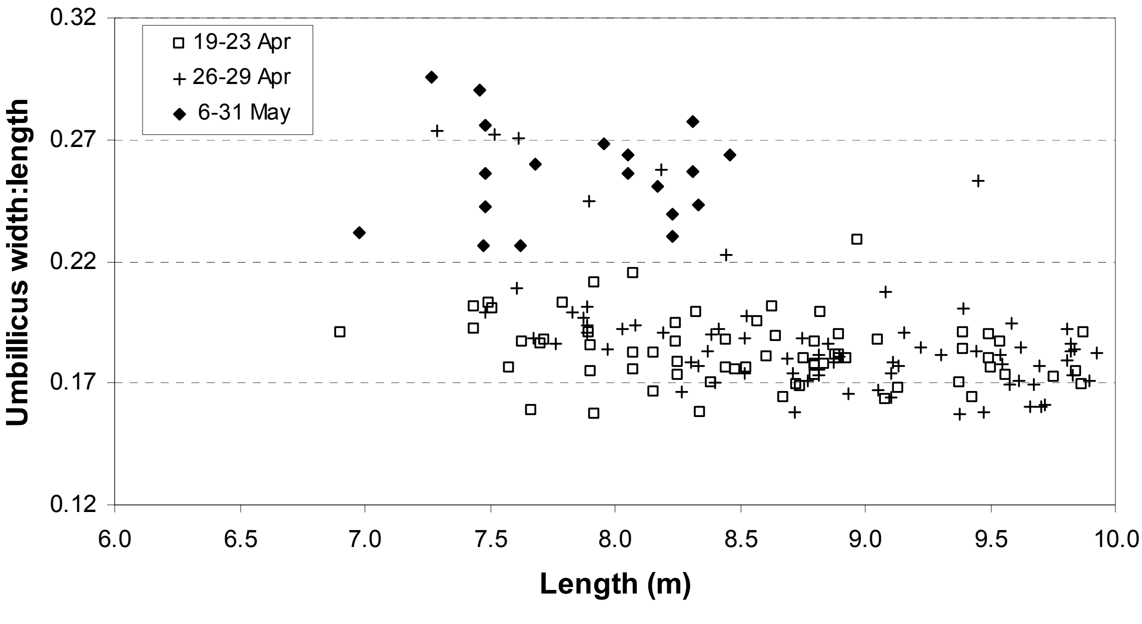

Fig. 6. Umbillicus width:length versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May.

