

Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*)
from the eastern Chukchi Sea

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University of Washington
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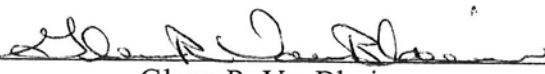
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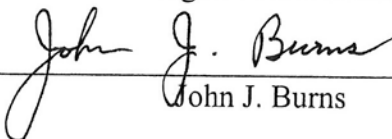
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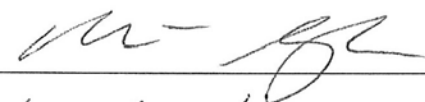
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Abstract

Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*) from the eastern Chukchi Sea

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Beluga whales (*Delphinapterus leucas*) are an important subsistence resource for many aboriginal peoples across the Arctic and subarctic. Environments of these whales are being subjected to considerable change, including increased human activities (e.g., oil and gas exploration and development) and climate change. To conserve belugas, we need to better understand their biology. Collection of biological samples of harvested whales and capture of live ones was possible because of an annual subsistence hunt at Point Lay in northwest Alaska along the eastern Chukchi Sea. Samples and measurements were collected from 688 harvested whales. These focused on aspects of age, growth, and reproduction. Measurements of standard length were compared with measurements from photographs taken during aerial surveys. Results indicated that the subsistence harvest was biased toward the larger, whiter animals and away from the smaller, darker ones. Measurements of harvested belugas showed that white males were longer than white females but the lengths of younger, darker animals were similar between sexes. Asymptotic lengths of males and females were 436 and 362 cm, respectively. The overall pregnancy rate was 0.56 but included females pregnant with near-term or small fetuses. When only accounting for small fetuses, the pregnancy rate was 0.41, which indicated a calving interval of 2 to 3 years. Production of young declined in older females (>~25 years).

Satellite transmitters were attached to 26 live-captured belugas and tracked for up to 520 days. After leaving the Point Lay area, whales moved north and east and mostly remained in the Beaufort Sea and Arctic Ocean during the summer and early autumn. Females and younger animals tended to remain near the shelf break while some large males moved far to the north ($\sim 80^\circ$ N) through deep, ice-covered waters. Some belugas were tracked south through the central and eastern Chukchi Sea. One animal provided the first known winter location for this stock, northwest of Saint Lawrence Island in the Bering Sea. Information on age, growth, reproduction, and movements of eastern Chukchi Sea belugas will allow for a greater ability to predict and mitigate impacts from changes occurring in the Arctic.

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CHAPTER 1

LENGTH DISTRIBUTION, COLOR COMPOSITION, AND EARLY GROWTH
OF BELUGA WHALES: EXAMINATION OF HUNTED AND PHOTOGRAPHED
ANIMALS FROM THE EASTERN CHUKCHI SEA

ABSTRACT

Beluga whales (*Delphinapterus leucas*) are an important subsistence resource for many aboriginal peoples across the Arctic and subarctic. Because hunters do not randomly harvest animals, the results from biological sampling for understanding of life history traits, could be biased. We examined biases by comparing average lengths and length distribution of harvested and free-ranging animals, which were measured on vertical aerial photographs. Average lengths of harvested whales were greater. Results of comparisons of length distribution differed between years. Lengths of all harvested belugas from 1987 to 1998 were longer than photographed whales. Small animals were underrepresented in the harvest and longer animals were underrepresented in the photographs. Biases in samples were likely caused by the age/sex segregation of belugas, hunting method, and hunter selectivity. Caution must be used when extrapolating results from biological sampling of hunted animals to the larger population and results should be appropriately qualified. We also extracted basic life history information for this population from the vertical photographs. We estimated length at birth to be about 157 cm and length of disassociation of calves and mothers to be about 246 cm, at about two years old.

INTRODUCTION

Beluga whales (*Delphinapterus leucas*) frequent certain coastal areas in many locations in the Arctic and subarctic during the summer and return to these areas year after year (Caron and Smith 1990, Frost and Lowry 1990). The animals' fidelity to summering areas provides a reliable resource for many aboriginal peoples. In some communities, belugas comprise a substantial component of the annual subsistence resource (Neakok et al. 1985, Heide-Jørgensen 1990, Fabijan et al. 1995). Human populations in the Arctic are usually quite small and dispersed, thus hunting of belugas is often sustainable. Belugas are susceptible to over-hunting though, when human populations are large, hunting needs change, or beluga populations are small (Heide-Jørgensen 1994, Moore and DeMaster 2000, Heide-Jørgensen and Rosing-Asvid 2002). Because belugas are harvested, understanding their population size, trend in abundance and biology are important for ensuring sustainable harvests. Lack of information can contribute to over-hunting or local extirpations (Heide-Jørgensen 1994, Moore and DeMaster 2000, Heide-Jørgensen and Rosing-Asvid 2002).

A great deal is known about many populations of beluga whales, even though some key information is still lacking (see Smith et al. 1990, Reeves et al. 1994, Reeves and St. Aubin 2001). For example, much has recently been learned about movements and distributions (Smith and Martin 1994, Richard et al. 2001a,b, Suydam et al. 2001), diving behavior (Heide-Jørgensen et al. 1998, 2001, Kingsley et al. 2001, Martin et al. 2001) and stock size (Frost and Lowry 1990, Richard et al. 1990, Harwood et al. 1996). Biological samples have often been collected from hunter-

killed animals to further our understanding of stock structure (Brennin et al. 1997, O’Corry-Crowe et al. 1998, 2002, de March et al. 2002, Innes et al. 2002, Palsbøll et al. 2002), contaminant burdens (Muir et al. 1990, Woshner et al. 2001), and health status (St. Aubin et al. 1990, 2001, Woshner et al. 2001). Also much can be learned from biological samples about life history traits such as age, growth and reproduction (Kleinenberg et al. 1969, Sergeant and Brodie 1969, Burns and Seaman 1986, Doidge 1990, Heide-Jørgensen and Teilmann 1994, Stewart 1994, Harwood et al. 2002).

Biological samples provide a great deal of information about belugas. Unfortunately, we do not know how representative those samples are of the associated population. As with many biological studies, small sample sizes have created problems with respect to making statistical comparisons among beluga populations (Steward 1994). An equally important consideration is whether biological samples from subsistence caught animals are representative of the population because of hunter selectivity or limited access to only specific types or sizes of animals. Researchers often assume, either explicitly or implicitly, that data or subsets of the data are representative of the population or a portion thereof (Heide-Jørgensen and Teilmann 1994, Stewart 1994, Harwood et al. 2002). Biases have been acknowledged but their influence on results is unknown (Burns and Seaman 1986, Harwood et al. 2002).

Harvested whales have been measured and sampled at Point Lay, Alaska, periodically since the 1970s (Burns and Seaman 1986, R. Suydam unpublished. data). Aerial surveys to document population size and trend also occur periodically in the

same area and about the same time as the hunt. Aerial photogrammetry, concurrent with surveys and the harvest, provides a means to collect information on the distribution of lengths and color composition of animals in a large sample of the population and to examine sampling biases associated with hunting. Color can be used as a proxy for age and maturity in belugas, thus understanding color composition can be useful. Belugas are born dark-gray or brownish and lighten as they age, ultimately becoming white. Some males and many females are sexually mature before they become white while all white animals are mature (Burns and Seaman 1986). Data on length and color of whales taken in the harvest can be compared with the lengths of animals measured in vertical aerial photographs and potential biases examined. Length and color comparisons between harvested and free-ranging belugas have never before been made.

In this study, we (1) documented the distribution of length and color composition of free-ranging groups of belugas from the eastern Chukchi Sea population through aerial photogrammetry, (2) compared the distribution of length and color composition of harvested belugas with animals that were photographed, and (3) examined early growth of belugas from vertical photographs.

METHODS

Study Area

This study was conducted near the community of Point Lay, located along the Chukchi Sea coast of northwest Alaska. Residents of Point Lay hunt belugas from

the eastern Chukchi Sea stock. Whales from this stock annually congregate along Kasegaluk Lagoon, especially at passes in the barrier islands (Frost and Lowry 1990, Frost et al. 1993). Once or twice a year, hunters drive a large group of belugas into the shallow lagoon (less than 2 m deep) using motorized skiffs. Once in the lagoon, the whales are hunted with high caliber rifles. Vertical photographs were taken of aggregations of belugas on the ocean side of the barrier islands of Kasegaluk Lagoon.

Harvested Belugas

From 1987 to 1998, we determined standard length (straight line measurement from the tip of the rostrum to the fluke notch), color, and sex of belugas that were taken in the harvest at Point Lay. Lengths were measured to the nearest cm. Colors were assessed subjectively and animals were placed into one of four color categories: white, gray-white, gray, dark gray. For this analysis, we combined the gray-white and gray categories into a single gray category to be consistent with the categorization of the color of whales determined in photographs. The harvested animals were not the same animals that were photographed.

Photogrammetry

Aerial surveys were flown along the eastern Chukchi Sea coast in late June and early July in 1996 (Lowry et al. 1996) and 1998 (DeMaster et al. 1998). Surveys were flown at a speed of approximately 225 km/hour and usually at about 300 m altitude. During the aerial surveys, vertical photographs of belugas were taken using

a KA-76 military reconnaissance camera mounted in the floor of a high-wing, twin engine AeroCommander aircraft. The camera had a 152 mm lens and a forward image motion compensation system that eliminates the loss of image resolution caused by the forward motion of the aircraft. All photographs were taken with Kodak SO-359 aerial transparency film. Each time a photograph was taken, a computer based data acquisition system captured a reading from the plane's radar altimeter and recorded the time. Photographic passes were made over belugas at altitudes of 227 to 910 m.

To test for biases in recorded altitude, we photographed known-sized objects at the end of the runway in Kotzebue, Alaska, from 152 to 333 m above the objects. We compared the calculated altitude (A_c) from each frame over the targets with recorded altitude (A_r) and found a consistent negative bias in the recorded readings of about 3%. We used the regression equation shown below to correct recorded altitude.

$$(1) \quad A_c = A_r * 1.027 - 14.5 \quad (r^2=0.995)$$

We counted numbers of photographed whales by viewing the original color transparencies through a dissecting microscope mounted on a light table. An acetate sheet was placed over the transparencies and each whale was marked as it was counted. Standard body length of individual animals was measured to the nearest 0.0001 mm on the film. Only those whales that were swimming close and parallel to the surface of the water were measured. Therefore not all animals in the group were

measured. The images of the selected whales were captured with a CCD camera and transferred to a computer. We used the program IMAGE, developed by the U.S. National Institute of Health, to enhance the images where necessary and make length measurements. Distances measured on the computer screen were converted to true lengths by multiplying the screen distance by the scale of the photograph (A_c /camera focal length). All of the measurements presented in this report were made on images taken between 4 and 6 July in both 1996 and 1998.

Whales that were clearly visible at the surface were divided into the following color categories: white, gray and dark gray. Small, dark gray or gray animals swimming in close association (i.e. less than about a body length of the calf) with a larger white whale were classified as calves and the associated larger animal was classified as an adult female. Our classification of adult females introduces a small positive bias in the sample of lengths of adult females. A female categorized as adult from the photographs has had at least a year to grow since becoming pregnant. For a female to have given birth and have an accompanying calf, she must have ovulated, become pregnant and carried the fetus to term over the previous 12-14 months. In contrast, a harvested female that was pregnant and carrying a small fetus would be mature but a year younger than a photographed female that was accompanied by a calf. In the case of tropical dolphins, this bias appears to be very small (Perryman and Westlake 1998). Beluga whales that were not swimming in the characteristic cow/calf configuration were classified as gray or white in color and not assigned a sex.

Length at Dissociation

Young whales remain with their mothers through lactation and in some cases for a period of time after weaning. We used regression techniques to model the probability that a young beluga whale would be found swimming in close association with its mother as a function of the length of the young animal. We maximized a log-likelihood function to fit the data to each of three possible logistic models, of the general form:

$$(2) \quad \ln (y/1-y) = \exp (\beta_0+\beta_1x+\beta_2x^2)$$

to estimate the probability of being associated (y) with its presumed mother at a given length (x). We tested three models: a quadratic model with three non-zero β coefficients, and two models with two non-zero β coefficients, where either β_1 or β_2 was set to zero. We compared calculated Akaike's Information Criterion (AIC) values (Burnham and Anderson 1998) for the three models and selected the model with the lowest value. The length at which there was a 50% probability that a calf was associated with a cow was taken as the estimated length at independence for calves; we call this the length at disassociation. Confidence intervals were computed by generating a bootstrapped distribution of 1000 estimated lengths at disassociation and then reporting the values located in the 2.5 and 97.5 percentiles of the distribution.

Statistical Comparisons

We compared the lengths of photographed, free-ranging whales with harvested animals in several ways. Lengths were compared for data collected in 1996, 1998, and a combination of all photographed whales with all harvested whales between 1987 and 1998. These comparisons were made using a Mann-Whitney U test. We also compared the length distribution of photographed and harvested whales using a Kolmogorov-Smirnov test. Burns and Seaman (1986) suggested that sexually mature animals were fully represented in the harvest. We test that assertion. Belugas of western Alaska attain sexual maturity at approximately 310 cm (Burns and Seaman 1986). Thus, we also compared length distributions for only those whales greater than or equal to 310 cm. We examined the color composition of the harvest using a chi-square goodness-of-fit test. We used the color composition of the photographed whales to calculate the expected color composition of the harvest.

RESULTS

Subsistence Harvest

Between 1987 and 1998, we collected data on 445 harvested whales at Point Lay. Forty percent were females and 60% were males. They ranged in length from 209 to 485 cm with an average length of 366.1 cm (SD = 45.9 cm).

Hunters from Point Lay harvested 34 belugas on 30 June 1996. The harvested animals consisted of 18 males and 16 females. No calves were taken in the hunt

although some may have been present but not taken by the hunters. Standard length for all animals averaged 365.2 cm (Table 1-1). For adult females the average lengths were 343.2 cm (se = 7.2) and ranged from 291 to 393 cm. Of the 34 harvested belugas in 1996, 26 were white in color and 8 were gray. The white animals were an average length of 378.2 cm and the gray 323.3 cm (Table 1-2).

Hunters harvested 47 belugas on 26 June 1998. All were males. The average length was 407.9 cm (Table 1-1). Of those 47 belugas, 44 were white and three were gray. The white animals averaged 410.5 cm in length and the grays 370.0 cm (Table 1-2). The distribution of lengths of harvested belugas for 1996 and 1998 are in Figure 1-1 and Figure 1-2, respectively.

Photogrammetry

Individual whales, including calves, were clearly visible in photographs taken throughout the range of altitudes. However, we could only adequately discern the rostrums and fluke notches of large, white whales in photographs taken at altitudes below 300 m and for smaller, darker whales in photographs taken below about 240 m.

In 1996, aerial photos were taken of a large group of belugas on 4 and 6 July. The group photographed on 4 July contained approximately 400 whales and the 6 July group contained approximately 350 animals. From these two groups, 243 whales were measured and categorized by color. For this data set, we selected passes made at altitudes of approximately 240 m and from different sections of the beluga aggregation. Although we attempted to measure each beluga only once, it is possible

that some animals were represented more than once in the data set. In 1998, aerial photos were taken of belugas on 5 and 6 July. For 5 July, 592 whales were counted on photographs and for 6 July, 1018 whales were counted. In total, 120 belugas were measured and categorized by color.

The average length for all whales photographed in 1996 was 338.2 cm and in 1998 the average length was 323.4 cm (Table 1-1). The distribution of lengths of photographed whales for 1996 and 1998, are in Figure 1-1 and Figure 1-2, respectively. Of the beluga whales measured in photographs, roughly 11% were dark gray, 21% were gray, and 67% were white (Table 1-2). The observed percentages of calves, gray, and white animals were consistent between 1996 and 1998. Dark gray and gray calves averaged about 210 cm in length and the smallest calf that we measured was 144 cm. Gray belugas were about 290 cm in length and white belugas were about 365 cm (Table 1-2).

In 1996, there were 37 whales, assumed to be adult females, which were accompanied by at least 23 dark gray calves (Table 1-1). In 1998, 17 adult females were accompanied by at least 26 calves (Table 1-1). The numbers of measured adult females and calves differ because in some cases either the adult or calf was not flat at the surface and therefore not measurable. More adult females were at the surface in 1996 and more calves were at the surface in 1998. A combination of data for all calves for both years shows three general size groupings, perhaps relating to the first three years of life (Figure 1-3). The average length for the first group is 156.8 cm (range 144-175 cm), 213.9 for the second (range 203-228), and 260.3 for the third

(range 240-292). Differences between means of each mode suggest growth of about 57 cm during the first year and 46 cm during the second year. Calves of the year represent 3.5% of our total measured sample. Our observed percentage of calves should not be considered as an estimate of calf production because it is likely that the photographs were taken prior to the end of the calving season and the smaller, darker calves were likely missed in the photos because they are more difficult to see.

We fit a logistic model to our data to estimate the average length of disassociation for this population (Figure 1-4) and found that at a length of 245.6 cm a calf was equally likely to be with its mother or swimming independently (95 % confidence intervals 234.6-255.3 cm). Based on the estimate of an average length of 260 cm at the end of a beluga's second year of age, we estimate that calves in this population leave their mothers prior to the beginning of their third year. Some whales much longer than our predicted length at 2 yrs were still seen in association with a white adult.

Statistical Comparisons

In 1996, the average length of all harvested whales was similar to that of all photographed whales (Table 1-1; $U = 3299$, $P = 0.0572$). When examined by color category, gray animals that were harvested were longer than those photographed (Table 1-2; $U = 73.0$, $P = 0.0042$), whereas white animals did not differ in length ($U = 1980.0$, $P = 0.4179$). The length distribution of all photographed and harvested whales were similar in 1996 (Figure 1-1; $Z = 1.15$, $P = 0.144$) as were the length

distribution of large (≥ 310 cm) whales ($Z = 0.75$, $P = 0.631$). The color composition of photographed and harvested whales was also similar ($\chi^2 = 0.0054$, $P = 0.94$).

In 1998, the average length of all harvested whales was greater than the average length of all photographed whales (Table 1-1; $U = 535$, $P < 0.0001$). When examined by color category, gray and white animals harvested were longer than those photographed (Table 1-2; gray: $U = 3.0$, $P = 0.0095$; white: $U = 433.0$, $P < 0.0001$). Additionally, length distributions were different for photographed and harvested whales for all animals and for only the larger (≥ 310 cm) ones (Figure 1-2; all: $Z = 4.30$, $P < 0.001$; only large: $Z = 3.50$, $P < 0.001$). The color composition of photographed and harvested whales was also different ($\chi^2 = 9.40$, $P = 0.002$).

When comparing all harvested whales, between 1987 and 1998, with all photographed whales the average length of harvested whales was greater ($U = 55260$, $P < 0.0001$). Length distributions differed between photographed and harvested belugas for all animals and for only the larger (≥ 310 cm) ones (all: $Z = 3.02$, $P < 0.001$; only large: $Z = 2.28$, $P < 0.001$).

DISCUSSION

Hunting and Sampling Biases

Determining underlying biases in estimates of various life history parameters derived from hunted animals is important for interpreting and understanding biological data collected from harvested animals, in this case beluga whales. Because lengths of belugas reach an asymptote long before old age, it would be most useful to

examine hunting biases in terms of age structure of belugas. Unfortunately we cannot determine ages from photographed whales, thus, we compared average lengths and length distribution of hunted and photographed whales. A comparison of lengths is useful, however, because length provides an indicator of age (Heide-Jørgensen 1994).

Modern aboriginal harvests, where belugas are hunted with rifles, consist primarily of larger animals. Smaller animals are often underrepresented in harvests (Burns and Seaman 1986, Heide-Jørgensen and Teilmann 1994, Harwood et al. 2002) because of hunter selectivity or beluga availability to the hunters. The conclusion that smaller animals were underrepresented in the harvest was not based on direct observation of length distribution of the population but rather on the low number of young or small animals in the harvest and the presumption that a greater percentage of small animals should be present in the population. Additionally, in some harvests there were more adult females, which had just given birth or were lactating, in harvests than recently born or nursing young (Burns and Seaman 1986, R. Suydam, unpublished data). Our results provide greater details about these biases and reinforce the observation that large belugas (>400 cm) are over-represented in some aboriginal harvests and small belugas (<300 cm) are under-represented.

Other hunting methods may be selective in different ways. For example, set nets tend to catch females and young more readily than adult males (Brodie 1971, Sergeant 1973, Burns and Seaman 1986).

Our data from vertical photographs provide contradictory results regarding the extensiveness of biases that are associated with hunting practices in the Point Lay

area. In 1996, lengths of harvested animals were generally similar to lengths of photographed ones, except that harvested gray animals were longer on average than photographed ones. These results indicated that biological samples were likely representative of the population, or at least of a portion of the population. Smaller animals were underrepresented in the harvest. Even though the length distributions were statistically similar, only one beluga less than 300 cm was taken in the harvest whereas 61 (25.1%) of the photographed whales were less than 300 cm. One reason small belugas are underrepresented in the harvest is because Point Lay hunters will usually hunt only the largest whitest animals even if small ones are available (R. Suydam, personal observation). The greater average length of harvested gray animals provides further evidence that hunters select the largest animals available.

In 1998, the harvest was unique and highly biased; it consisted entirely of large adult males. Contrary to 1996, harvested animals in 1998 were longer than photographed animals in all comparisons. Length distributions were different, regardless of whether all whales were included or just those over 310 cm in length. Additionally, five belugas were live captured in Kasegaluk Lagoon after the hunt and fitted with satellite transmitters. All five of these were also males (Suydam et al. 2001). Apparently the belugas driven into the lagoon in 1998 belonged to an all-male group that consisted of large animals. Thirty-three of the 47 harvested males were greater than 400 cm in length and the smallest was 331 cm (R. Suydam, unpublished data). The aerial photographs, in contrast, included 36 belugas (of 120) that were smaller than 300 cm and at least 26 of those appeared to be calves. The vertical

photographs and the harvest sampled different portions of the population. In the vertical photographs we sampled adult, immature and young animals of both sexes, while in the harvest, the sample consisted entirely of large males. Thus, it is not surprising that the length structures were different as adult male belugas are larger than females.

Burns and Seaman (1986) reported a similar situation at Little Diomed Island, Alaska. Inhabitants of Little Diomed recognized that the first belugas passing north in the spring were typically all males. Some males, the females and young all migrated later. The 1998 hunt at Point Lay was the earliest since at least 1987 and the belugas that were hunted were probably from the first group to pass that year (R. Suydam, unpublished data). Subsequent groups likely included females and young. Beluga groups of all males can also occur at other times. In early August 1999, a group of about 100 belugas was seen at Barrow, Alaska. All the whales were large and white, presumably males, and there were no calves or gray animals. Additionally, three whales were taken from this group, all of which were males (R. Suydam unpublished data). Thus, it is not surprising that our photogrammetry data did not agree with the harvest data. The two datasets captured different components of the population.