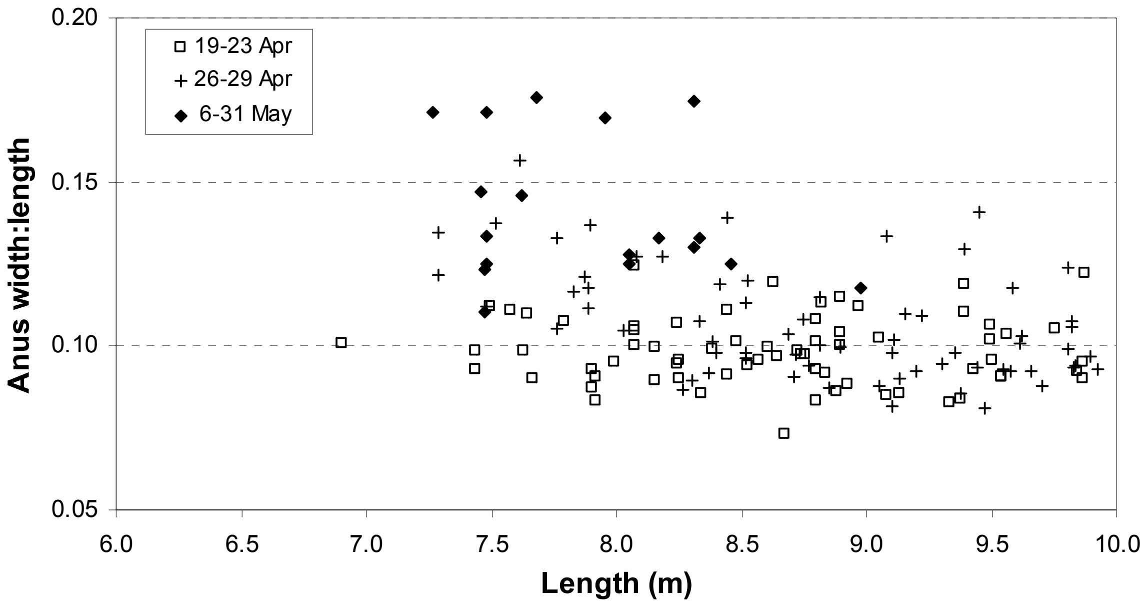

Fig 7. Anus width:length versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May.

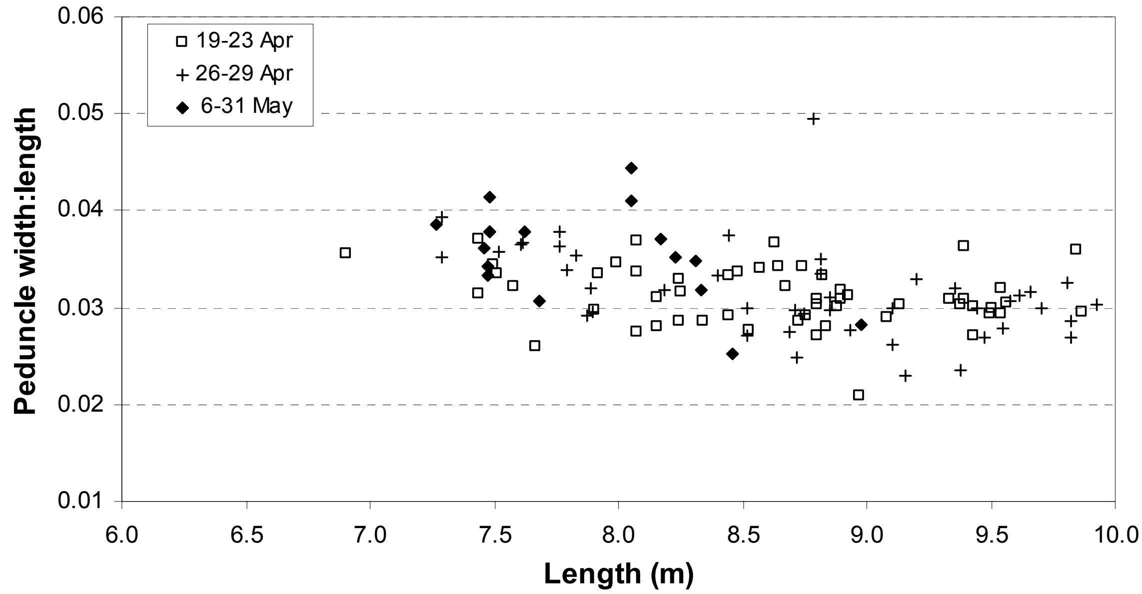

Fig. 8. Peduncle width:length versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May.

Past studies indicate that the heads of bowhead whale calves are relatively small compared to those of larger whales (George, 2009; Koski *et al.*, 1990; 1993). George (2009) found that the head:body length increased rapidly during the first 2-5 years of life and so the ratio of the head to body length should be a good predictor of age in small bowheads. Our sample of snout-to-blowhole distance:length from 2004 photographs is small (Fig. 10) and more measurements are needed to establish reliable criteria for separation of yearlings from older bowheads based on snout-to-blowhole distance measurements. Similarly the shape and width of flukes may be a reliable indicator of age in very young bowheads but too few measurements were obtained to establish reliable criteria for fluke width:length (Fig. 11).

Table 3 shows the tentative criteria established in Table 1 for distinguishing yearlings from older whales based on the above figures and evaluates their usefulness. The criteria shown here will be refined when measurements from the other seven years of data are available. Table 4 shows the number of whales classified by

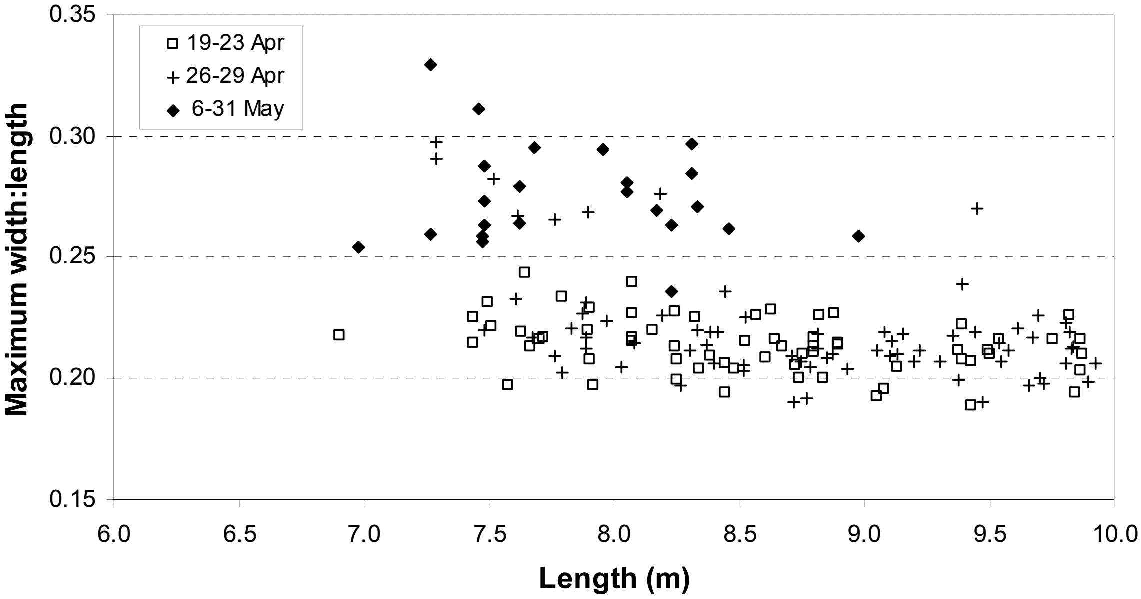

Fig. 9. Maximum width versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May.