Burns and Seaman (1986) suggested that animals were fully recruited into the harvest, and thus the biological sampling was representative of the population, by the time of sexual maturity, approximately the age of six or at an approximate length of 310 cm. Because we were unable to determine the ages of photographed whales, we

compared the lengths of whales longer than 310 cm. Our comparisons showed that in some years biological samples were representative of mature animals while in other years they were not. This result is likely attributable to selectivity of hunters as well as the non-random composition of the groups that were hunted. Heide-Jørgensen and Teilmann (1994) used a similar approach when comparing beluga harvests in west Greenland during two different time periods. They still found differences in whale lengths when only comparing whales larger than 300 cm.

We assumed that aerial photos provided a reasonably representative sample of the eastern Chukchi Sea population of belugas for comparison to samples of harvested animals. Our aerial photogrammetry data may have provided a more objective view of the length distribution of beluga whales than harvested animals because issues such as hunter selectivity were removed. We would have expected to see two peaks of approximately the same amplitude in the length frequency data, one for females and another for males, if the photogrammetry data would have been representative of the population. The peaks should have been of approximately the same height because longevity and survival are similar between the sexes (Sergeant 1973, Burns and Seaman 1986). The aerial photos, however, contained relatively few whales from 420 to 450 cm in length (Figure 1-5) indicating that adult males were underrepresented. Some previous studies of belugas show two peaks of similar amplitude (Vladykov 1944, Sergeant and Brodie 1969, Sergeant 1973, Harwood et al. 2002) while others do not (Brodie 1971, Heide-Jøregensen and Teilmann 1994). The ones that show peaks of different amplitude attribute some type of sampling bias associated with

hunting technique. Segregation of different age classes and sexes of belugas can lead not only to biases in biological samples from harvested whales but also to data collected in a more random fashion, i.e. photogrammetry samples. Even though our photogrammetry data may have missed a portion of a segment of the population, the data do contain animals of all lengths. Thus, the photogrammetry data are likely more representative than the harvest data, which contain few small animals.

As our results indicate, the collection of data, especially biological samples from subsistence harvested animals but also photogrammetry data can be misleading. Knowing the biology of the study species and designing studies appropriately, with a sufficient sample size and over a sufficient time period, can reduce these biases. As mentioned above, all belugas in a population might not be available to hunters at all times because of sex and age/size segregation (Tomilin 1957, Burns and Seaman 1986, Heide- Jørgensen 1994, Smith et al. 1994). Furthermore, sampling biases associated with hunting may also be related to hunting method. There are several methods used for hunting belugas, some of which are inherently more selective of specific size or age classes than others. Finally hunters will frequently choose to take the larger, whiter whales and avoid young animals or females with young (Burns and Seaman 1986, Harwood et al. 2002). Accumulating biological samples over multiple years of harvesting should improve how representative the samples are of the entire population. Our results indicate that care must still be taken even when sample sizes are large. Harvest data from belugas may not adequately sample from small animals

in the population while aerial photos may under sample the larger animals in the population.

Our analysis provides insight into the extent of biases associated with sampling harvested and free-ranging animals but does not suggest how those biases might in turn influence analysis of life history data. If the sample size was large enough and samples came from all portions of the population, the biases might be biologically insignificant. For example, calculation of asymptotic lengths and growth coefficients might not be influenced much by hunter selection or beluga availability, as long as most age/size classes were represented in the sample. In contrast, analysis of reproduction might be greatly influenced. If a sample consisted of mostly young but mature females, estimated pregnancy rates would likely be higher than if the sample were from mostly older females (Burns and Seaman 1986). In summary, care must be taken when evaluating results of some types of biological information derived from harvested animals or from data presumed to be collected objectively. Understanding the biology of the species being studied and any possible biases should be evaluated as much as possible and results should be appropriately qualified.

Early Growth

Estimates of life history parameters based on analysis of measurements from vertical photographs agree well with those based on specimens taken in the field. We estimated length at birth to be about 157 cm while published estimates from specimens include 159.6 cm (Brodie 1971), 151 cm (Sergeant 1973), and 156 cm

(Burns and Seaman 1986). We also estimated that whales from this population averaged 214 cm in length at 1 year, which is similar to estimates of 216 cm and 219 cm from Brodie (1971) and Burns and Seaman (1986), respectively. Estimates of length at the end of the second year, 260 cm (this study), 236 cm (Burns and Seaman 1986), and 250 cm (Brodie 1971), are questionable. They are questionable in our study because of the likely presence of animals older than 2 years in the photographs and in the other studies because of the small number of animals with estimated ages (Brodie 1971, Burns and Seaman 1986). Our data indicate that calves separate from their mothers on average at about 2 yrs of age, but that some individuals may have remained with their mothers at lengths that were likely representative of 3 yr old animals. Brodie (1971) found that calves continued to nurse for longer than 2 years, while Burns and Seaman (1986) suggested that the dependent nursing period lasts 6-12 months. Our data do not provide evidence of when weaning occurs as calves may remain with their mothers for some time after they have stopped suckling.

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Table 1-1. Average length, standard error (SE) and range of lengths of belugas measured in vertical photographs and the harvest in 1996 and 1998 in the eastern Chukchi Sea, Alaska.

Grouping	n	Avg. length (cm.)	SE	Range (cm.)
<i>1996 Aerial Photos</i>				
All belugas	243	338.2	4.1	144.5-448.4
Associated w/ calves	37	359.4	2.8	328.1-402.0
Calves	23	209.1	8.2	144.5-266.0
<i>1996 Harvested belugas</i>	34	365.2	7.2	291-427
<i>1998 Aerial Photos</i>				
All belugas	120	323.4	5.9	147.6-433.3
Associated w/ calves	17	360.7	6.4	307.2-413.8
Calves	26	225.7	8.6	147.6-292.0
<i>1998 Harvested belugas</i>	47	407.9	4.0	331-462

Table 1-2. Average length, standard error (SE), and range of lengths of white, gray and dark gray belugas measured in vertical photographs and harvested in 1996 and 1998 in the eastern Chukchi Sea, Alaska.

Grouping	n	Avg. length (cm)	SE	Range (cm)
<i>1996 Aerial Photos¹</i>				
White	169	371.8	2.6	288.1-448.4
Gray	50	287.7	4.3	213.0-357.6
Dark Gray (All calves)	23	209.1	8.2	144.5-266.0
<i>1996 Harvested belugas</i>				
White	26	378.2	7.5	304-427
Gray	8	323.3	8.1	291-356
<i>1998 Aerial Photos</i>				
White	75	361.2	3.9	289.1-433.3
Gray (includes 8 calves)	27	294.2	6.1	240.4-348.6
Dark Gray	18	210.1	10.1	147.6-278.5
<i>1998 Harvested belugas</i>				
White	44	410.5	3.8	331-462
Gray	3	370.0	19.5	339-406

¹ Only 242 (of 243) whales were assigned a color.

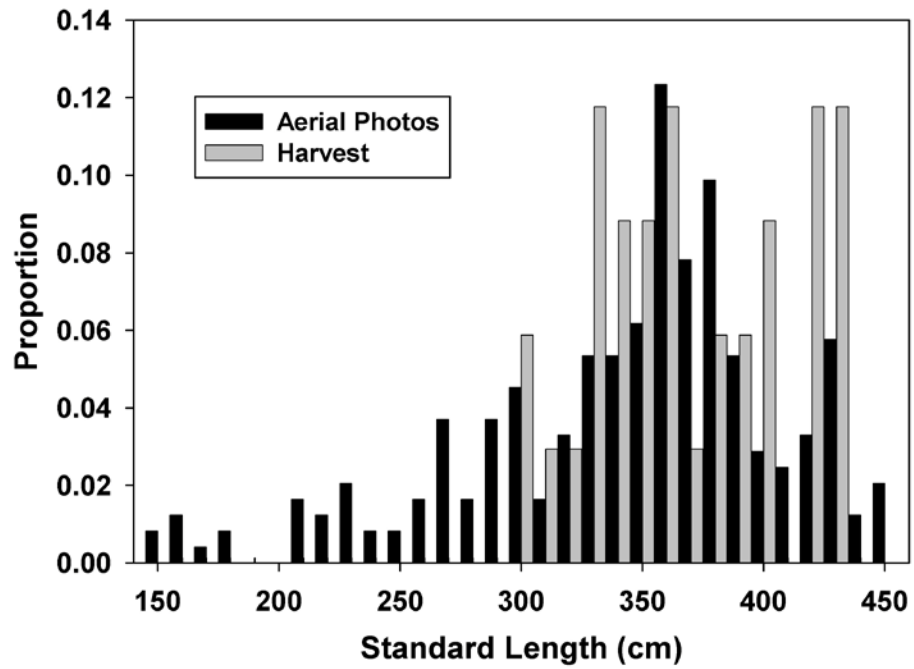


Figure 1-1. Length distribution (grouped in 10 cm bins) of beluga whales that were either harvested or photographed in the eastern Chukchi Sea, Alaska, in 1996.

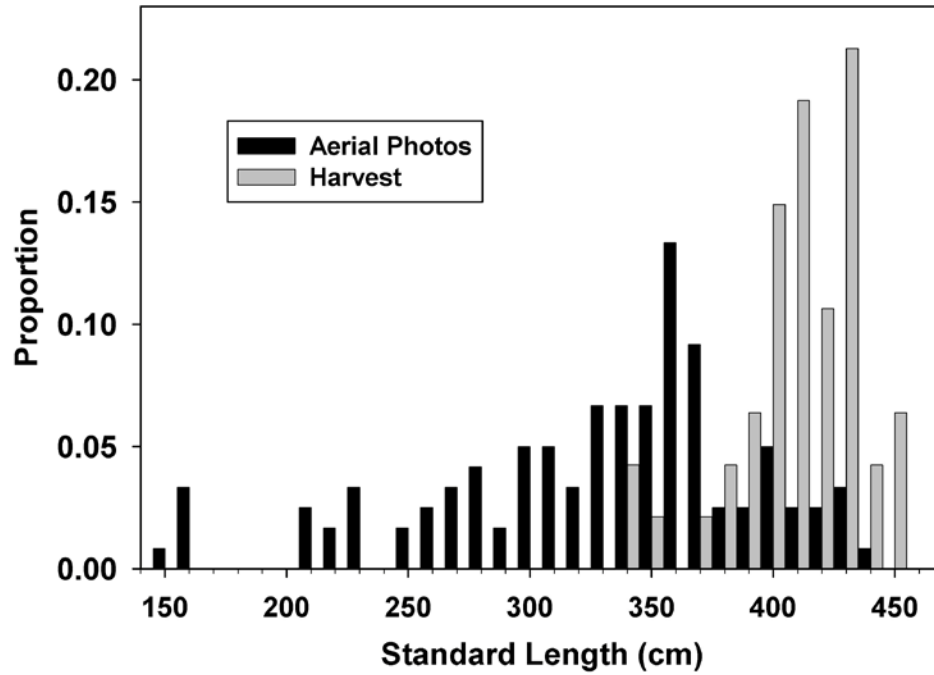


Figure 1-2. Length distribution (grouped in 10 cm bins) of beluga whales that were either harvested or photographed in the eastern Chukchi Sea, Alaska, in 1998.

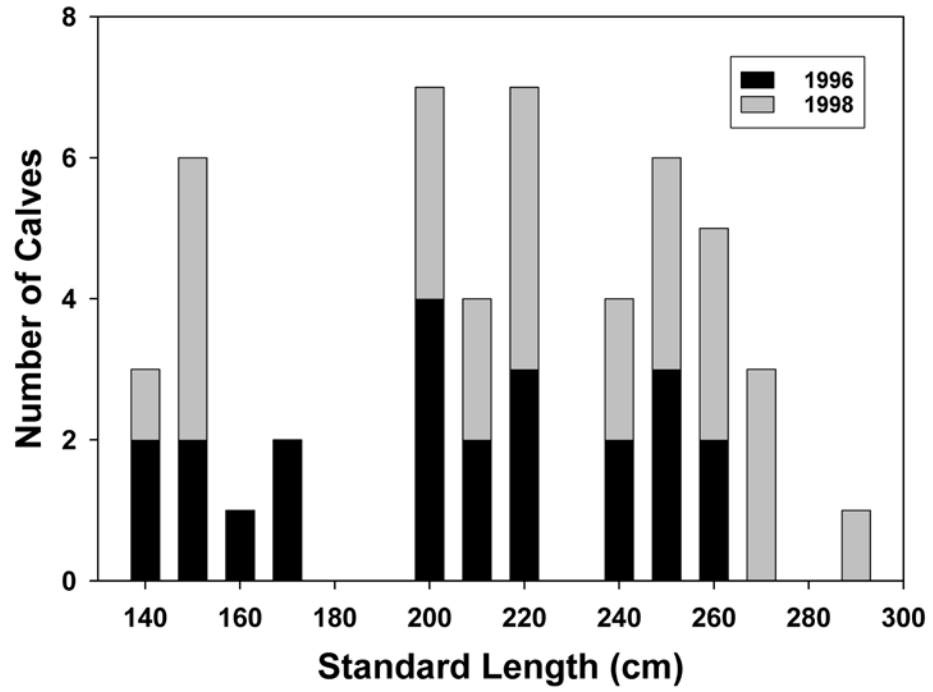


Figure 1-3. Numbers and lengths of calves photographed in the eastern Chukchi Sea, Alaska, 1996 and 1998.

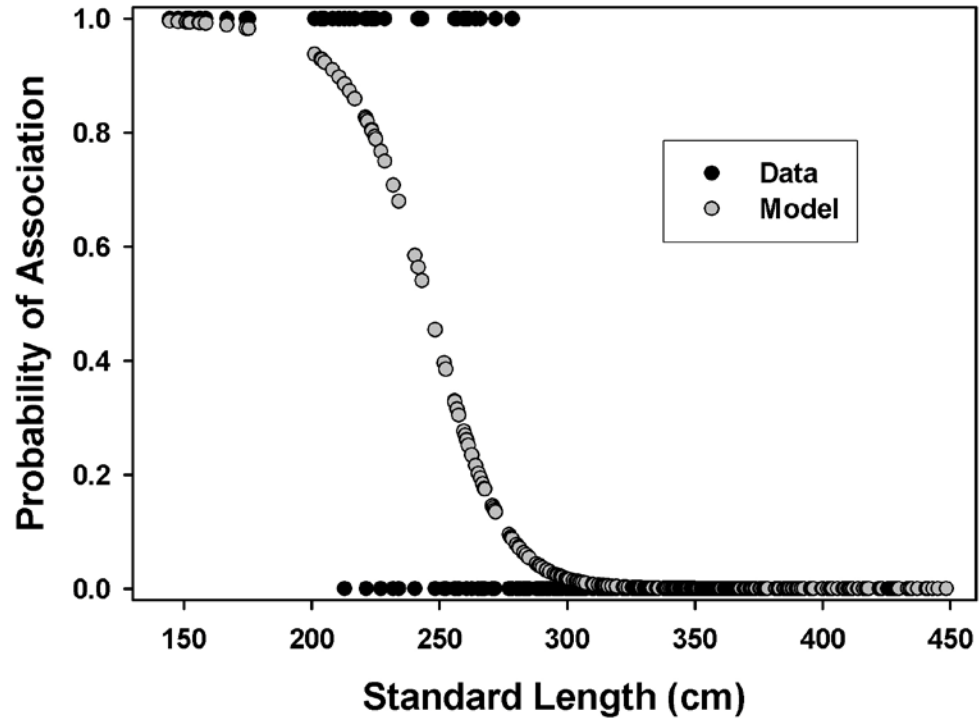


Figure 1-4. Length of disassociation of beluga whale calves from their mothers based on length measurements of calves photographed in the eastern Chukchi Sea, Alaska, 1996 and 1998.

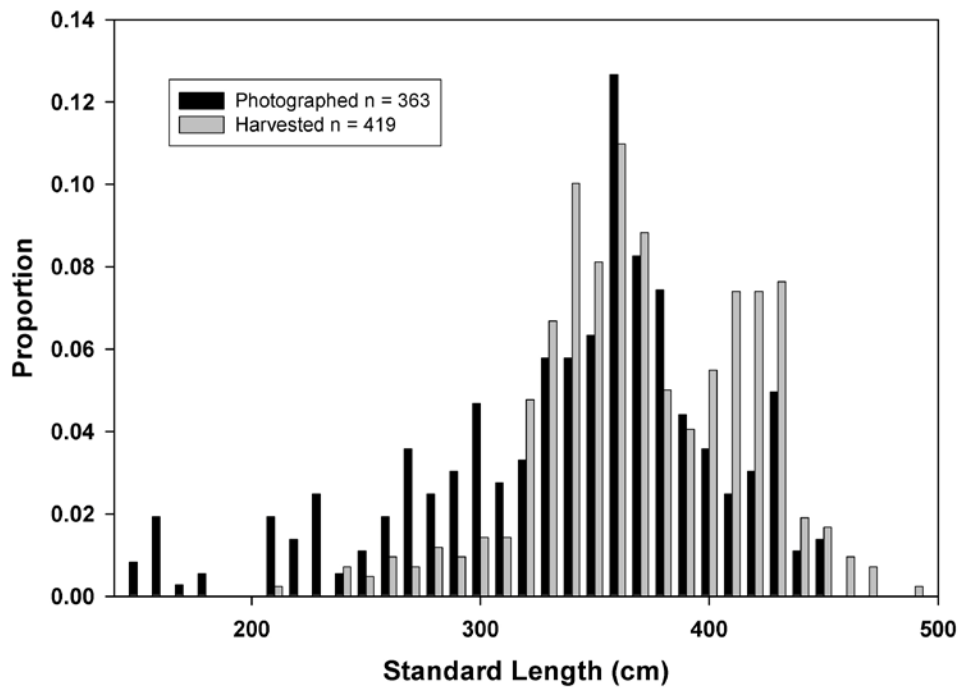


Figure 1-5. Length distribution (grouped in 10 cm bins) of belugas that were either harvested (1987 to 1998) or photographed (1996 and 1998) in the eastern Chukchi Sea, Alaska.

CHAPTER 2

AGE, GROWTH, AND REPRODUCTION OF BELUGA WHALES
FROM THE EASTERN CHUKCHI SEA, ALASKA

ABSTRACT

We collected measurements and biological samples from most of the 688 beluga whales (*Delphinapterus leucas*) killed in the subsistence drive hunt by Alaska Natives at Point Lay, Alaska from 1987 to 2005. Belugas in this harvest are from the eastern Chukchi Sea stock. Additionally, we provide some data and results from belugas harvested in Kotzebue Sound, Bristol Bay and Cook Inlet, Alaska. Hunters at Point Lay tend to selectively take larger, older animals, so few small, young whales were represented in the harvest. This bias for larger whales resulted in more males and fewer females being taken. Although age and length data were skewed to older and larger animals, several aspects of beluga biology, such as growth, female reproduction, gestation and age at first pregnancy, are likely not influenced by the biased harvest. Younger aged whales of both sexes had similar lengths. Color change from gray to gray-white to white has long been known to be age related. We found that lengths in both sexes were comparable until the whales turned white. Adult males were longer than females. The asymptotic length of males was 436 cm and that of females was 362 cm. The overall pregnancy rate was 0.56, which included females pregnant with small or near-term fetuses and some animals that were recently post-parturient. The pregnancy rate for females with only small fetuses was 0.41, which would indicate a

calving interval of between 2 to 3 years. Pregnancy rates of females declined after about 25 years of age. The lower reproductive output of older females was also reflected in corpora counts. Numbers of corpora were found to level off and may decline after about 40 years of age. We estimated a gestation length of 454 days (14.9 months), slightly less than the known gestation period of captive females. We estimated age at first birth to be about 8.5 years.

INTRODUCTION

Beluga whales (*Delphinapterus leucas*) occur across most of the Arctic and in many portions of the subarctic. In Alaska, they are found seasonally in coastal waters of northern, western and southcentral Alaska. The majority of belugas in Alaska reside in the Bering, Chukchi, and Beaufort seas while a small stock also occurs in Cook Inlet (Seaman et al. 1988, Frost and Lowry 1990, O’Corry-Crowe et al. 1997). These whales predictably concentrate during the summer in Cook Inlet and four areas in western Alaska, namely Bristol Bay, the eastern Bering Sea, Kotzebue Sound, and the eastern Chukchi Sea (Seaman et al. 1988, Frost and Lowry 1990), and in the eastern Beaufort Sea in northwestern Canada (Harwood et al. 1996). This predictable distribution was originally used to identify provisional management stocks, although animals from Kotzebue Sound and the eastern Chukchi Sea were considered the same stock (Seaman et al. 1988, Frost and Lowry 1990). Genetic analysis confirmed that most of the summer concentrations represent distinct stocks (O’Corry-Crowe et al. 1997) but more recent genetics data indicate that whales using Kotzebue Sound comprise a separate stock (G. O’Corry-Crowe, personal communication).

At least three stocks occur in the Chukchi Sea. The Beaufort Sea stock migrates from the Bering Sea to the Mackenzie River Delta in northwest Canada during the spring when the ocean is still mostly ice covered. They migrate through leads and polynyas in the sea ice that form each year. After spending the summer in waters of northwest Canada, they migrate back to the Bering Sea for the winter (Harwood et al. 1996, Richard et al. 2001). Little is known about the movements of

Kotzebue Sound belugas, except that they occur in that area primarily in June and are now greatly reduced in number.

Our study focused on the eastern Chukchi Sea stock. In late June or early July, these whales move into coastal waters of the eastern Chukchi Sea, primarily near Kasegaluk Lagoon, remaining for 2 to 4 weeks (Frost and Lowry 1990, Frost et al. 1993). It is likely that belugas aggregate near Kasegaluk Lagoon to facilitate their annual skin molt (St. Aubin et al. 1990, Frost et al. 1993) although they may also feed in the area (Huntington et al. 1999). Where they traveled after leaving the eastern Chukchi Sea coast was unknown until recently. A satellite telemetry study showed that this stock of belugas predominantly inhabits the Arctic Ocean and the shelf break of the northeastern Chukchi and Beaufort seas during summer and early fall (Suydam et al. 2001, 2005, chapters 3 and 4 of this dissertation). The same telemetry study also showed for the first time that belugas of the eastern Chukchi Sea stock winter in an area northwest of St. Lawrence Island, based on the known movement of a single adult male (chapter 4 of this dissertation).

Belugas are an important subsistence resource for residents of many Alaska Native coastal villages. The Beaufort Sea stock is hunted by villages in western and northern Alaska, in northwestern Canada (Harwood et al. 2002), and occasionally in Russia. Kotzebue Sound belugas are hunted by several villages in that area. The eastern Chukchi Sea stock is hunted primarily by the villages of Point Lay and Wainwright, which are situated near Kasegaluk Lagoon, in late June and early July (Burns and Seaman 1986). In Point Lay, belugas comprise a large portion of the

subsistence resources available to the village and are harvested each year in a cooperative drive hunt.