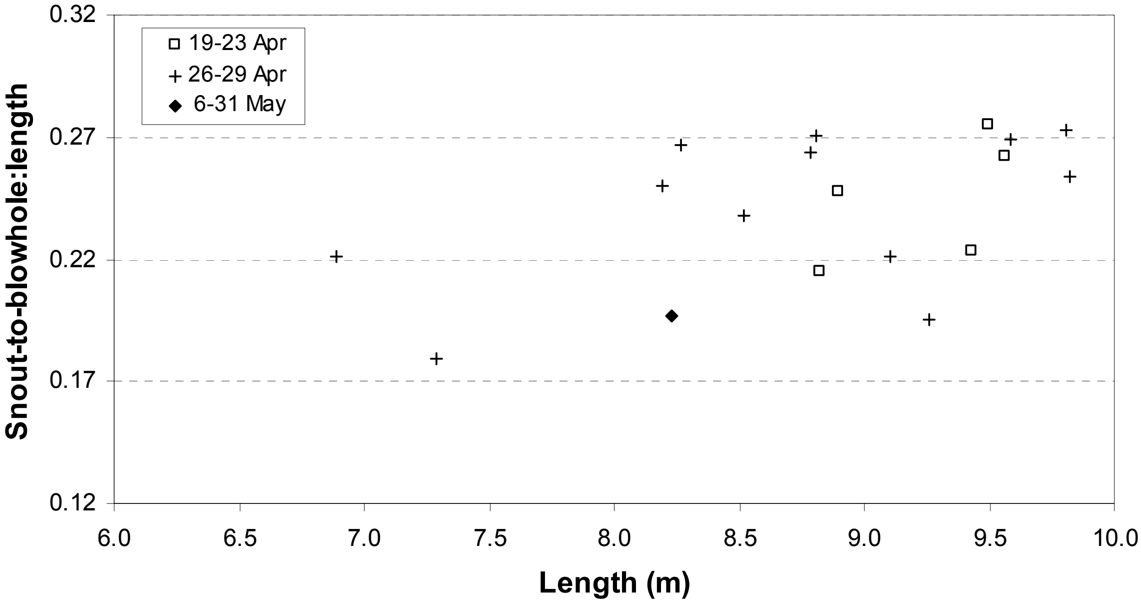

Fig. 10. Snout-to-blowhole distance:length versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May.

each criterion and overall and Fig. 12 shows the breakdown by date into yearlings, unknown and 2+ year old animals. Eighty five percent of whales <10.0m long were classified as yearlings or 2+ year old animals based on the preliminary criteria established in this paper. A total of 613 classifications were made on the 245 measured images, excluding seven measured images where yearlings were accompanied by their mother. We excluded the yearlings still with their mother because their growth was not complete and so their physical measurements might not be representative of older whales that were weaned. Some measured images could not be classified because the only measurement available was length. Where more than one classification was made on a whale because a whale had more than one variable measured, only two classifications did not agree with the others. Those two were based on anus width:length, which had the most overlap of the criteria that were used (Fig. 7).

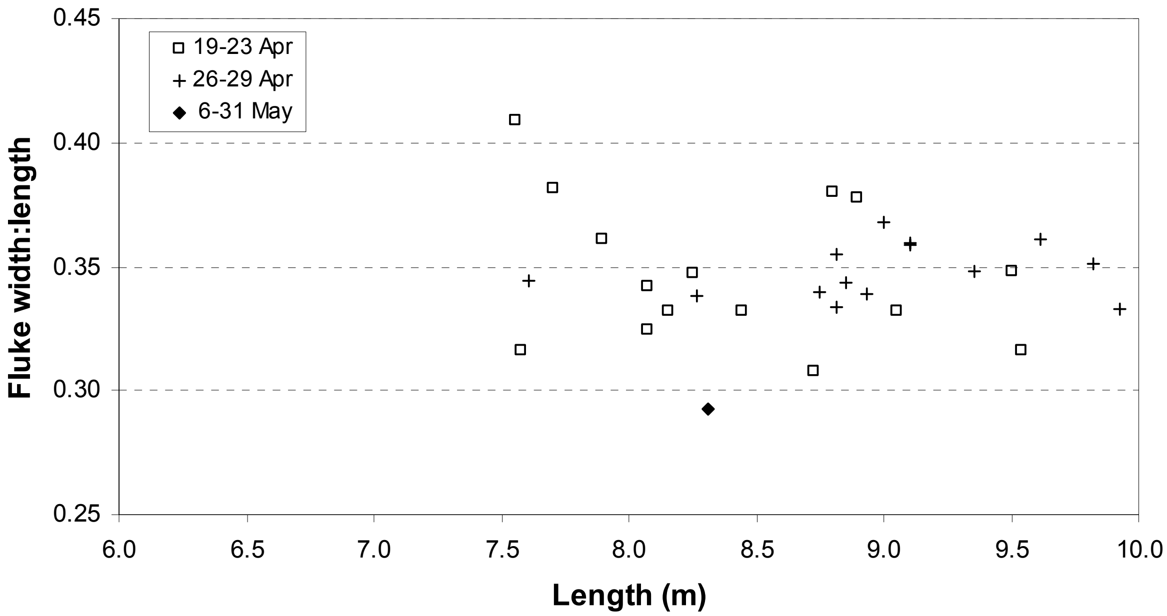

Fig. 11. Fluke width:length versus length for non-calf bowhead whales <10m photographed in 2004 during the periods 19-23 April, 26-29 April and 6-31 May.

Table 3.

Evaluation of criteria for classifying small whales during spring as yearlings or older.