At Point Lay, the annual hunt provides a reliable opportunity to collect measurements and biological samples, which are necessary for understanding various aspects of the biology of belugas. In this study we focused on collecting information related to age, growth and reproductive status (i.e., pregnancy), primarily for females. We also collected a limited amount of morphometric data for comparison with other stocks. These data are important for understanding and evaluating population dynamics and to help ensure a sustainable harvest.

The objectives of this paper are to report results of our analyses and characterizations of data on the age, growth and reproductive status of beluga whales from the eastern Chukchi Sea and compare the results to similar data from other stocks.

METHODS

Sampling and Measurements

Biological samples and morphometric measurements were collected from beluga whales harvested at Point Lay from 1987 to 2005, except for 1997 and 2000. In 1997, very few animals were seen and only three were taken in a hunt that occurred unusually distant from the village. In 2000, shore-fast ice remained along the coast near Point Lay well into summer. The ice conditions prevented hunters from accessing the ocean and the belugas. In a typical year, hunters drive belugas traveling along the

outside coast into Kasegaluk Lagoon through one of the passes in the barrier islands that define the seaward side of the lagoon. The whales are herded to a shallow area near the village, where they are killed. After the hunt, the carcasses are pulled onto the beach of the island and butchered. We measured and sampled the whales at the butchering site. Each was given a unique number. We determined sex by palpation of the genitalia and recorded color (white, gray-white, gray, dark gray) and measurements of standard length (straight line measurement from snout to fork of tail) and fluke. We collected biological samples from animals, as possible, including mandibles (teeth for ageing) and reproductive tracts, primarily ovaries. We were not able to collect all information from all harvested animals.

Age Determinations

Mandibles were macerated in water until teeth became loose and could be easily removed. Three of the largest and least worn teeth (assessed subjectively) were glued to a wooden block with epoxy and sectioned with an Isomet© low-speed saw. Thin longitudinal sections were cut from at least two teeth per beluga and examined under a binocular microscope using transmitted light. We determined age for each whale by counting the number of dentinal growth layer groups (GLGs) in each thin section. GLGs in each tooth section were counted at least twice. If the results were similar for the two sections and the two readings the count was accepted. If the results were dissimilar (i.e. greater than ~10% difference), a third tooth was sectioned and

GLGs counted. We assigned age based on concurrence of readings from two of the three tooth sections.

The conventional wisdom has been that two GLGs are deposited in the teeth of belugas each year (Goren et al. 1987, Brodie 1982, Heide-Jørgensen et al. 1994). Recently, there has been some disagreement about the deposition rate of GLGs in belugas (Hohn and Lockyer 1999, Stewart et al. 2006, Lockyer et al. 2007). Stewart et al. (2006) provided convincing evidence that age data best fit the hypothesis that only 1 GLG is deposited annually. There is still some question whether one GLG is deposited per year in immature whales (Luque et al. 2007). Regardless of deposition rate, GLGs are lost as the result of normal tooth wear and abrasion especially in older animals. Thus, ages may be minimal estimates. The ages we present here are simply the enumerations of GLGs counted in the dentine.

Growth Curves

We plotted standard lengths against ages and fitted a Gompertz growth curve to the data, as follows:

$$(1) \quad \text{Standard Length} = L_{\infty} * (\exp(-b * \exp(-k * x)))$$

where L_{∞} equals asymptotic length, b and k are derived constants, and x is age in years as estimated by counting GLGs in tooth sections. We used the Gompertz model because of its prevalent use in examining growth of cetaceans, including belugas

(Doidge 1990a,b, Heide-Jørgensen and Teilmann 1994). We used Sigma Plot © (2002, Version 8.02, www.sigmaplot.com) for fitting growth curves (with least squares) and estimating parameter values and their variances.

Ovarian Analysis

Initial inspection of reproductive tracts occurred in the field. Uteri and ovaries were grossly examined for evidence of recent or current pregnancy. Ovaries and occasionally uteri were collected and fixed in 10% formalin. Small fetuses were collected, measured, weighed, and fixed in 10% formalin. Large fetuses were measured but often not weighed.

Reproductive tracts were processed as described by Burns and Seaman (1986). Ovaries were trimmed of excess tissue, weighed, and measured after being fixed in formalin, then were sectioned longitudinally. A two-dimensional diagram of the ventral aspect of each pair of ovaries was made on 5 x 7 cards. Additional drawings were made of follicles, corpora, and calcified bodies observed in the sections. Number of corpora lutea (CL) and corpora albicantia (CA) were summed for each female and plotted by age. A 3-parameter log-normal curve was fit to the age and CA data. These plots were examined for changes in reproductive status that may be associated with age.

Gestation

As with others (Perrin et al. 1976, Perrin and Reilly 1984, Ferrero and Walker 1996), we estimated the length of gestation using the approach of Laws (1959). Law's equation provides an estimate of the duration of gestation:

$$(2) \quad L = a (t_g - t_0)$$

where L is length at birth, a is the slope of the fetal growth curve during the “linear” portion of growth, t_g is the total gestation time and t_0 is the time during the initial fetal growth period that is slow and “nonlinear” (Hugget and Widdas 1951, Laws 1959).

We used length at birth equal to 165 cm (Burns and Seaman 1986). We calculated the slope of the linear portion of fetal growth by plotting fetal lengths against date. Laws (1959) suggested that t_0 for length data is less than t_0 for weight data; therefore t_0 for length requires correction. We used 0.1 for the correction (Laws 1959) and solved for t_g iteratively.

Average Age at First Birth

We estimated age at first birth following DeMaster (1981). This technique is appropriate for belugas because it does not assume that each female in the population will conceive in each year but instead analyzes animals that are “available” for reproduction. If ovaries of a young female contained a CL and a near term fetus was present, she was included in the analysis in the next youngest age category because she

clearly had conceived in the prior year. We calculated the average age at first birth as follows:

$$(3) \quad \hat{y}(x) = t(x) / n(x)$$

where x is female age, $y(x)$ is the estimated proportion of females of age x that were pregnant or had recently given birth, $t(x)$ is the number of females of age x that were pregnant or had recently given birth in the sample, and $n(x)$ is the number of females of age x observed in the sample.

The estimated probability of having a later term pregnancy at or before age x , $z(x)$, was calculated as follows:

$$(4) \quad \hat{z}(x) = \hat{y}(x) + [1 - \hat{y}(x)][\hat{z}(x-1)]$$

The probability of giving birth for the first time at age x , $r(x)$, plus the probability of giving birth at or before age $x-1$, $z(x-1)$, equals $z(x)$. The probability of giving birth for the first time at age x was calculated as:

$$(5) \quad \hat{r}(x) = \hat{z}(x) - \hat{z}(x-1)$$

Estimated average age at first birth is:

$$(6) \quad \bar{x} = \sum_{x=0}^w x \hat{r}(x)$$

where w = the minimum age where $z(x) = 1.0$

and variances were estimated as follows:

$$(7) \quad \text{var } \hat{y}(x) = \frac{\hat{y}(x)[1 - \hat{y}(x)]}{n_x - 1}$$

$$(8) \quad \text{var } \hat{z}(x) = \text{var } \hat{z}(x-1) + \text{var } \hat{y}(x) + [\hat{y}(x)]^2 \text{var } \hat{z}(x-1) + [\hat{z}(x-1)]^2 \text{var } \hat{y}(x)$$

$$(9) \quad \text{var } \hat{r}(x) = \text{var } \hat{z}(x) + \text{var } \hat{z}(x-1)$$

and

$$(10) \quad \text{var}(\bar{x}) = \sum_{x=0}^w x^2 \text{var } \hat{r}(x)$$

We also fitted a logistic curve (with least squares) to female maturity data and estimated the age and length at which the proportion of sexually mature animals was equal to 0.50. Various authors have used a similar approach, although they grouped

animals by age and estimated where 50% were sexually mature (Perrin et al. 1976, DeMaster 1984, Ferrero and Walker 1993)

Comparison with other stocks

We compared the growth in belugas of the eastern Chukchi Sea stock with that of three other Alaskan stocks. We used data collected by Burns and Seaman (1986) for belugas from Kotzebue Sound, Lensink (1961) collected data for Bristol Bay, and Vos (2003) provided data for Cook Inlet belugas. We compared the 95% confidence intervals of the Gompertz growth parameters for overlap among the stocks.

RESULTS

A total of 688 belugas was taken at Point Lay between 1987 and 2005 (Table 2-1).

Sex Ratio

We determined the sex of 667 of the harvested belugas and found that the combined catch was strongly biased toward males (408 males [61.2%] to 259 [38.8%] females). There was great annual variation (Figure 2-1). For example, in 1989, 14 of the 16 whales landed were females. In 1998, the 49 landed animals were all males. The sex ratio was still skewed even if the all-male harvest of 1998 is excluded from the analysis (359 males: 259 females; $\chi^2=16.2$, $df=1$, $P<0.001$).

Ages

GLGs were counted for 216 whales, 86 males and 130 females. Males were predominantly between 11 and 30 years old and the oldest was at least 46. The older male's teeth were worn and did not include a neonatal line, thus its age is a minimal estimate. Females were predominantly between 6 and 30 years old and the oldest was at least 57. Age structure of the harvest was biased especially for males. There were notably few animals (11 males and 27 females) in the sample with less than 10 GLGs (Figure 2-2).

We did not determine the age of the one dark gray animal that was hunted. Gray colored males ranged in age from 2 to 10 GLGs, females from 2 to 12 (Figure 2-3). Both sexes of gray animals were similar in age (*Mann-Whitney* $U = 33.0$, $df = 24$, $P = 0.24$). Gray-white males ranged from 8 to 23 and females ranged from 5 to 35. Both sexes of gray-white animals were also similar in age (*Mann-Whitney* $U = 146.5$, $df = 44$, $P = 0.08$). White males ranged in age from 9 to 46 GLGs and females ranged from 10 to 57. White animals were also similar in age (*Mann-Whitney* $U = 2535.5$, $df = 145$, $P = 0.66$).

Lengths

Of the 688 harvested belugas, we measured 530 and categorized the color of 528 of these. Males were significantly longer than females (*Mann-Whitney* $U = 12766.5$, $P < 0.01$). Lengths of males ranged from 240 to 485 cm (average = 383.3, SE = 2.34, $n = 330$) and females from 209 to 410 cm (average = 338.4, SE = 2.26, $n =$

198). In addition to the greater mean length, the modal length for males is approximately 70 cm greater than for females (*Kolmogorov-Smirnov* $Z = 6.02$, $P < 0.001$). Figure 2-4 presents the length composition of harvested belugas. Length structure is biased in a similar manner to the age structure. Very few small young whales of either sex were taken in the harvest.

We examined average lengths of whales based on color and sex. The single dark gray animal taken in the harvest was 240 cm in length and gray colored males ranged in length from 248 to 322 cm, females from 209 to 359 cm. Gray animals were similar in length by sex (*Mann-Whitney* $U = 99.5$, $df = 30$, $P = 0.67$; Table 2-2; Figure 2-5). Gray-white males ranged from 280 to 406 cm and females ranged from 272 to 378 cm. Gray-white animals were also similar in length by sex (*Mann-Whitney* $U = 682.5$, $df = 82$, $P = 0.09$). White males ranged in length from 307 to 485 cm, females from 304 to 410 cm. Males white in color were significantly longer than females (*Mann-Whitney* $U = 5425.5$, $df = 409$, $P < 0.01$).

There is a close relationship between standard length and fluke width for both male and female belugas (Figure 2-6). The increase in fluke width with body length is similar for males ($n = 278$) and females ($n = 181$; i.e., the slopes of the regression lines are similar; $t = 0.58$, $df = 456$, $P > 0.50$). The elevation of the male regression line is significantly higher than that of females ($t = 6.33$, $df = 456$, $P < 0.01$), an indication that the width at length of males' flukes in general is greater than that of females. The linear relationship between fluke width and standard length for males is best described by the equation:

$$(11) \quad \text{Fluke Width} = -3.97 + 0.25 * \text{Length}; r^2 = 0.76$$

The linear relationship between fluke width and standard length for females is best described by the equation:

$$(12) \quad \text{Fluke Width} = 7.76 + 0.20 * \text{Length}; r^2 = 0.60$$

Growth Curves

The asymptote of the growth curves for females occurred at about 20 years of age and at a length of 362 cm (n = 130; Figure 2-7). For males, the asymptotic length was 436 cm (n = 83) at about 25 to 30 years. Estimates of parameter values for the growth equation are listed in Table 2-3. Asymptotic lengths for Kotzebue Sound animals were 435 cm for males (n = 48) and 356 cm for females (n = 65; Figure 2-8). Asymptotic lengths for Cook Inlet belugas were 432 cm for males (n = 28) and 361 cm for females (n = 17; Figure 2-9). Asymptotic lengths for Bristol Bay belugas were 405 cm for males (n = 13) and 351 cm for females (n = 9; Figure 2-10). Estimates for growth parameters for these four stocks were similar (Figures 2-11, 2-12, and 2-13).

Pregnancy Rates and Corpora Counts

A majority of females killed in the subsistence harvest at Point Lay were pregnant. We examined 149 mature females (i.e., females with a least one corpora).

Those females were pregnant with either a small fetuses, near-term fetuses, had recently given birth, or were non-gravid (Figure 2-14). The overall pregnancy rate was 0.56; however, this value is vulnerable to misinterpretation because it includes females that became pregnant in the previous year as well as those just recently pregnant. Further, it is unlikely that females became pregnant after late June, the approximate time of the harvest. If many had, we would likely have observed a fetus of a length that would have indicated a birth date of August or September. Thus, we used only the percentage of females with small fetuses to represent the annual pregnancy rate, which was 0.41. This rate is consistent with a calving interval of two to three years.

The production of calves appears to decrease with age in female belugas. Pregnancy rates remained relatively high until about 25 years of age (i.e., based on GLG counts) and declined in older animals (Figure 2-15). A lower pregnancy rate among older females, especially the oldest females in the sample, is also supported by analysis of corpora counts. CAs steadily accumulated until about 40 years of age. In later years the number of CAs appear to decrease slightly although the sample size of older females is small (Figure 2-16). The number of CLs provides further insight into the decline in reproductive output with age. No female over the age of 41 ($n = 5$) had a CL. By combining our data from Point Lay with data collected by Burns and Seaman (1986) from northwest Alaska, the resulting sample was much larger and the results were similar (Figure 2-17).

Of the 70 females for which we sectioned and examined ovaries, 60 were sexually mature. Of those 60 25% had more than one CL, and of those one had 5. For

females with a CL, the average number of CLs was 1.62. Accessory corpora result from the luteinization of ruptured or unruptured follicles in addition to the corpus associated with pregnancy (Brodie 1971, 1972). These accessory corpora support the pregnancy and regress after parturition.

Gestation

We calculated a gestation length of 454 days or 14.9 months based on lengths of 51 fetuses ranging from 5.1 to 175 cm. The initial phase of fetal growth was 45 days and the linear portion of fetal growth was 409 days. We calculated a gestation of 452 days for belugas that were landed in Kotzebue Sound during the 1970s and 1980s (Burns and Seamen 1986).

Average Age at First Birth

We estimated the average age at first birth to be 8.27 years (SE = 2.88, n = 87). When examining ovaries, females were first pregnant (i.e., with a CL but no CA) at 9, 10, 10, and 11 years old, but there was also an eight year old that had one CL and one CA. The estimated age at which 50% of females were sexually mature was 8.25 years (n = 87; Figure 2-18). The length at which 50% of females were sexually mature was 288.5 cm (n = 48; Figure 2-19).

DISCUSSION

Age, growth and reproduction of belugas have been relatively well studied. Because belugas are an important subsistence resource, there is need and opportunity to collect samples and study various biological parameters. Aspects of growth and reproduction have been examined in many different areas of the Arctic and subarctic. In Russia, information was provided by Kleinenberg et al. (1969) and Ognetrov (1981), in Greenland by Heide-Jørgensen and Teilmann (1994), in Canada by Brodie (1971), Sergeant (1973), Doidge (1990a,b), and Stewart (1994), and in Alaska by Burns and Seaman (1986) and Vos (2003). Information on growth and reproduction of captive belugas has also been published (Robeck et al. 2005). Much of the previous work was based on age estimates with a GLG deposition rate of two per year, contrary to recent findings of a deposition rate of one per year (Stewart et al. 2006). Here we have provided information on age, growth and reproduction for another stock of belugas, the eastern Chukchi Sea stock. We also reexamined data collected by Burns and Seaman (1986), and compared data on growth and reproduction for other Alaskan stocks, based on a deposition rate of one GLG per year for age estimates.

Selectivity of Hunters

Hunters at Point Lay choose to shoot larger, older belugas and purposely avoid smaller, darker ones, which are therefore underrepresented in the harvest. The length composition of the Point Lay harvest is very similar to that reported for harvests in western Greenland during the 1920s, where there was also strong selectivity for larger

belugas (Degerbøl and Nielson 1930). More recently, Heide-Jørgensen and Tielmann (1994) asserted that their samples from western Greenland were less biased than the former harvests, but that shorter belugas were still underrepresented. Sergeant and Brodie (1969) observed that hunters who harpoon and shoot their prey tend to select larger animals. They also speculated that when nets are used to catch belugas, all sizes of animals may be taken but there is a tendency to take smaller whales, possibly because larger animals may be less curious, less naïve, or tend to avoid shallower water where nets are usually set.

Suydam et al. (chapter 1 of this dissertation) examined the bias in the harvest at Point Lay. They suggested that the composition of the harvest there is due to a combination of factors including hunter selectivity and segregation of animals by sex and possibly by age. If the entire stock does not frequent the lagoon, then the harvest may not be representative of the population, regardless of any hunting biases. (See Sex Ratio, below, for a more thorough discussion about segregation by sex and age or size.)

It is likely that the length and age compositions of the harvest at Point Lay are not representative of the entire population. Even though there is a bias in the harvest, it is likely small enough, and sample sizes large enough, that information obtained from measurements and biological samples are representative for some aspects of age, growth and reproduction. The selectivity of the hunters or a non-random distribution of belugas will likely not influence some results, such as age of sexual maturity, length at age, and gestation period, but will influence other data, such as length and age composition and sex ratio of the harvest.

Sex Ratio

The sex ratio of belugas taken in subsistence hunts is typically skewed toward males, presumably because of the tendency of hunters to take larger animals. While some hunts in some years may secure more females than males, the overall sex ratio in most locations favors males. One explanation is that when driven into shallow water, larger whales create more turbulence and therefore are easier to follow and present a larger target. Because males are larger than females, males are taken more frequently than females. To our knowledge, no studies based on subsistence hunts have found overall sex ratios favoring females.

Loseto et al. (2006) evaluated satellite-tracking data from belugas tagged in the eastern Beaufort Sea. Tracked animals segregated by age, sex and reproductive status during summer months. Harvests reflect this segregation. In Greenland there is a strong spatial and temporal size and age segregation (Heide-Jørgensen and Tielmann 1994). Burns and Seaman (1986) provided evidence that male and female belugas were segregated during some times of the year. Even though they found an overall 1:1 sex ratio in the harvest, some hunts landed predominantly one sex or the other. In one case the harvest at Wainwright, Alaska, in 1979, was comprised of 70% males and in another instance at Kotzebue Sound in 1981, the harvest was comprised of only 13% males (Burns and Seaman 1986). Studies in other locations found equal sex ratios (Doan and Douglas 1953, Sergeant 1973, Finley 1982) or sex ratios skewed toward males (Degerbøl and Nielsen 1930, Lensink 1961, Ognetev 1981, Fraker 1980, Heide-

Jørgensen and Teilmann 1994, Harwood et al. 2002). The most skewed sex ratios were in the harvests in the Mackenzie River Delta in the eastern Beaufort Sea (2.3 males: 1 female; Harwood et al. 2002), the White Sea (3.65 males: 1 female; Ognetrov 1999), and the Kara Sea (1.42 males : 1 female; Ognetrov 1999). The skewed harvest in the Mackenzie River Delta is due to hunter selectivity to avoid taking females (Harwood et al. 2002).

The hunters in Greenland, possibly Point Lay, and other areas may have greater access to certain portions of the population. Absence or presence of male herds greatly influences sex ratio and length frequency of the whales taken in the harvest. The sex ratio at Point Lay is dramatically skewed toward males although it varies greatly among years. The most dramatic example was in 1998 when the entire harvest consisted of males. The skewed sex ratio of the harvest at Point Lay and elsewhere could be attributed to two primary factors, (1) hunters select larger belugas, and therefore more males are harvested, as described, above, or (2) there is a greater prevalence of males near Point Lay. Our result is most likely a combination of the two factors.

It is curious that harvests are skewed toward males because it appears that females tend to occur closer to shore than males in some areas and thus might be more susceptible to hunting. Smith et al. (1994) observed adult females with young in estuaries while large males spent little time there. Furthermore, Richard et al. (2001) observed that most females remain close to the shoreline and some males moved farther offshore and to more remote locations. It is unlikely that females avoid coastal

areas. It is not apparent that whales from the eastern Chukchi Sea stock behave differently than belugas from most other areas.

Sergeant (1973) concluded that the sex ratio was close to unity, and thus mortality rates were similar between the sexes. The sex ratios of term fetuses from various locations provide contrary evidence of an equal sex ratio. At Point Lay, of 13 term fetuses, 69% were males. Further, Burns and Seaman (1986) determined sex for 54 term fetuses, of which 65% were males. Finally, the sex ratio of 23 calves born in captivity was 61% male and 39% female (Robeck et al. 2005). Combined these data indicate that the sex ratio of newly born calves may not be equal ($\chi^2=7.51$, $df=1$, $P=0.006$), although more information is needed to substantiate this preliminary finding.

The sex ratios of fetuses or young of other cetaceans have generally been equal. For example, in spotted dolphins (*Stenella attenuata*), the sex ratio was near parity at birth but the mortality of males was higher than females, thus the sex ratio of older animals was skewed toward females (Perrin et al. 1976). Bowhead whales (*Balaena mysticetus*) had an equal sex ratio of fetuses, 13 males to 12 females (J.C. George, North Slope Borough, Barrow, AK, pers. comm.). The sex ratio of juvenile northern right whale dolphins (*Lissodelphis borealis*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) did not differ from one (Ferrero and Walker 1993, 1996, respectively). Lockyer (1984) summarized the fetal sex ratios of baleen whales. They were generally one to one, but occasionally were slightly skewed to males or females.

Size and Color Change

Beluga whales are sexually dimorphic. Adult males are considerably larger than adult females (Heide-Jørgensen and Tielmann 1994, Doidge 1990a, Stewart 1994, Burns and Seaman 1986). Our data from the Point Lay harvests also show size dimorphism at least in white-colored animals. The length at age of younger (i.e., gray and gray-white) males and females were not different but the size dimorphism is obvious once belugas have turned white. Burns and Seaman (1986) also reported that size differences between males and females were evident but only for the older animals that were white. Robeck et al. (2005) showed no differences in length or growth of immature male and female belugas. Few other studies have presented data on lengths of males and females relative to color and color change with age.

Fluke Width and Standard Length

There is a close relationship between standard length and fluke width in belugas (Heide-Jørgensen and Tielmann 1994, this study). This relationship is useful for estimating standard length in situations where that measurement could not be obtained, such as when an animal was butchered before it could be measured. For Greenland belugas this relationship was estimated in two different studies and was expressed as:

Fluke Width = $8.16 + 0.20 * \text{Standard Length}$ ($r^2 = 0.56$; Degerbol and Nielsen 1930)

Fluke Width = $0.492 + 0.23 * \text{Standard Length}$ ($r^2 = 0.90$; Heide-Jorgensen and Teilmann 1994)

The relationship of fluke width and standard length for Greenland whales is similar to that of eastern Chukchi Sea belugas, although Greenland animals are larger (Heide-Jorgensen and Teilmann 1994).

Age and Growth

Belugas are aged by the enumeration of GLGs in longitudinal thin sections of teeth. For many years it was assumed that two GLGs were deposited per year. Lockyer and Hohn (1999) challenged that assumption. Further examination of teeth from animals reared in captivity for a portion of their lives was equivocal (Lockyer et al. 2007). Stable isotope analysis of teeth helped resolve the controversy and provided evidence of a deposition rate of one GLG per year (Stewart et al. 2006). We used a deposition rate of one GLG per year as a basis for aging belugas harvested at Point Lay. It is unlikely that deposition of GLGs differ among populations of belugas (Sergeant 1973). A deposition rate of one GLG per year instead of two means that previously published estimates of longevity and other age-related life history parameters need to be adjusted accordingly to be comparable with the findings reported herein.

Our improved understanding of age determination of belugas, which means a greater longevity, fits with our understanding of other arctic cetaceans. Low

reproductive rates and long lives may be adaptations to the rigors and variability of living in the Arctic. Bowhead whales and narwhals have been aged by analysis of aspartic acid racemization of the eye lens. Although standard errors are relatively large, the point estimates indicate a greater longevity than previously thought. Some bowheads may live longer than 150 years, with corroboration of the estimates from stone harpoon points found in blubber of recently harvested whales (George et al. 1999, Rosa et al. 2004). Aspartic acid racemization showed that narwhals also lived longer than previously determined; one female was estimated to be 115 years old (Garde et al. 2007). Narwhals are about the same size as belugas, they reach sexual maturity at about the same age, and their habitats overlap in some portions of the Arctic. It seems reasonable to assume that belugas may also live as long as narwhals. Because of the changes in our understanding of GLG deposition rates, estimates of longevity of belugas have increased to at least 60 or 70 years. These ages are likely underestimates. Beluga teeth wear down as the animals age. Therefore, age determinations based on counts of GLGs in older animals likely result in underestimates of actual ages because some of the GLGs are lost. Determining ages of belugas via aspartic acid racemization may be warranted to obtain better estimates of longevity. If belugas do live as long as narwhals, age estimates, previously published estimates of survival, and lifetime reproductive output will also have to be adjusted accordingly.

The combination of hunter selectivity and non-random availability of belugas, influences the linked parameters of age and length in a similar manner. Younger,

smaller animals are underrepresented in the harvest. Even though age and length compositions have some similarities, there are also some differences. The length composition reflects the sexual dimorphism of beluga whales, males being longer than females. Age compositions of males and females, however, are similar. Age compositions of the harvest of belugas in northwest Alaska, in the late 1970s and early 1980s (Burns and Seaman 1986) and in Hudson Bay, Canada (Sergeant 1973), are similar to our results. Age composition of the harvest in west Greenland, however, is quite different. In one area, it was essentially uniform for younger to older whales but in another area the harvest consisted of mostly young belugas (Heide-Jørgensen and Tielmann 1994). Differences in age composition between Alaska and Greenland may be due to differing hunter selectivity or hunting technique, differing components of each stock being available to hunters, or differences in the age composition between stocks. The age composition may be different between the two areas just from the fact that the population of belugas in the eastern Chukchi Sea stock is apparently stable (Lowry et al. 1999) while the western Greenland stock is declining (Heide-Jørgensen and Tielmann 1994).

Different stocks of beluga have different asymptotic lengths (Sergeant and Brodie 1969, Doidge 1990a, Heide-Jørgensen and Tielmann 1994, Stewart 1994). Belugas from western Greenland and the Sea of Okhotsk are the longest, those from Hudson Bay and Northern Quebec, Canada are the shortest, and those from northwestern Alaska, the western Canadian Arctic, and the White and Kara seas are of intermediate length. The asymptotic lengths we observed were similar to those for

belugas from northwestern Alaska reported by Burns and Seaman (1986) and do not change our understanding of the relationship of asymptotic lengths among belugas stocks that have been previously studied.

Size differences among stocks have been suggested to be indicative of ecological differences. Sergeant and Brodie (1969) suggested that amount of food available in the winter environment might be the most important factor determining the size attained by belugas. Stocks of the smallest belugas use estuarine environments in the subarctic, medium sized animals use the high Arctic, and large belugas occur at some times of the year in oceanic waters of the subarctic. Satellite tracking has revealed that stocks using estuarine environments in the subarctic (e.g., Cook Inlet) migrate shorter distances or not at all, whereas high Arctic and oceanic subarctic stocks (e.g. eastern Chukchi Sea, eastern Beaufort Sea) migrate considerable distances. The size pattern observed in belugas in other areas of the Arctic and subarctic was not the case in Alaska. Animals from Cook Inlet, Bristol Bay (both stocks inhabiting estuarine environments in the subarctic), and the eastern Chukchi Sea (in the high Arctic) were of similar size. Additionally, diets of belugas from these three stocks are likely different. Although there is not a great deal of current information about beluga diets, fish, especially salmon (*Oncorhynchus* spp.), play an important role in diets of those whales in Cook Inlet and Bristol Bay, while cephalopods, shrimp, saffron cod (*Eleginus gracilis*) and arctic cod (*Boreogadus saida*) are important foods in the Chukchi and Beaufort seas (Seaman et al. 1982). Perhaps size differences are a result

of several factors including diet and possibly genetic founder's effects resulting from previous periods of glaciation and limited breeding among some stocks.

Pregnancy Rate and Corpora Counts

Comparing pregnancy rates among stocks or studies is not simple. Hunts occur at different times of the year. Thus, the timing of breeding, the stage in the pregnancy, the size of fetuses, and other factors affect the observed rates in a given area. Based on the information that is available from animals taken in hunts, pregnancy rates for beluga whales varied from 0.26 to 0.65, but most studies reported rates of about 0.33 when considering only small or term fetuses independently (Kleinenberg et al. 1969, Sergeant 1973, Ognetrov 1985, Burns and Seaman 1986, Doidge 1990b, Heide-Jørgensen and Teilmann 1994). A pregnancy rate of 0.33 indicates a calving interval of three years, with approximately one-third of the mature females being newly pregnant in any given year. An exception to this average three-year calving interval was in Hudson Bay, Canada. Beluga whales from Hudson Bay had a pregnancy rate of 0.47, which indicates a two-year calving interval (Sergeant 1973, Doidge 1990a). Data for Point Lay showed a pregnancy rate of 0.41, also signifying a two- to three-year calving interval. Our observed pregnancy rate appears to be slightly greater than that presented by Burns and Seaman (1986) of 0.34 for belugas also from northwestern Alaska. Our observation of a higher pregnancy rate compared with that reported by Burns and Seaman (1986) could have multiple explanations: (1) An improved environment with more resources could allow for more resources per capita so that

females could calve more frequently. (2) The stock size is smaller now also allowing for more resources per capita. (3) There may be disparity in age composition among samples. Older females have a marked decline in pregnancy rate (Burns and Seaman 1986, this study). If a sample consisted of mostly young females, a higher pregnancy rate would be expected than if the sample consisted of mostly older females. (4) The age of senescence differed between the studies. It is difficult to separate these factors or a combination of them. Any could allow for an increased pregnancy rate and multiple factors may apply. We do not know of any large mortality events in Alaskan waters but the Chukchi and Beaufort seas have changed dramatically in the past 30 years due to climate warming (Serreze et al. 2007). Sea ice has reduced in thickness and extent. Therefore, it is reasonable to hypothesize that the availability of resources to belugas may have improved, although changes in ecosystem productivity associated with the observed loss of sea ice (and overall global warming) may have been adverse in terms of the carrying capacity for this population.

The decline in pregnancy rate of older females is also reflected in corpora counts. The number of CAs generally increased up to about 40 years of age based on the literature and the results from our study (Brodie 1972, Heide-Jørgensen and Teilmann 1994, this study). However, Sergeant (1973) and Khuzin (1963) did not observe a decrease in number of CAs with age, instead documenting an increase in older animals, to 48 and 38 years, respectively. In our study, there was a decrease in the number of CAs after about 40 GLGs. Fewer CAs in older females are probably the result of an overall lower pregnancy rate. With fewer ovulations or pregnancies there

are fewer CLs to become CAs. Additionally fewer CAs in older females likely occur because the older CAs become progressively smaller and more difficult to detect. Corpora counts and pregnancy rates both indicate that older females have lower reproductive rates than younger females.

Other species of cetaceans also show a decline in reproduction with age. Perrin et al. (1976) observed a decline in pregnancy rates of spotted dolphins (*Stenella attenuata*) with age. Approximately 60% of younger (i.e. 8 to 9 GLGs) females were pregnant while only 30% of older (i.e. 16 to 17 GLGs) females were. Mizroch (1981) observed that the number of CAs appears to be curvilinear with age in fin whales (*Balaenoptera physalus*). Numbers increased to a certain age and then leveled off or even declined. Short-finned pilot whales showed a similar pattern (March and Kasuya 1984).

In studies of other species, corpora counts can be used as a reasonable index of pregnancies (Perrin et al. 1976, George et al. 2005). Interpreting corpora counts of belugas is complicated because of the occurrence of accessory corpora (Brodie 1971, 1972, Burns and Seaman 1986). Sergeant (1973) found that accessory CLs accounted for 32% of all CLs. Burns and Seaman (1986) found that approximately 23% of CLs were accessory. Approximately 38% of the CLs in our study were accessory. It is not clear whether the production of accessory CLs varies with age. It is feasible that younger females may produce more accessory CLs than older ones (Brodie 1971).

Gestation

Estimates of the length of gestation in belugas are quite variable, ranging from 11 to 16 months. Belugas in west Greenland and northwestern Russia were reported to have a gestation period as short as 11 months (Ognetov 1985, Heide-Jørgensen and Teilmann 1994). Kleinenberg and Yablokov (1960) estimated 11-12 months for gestation but Sergeant (1973) reanalyzed their data and revised the estimate to nearly 14 months. Other authors also estimated gestation at about 14 months (Laws 1959, Burns and Seaman, 1986). Brodie (1971) estimated a gestation length of 14.5 months for animals in Cumberland Sound, Canada, while Sergeant (1973) suggested that gestation lasted 16 months based on length at birth and growth curves. Sergeant's (1973) estimate may have been biased due to the small sample of lengths at birth. Differences in methodology and assumptions of fetal growth have likely contributed to the variation. Even though the estimates of gestation from harvested belugas are varied, it is unlikely that whales from different stocks would have a gestation period varying to such a great extent.

The hunt of belugas in the eastern Chukchi Sea occurs during the time of calving. Thus, pregnant females may be carrying a term fetuses, or a small one from a recently initiated pregnancy. These observations indicate a gestation period of greater than 12 months. Our estimation of gestation, based on recent data from Point Lay, is 454 days (14.9 months) and our recalculation from the data of Burns and Seaman (1986) indicates a gestation period of 452 days.

Data from 9 captive belugas, for whom the beginning and ending of gestation were precisely known, indicated a gestation period of 475 days or 15.6 months (SE = 6.8 days; Robeck et al. 2005). Those animals originated from western Hudson Bay, Canada (T. Robeck, personal communication). Almost all estimates of gestation based on samples from harvested belugas are apparently underestimates. Estimates of length at birth are probably accurate given that lengths of new-born young are known and are similar to lengths of term fetuses. Therefore, gestation estimates from harvested animals do not appropriately account for the slow growth of early gestation.

Age at Sexual Maturity, First Birth, or Associated Parameter

Published estimates of age at sexual maturity also vary greatly. This in part may be due to different definitions of sexual maturity but it also relates to age determination of belugas. Whether one or two GLGs are deposited annually in beluga teeth greatly influences estimates of age, and therefore estimates of age at sexual maturity. Here, we discuss age at sexual maturity (or related statistic) relative to a deposition rate of one GLG per year and the age of first pregnancy.

Published estimates of age at sexual maturity ranged from 4 to 14 years for females (see Braham 1984, Heide-Jørgensen and Teilmann, 1994). In many cases authors were not explicit about whether their estimates were age at first ovulation, first conception, or first birth. These estimates differ by at least 15 months (i.e., length of gestation). Another confounding factor among estimates is that not all females will become pregnant during their first ovulation.

Ognetov (1981) estimated that some females attained sexual maturity (most likely age at first ovulation) at the age of 2 to 3 years, most were mature by 5 and all were mature by 9 years. Most other researchers estimated sexual maturity in females to be attained by about 3 to 7 years (Khuzin 1963, Brodie 1971, Sergeant 1973, Heide-Jørgensen and Teilmann, 1994). Those estimates were based on a deposition rate of 2 GLGs per year. Estimates of age at sexual maturity would therefore be about twice as high, between 6 and 14 years of age, if one assumes the convention that one GLG is deposited per year. Those estimates generally correspond to our estimate of age at first birth of 8.3 years (95% CI = 2.7 to 13.9). The ≥ 15 month difference between age at first ovulation and age at first birth would suggest that previous estimates were too high or ours was too low.

Robeck et al (2005) observed first luteal concentrations of progesterone in the blood at 6.9 years (SE = 0.5, n = 6) in their study of captive animals. First conception was at 9.1 years (SE = 0.7, n = 9), which is in agreement with our estimates for wild animals. Captive animals may mature at different ages than wild ones. Some of the factors that need to be considered include the social system and diet of captive animals. The social system of captive animals is dramatically different than that of wild animals, possibly influencing reproductive chronologies. If large groups of animals facilitate breeding and maturity as in some species, the smaller group sizes of captive animals may delay maturity. On the other hand, nutrition may be better in captivity, which might lower age of maturity.

Conclusion

Modeling the dynamics of wildlife populations that are harvested is an essential component of conservation and sustainability. Key components of these models are data on age, growth, and reproduction or vital rates estimated from those data. Furthermore, the information is useful for understanding impacts from a changing Arctic environment. For example, reproductive rates, estimates of age at maturity, or length at age could change as the ability of the environment to sustain populations changes. Environmental conditions for belugas could improve or worsen as the Arctic environment warms. We have provided a great deal of new information for the eastern Chukchi Sea stock of belugas that will be useful for managing the sustainability of the harvest and for understanding impacts from a changing environment.

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Table 2-1. Year, date, number, and sex of beluga whales harvested at Point Lay, Alaska from 1987 to 2005.

Year	Date	Total Harvested	Males	Females	Undetermined
1987	3 and 8 July	22	13	6	3
1988	27 June	40	24	13	3
1989	2 July	16	2	14	0
1990	11 July	62	35	27	0
1991	28 June	35	11	24	0
1992	6 and 7 July	24	16	8	0
1993	4 July	77	48	29	0
1994	27 June	56	30	24	2
1995	30 June	31	17	12	2
1996	30 June	34	18	16	0
1997	5 July	3	0	0	3
1998	26 June	49	49	0	0
1999	29 June	37	32	5	
2000	-- ¹	0			
2001	3 July	33	16	13	4
2002	7 July	45	27	18	
2003	28 June	36	18	16	2
2004	18 June	47	22	23	2
2005	26 June	41	30	11	
Totals		688	408	259	21

¹ No belugas were harvested in 2000 because sea ice remained close to the beach into July preventing hunters from accessing the ocean.

Table 2-2. Average length (95% confidence interval) and sample size of male and female beluga by color.

Sex	Gray	Gray-white	White
	284.8	340.5	394.7
Males	(267.61 - 301.99) n = 10	(330.70 - 350.22) n = 46	(390.67 - 398.63) n = 273
	281.0	329.4	350.0
Females	(264.43 - 297.47) n = 22	(322.29 - 336.55) n = 38	(346.48 - 353.44) n = 138

Table 2-3. Estimates (95% Confidence Interval) for parameters of Gompertz growth equation for male and female beluga whales. Parameters B and K are not directly comparable with animals from Greenland and the White/Kara seas because of differences in age determinations.

Location	L_{∞}	B	K
<i>Males</i>			
W. Greenland (2 GLG/yr) ¹	483 (458-509)	0.95 (0.89-1.01)	0.22 (0.18-0.35)
Eastern Chukchi Sea	436.46 (420-453)	0.61 (0.54-0.76)	0.08 (0.07-0.11)
White Sea/Kara Sea (2 GLG/yr) ¹	434 (427-441)	0.75 (0.71-0.79)	0.21 (0.19-0.23)
Beaufort Sea ²	432 (427-436)		
Kotzebue Sound	432.46 (416-449)	0.73 (0.64-0.82)	0.06 (0.05-0.08)
Cook Inlet	431.75 (401-461)	1.01 (-0.2-2.2)	0.16 (0.02-0.30)
Bristol Bay	405.41 (385-424)	1.02 (0.92-1.12)	0.15 (0.11-0.18)
<i>Females</i>			
W. Greenland (2 GLG/Yr) ¹	386 (374-398)	0.62 (0.56-0.67)	0.27 (0.21-0.32)
Chukchi Sea	362.38 (355-368)	0.54 (0.44-0.64)	0.13 (0.11-0.17)
White Sea/Kara Sea (2 GLG/yr) ¹	375 (370-379)	0.65 (0.60-0.70)	0.31 (0.27-0.34)
Beaufort Sea ²	386.2 (377.4-394.9)		
Kotzebue	356.96 (350-363)	0.74 (0.62-0.86)	0.16 (0.13-0.19)
Cook Inlet	360.86 (351-370)	0.84 (0.57-1.11)	0.35 (0.09-0.61)
Bristol Bay	350.72 (298-403)	0.69 (0.39-0.98)	0.13 (0.01-0.26)

¹ Heide-Jørgensen and Teilmann 1994

² Harwood et al. 2002

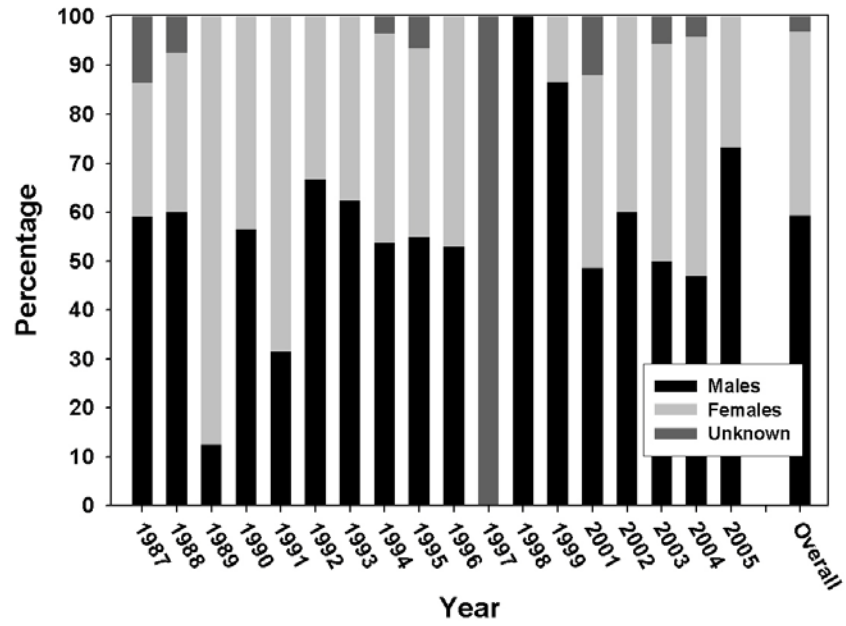


Figure 2-1. Percentage of male and female beluga whales taken in the subsistence harvest at Point Lay, Alaska, 1987 to 2005.

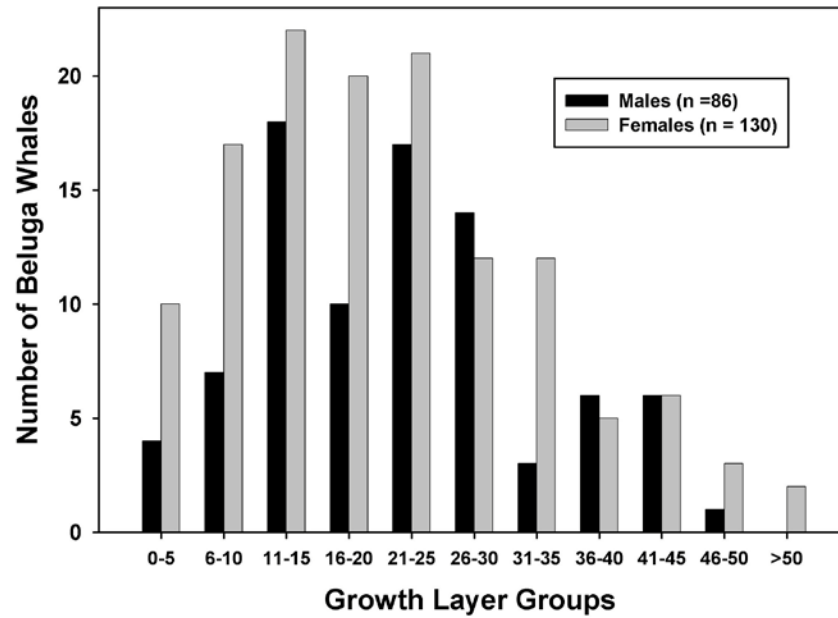


Figure 2-2. Number of beluga whales, by age, taken in the subsistence harvest at Point Lay, Alaska, 1987 to 2005.

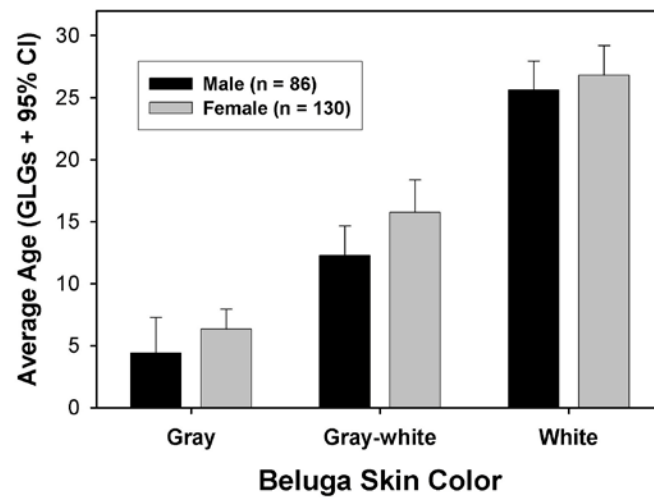


Figure 2-3. Average age of belugas, by color, taken in the subsistence harvest at Point Lay, Alaska, 1987 to 2005.