Characteristic	Reliability	Usefulness
Presence of mother	Highest	Few yearlings are accompanied by their mother in spring
Date: after 5 May	High	Extremely useful. Confirms morphology measurements suitable for other periods
Date: before 24 April without mom	High?	Useful but date needs confirmation from more data
Length	Not reliable except for largest whales	Useful to classify largest whales
Axillary width:length	High	Very useful. Minor overlap between skinny yearlings and fat older whales
Umbillicus width:length	High	Very useful. Some overlap between skinny yearlings and fat older whales
Anus width:length	High	Useful but overlap between skinny yearlings and fat older whales is greater than for axillary and umbillicus widths
Peduncle width:length	Unreliable	Almost complete overlap between yearlings and older whales
Snout-to-blowhole distance:length	Probably medium	Measurement rarely obtained but separation probably good
Fluke width:length	unknown	Potentially useful but too few data in this sample to evaluate

Table 4.

Classification of small non-calf whales based on Tables 1 and 3. The three columns to the left show the classification based on the individual criterion in that row and the three columns to the right show the cumulative classifications based on sequential application of that criterion and all criteria above it.

	Based on criterion			Classified after all criteria used		
Characteristic	Yearling	Unknown	2+ yr old	Yearling	Unknown	2+ yr old
Total whales <10.0m	0	252	0	0	252	0
Presence of mother	7	245	0	7	245	0
Date after 5 May	28	224	0	32	220	0
Date before 24 April without mom	0	161	91	32	130	90
Length <6.9m	0	252	0	32	130	90
Length >9.5m	0	216	36	32	104	116
Axillary width:length >0.249	30	222	0	40	96	116
Axillary width:length <0.231	0	130	122	40	50	162
Umbillicus width:length >0.229	23	229	0	40	50	162
Umbillicus width:length <0.211	0	122	130	40	43	169
Anus width:length >0.129	20	229	0	41	42	169
Anus width:length <0.110	0	154	98	41	42	169
Snout-to-blowhole distance:length <0.200	3	229	0	42	43	169
Snout-to-blowhole distance:length >0.220	0	238	14	42	39	171
Fluke width:length <0.300	1	251	0	42	39	171
Fluke width:length >0.330	0	227	25	42	37	173