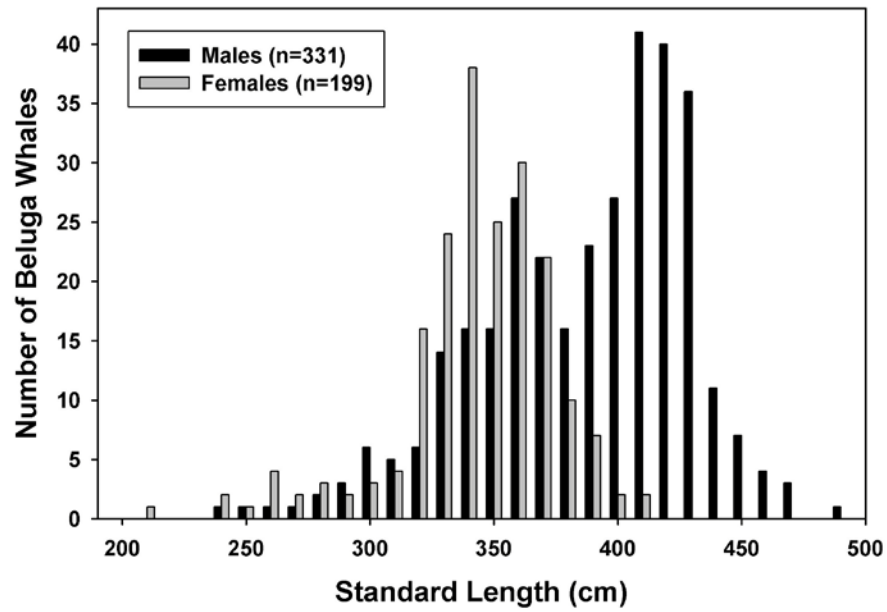


Figure 2-4. Number of beluga whales, by length, taken in the subsistence harvest at Point Lay, Alaska 1987 to 2005.

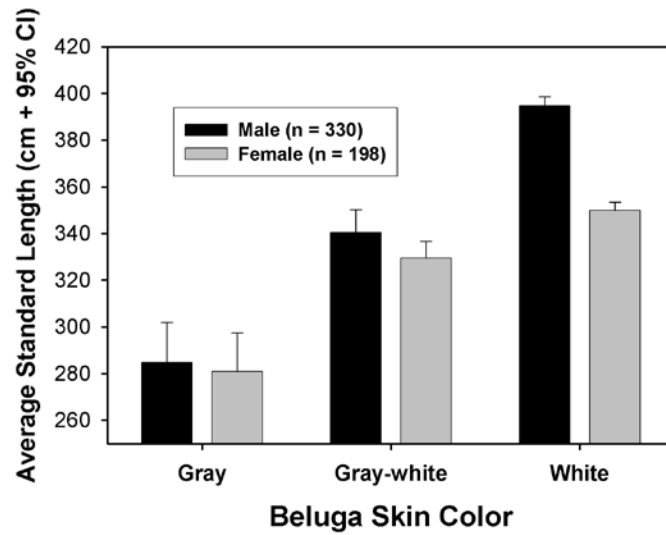


Figure 2-5. Standard length (95% confidence intervals), by color, of beluga whales from the eastern Chukchi Sea stock.

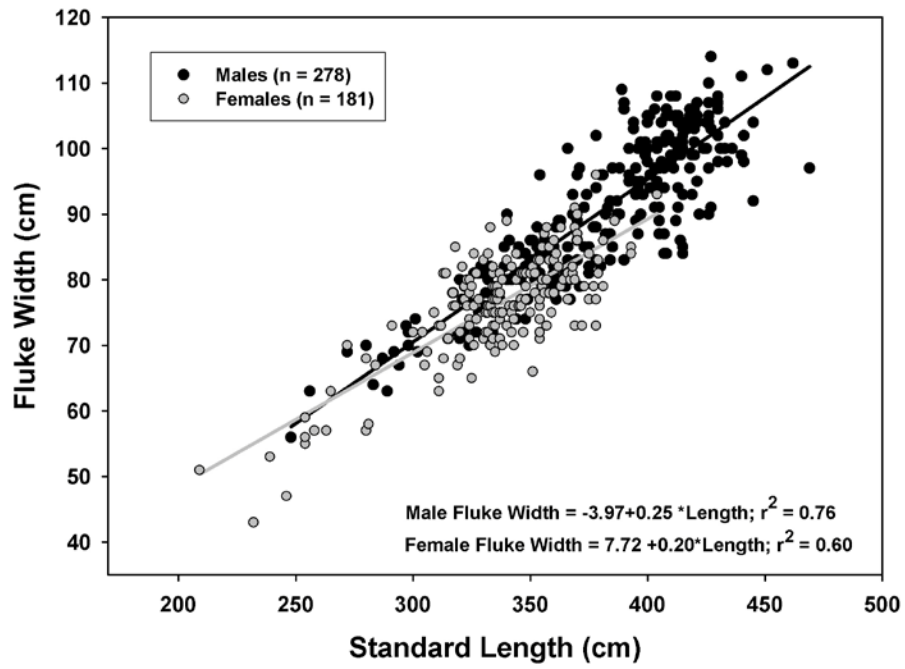


Figure 2-6. Relationship of fluke width to standard length of belugas whales harvested from the eastern Chukchi Sea stock.

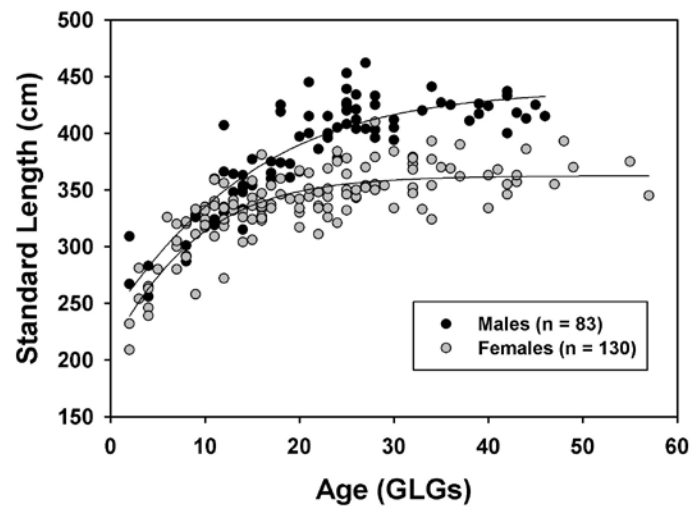


Figure 2-7. Gompertz growth curves for male and female beluga whales harvested from the eastern Chukchi Sea stock.

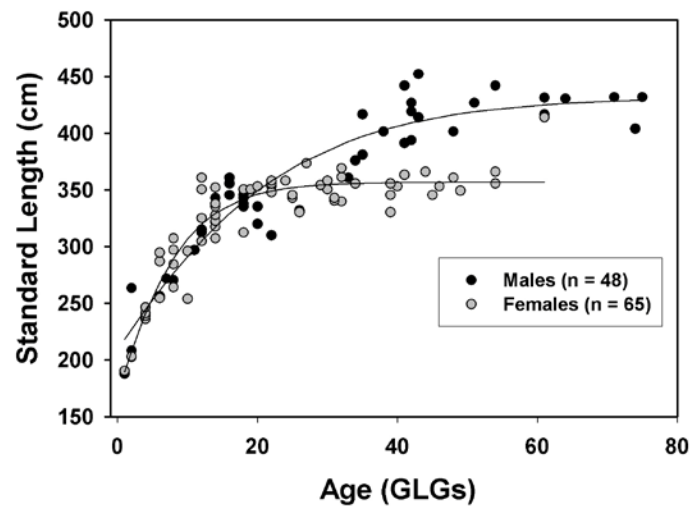


Figure 2-8. Gompertz growth curves for male and female belugas whales harvested from Kotzebue Sound.

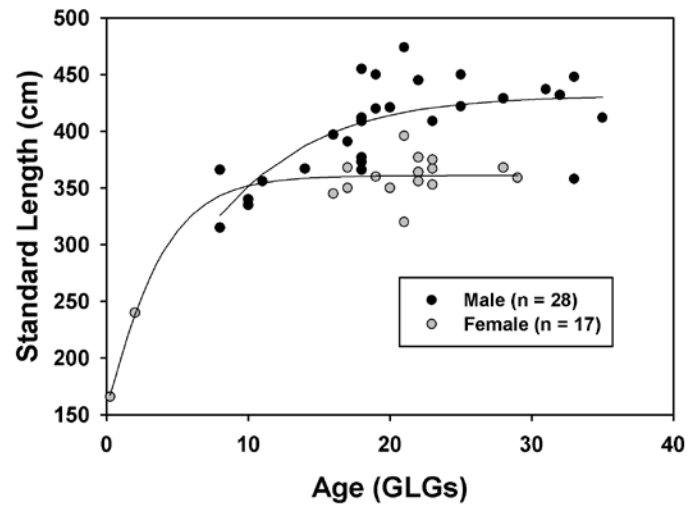


Figure 2-9. Gompertz growth curves for male and female belugas whales sampled in Cook Inlet.

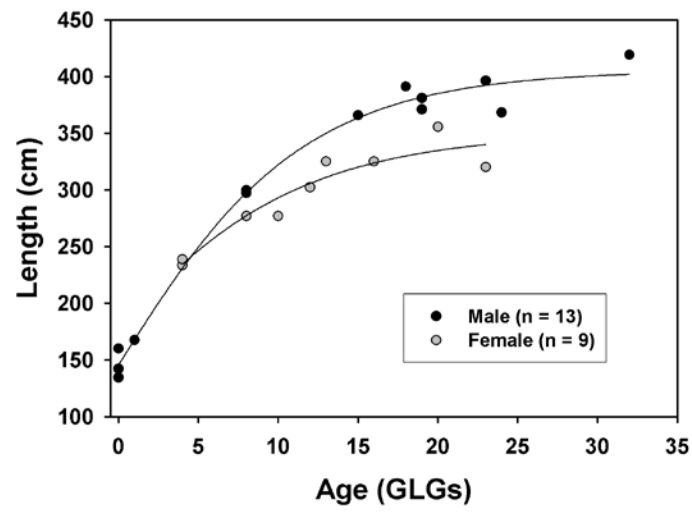


Figure 2-10. Gompertz growth curves for male and female belugas whales sampled in Bristol Bay.

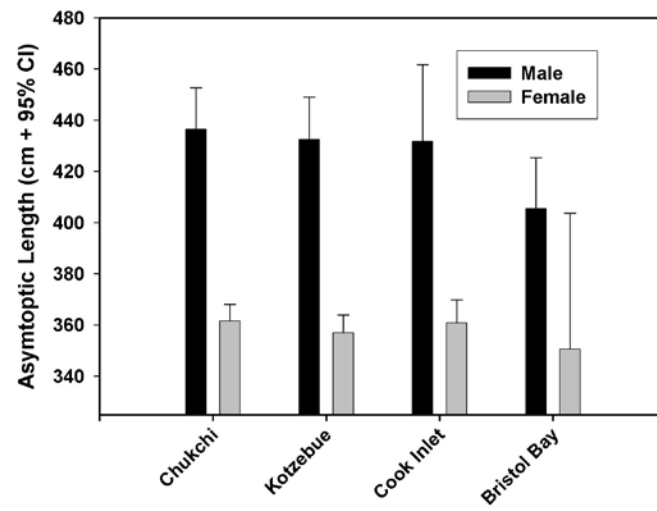


Figure 2-11. Estimates (and 95% confidence interval) of the L_{∞} parameter from the Gompertz growth curve for belugas from the Chukchi Sea, Kotzebue Sound, Bristol Bay and Cook Inlet.

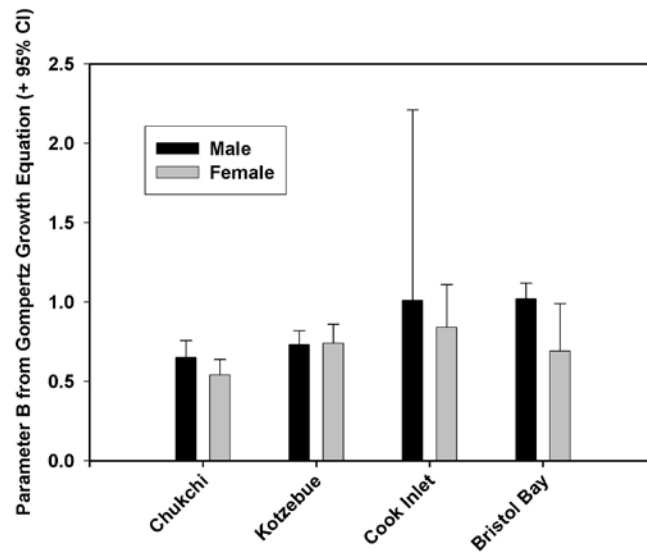


Figure 2-12. Estimates (and 95% confidence interval) of the B parameter from the Gompertz growth curve for belugas from the Chukchi Sea, Kotzebue Sound, Bristol Bay and Cook Inlet.

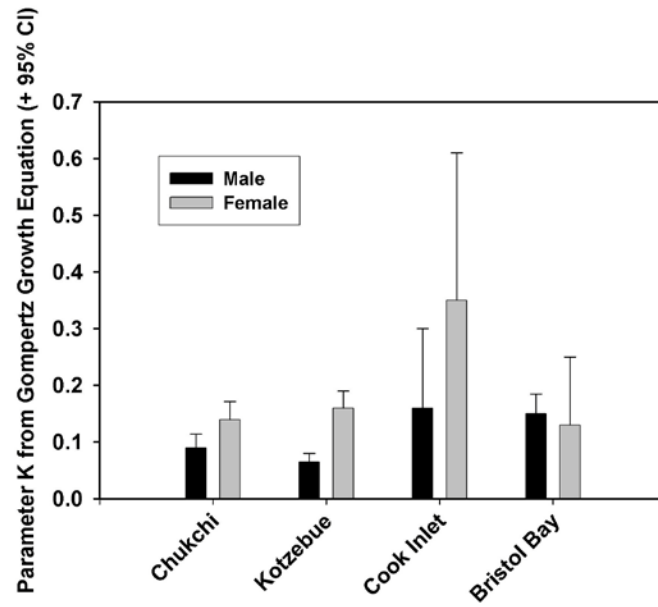


Figure 2-13. Estimates (and 95% confidence interval) of the K parameter from the Gompertz growth curve for belugas from the Chukchi Sea, Kotzebue Sound, Bristol Bay and Cook Inlet.

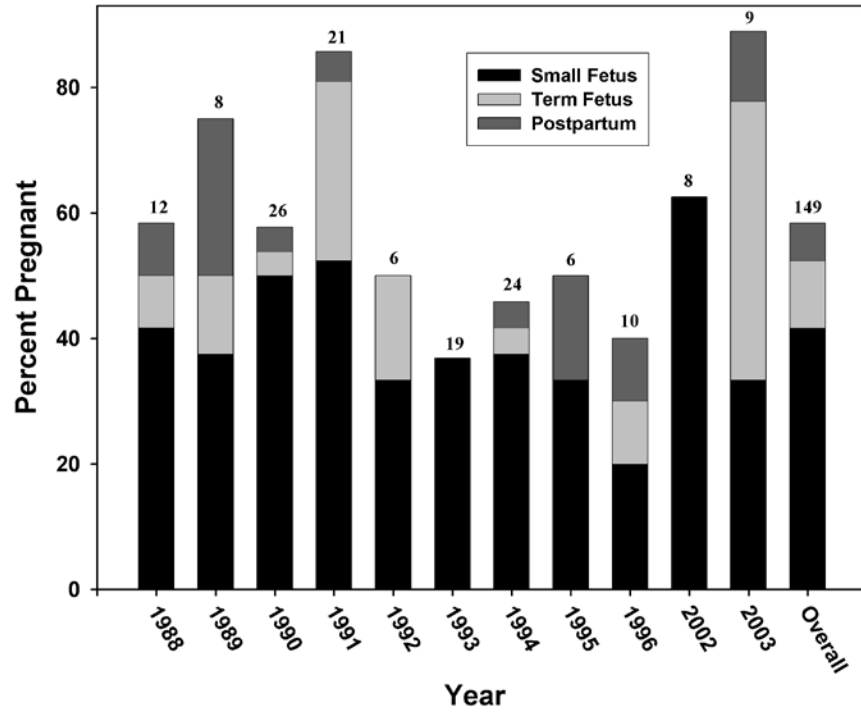


Figure 2-14. Percentage of mature female beluga whales that were pregnant (or had recently given birth) and taken in the subsistence harvest at Point Lay, Alaska, 1987 to 2003.

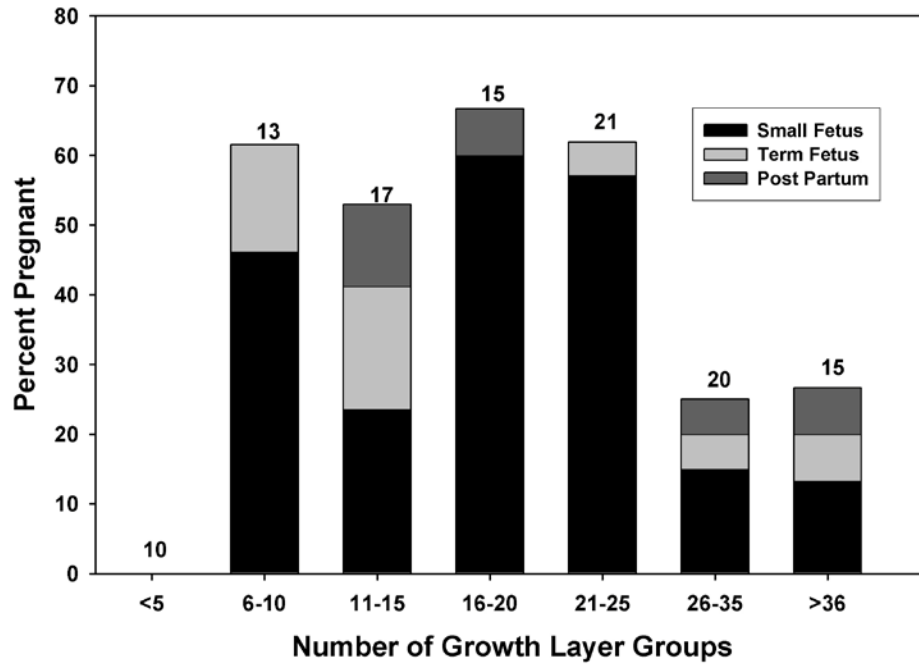


Figure 2-15. Percentage of female beluga whales, by age, that were pregnant (or had recently given birth) and taken in the subsistence harvest at Point Lay, Alaska, 1987 to 2003. Numbers above the bars represent sample sizes.

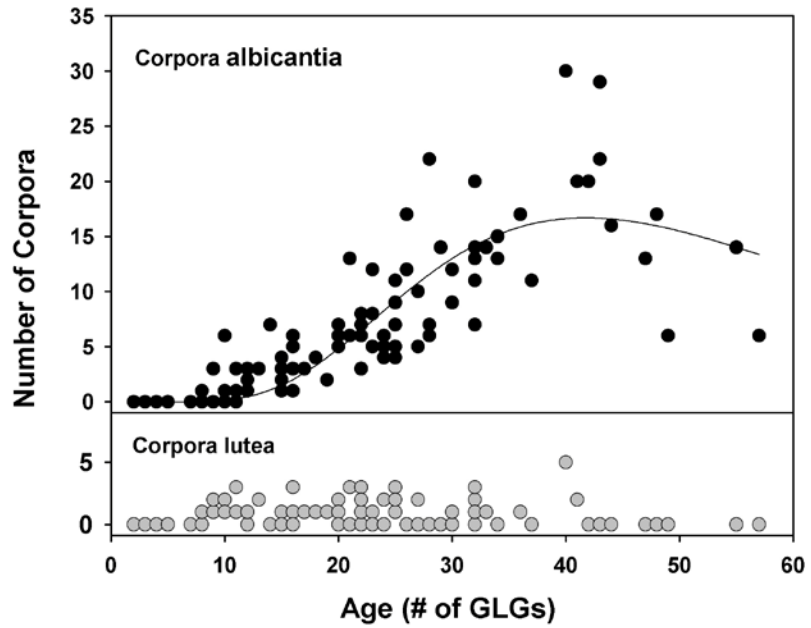


Figure 2-16. Number of corpora lutea and corpora albicantia, by age, in ovaries of beluga whales taken in the subsistence harvest at Point Lay, Alaska, 1987 to 2003.

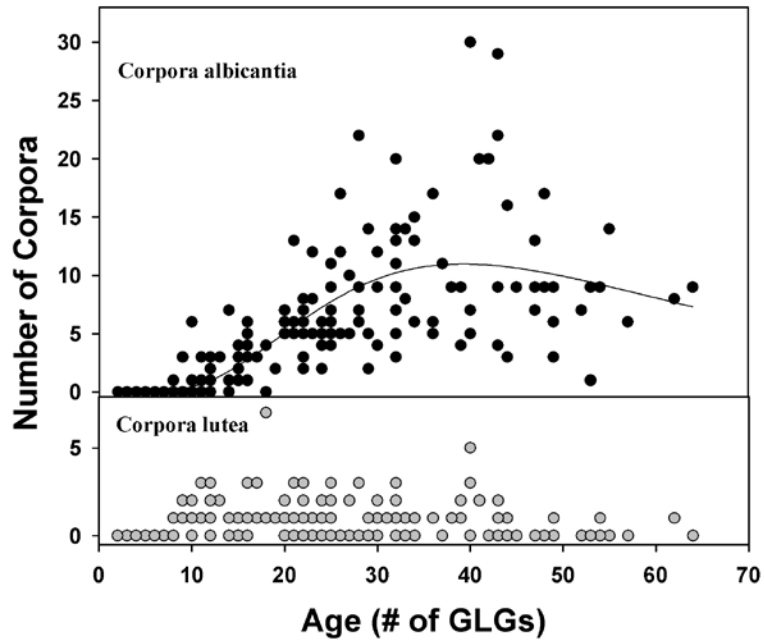


Figure 2-17. Number of corpora lutea and corpora albicantia, by age, in ovaries of beluga whales taken in the subsistence harvest in northwestern Alaska. Data from this study were combined with data collected by Burns and Seaman (1986).

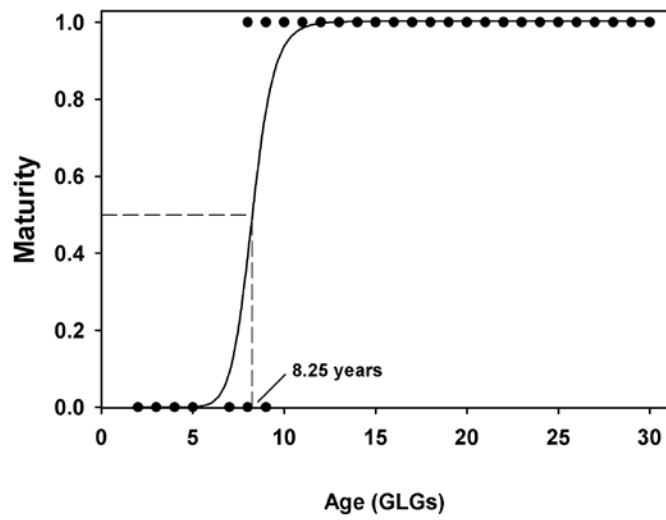


Figure 2-18. Age at sexual maturity for female beluga whales from the eastern Chukchi Sea stock.

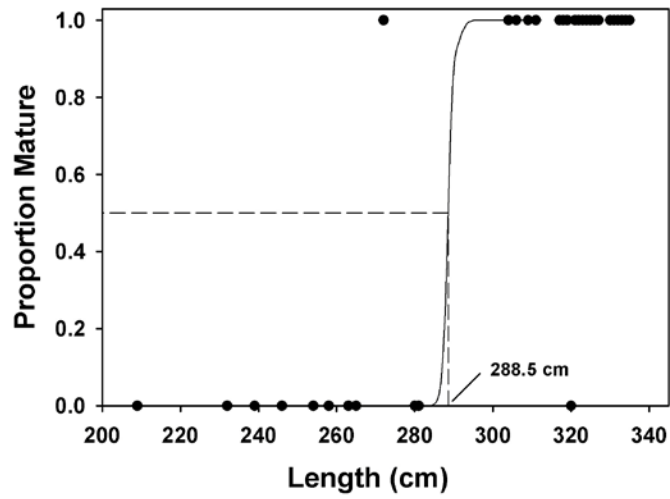


Figure 2-19. Length at sexual maturity for female beluga whales from the eastern Chukchi Sea stock.

CHAPTER 3

SATELLITE TRACKING OF EASTERN CHUKCHI SEA BELUGA WHALES
INTO THE ARCTIC OCEAN

ABSTRACT

Beluga whales (*Delphinapterus leucas*) congregate in nearshore waters of the eastern Chukchi Sea, especially in Kotzebue Sound and Kasegaluk Lagoon, in June and July. Where they travel after they leave this area was unknown before this study. We live captured five belugas in Kasegaluk Lagoon and attached satellite-linked depth recorders to them. The belugas were caught between 26 June and 1 July 1998 and included 4 males and 1 female ranging in length from 398 to 440 cm. A large calf was accompanying the female. Two tags transmitted for only about two weeks during which time one animal remained in the vicinity of Icy Cape, 80 km north of the capture site, and the other traveled to Point Barrow, about 300 km north. The other three tags operated for 60-104 days and the belugas traveled more than 2000 km and reached 80° N and 133° W, almost 1100 km north of the Alaska coast. This required them to move through 700 km of >90% ice cover. Two of the whales then moved southward into the Beaufort Sea north and east of Point Barrow. Two whales later moved to an area north of the Mackenzie River delta where they spent 2-3 weeks before once again heading southwest towards Barrow.

INTRODUCTION

Beluga whales (*Delphinapterus leucas*) occur in coastal and offshore waters of western and northern Alaska (Hazard 1988; Seaman et al., 1988; Frost and Lowry, 1990).

During summer months they predictably concentrate in certain coastal locations to feed, calve, and molt. This predictable distribution was used to identify three provisional management stocks in western Alaska (Seaman et al., 1988; Frost and Lowry, 1990). Studies of mitochondrial DNA have confirmed the existence of three stocks that occur during summer in western Alaska and a fourth in northwestern Canada. These are the belugas of Bristol Bay, the eastern Bering Sea, the eastern Chukchi Sea, and the eastern Beaufort Sea (O'Corry-Crowe et al., 1997).

Beluga whales have been seen all along the coast of the eastern Chukchi Sea during summer but they are most common in Kotzebue Sound and near Kasegaluk Lagoon (Frost and Lowry, 1990). Belugas apparently have been using the Kasegaluk Lagoon region during summer for many years. Warren Neakok described hunting them there in about 1930 (Neakok et al., 1985). In recent years, the occurrence of belugas at Kasegaluk Lagoon has been quite predictable, and they usually arrive in late June or early July (Frost and Lowry, 1990; Huntington et al., 1999). The latest sightings of belugas near the lagoon usually occur in mid to late July (Frost and Lowry, 1990; Huntington et al., 1999) and the distribution and movements of the whales after that time were completely unknown prior to this study. We suspected that they moved north and spent the summer along the edge of the pack ice in the Chukchi or western Beaufort seas.

Our understanding of the biology of beluga whales from the eastern Chukchi Sea stock is very limited. Aerial surveys provided some information on distribution and movements during June-July (Seaman et al., 1988; Frost and Lowry, 1990), examination of biological samples from belugas taken in subsistence hunts have provided insights into growth and reproduction (Burns and Seaman, 1988), and genetic analyses have provided a better understanding of stock relationships (O'Corry-Crowe et al., 1997). Recent advances in technology, such as satellite-linked tags, have provided opportunities to study belugas and other marine mammals in new ways.

Frost et al. (1985) first used telemetry to study the movements and behavior of belugas. They attached VHF radios to the dorsal ridges of two belugas in Bristol Bay, Alaska, and tracked their movements for about two weeks. Subsequently, similar techniques have been used to attach satellite-linked transmitters to beluga whales in several areas of the Canadian Arctic (Martin et al., 1993; Smith and Martin, 1994; Richard et al., 1997, 1998a,b). Satellite-linked transmitters have allowed belugas to be tracked over greater areas and for longer periods of time.

Beluga whales from the eastern Chukchi Sea stock are an important subsistence resource for residents of the village of Point Lay, adjacent to Kasegaluk Lagoon, as well as other villages in northwest Alaska. Each year, hunters from Point Lay drive belugas into the lagoon to a traditional hunting location. This technique provides opportunities to live-capture belugas that remain in the lagoon after the hunt.

In this paper, we present results from a project initiated by the Alaska Beluga Whale Committee (ABWC) to live-capture and attach satellite-linked depth recorders

(SDRs) to belugas. In 1998, we worked cooperatively with people from the village of Point Lay to capture and tag five whales in Kasegaluk Lagoon. Our objectives were to track movements and document diving behavior of belugas once they leave the area of Kasegaluk Lagoon. In this paper we present only movement data. Dive data will be presented in the future when our sample size is larger.

METHODS

Capture and Tagging of Whales

In 1996 and 1997, we were not successful in our attempts to capture belugas in or near Kasegaluk Lagoon. In 1996, no belugas remained in the lagoon after the drive hunt and in 1997 few belugas were seen near Point Lay. On 26 June 1998, the hunters of Point Lay drove approximately 80 belugas into Kasegaluk Lagoon; 48 were killed and approximately 30 remained alive in the lagoon. Between 26 June and 1 July 1998, we captured five of these remaining belugas (4 males and one female) in two different ways. The first animal was captured during the drive hunt as it attempted to escape; a hoop net as described by Martin and Smith (1992) was used. The other four were captured with a set net, 200 m long, 4 m deep, and with 37.5 cm stretched mesh. The net was set across the channel of the lagoon. Individual whales were driven into the net where they became entangled. They were further secured with a hoop net over their head and flippers. A padded rope was secured around the caudal peduncle and the beluga was towed to shore. They were held in water shallow enough that their dorsum was exposed. They were released immediately after the transmitters were attached.

The transmitters, manufactured by Wildlife Computers, were attached to a nylon saddle. Each tag with saddle weighed ~750 gm and measured 14.8 x 10.0 x 3.8 cm. The tags were powered by 4 C cell lithium batteries and their output was 0.5 watts; they collected data continuously but a conductivity switch allowed transmissions only when the tag was out of the water. The transmitters were attached with 4 nylon or dacron pins, approximately 0.33 m long. These pins were inserted through the skin and blubber of the dorsal ridge. They fit through pre-cut holes in the saddle of each transmitter, and nylon or dacron washers and nuts held the saddle and transmitter to the back of each animal. This attachment technique reportedly has little long-term impact on beluga whales (Orr et al., 1998). Pins migrate out of the dorsal ridge leading to release of the transmitter and loss of signals. Using different materials for the pins may influence time of tag retention, although we observed no association between tag longevity and pin type.

The whale that was captured and tagged during the drive hunt was guided out of Kasegaluk Lagoon shortly after tagging. The other belugas remained in the channels of the lagoon for 2-5 days after they were tagged. We attempted to drive them out on 2 July but they remained in the deeper channels and would not cross over shallow areas. On 3 July, the water level in the lagoon rose and the belugas left of their own accord.

Satellite Tag Data Analysis

Data from the satellite-tagged belugas were obtained from Service ARGOS (see ARGOS, 1988 and Fancy et al., 1988 for a detailed description of the ARGOS data

collection and location system). Data included a location for the SDR if sufficient signals were received during a satellite pass, or dive and battery strength data if only one uplink occurred. Service ARGOS assigns a location quality code to each location record that it provides. In our analysis we used all location qualities except class "Z", which consists of those that do not pass ARGOS plausibility tests. ARGOS predicts that locations of quality code 3 are within 150 m of the actual location, code 2 are within 350 m, code 1 are within 1 km, and code 0 are >1 km (ARGOS 1988), although there is evidence that the locations are not this accurate (Burns and Castellini, 1998; Goulet et al., 1999).

We screened location records using a computer program that calculated the time, distance, and speed between sequential pairs of locations. The program identified pairs of records that were improbable or that indicated apparent speeds greater than 20 km/hour over periods longer than 10 minutes. The identified records were inspected visually and the ones that appeared erroneous were deleted. The location records used in this paper include only those that remained after the screening process.

For analysis and presentation, dates and times reported by Service ARGOS were converted from Greenwich mean time to true local time by subtracting 11 hours. A computer program calculated the average daily position for each whale based on all records obtained during a 24 hour period, local time.

Data on sea ice coverage were obtained from the National Oceanic and Atmospheric Administration's National Ice Center. Average daily positions for

belugas and sea ice coverage maps were displayed and analyzed with the geographic information systems ArcInfo and ArcView.

RESULTS

The four male belugas ranged in length from 414 to 440 cm and the female measured 398 cm. The female was accompanied by a 310 cm gray colored male, presumed to have been her calf. We refer to the whales by their SDR identification number (Table 3-1).

SDRs provided location information over periods ranging from 13 to 104 days. Two of the tags failed after approximately 2 weeks while the other three operated for 2 to 3.5 months. Individual whales were located on 68-93% of the days they were tracked. In most cases location data were received for each whale every day. The main exception was beluga 2285 for which no locations were received, for unknown reasons, from 30 August through 18 September. The average number of locations received per day per SDR ranged from 8.1 to 24.0.

From the time they were tagged through 12 July, the belugas stayed in the northeastern Chukchi Sea between Point Lay and Point Barrow (Figure 3-1). Beluga 11035 moved out of Kasegaluk Lagoon shortly after it was tagged and remained in open water off the northern part of Kasegaluk Lagoon until 8 July (when signals stopped). The other four tagged belugas left the lagoon on 3-4 July and moved northward, then northeastward to the vicinity of Point Barrow. Three of them (11036, 2282, 2285) then moved back westward toward Icy Cape during 8-10 July; no signals

were received from the fourth animal (2284) during those days. The maximum distances between average daily locations of the four whales were 11-100 km. On 12 July the four belugas with transmitting SDRs were all north of Point Barrow, and their average locations for that day were within 17 km of one another. All locations for these four whales during 5-12 July were in ice cover of greater than 90%.

From 12-31 July, the three belugas with functioning tags moved steadily northward (Figure 3-2). They traveled as a group; the greatest distance between average daily locations during this period was 45 km. The whales moved through ice of greater than 90% coverage to a point north of 80° N, about 1100 km north of the Alaska coast. They traveled 1120 km in 19 days, averaging 59 km per day. After they reached their northernmost location, two of the animals (11036 and 2282) immediately headed south, again traveling together through ice of >90% coverage. They reached open water on 8 August, having moved 620 km in 8 days (78 km/day). The other whale (2285) remained in the north until 5 August, after which time it moved south along a different route. It reached open water on 16 August, having covered 630 km in 8 days (79 km/day).

Belugas 2282 and 11036 continued traveling southward together in open water until 10 August when they separated; 11036 moving to an area of loose ice east of Point Barrow while 2282 turned back northward into heavy pack ice (Figure 3-3). When it reached open water beluga 2285 swam westward approximately 500 km to the edge of loose pack ice, which it then followed back toward the east. During August-September the three belugas moved independently covering a large part of the Beaufort

Sea and adjacent Arctic Basin. All three used an area just north of the shelf break between Point Barrow and Prudhoe Bay, and a region of pack ice 400-600 km north of the Mackenzie River delta. The maximum distance apart for pairs of tagged whales on individual days was 620-717 km (Figure 3-4). The three belugas were separated to the greatest extent on 22 August, when the closest pair of locations was more than 400 km apart. On 29 August they were all near the shelf break northeast of Barrow, within 55-120 km of one another. On 22 September the two whales with functioning tags (11036 and 2285) were only 7 km apart at a location 600 km north of the Mackenzie Delta. Six days later those whales were 294 km apart, after one had moved to the southeast and the other to the southwest. The last signals were received from beluga 11036 on 10 October, when she was approximately 400 km northeast of Point Barrow.

Based on location data and ice maps, two of the tagged belugas spent 34 days (60.7% of days with locations) and one spent 42 days (46.2% of days with locations) in ice of greater than 90% coverage. When moving steadily they covered average distances of 59-79 km/day (2.5-3.3 km/h) through the ice.

DISCUSSION

Initial movements of the tagged belugas were as expected. All five whales moved northeastward from the capture location near Point Lay. One remained relatively nearshore in open water near Icy Cape. The telemetry locations from this whale, animal 11035, allowed an aerial survey crew to locate a large group of belugas on 6 July; 1172 whales were counted near Icy Cape and in the ice just offshore (Lowry

et al., 1999). Such an aggregation is normal for that time of year. Frost et al. (1993) flew 24 aerial surveys in the Kasegaluk Lagoon region during 3-14 July 1990 and 4-16 July 1991. Belugas were seen on every flight, with the highest single-day count of 1212 whales on 6 July 1991. The other four tagged belugas moved into heavy ice cover about 180 km north of Icy Cape, and were there at the same time that the large group was counted near Icy Cape. We do not know how many additional whales may have been associated with these four tagged individuals.

Movements of tagged belugas, after the initial northeastward movement, were unexpected. They traveled far north into the Arctic Ocean and deep into the pack ice. The reasons for the observed movements are unknown. Since two of the belugas immediately headed south after reaching their northernmost point, it seems reasonable to conclude that the circumstances there were not particularly suitable. However, one beluga did remain at 80° N for almost a week. The direct and coordinated movements of the three animals were purposeful, possibly indicating prior knowledge of a resource. One such resource, arctic cod (*Boreogadus saida*), can occur in dense patches and is an important food of marine mammals in the Arctic (Finley et al., 1990; Welch et al., 1993). However, there are no data on distribution or concentrations of arctic cod or other beluga food items so far north.

During summer the tagged belugas, including the female and possibly her calf, moved to deep offshore waters (~3000 m) with heavy ice cover (>90%). Use of deep, offshore habitat is different than previously reported for summer. Tagged belugas from other areas have tended to remain in relatively nearshore waters, although often in deep

water (Smith and Martin, 1994; Richard et al., 1997, 1998a,b). Belugas tagged in the eastern Canadian Arctic remained within the Canadian archipelago and mostly within or near estuaries (Smith and Martin, 1994). Female belugas tagged in the Mackenzie River delta also remained mostly near shore and in relatively shallow water, while males spent little time in the delta and traveled north, presumably to feed in nearshore water with heavy ice cover (Richard et al., 1997, 1998b). Smith and Martin (1994) thought that ice melt in summer dictated when and where belugas could move within Peel Sound. It is obvious that ice did not restrict movements of the tagged belugas we tracked in the Arctic Ocean, but the ice conditions there may be less hazardous for belugas to navigate than in the geographically complex Canadian Archipelago.

The belugas we tagged moved far to the north, in a short period of time, and to a place that we did not anticipate. It is unknown whether those movements were typical of eastern Chukchi Sea belugas. Prior to this study there was no information on where eastern Chukchi Sea belugas spent the summer after leaving the area near Kasegaluk Lagoon. It is feasible that the entire stock spends the summer in the pack ice of the Arctic Ocean. Regardless of why belugas moved so far north, the tagged whales showed that they are capable of moving great distances in almost complete ice cover

The three whales that traveled farthest north provided insight into association/grouping patterns in this species. They were caught from the same herd, traveled together most of the time when moving through heavy ice and moved more independently after they reached areas of open water and looser ice. Locations paired

by date show that the whales were frequently separated by more than 400 km. Nonetheless, they either deliberately managed to find one another again or happened to converge on the same area. Two whales that were more than 700 km apart on 13 August were only 7 km apart on 23 September.

During fall migration, tagged belugas in eastern Canada, typically used deeper waters between islands (Smith and Martin, 1994). In the Beaufort Sea, they mostly moved along the shelf break although a small number migrated through the heavy ice near 75° N, far north of the shelf break (Richard et al., 1997, 1998b). The westward fall migration of the eastern Beaufort Sea stock, occurs in mid to late September and October (Richard et al., 1997, 1998b; Treacy 1994). Our tagged belugas from the eastern Chukchi Sea likely occurred in similar places at similar times as those from the eastern Beaufort Sea stock, assuming that the latter stock's migration occurred at the same time in 1998 as in previous years. The significance of the apparent overlap or mingling of these two stocks in early fall is uncertain.

Estimated swimming speeds (2.5-3.3 km/h), derived from distances covered by our belugas, are similar to other studies. Smith and Martin (1994) estimated swimming speeds of 1.1-1.85 km/h during the entire period of their study, which included considerable time spent by the whales in estuaries. They calculated speeds of 1.6-5.99 km/h during the fall migration. Richard et al. (1998b) observed belugas moving mostly at 1-10 km/h during the fall but they also calculated several speeds in excess of 20 km/h. Undoubtedly, the speeds at which belugas travel depend upon the season and

activity. They would be expected to travel faster while on migration than while feeding or molting.

Our tag longevity, 13 to 104 days, was similar to that experienced in other studies of beluga whales. Smith and Martin (1994) received signals for <1 to 75 days, Richard et al. (1997) for 7 to 91 days, Richard et al. (1998a) for 37 to 60 days, and Richard et al. (1998b) for 56 to 120 days. The longevity of the tags appears to be limited by the attachment technique. The nylon pins holding the tag onto the beluga eventually pull out of the blubber and skin of the dorsal ridge and the tag falls off (Orr et al., 1998). To obtain greater tag longevity, a different attachment technique, a modified transmitter size or shape, or both are needed.

Our results show that beluga whales are not necessarily limited by heavy ice cover and illustrate that they are capable of moving great distances in relatively short periods of time. Mixed groups of whales may remain in cohesive units for periods of weeks or months, or alternatively, separate and move as much as 700 km apart only to converge at a later time. Furthermore, during the summer belugas from the eastern Chukchi Sea stock use offshore areas with heavy ice cover, as well as loose ice cover, open water, and nearshore waters. Interpretation of our results is limited by the very small sample size. Further tagging studies, to increase sample size, will help elucidate movement patterns and habitat use by beluga whales of the eastern Chukchi Sea.

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Table 3-1. Performance of satellite-linked depth recorders attached to beluga whales at Kasegaluk Lagoon, Alaska, June-July 1998.

SDR*	Whale Length (cm)	Sex	Date Attached	Date of Last Location	Total Days Operational	No. Days w/ Locations	Total No. Locations
11035	440	M	6/26/98	7/8/98	13	12	312
11036	398	F	6/29/98	10/10/98	104	91	1267
2282	414	M	7/1/98	8/29/98	60	56	801
2284	432	M	6/28/98	7/12/98	15	11	172
2285	415	M	6/29/98	9/28/98	92	63	745

* SDR = Satellite-linked depth recorder number.

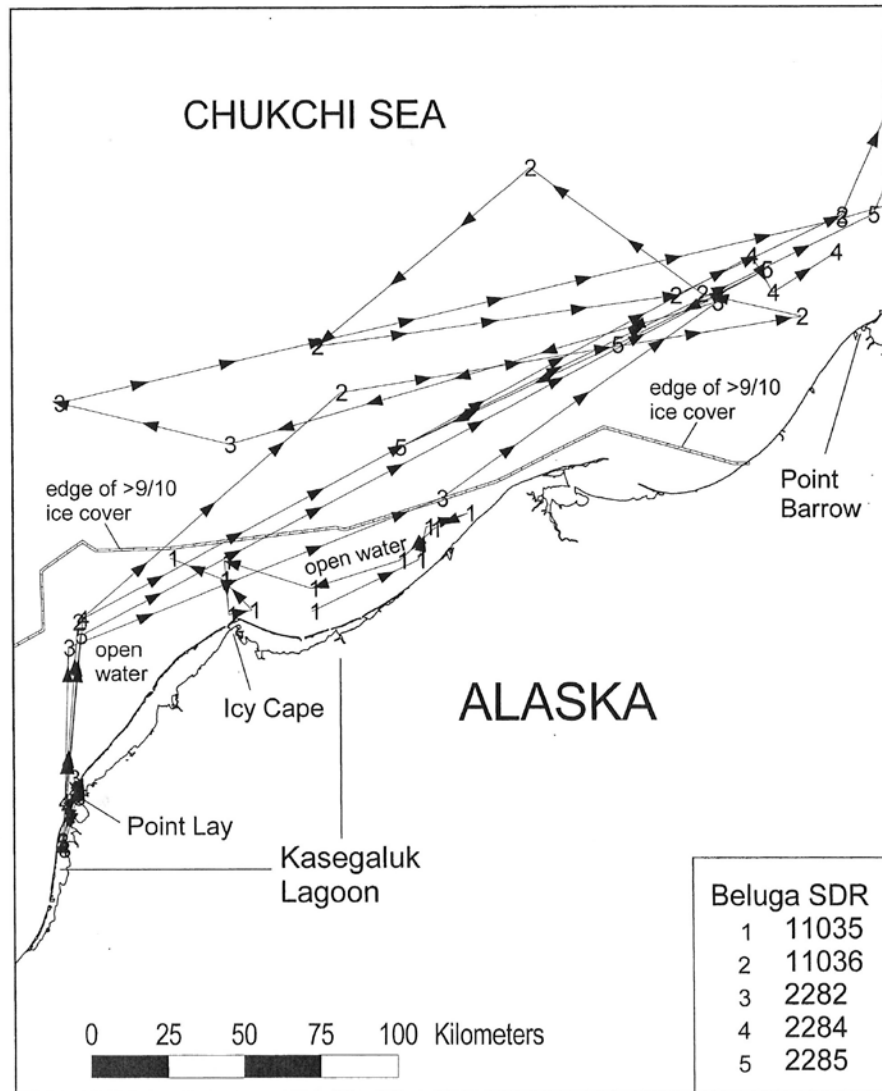


Figure 3-1. Movements during 26 June-12 July 1998 of beluga whales satellite tagged near Point Lay, Alaska.