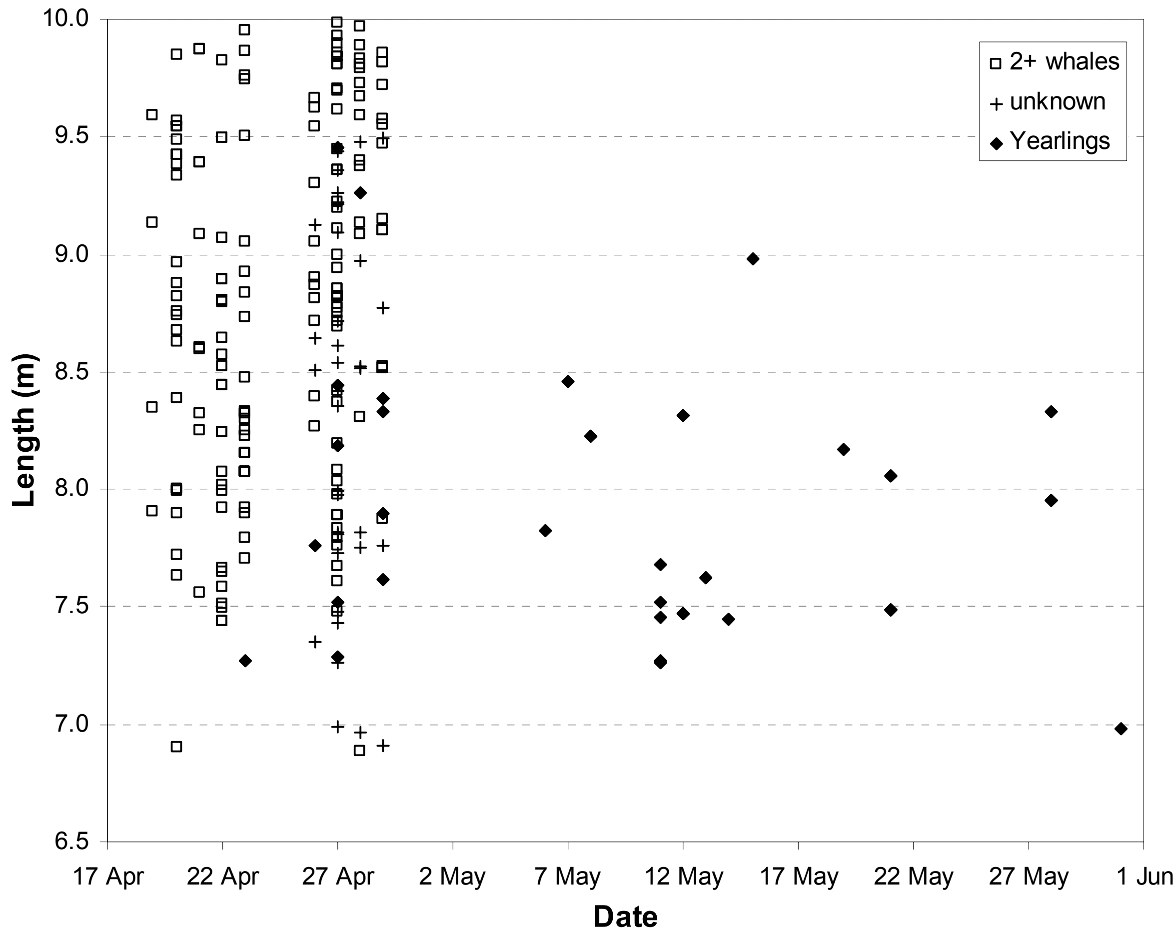

Fig. 12. Classification of 252 non-calf bowhead whales <10.0m long based on criteria in Table 1. Determination of status is summarized in Table 4.

DISCUSSION

Aerial photographs collected near Barrow, Alaska, during the spring of 2004 were analysed to see whether yearling bowhead whales could be reliably distinguished from older whales. A tree model was constructed to classify small bowheads as yearlings or 2+ old animals. The branches in the model were selected based on relative timing during the migration period and a suite of measurements taken from the photographs. Analyses of additional years of data may permit refinement of the criteria used in the tree model and may permit more complete categorization of photographs. In addition, some modifications of the criteria may be necessary to take into account inter-annual variation in migration timing when more years of data are included. The model permitted classification of 85% of images with greater than 99% agreement among the different criteria for distinguishing yearlings from older whales for animals that were not accompanied by their mothers.

Methods to classify the remaining 15% of small whales have not been explored but will be pursued. A second attempt will be made to obtain measurements, which will be less precise than our current measurements, from unclassified whales; however, those measurements might still be accurate enough to unambiguously categorize the whale as a yearling or older after allowing for greater uncertainty in the measurement. Other methods, such as mixture models (e.g., Gelman *et al*., 2004) and statistically fitted tree-based models (Breiman *et al*., 1984), will be considered in future analyses in order to quantify the number of yearlings in a more statistically robust framework. Likewise, it may be possible to eventually combine the photo data and independent length-at-age estimates (e.g., George *et al*., 1999; Lubetkin *et al*., 2008) in an integrated framework (e.g., Eveson *et al*., 2004) in order to improve our understanding of bowhead growth patterns.

Once images have been classified as yearlings or older, the approach of Koski *et al*. (2006; 2008) will be used to estimate the proportion of yearlings in the population for each year by accounting for biases in sampling effort and the variable proportions of the population that pass Barrow during each weekly period during the spring migration. Estimates of calf to yearling survival can then be made by comparing the proportion of yearlings in a sample year to the proportion of calves in the preceding year. When analyses are complete, there will be eight years with estimates of the proportion of yearlings in the population (1985-6, 1989-92 and 2003-4) and five estimates of calf to yearling survival (1985-6, 1989-90, 1990-1, 1991-2 and 2003-4). In addition, the proportions of yearlings in 1985, 1989 and 2003 will provide information to assess, in a general way, calf production in 1984, 1988 and 2002.