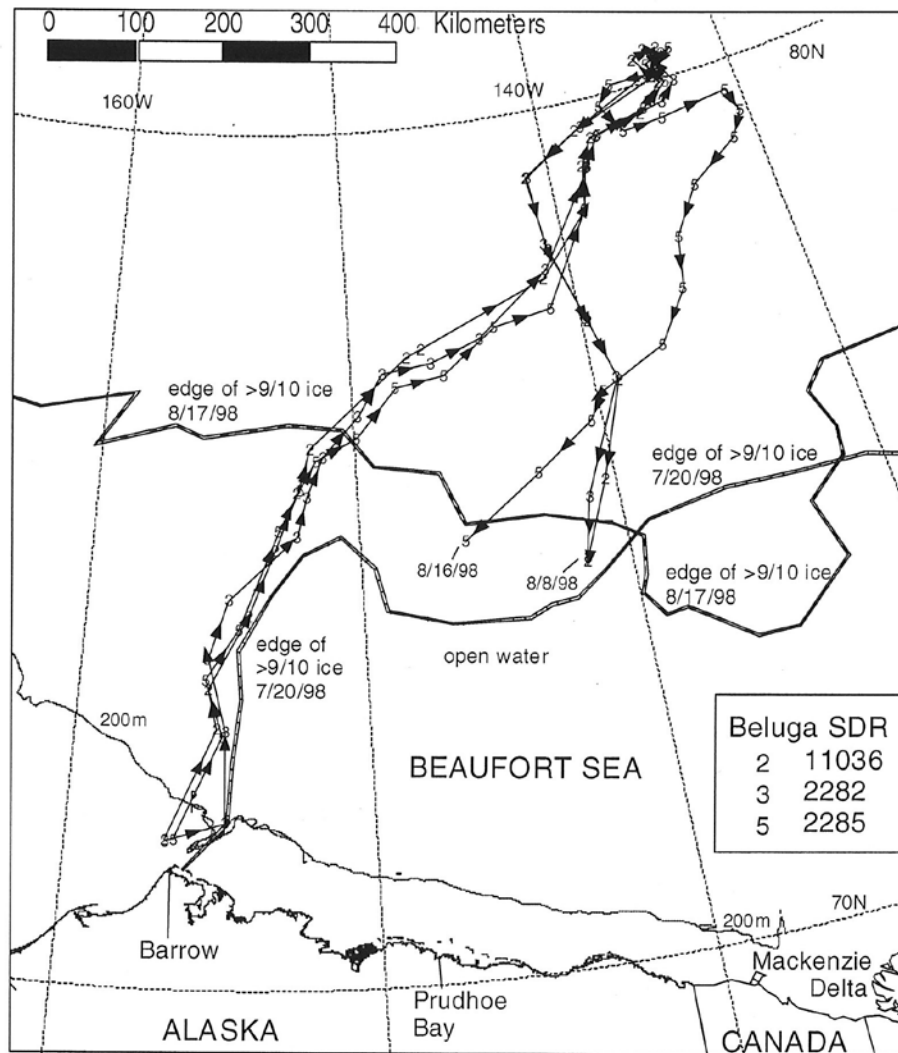


Figure 3-2. Movements during 12 July-19 August 1998 of beluga whales satellite tagged near Point Lay, Alaska.

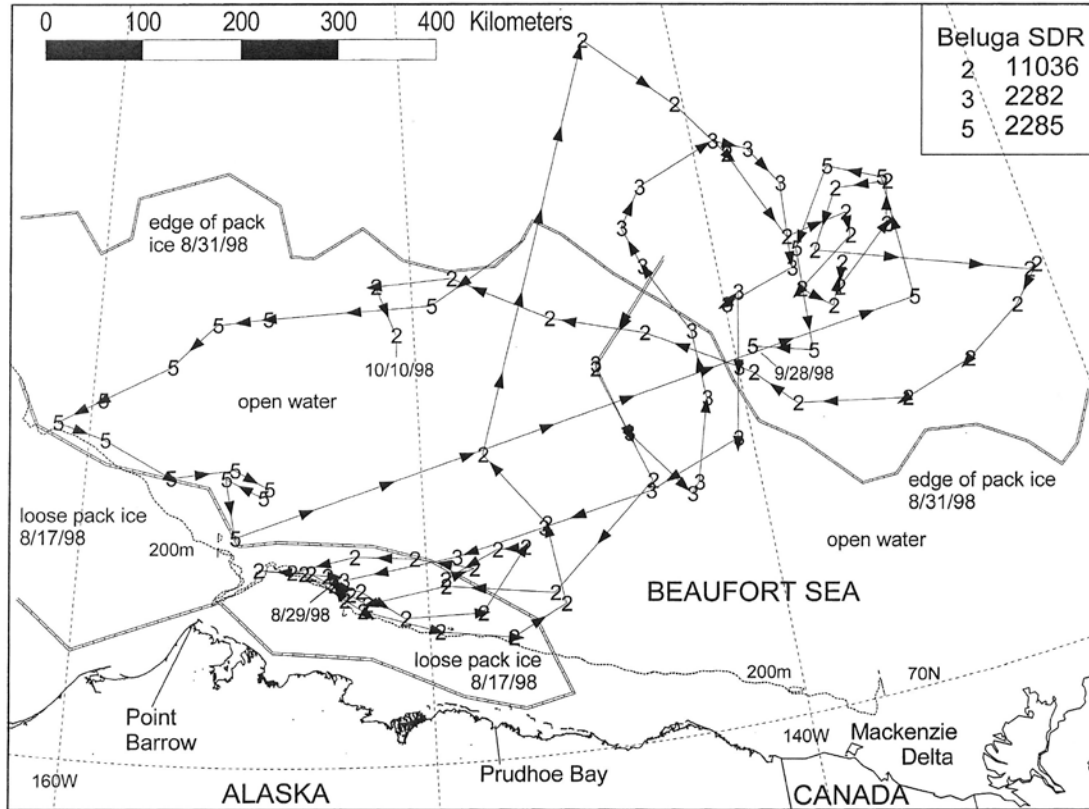


Figure 3-3. Movements during 19 August-10 October 1998 of beluga whales satellite tagged near Point Lay, Alaska.

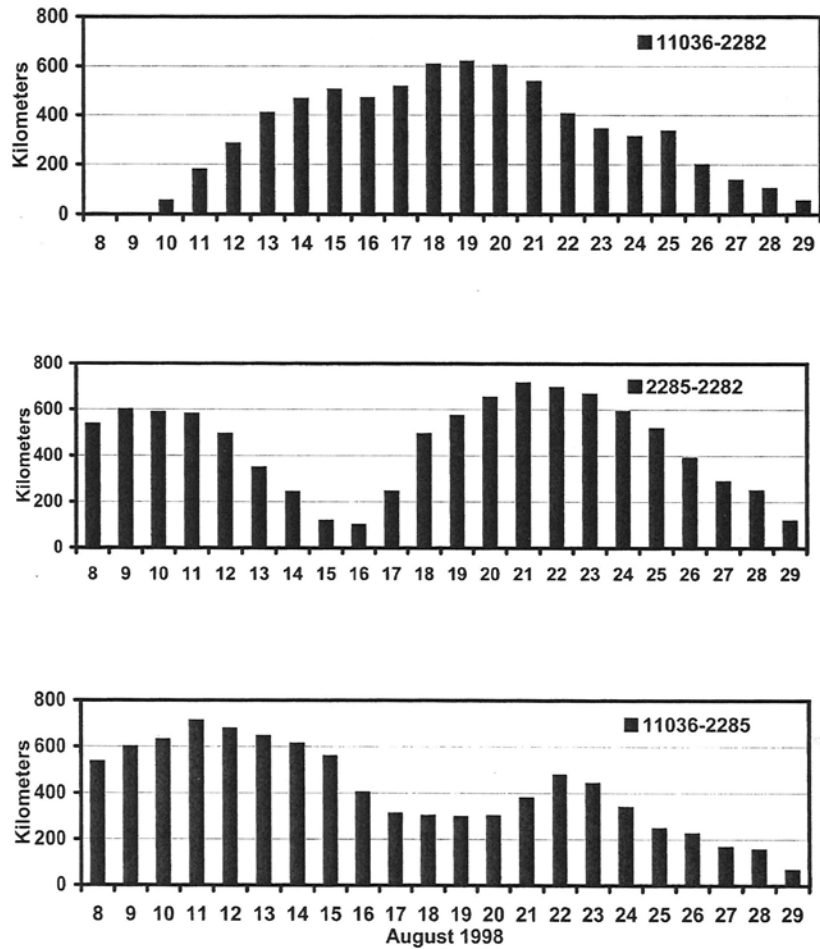


Figure 3-4. Daily distance in kilometers between belugas #11036, #2282, and #2285 during 8 to 29 August 1998.

CHAPTER 4

DISTRIBUTION AND MOVEMENTS OF BELUGA WHALES FROM THE
EASTERN CHUKCHI SEA STOCK DURING SUMMER AND EARLY AUTUMN

ABSTRACT

At least five stocks of beluga whales (*Delphinapterus leucas*) occur in Alaska. One of these, the eastern Chukchi Sea stock, is most commonly seen in coastal waters near Kasegaluk Lagoon in northwestern Alaska during June and July. Relatively little was known about the movements and seasonal distribution of these whales during the rest of the year. During June and July from 1998-2007 we instrumented 26 belugas with satellite-linked depth recorders (SDRs), including 13 adult males, 5 immature males, 4 adult females and 4 immature females. SDRs provided location information for an average of 89 days (range 5-520). “Saddle mount” tags averaged 52 days, “side mounts” 81 days, and “spider mounts” 141 days, although there was no statistical difference in mean longevity among attachment types. Animals moved north and east through the northern Chukchi Sea and into the western Beaufort Sea after capture. From mid July to September they rarely occurred in continental shelf waters (depth <200 m) and primarily ranged along the shelf break (~200 m) and across deep waters (200 to 4,000 m) of the central and eastern Beaufort Sea and the Arctic Ocean. Some penetrated the pack ice as far as 80°N. Sample size limits our ability to analyze movements by age and gender, although all belugas that moved north of 75° N were

males. Adult males may use deeper waters than adult females and immature animals, the latter two categories apparently remaining closer to the shelf break throughout summer and early fall. Heavy ice apparently did not inhibit the movements of large adult males in summer because they traveled through and were often located in water with >90% ice cover. Six tagged belugas transmitted data after October. Those animals used the central and eastern Chukchi Sea during autumn migration. One provided the first winter locations of a tagged Chukchi Sea beluga in the northern Bering Sea, between Saint Lawrence Island, the Bering Strait, and Providenya, Russia.

INTRODUCTION

Movements and migrations are important components of life histories of vertebrates. In deciding where and how to move, animals must balance the energetic costs of movement while maximizing long-term reproductive success (Rodgers 1983). Movements among habitats are driven by both abiotic and biotic factors (Dingle 1972). All habitats have a seasonal component and some time periods are relatively better for animals than others (Sinclair 1975). This is especially the case in the Arctic, where abiotic factors, such as cold, darkness, and ice cover limit primary production and likely reduce foraging opportunities for vertebrates. Furthermore, risks to survival in the Arctic during winter may increase due to cold or ice entrapment. The predominant biotic factor in the Arctic and subarctic is the highly seasonal productivity that can provide a large food resource. Some species of Mysticete whales are examples of animals that have taken advantage of the seasonality of the Arctic. They feed at a low trophic level and have balanced survival and reproduction by moving toward the Arctic during the productive summer months where they feed extensively. In the winter, they move toward equatorial regions where there is little food but warmer water may increase calf survival (Norris 1967). The thick blubber layer, which stores energy, allows Mysticetes to go long periods of time without feeding and may be more important as a food store than as insulation (Norris 1967). Another biotic factor that may play a role in movement is predation, especially from killer whales (*Orcinus orca*; Corkeron and Conner 1999).

By comparison, most Odontocetes are smaller and cannot store as much energy as the Mysticetes. The result is that smaller size precludes long migrations (Sinclair 1983). Odontocetes also typically forage at a higher trophic level meaning that their food resources are not as subject to the extreme seasonal changes as Mysticetes. Belugas (*Delphinapterus leucas*) are one of the more prominent cetaceans in the Arctic. They exhibit a wide range of migratory behaviors. Some stocks, principally the more southerly ones, remain in the same general area throughout the year (e.g., Cook Inlet belugas, Hobbs et al. 2005), while others make long movements (e.g., Beaufort Sea stock, Richard et al. 2001). Understanding movements of belugas and other arctic marine mammals is especially important in light of recent dramatic reductions in the sea ice and increase in human activities.

Understanding movements, distribution and behavior of wildlife, especially marine mammals, has been greatly enhanced through the use of electronic technology. The attachment of VHF radio transmitters (Frost et al. 1985) and subsequently the attachment of satellite-linked transmitters to belugas (Martin et al., 1993; Smith and Martin, 1994; Richard et al., 1997, 1998a,b, 2001a,b; Lydersen et al. 2001, Suydam et al. 2001) has allowed near real-time tracking of individual animals. Satellite-linked transmitters in particular have enabled researchers to track whales over large areas and for long periods of time. More belugas have been instrumented with satellite transmitters than any other species of cetacean (Reeves and St. Aubin 2001). Satellite tagging offers a proven, cost-effective and technologically sound approach to obtaining information on beluga distribution and movements.

Beluga whales occur throughout much of the Arctic and are an important subsistence resource for many aboriginal people. This is especially true in northern and western Alaska where approximately 300 belugas are harvested annually (Frost and Suydam, in review). Additionally, whales from northern and western Alaska may migrate through Alaskan, Russian and Canadian waters where they are the subjects of increasing interest in international cooperative management (Adams et al. 1993). Further, many belugas may migrate through or occur in offshore oil and gas leasing areas in Alaska and Canada. Concerns about potential effects of offshore oil and gas exploration and development on beluga whales exist at local, national, and international levels. Despite the importance of belugas as a subsistence resource and the potential impacts on this species from increasing interests in oil and gas activities, we know little about late summer distribution, autumn and spring migration patterns, and wintering locations for many stocks.

In Alaska, there are at least five demographically discrete stocks of belugas. These stocks were initially identified based on traditional summering areas (Frost and Lowry 1990) and later confirmed by genetic analysis (O'Corry-Crowe et al. 1997, 2002). Two of these stocks, the eastern Beaufort Sea and the eastern Chukchi Sea stocks, occur seasonally in areas. The Beaufort Sea stock migrates north and east through openings in the sea ice, called leads and polynyas, in April and May. They move from the Bering Sea to the eastern Beaufort Sea and the waters of the western Canadian Arctic Archipelago and return west through the Beaufort Sea in September and October (O'Corry-Crowe et al., 1997; Richard et al. 2001b). Belugas of the eastern

Chukchi Sea stock were thought to arrive in Kotzebue Sound in early to mid-June and then move north to areas near Kasegaluk Lagoon in late June and early July (Frost and Lowry, 1990). Recent genetic evidence indicates that Kotzebue Sound belugas are distinct from those occurring near Kasegaluk Lagoon (O’Corry-Crowe, unpublished data). Whales have been recorded as using coastal waters in northwest Alaska during summer for many years, with the earliest records of hunting at Kasegaluk Lagoon dating to 1930 (Neakok et al., 1985) and at nearby Corwin Bluffs as far back as 1884 (Brower, 1942). It is likely that beluga hunting has been occurring in the area for much longer, perhaps centuries.

In recent years, the occurrence of belugas at Kasegaluk Lagoon has been quite predictable. They usually arrive in late June or early July. The latest sightings of belugas near the lagoon usually occur in mid to late July (Frost and Lowry, 1990; Huntington et al., 1999) and the distribution and movements of the whales after that time were unknown prior to satellite tracking (this study; Suydam et al. 2001). Before the current study, we suspected that the whales likely moved north and may have spent the summer along the southern edge of the pack ice near the shelf break in the Chukchi or western Beaufort seas, although there were few sightings to provide support for this hypothesis. The ice edge and upwelling at the shelf-break may provide feeding opportunities for belugas.

An annual subsistence drive hunt for belugas at Point Lay, Alaska, offers opportunity to capture and tag belugas from the eastern Chukchi Sea stock. Alaska Native residents of this village, adjacent to Kasegaluk Lagoon, drive belugas into the

lagoon to a traditional hunting location. Whales not harvested may be live-captured in the shallow lagoon after the hunt. We worked cooperatively with hunters from the village of Point Lay from 1996 to 2007 to capture and tag belugas. Our primary objective was to track movements to understand what areas and habitats are used by belugas of the eastern Chukchi Sea stock once they left the area of Kasegaluk Lagoon.

METHODS

Capturing and Tagging of Whales

We attempted to capture belugas beginning in 1996 but were unable to do so in that year, or in 1997 and 2000. In 1996, few belugas were available for capture after the harvest. Ice conditions, weather, or few animals prevented tagging in 1997 and 2000. We were successful at capturing and tagging whales in 1998, 1999, 2001, 2002 and 2007. In each of those years 10 to 40 belugas remained alive in the lagoon after the annual subsistence drive hunt.

Orr et al. (2001) described three techniques for capturing belugas: (1) hoop net, (2) stationary net, and (3) seine net. We used two of those and one additional technique not previously described in the literature. We captured one animal using the hoop net technique during the drive hunt in 1998. With this technique, a person jumps from a moving boat and puts a hoop net over a beluga's head as it comes to the surface. Using the second technique, Orr et al. (2001) monitored a stationary net while waiting for a beluga to swim into it and become entangled. We modified this second technique slightly. We set an unanchored net (~50 m long, 4 m deep, and with 37.5 cm stretched mesh) across a channel of the lagoon and drove one or two belugas at a time into the

net. The third technique we used was to drive belugas into very shallow water, using small boats (usually inflatable) with outboard motors, until the whales could no longer maneuver easily. A person would jump into the water, wade to the whale and place a hoop net over the animal's head. This technique was especially successful in Kasegaluk Lagoon where there are extensive areas of shallow water. This technique also minimized danger to the whale and people by eliminating the use of long, sometimes unwieldy nets or the need to leap out of moving boats. In 1999 we also tagged four whales that had already become stranded in shallow water during the drive hunt.

After belugas were caught we handled them as described by Orr et al. (2001). We secured whales with a hoop net over their head and flippers. A padded rope was placed around the caudal peduncle and the beluga was slowly pulled to shore. The animals were held in water shallow enough that their dorsum was exposed. We released the whales immediately after the transmitters were attached, with the exception of the animals captured in 2007. In that year we collected blood samples before release. Whales were held for 20 to 60 minutes. Most belugas that we captured remained in the channels of Kasegaluk Lagoon for 2 to 5 days after they were tagged, although four whales (one in 1998 and the three in 2007) left the lagoon of their own accord shortly after tagging.

We used 0.5-watt output satellite data recorders (SDRs) manufactured by Wildlife Computers (Redmond, WA, USA). SDRs deployed in 1998 and 1999 (and one in 2001) used ST-10 transmitters, while most of those deployed in 2001 and 2002

used ST-16 transmitters. In 2002, we also deployed one SPOT2 transmitter (location only). In 2007 we deployed SPLASH tags. Eighteen of the SDRs were glued to nylon belting in one of two configurations, saddle mount (n=9) or side mount (n=9; Figure 4-1). We also deployed eight tags with spider mount configurations (Figure 4-1, Table 4-1).

Each saddle mount weighed ~750 gm and measured 14.8 x 10.0 x 3.8 cm. Four C-cell lithium batteries powered the tags. The side mounts weighed ~300 gm and the spider mounts about 330 gm, except the spider mounts in 2007, which weighed about 200 gm. Side, spider and SPOT tags measured approximately 13 x 5 x 3 cm and were powered with either two 2/3A batteries or 4 M1 (military grade) batteries. SPLASH tags were ~12.5 x 3.5 x 3.5 cm and powered with one C cell battery. All transmitters collected data continuously but a conductivity switch allowed transmissions via satellite uplink only when the antenna was out of the water. Transmitters were attached with three (for spider mounts) or four (for saddle and side mounts) nylon or dacron pins, approximately 0.33 m long. The pins were inserted through the skin and blubber of the dorsal ridge (i.e., through a hole made with a trocar) or just anterior to the ridge and fit through pre-cut holes in the belting of each transmitter or through adjustable loops of the spider mounts. Nylon or dacron washers and nuts screwed onto the pins held the transmitter to the back of each animal.

Data Acquisition and Analysis

Data from the satellite-tagged belugas were obtained from Service ARGOS (see ARGOS, 1988 and Fancy et al., 1988 for a detailed description of the ARGOS data collection and location system). Data included a location for the SDR if sufficient signals were received during a satellite pass, or dive and battery strength data if only one uplink occurred. Service ARGOS assigns a location quality code to each location record that it provides. In our analysis we used all location qualities except class "Z", which consists of those that do not pass ARGOS plausibility tests. ARGOS predicts that locations of quality code 3 are within 150 m of the actual location, code 2 are within 350 m, code 1 are within 1 km, and code 0 are >1 km (ARGOS 1988), although there is evidence that the locations may not be this accurate in some cases (Burns and Castellini, 1998; Goulet et al., 1999; Vincent et al. 2002).

We screened location records using a computer program that calculated the time, distance, and speed between sequential pairs of locations. The program identified pairs of records that indicated apparent speeds greater than 20 km/hour over periods longer than 10 minutes, an implausible speed for belugas. The identified records were inspected visually and the member of the pair that appeared erroneous was deleted. The location records used in this paper include only those that remained after the screening process. This screening process was similar to that used by Lowry et al. (1998).

For analysis and presentation, dates and times reported by Service ARGOS were converted from Greenwich Mean Time to true local time (Alaska Standard Time) by subtracting 9 hours. A computer program calculated the average daily position for each whale based on all records obtained during a 24 hour period, local time.

Bathymetry was assigned to each averaged daily location using the 2008 International Bathymetry Chart for the Arctic Ocean (IBASCO), which has a resolution of 2 km (Jakobsson et al. 2008).

Data on sea ice coverage were obtained from the National Oceanic and Atmospheric Administration's National Ice Center. Average daily positions for belugas and sea ice coverage were displayed and analyzed with the geographic information systems ArcInfo and ArcView 9.0.