Photographic surveys during the spring migration of the BCB stock of bowhead whales near Barrow, Alaska, have provided much of the life-history data that are used for managing harvests from this stock. The additional information obtainable on yearling whales that was investigated during this study adds to the value of past and future surveys by providing information that can be used to estimate calf to yearling survival and by providing some information on calving the year before the survey. The latter information helps to fill gaps in sampling histories. Given concerns about the effects of environmental changes on calf production and survival (either positive or negative), it is recommended, that to the extent possible, future surveys be conducted on an annual basis for a period of three to four years followed by a gap of several years rather than spacing surveys more evenly over three to four years in a 10-yr period.

ACKNOWLEDGEMENTS

Many people have assisted in the acquisition of photographs and data from harvested whales that are present in the current bowhead whale photographic database. People who have contributed significantly to several of the photographic studies include Robyn Angliss, Lisa Baraff, Howard Braham, Jim Cubbage, Rolph Davis, Bob Evans, Gary Miller, Mary Nerini, John Richardson, Kim Shelden, Dave Withrow and Bernd Würsig. Steve McLean of LGL and Devin Bates of the NSB-DWM were primary observers and data recorders during the 2004 aerial surveys. Rita Acker, Paula Earp and several other members of the NSB-DWM assisted as observers. Marco Colella and Ralph Aiken of Commander Northwest piloted the aircraft. The staff at the NSB-DWM, including Directors Taqulik Hepa and Charles Brower, were particularly helpful and supportive of the studies.

We thank Charlie Brower and Harry Brower for their long discussions about bowhead whale behaviour and movements and for passing on local and traditional knowledge about the late season movements of Ingutuks past Barrow, which inspired the current analyses. We especially thank the Whaling Captains Association at Barrow for allowing us to conduct these studies near their village during the whaling seasons.

We thank Rolph Davis of LGL Limited and Dave Rugh of NMML for reviewing and providing comments that improved the paper.

Photographic surveys were conducted under Scientific Research Permits 580, 791, 782-1438 and 782-1791 (NMML) and 670 (LGL) issued by NMFS under the provisions of the US Marine Mammal Protection Act and US Endangered Species Act.

REFERENCES

Angliss, R.P., Rugh, D.J., Withrow, D.E. and Hobbs, R.C. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort seas stock of bowhead whales (*Balaena mysticetus*). *Rep. int. Whal. Commn* 45:313-24.

Brandon, J.R. and Wade P.R. 2006. Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using Bayesian model averaging. *J. Cetacean Res. Manage.* 8(3):225-239.

Breiman, L., Friedman, J.H., Olshen, R. and Stone, C.J. 1984. *Classification and Regression Trees*. Wadsworth International Group, Belmont, CA. 358pp.

da Silva, C.Q., Zeh, J., Madigan, D., Laake, J., Rugh, D., Baraff, L., Koski, W. and Miller, G. 2000. Capture-recapture estimation of bowhead whale population size using photo-identification data. *J. Cetacean Res. Manage*. 2(1):45-61.

da-Silva, C.Q. , Gomes, P.V.S. and Stradioto, M.A. 2007. Bayesian estimation of survival and capture probabilities using logit link and photoidentification data. *Computational Stat. Data Anal.* 51:6521-34.

Eberhardt, L.L. 1977. “Optimal” management policies for marine mammals. *Wildl. Soc. Bull*. 5(4):162-9.

Eveson, J.P., Laslett, G.M. and Polacheck, T. 2004. An integrated model for growth incorporating tag-recapture, length-frequency, and direct aging data. *Can. J. Fish. Aquat. Sci.* 61:292-306.

Gelman, A., Carlin, J.B., Stern, H.S. and Rubin, D.B. 2004. *Bayesian Data Analysis*, second edition. Chapman and Hall/CRC, Boca Raton, FL. 668pp.

George, J.C. 2009. Growth, morphology and energetics of bowhead whales (*Balaena mysticetus*). Unpublished Ph.D. Thesis, University of Fairbanks, Fairbanks, Alaska. 168pp.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* 77: 571-580.

IWC. 2003. Report of the Scientific Committee, Annex E. Report of the Standing Working Group on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP). *J. Cetacean Res. Manage.* (Suppl.) 5: 154–255.

IWC 2009. Report of the Scientific Committee. Annex D. Report of the sub-committee on the revised management procedure (RMP). *J. Cetacean Res. Manage*. 11 (supplement):91-124.

IWC. 2010. Report of the Scientific Committee. *J. Cetacean Res. Manage.* 11 (Supplement part 2):1-108.

Koski, W.R., Miller, G.W. and Davis, R.A. 1990. Growth rates and morphology of bowhead whale calves: photogrammetric evidence. Extended abstract presented at the 5th Conference on the Biology of the Bowhead Whale, *Balaena mysticetes*, April 1990, Anchorage Alaska.

Koski, W.R., Davis, R.A, Miller, G.W. and Withrow, D.E. 1992. Growth rates of bowhead whales as determined from low-level aerial photogrammetry. *Rep. int. Whal. Commn* 42:491-99.

Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1993. Reproduction. pp. 239-74. *In*: J.J. Burns, J.J. Montague and C.J. Cowles (eds) *The Bowhead Whale*. Special Publication. No. 2. Society for Marine Mammalogy, Lawrence, Kansas. 787pp.

Koski, W.R., Miller, G.W., Richardson, W.J. and Würsig, B. 2004. Bowhead whale (*Balaena mysticetus*) mothers and calves during spring migration in the Alaskan Beaufort Sea: movements, behaviour and life history data. Paper SC/56/BRG27 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 31pp.

Koski, W.R., Rugh, D.J., Punt, A.E. and Zeh, J. 2006. A new approach to estimate the length-frequency distribution of bowhead whales (*Balaena mysticetus*) using aerial photogrammetric data. *J. Cetacean Res. Manage.* 8(1):45-54.

Koski, W.R., Zeh, J. and George, J.C. 2008 A calf index for monitoring reproductive success in the Bering-Chukchi-Beaufort Seas bowhead whale (*Balaena mysticetus*) population. *J. Cetacean Res. Manage*. 10 (2): 99-106.

Koski, W.R., Zeh, J., Mocklin, J, Davis, A.R., Rugh, D.J., George, J.C. and Suydam, R. In Press. Abundance of Bering-Chukchi-Beaufort bowhead whales (*Balaena mysticetus*) in 2004 estimated from photo-identification data. *J. Cetacean Res. Manage.*

Lubetkin, S.C., Zeh, J.E. and George, J.C. 2008. Age estimation for young bowhead whales (*Balaena mysticetus*) using annual baleen growth increments. *Can. J. Zool.* 86:525-38.

Miller, G.W., Davis, R.A., Koski, W.R., Crone, M.J, Rugh, D.J. and Fraker, M.A. 1992. Calving intervals of bowhead whales - an analysis of photographic data. *Rep. int. Whal. Commn* 42:501-6.

Nerini, M.K., Braham, H.W., Marquette, W.M. and Rugh, D.J. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). *J. Zool., Lond.* 204:443-68.

Rugh, D.J., Miller, G.W., Withrow, D.E. and Koski, W.R. 1992b. Bowhead whale calving intervals established through photographic reidentifications. *J. Mammal.* 73:487-490.

Schweder, T. 2003. Abundance estimation from multiple photo surveys: confidence distributions and reduced likelihoods for bowhead whales off Alaska. *Biometrics* 59:974-83.

Schweder, T., Sadykova, D., Rugh, D.J. and Koski, W.R. 2010. Population estimates from aerial photographic surveys of naturally and variably marked bowhead whales. *J. Agric. Biol. Environ. Stat.* 15(1):1-19.

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, KS. 787pp.

Zeh, J., Poole, D., Miller, G., Koski, W., Baraff, L., and Rugh, D. 2002. Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981-1998 photoidentification data. *Biometrics* 58:832-40.