RESULTS

Capture and Tagging

We captured and tagged 26 belugas near Point Lay (Table 4-1). Some of the 1998 data were presented in an earlier paper (Suydam et al., 2001). In late June 1998 and 1999, the hunters drove belugas into the lagoon from among the first groups of animals to migrate north along the barrier Islands. These early groups consisted almost entirely of males. In 1998, all whales hunted (n=48) and tagged (n=5) were adult males. In 1999, 28 of 33 hunted and four of five tagged animals were adult males. The hunts in 2001 and 2002 occurred later in the season and included many more females and young animals. In 2001, 16 males and 13 females were taken in the hunt and we

tagged five males (three adults and two immature) and three females (one adult and two immature). In 2002, 27 males and 18 females were taken in the hunt and we tagged three males (all immature) and two females (one adult and one immature). In 2007, 54 males, 10 females and one animal of undetermined sex were taken in the hunt and we tagged one adult male and 2 adult females. In total we tagged 13 adult males, 5 immature males, 4 adult females and 4 immature females. The 18 males ranged in length from 267 to 441 cm and the 8 females from 266 to 398 cm (Table 4-1).

SDRs provided location information from 5 to 520 days. Two of the tags failed within the first week, another 6 transmitted for two to six weeks and the remaining 18 lasted about two months or longer. The longest lasting tag was a SPLASH tag that was positioned just anterior to the dorsal ridge. Most of the tags were placed on the dorsal ridge. On average, tags transmitted data for 89 days. Saddle mounts averaged 52 days, side mounts 81 days, and spider mounts 141 days, although there was not a significant difference in longevity of tag types (Kruskal-Wallis: $\chi^2=3.88$, $p=0.14$). One tag failed in 1999 because a polar bear (*Ursus maritimus*) killed the whale while it was still in Kasegaluk Lagoon. We do not know why the other tags failed; however, we suspect most failed because the tags fell off, were rubbed off, or the antennae broke when belugas rubbed against ice, the sea floor, or one another. Henceforth we discuss only those tags that operated for more than five days.

Movement Patterns

After capture and tagging in 1998, the animals moved northeast from Kasegaluk Lagoon paralleling the coast toward Point Barrow. They encountered dense ice for much of the way. There was some movement back toward the southwest but the overall movement was to the northeast. The three whales with functioning tags after July 12 traveled together due north and northeast of Barrow through >90% ice cover (Figure 4-2). They ceased their northward movement in early August just north of 80°N 134°W, approximately 1,100 km north of the Alaskan coast, and turned to the south after remaining near 80°N for five or six days. After turning south, they separated and ranged over a large portion of open water and loose pack ice in the Beaufort Sea and Arctic basin at least until the tags failed, between late August and mid-October.

In 1999, initial movements of the tagged whales were similar to 1998, northeastward from Kasegaluk Lagoon to an area north of Point Barrow by July 20 (Figure 4-3). The immature female (99-2) remained near the shelf break (200m isobath) just north of Barrow (near Barrow Canyon, an underwater canyon that extends from the relatively shallow Chukchi Sea north to the deep waters of the Arctic Ocean.) throughout the summer. One of the males (99-1) moved north and east of Point Barrow into deeper waters and through >90% ice cover to approximately 77°N 126°W, then turned south. The two remaining males (99-3 and 99-4) followed almost the same northern/northeastern route through dense pack ice as was used in 1998. In 1999, the whales turned south at about 79°N after remaining there for approximately four days.

Again, the males ranged over a large portion of the Beaufort Sea during the late summer.

Belugas tagged in 2001 also moved north and east from Kasegaluk Lagoon to an area east of Point Barrow (Figure 4-4). Most of the whales spent July and August along the shelf break between Point Barrow and the Canadian border. In July, several animals (01-1, 01-3 and 01-4) moved north into deeper water, to between 73° N and about 75°N, for excursions that lasted 5 to 6 days, but then returned to the shelf break. Two of those animals also moved east, one (01-4) as far northeast as 76°N, 128°W in mid-September. The summer movements of the tagged animals encompassed much of the offshore areas of the Beaufort Sea. Four whales with tags still functioning moved southwest from the Beaufort Sea into the Chukchi Sea in October. They moved west a considerable distance, into Russian waters, before returning to U.S. waters. Three of the tags continued sending signals into November and early December. At that time, the whales moved south through the eastern portion of Bering Strait. The last signals were received in the Bering Sea north of St. Lawrence Island (Figure 4-4).

In 2002, the initial movements of belugas differed from other years. Instead of moving northeast toward Point Barrow, the animals tended to move to the west before turning north (Figure 4-5). In one case, an immature female (02-1), moved southwest along the coast before turning to the north. She then traveled approximately 900 km to the west before returning east to the shelf break north of Point Barrow. As in 2001, the animals tagged in 2002 tended to stay along the shelf break through the summer. One

animal (02-4), an immature male, made an excursion through dense pack ice (>90%) to 76°N that lasted for several days.

In 2007, the two adult females generally followed a similar pattern to previous years. They moved north from Point Lay and spent the early summer along the shelf break of the western Beaufort and eastern Chukchi seas, including the vicinity of Barrow Canyon. In middle to late summer they ventured north of the shelf break into the northern Beaufort Sea before returning to the Barrow Canyon. Autumn migration toward the south began in early November. The last signals from these two animals were received in early to mid-November.

The adult male (07-1) tagged in 2007 provided more than 17 months (520 days) of location data. His tag sent signals from 1 July 2007 until 4 December 2008. The early summer movements of this whale differed markedly between the two years. In 2007, he spent most of the early summer near Barrow Canyon before moving east in early September. In 2008, he followed a path far to the north, similar to that used by the large males in 1998 and 1999. In early August, he moved to 81°, but only remained there for about two days before returning south. In both years, the whale spent much of late September and early October in the Canadian sector of the Beaufort Sea.

Beluga 07-1 began the southward autumn migration in early November and moved through the Bering Strait in late November, a couple of weeks later than the belugas in 2001. The beluga spent December through March in an area between Bering Strait, the west end of Saint Lawrence Island, and Providenya, Russia. He started moving north again in mid-April but did not venture through the Bering Strait.

Instead, he remained near King Island in the northeastern Bering Sea. In late May, the animal moved north through the strait. Throughout June he was in the Russian sector of the Chukchi Sea before heading toward Barrow. Instead of moving to the coastal waters of Kasegaluk Lagoon, he returned to the Barrow Canyon area near Barrow. Finally in late June he returned to the northern end of Kasegaluk Lagoon.

Movements Relative to Bathymetry, Ice Cover, and Distance Traveled

We did not find any statistical differences ($p > 0.05$) in average water depth at the average daily locations by month (i.e., July, August, September and October) between males and females, even when controlling for age (i.e., adult vs. immature). Average water depth for adult males ranged from 1407 to 1996 m, and for adult females from 98 to 2420 m (Table 4-2). Immature males were found in water depths averaging 573 to 1292 m and for immature females from 423 to 1083 m. Whale 07-1 was the only animal that we were able to track over an entire year. Figure 4-6 shows how the average water depth at the average daily locations for this animal was relatively shallow most of year because it was in the relatively shallow Chukchi and northern Bering seas. During August, September, and October, however, the whale was in the deeper waters of the Arctic Basin.

Ice cover was greater than 90% for many of the beluga locations in late June and early July. For the whales that traveled into the northern Beaufort Sea and Arctic Ocean, ice cover was also frequently 90% or greater. Several whales penetrated up to 1,100 km into ice of this density. The pack ice melts and retreats to the north during the

summer, typically reaching its northernmost retreat in late September or early October. In 1998, 2002, and 2007 ice retreat was among the most extreme ever observed, while 1999 and 2001 were closer to average. Figures 4-2 to 4-5 show ice concentrations in mid-July and early September along with beluga locations throughout the summer in each year. It is unknown how the extent of ice retreat in August and September affected beluga movements; however, movements in June and July did not seem to be limited by ice as it covered most of the areas of the Beaufort Sea and northern Chukchi Sea that were used by tagged belugas.

We compared distance between average daily locations of males with females, controlling for month and age. With the exception of a comparison of adult males and females in September, we found no differences in average daily travel distance between males and females (Table 4-3; $p > 0.05$).

DISCUSSION

Movements and Distribution

Most belugas move into shallow coastal or estuarine waters during at least a portion of the summer (Caron and Smith 1990; Frost and Lowry 1990). These summer concentration areas are consistently used from year to year and the waters are usually brackish and relatively warm. The reasons for occupying coastal areas are not completely known but may include feeding (Frost et al. 1983; Seaman et al. 1988; Huntington et al. 1999), calving (Sergeant 1973; Fraker et al. 1979; Brodie et al. 1981), and molting (St. Aubin et al. 1990). Coastal areas may also provide a thermal

advantage to adults and particularly neonates (Sergeant and Brodie 1969; Fraker et al. 1979). Eastern Chukchi Sea belugas move into coastal areas along Kasegaluk Lagoon in late June and animals are sighted in the area until about mid-July (Frost and Lowry 1990, Frost et al. 1993). The absence of substantial stomach contents in belugas killed in the subsistence hunt suggests feeding is not the major reason for their presence near Kasegaluk Lagoon (Suydam, unpublished data). Frost et al. (1993) suggested that belugas likely congregate near Kasegaluk Lagoon to molt. Some of the largest gravel beds along the Chukchi Sea coast are located near the passes of Kasegaluk. Belugas often occur very near shore (sometimes only a few meters from shore) in these areas and stir up bottom sediments, possibly from rubbing to slough off old skin. The warmer, low saline water exiting the lagoons may facilitate the molting process. Belugas with both “old skin” and “new skin” are taken in the Point Lay hunt.

Prior to this study, the actual movements of eastern Chukchi Sea belugas, after they left the Kasegaluk Lagoon area, were unknown. Initial movements of the whales we tagged were as expected. Frost and Lowry (1990) noted that sightings of belugas in ice-free waters along the Chukchi Sea coast tended to occur progressively from south to north. Our results fit those observations as the belugas generally moved from the south to the north.

Movements of tagged belugas, after the initial northeastward movement, were unexpected in some cases. This is especially true for the adult males that moved to 80° or 81° north. They reached their northernmost locations by late July or early August, similar to whales of the Beaufort Sea stock that were tagged from 1993-1997 in the

Mackenzie River Delta (Richard et al. 2001b). By late summer, many of the females and immature animals moved east into the central and eastern Beaufort Sea. One individual was recorded within 100 km of Banks Island in the Canadian Arctic Archipelago in September. This was unanticipated. We presumed that these waters were the domain of the larger eastern Beaufort Sea stock, which summers in the Mackenzie Delta, the eastern Beaufort Sea and adjacent waters of the Canadian Arctic Archipelago (Richard et al., 2001a). The use of deep, offshore, ice-covered habitats during the summer was also unexpected. Other researchers showed that belugas migrated through deep, offshore habitats during the summer but tended to remain in coastal waters, bays and estuaries, although occasionally moving into deep offshore waters (Smith and Martin, 1994; Richard et al. 2001a, b). Our results show that belugas from the eastern Chukchi Sea consistently use deep, ice-covered, offshore areas after leaving the northeastern Chukchi Sea in mid-summer.

The reasons for the observed movements far to the north are unknown. Movements of the three animals in 1998 and two animals in 1999 were direct and coordinated, possibly indicating prior knowledge of a resource. Belugas may move north to exploit an abundant food resource (Martin and Smith 1992; Smith and Martin 1994; Richard et al 2001b). One such resource, arctic cod (*Boreogadus saida*), can occur in dense patches and is important prey of many marine mammals in the Arctic (Frost and Lowry 1981; Lowry and Frost 1981; Welch et al., 1993). To our knowledge there are no available data on the distribution or abundance of arctic cod or other beluga food items so far north. However, there are oceanographic studies that showed

a surface front at approximately 80° N between 130° and 150°W (Timmermans et al. 2008) and possible eddies that advect Pacific water into the Arctic Ocean (Spall et al. 2008, Timmermans et al. 2008). These oceanographic features could concentrate the belugas' prey.

During autumn migration, belugas tagged in the eastern Beaufort Sea mostly moved west along the shelf break of the Beaufort Sea, although some migrated far north of the shelf break through heavy ice near 75° N (Richard et al. 1997, 1998b, 2001b). Aerial surveys confirm the importance of shelf break habitat for belugas in the Beaufort Sea during autumn migration (Moore et al. 2000). It is unclear why the shelf break is important for migrating belugas. Perhaps they forage during migration. Stomachs of spring migrating belugas, taken in the hunt at Point Hope, often contained food items (Suydam, unpublished data). Whales may also forage during autumn migration.

The westward autumn migration of the eastern Beaufort Sea stock begins in late August to mid-September (Richard et al., 1997, 1998b, 2001b) with whales moving as far west as Russian waters by mid- to late September. Those whales may remain near Wrangel Island for weeks before moving south into the Bering Sea mainly starting in October (Richard et al. 2001b). Whales occasionally remained in certain areas for periods of days, weeks or even a month, possibly to feed (Richard et al. 1998a). By contrast, the whales we tagged initiated autumn migration out of the Beaufort Sea in October or November, much later in the year than eastern Beaufort Sea belugas. Belugas of the eastern Beaufort Sea stock appear to migrate past whales from the

eastern Chukchi Sea stock someplace in the mid-Beaufort Sea region. During June, July and part of August it is likely that the ranges of these two stocks do not overlap much. In August and later in the year, eastern Chukchi Sea and eastern Beaufort Sea belugas may occur in similar places at similar times, assuming that the relatively small sample sizes over a few years of tagging are representative of typical movement patterns. The significance of the apparent overlap or mingling of these two stocks in early fall is uncertain, particularly since studies of mitochondrial DNA clearly indicate the two stocks are genetically discrete (O’Corry-Crowe et al. 1997, 2002).

Gender and age-related differences in movements

Loseto et al. (2006) modeled habitat selection of eastern Beaufort Sea belugas based on data collected during satellite tagging studies of Richard et al. (2001b). Their results showed that the large adult males selected areas with dense ice cover, females with calves and smaller males selected open-water habitats near shore, and smaller males and females with older calves selected ice edge habitats. Habitat segregation between adult males and females and young may be driven by body size dimorphism in relation to different resource demands related to size (Ruckstuhl and Neuhaus 2002, Bowyer 2004, Loseto et al. 2006). We have not yet modeled habitat selection for eastern Chukchi Sea belugas but our results qualitatively align with those of Loseto et al. (2006). Although not statistically significant, our tagged adult males appeared to use deeper waters farther to the north than females and immature animals. Increased

sample size will help to better understand habitat selection of the eastern Chukchi Sea whales.

The behavior of the eastern Chukchi Sea stock of belugas may parallel that of another but much larger odontocete, the sperm whale (*Physeter catodon*). Large male sperm whales tend to occur at higher latitudes than females and immature animals except during the mating season when large males will accompany females groups (Whitehead 1993, Whitehead and Weilgart 2000). Males are larger than females in both sperm and beluga whales. The larger body sizes of male belugas may enable them to better exploit ice-covered waters than can females and young (Martin and Smith 1999). Larger animals should be able to dive deeper and longer than smaller ones, thus providing more security for finding openings in the ice for breathing and for accessing prey resources.

Movements in relation to ice and bathymetry

Ice influences the movements and distribution of marine mammals, including beluga whales (Fay 1974). Belugas are frequently associated with sea ice (Frost and Lowry 1990; Moore et al. 2000). The association with ice was typically thought to be weakest in summer (Hazard 1988). This perception was probably due to the limited ability to collect data using traditional visual methods. Observing belugas in broken ice or ice-cover greater than 90% is difficult, at best. The use of satellite telemetry has allowed new insights into beluga's association with and penetration of pack ice.

Some of the belugas we tagged penetrated deep into the pack ice of the northern Beaufort Sea and adjacent southern Arctic Ocean. Belugas tagged in the Mackenzie Delta of the eastern Beaufort Sea also penetrated deep into the ice, especially between the islands of the western Canadian Archipelago (Richard et al. 2001b). In both these studies, ice-cover was often greater than 90%; however, during summer when belugas are present the ice is in motion and cracks form as it melts and shifts. The relatively warm summer temperatures keep that open water from freezing quickly. Movement of the ice in combination with warm temperatures should allow belugas to easily find breathing holes in the pack ice, and the movements of the belugas tagged in this study and that of Richard et al. (2001b) strongly suggest that ice-cover in the Beaufort Sea and Arctic Ocean does not limit movements of larger adults and possibly smaller animals during the summer.

Other stocks of belugas are apparently more restricted by ice. In the high Canadian Arctic, ice between islands blocks movements of belugas (Smith and Martin 1994; Richard et al. 2001a). Ice behaves differently between islands and in fjords than in an ocean basin. In the open ocean, ice is usually in motion. As it moves, cracks, leads, or polynyas form providing belugas access to the ocean surface to breath. Ice between islands or in fjords does not move or shift as readily. Therefore, there may be a greater risk of entrapment to belugas that penetrate ice in narrow passages between landmasses than on the open ocean. Entrapments of belugas have occurred in areas other than between islands or in fjords, but usually only when rapid extreme freezing conditions exist (e.g. air temperatures are very low and there is no wind) (Burns

and Seaman 1986; Siegstad and Heide-Jørgenson 1994). When the sea surface freezes quickly and ice becomes stationary belugas may become entrapped and are easily hunted by humans or preyed upon by polar bears (*Ursus maritimus*; Burns and Seaman 1986; Lowry et al. 1987; Siegstad and Heide-Jørgenson 1994; Heide-Jørgenson et al. 2002). Ice did not generally restrict movements of the larger belugas we tracked in the Arctic Ocean during the summer.

Information from tagging studies has dramatically changed our understanding of habitat use, distribution and movements of belugas. Prior to satellite tagging efforts, few would have suggested that belugas regularly use the deep offshore waters of the northern Beaufort Sea and Arctic Ocean to any great extent except perhaps during migration. Most observations showed that these whales used the shelf waters (Frost and Lowry 1990) or the shelf break (Moore et al. 2000). It is now clear that many of the belugas tagged in the eastern Beaufort and the eastern Chukchi seas do not remain in shallow, nearshore waters but travel hundreds of kilometers to the north through heavy pack ice, presumably to feed. While there, they often dive to depths exceeding 400 m (Martin et al. 1998; Martin and Smith 1999; unpublished data this study). Those that do not move into deep, ice covered waters mostly remain near the shelf break, which is approximately 50 to 100 km north of the coast of Alaska, and make dives of 100-300 m (Moore et al. 2000).

Tag attachments and longevity

The attachment technique we used likely leaves lifelong scars but appears to have inconsequential, long-term impact on tagged belugas. Orr et al. (1998) reported recaptures and observations of three belugas previously tagged with SDRs, similar to those we deployed. They speculated, based on scarring patterns, that the nylon pins migrated out of the dorsal ridge leading to release of the transmitter and loss of signals. The three belugas they observed showed no sign of infection or excessive scarring. In 1999, Point Lay hunters harvested one of the belugas we tagged in 1998 (98-5, Figure 4-7). This was later confirmed by genetic analysis (G. O’Corry-Crowe, unpubl. data). This beluga was driven into the lagoon on 26 June in 1998 and on 30 June in 1999. The animal was obviously scarred but with no apparent adverse impacts. The scars appeared to be healed. Based on the scarring pattern on this beluga, it appeared that the pins at the anterior end of the tag had migrated out of the dorsal ridge first followed by the posterior pins at some later date.

Other studies of belugas had tag longevity that lasted up to 129 days (Smith and Martin 1994, Richard et al. 2001a,b). Longevity of the tags we applied was 5 to 520 days, was mostly similar to that experienced in other studies of beluga whales, with one exception. The tag on beluga 07-1 lasted for more than 17 months.

The longevity of the tags appears to be limited by the attachment technique and not battery power (Richard et al., 2001a). The nylon pins holding the tag onto the beluga eventually migrate out of the blubber and skin of the dorsal ridge and the tag falls off (Orr et al., 1998). The tag on beluga 07-1 was smaller than the earlier tags and

we used thin cable to attach the transmitters instead of belting as was used in 1998 and 1999. The smaller transmitters, cabling instead of belting, and placement just anterior to the dorsal ridge likely contributed to the increasing longevity of beluga tags.

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Table 4-1. Beluga whales instrumented with tags at Point Lay, Alaska in 1998, 1999, 2001, 2002, and 2007.

ID #	Capture Date	Sex	Age class	Color	Length (cm)	PTTID	PTT Type	Last Date	Tag Duration (days) ¹
1998									
98-1	26 June	Male	Adult	White	440	11035	Saddle	8 July	13
98-2	28 June	Male	Adult	White	432	2284	Saddle	12 July	15
98-3	29 June	Male	Adult	White	398	11036	Saddle	10 October	104
98-4	29 June	Male	Adult	White	415	2285	Saddle	28 September	92
98-5	1 July	Male	Adult	White	414	2282	Saddle	29 August	60
1999									
99-1	30 June	Male	Adult	White	418	11035	Side mount	24 September	87
99-2	30 June	Female	Imm. ²	Gray	266	11036	Side mount	18 September	81
99-3	30 June	Male	Adult	White	424	11037	Saddle	25 August	57
-----	30 June	Male	Adult	White	441	11039	Saddle	4 July	5
99-4	30 June	Male	Adult	White	424	11041	Saddle	22 September	85
2001									
01-1	3 July	Male	Adult	White	381	2093	Spider	9 August	38
01-2	3 July	Female	Adult	White	359	2094	Spider	21 July	19
01-3	5 July	Female	Imm.	Gray	316	11038	Side mount	28 November	147
01-4	5 July	Male	Imm.	Gray	324	11041	Side mount	5 December	154
01-5	5 July	Female	Imm.	Gray	335	2280	Side mount	22 October	110
01-6	7 July	Male	Adult	White	340	11037	Spider	16 November	133
01-7	7 July	Male	Imm.	Lt. Gray	320	2281	Side mount	23 July	17
01-8	7 July	Male	Adult	White	373	2282	Saddle	12 August	37
2002									
02-1	7 July	Female	Imm.	Gray	320	11036	Spider	13 September	69
-----	7 July	Female	Adult	White	368	11042	Side mount	11 July	5
02-2	7 July	Male	Imm.	Gray	276	11044	Spider	29 September	85
02-3	7 July	Male	Imm.	Gray	274	2090	Side /SPOT	5 September	61
02-4	8 July	Male	Imm.	Gray	267	2088	Side mount	12 September	67
2007									
07-1	1 July	Male	Adult	White	430	22149	Spider	3 Dec. 2008	520
07-2	1 July	Female	Adult	White	386	77015	Spider	12 November	135
07-3	1 July	Female	Adult	White	398	36516	Spider	4 November	127

¹ Tag duration = the number of days from tag attachment to the last reception of a good location that passed data screening.

² Imm. = classified as immature based on color and length.

Table 4-2. Average water depth (SE; n) at the average daily location by month for adult and immature belugas from the eastern Chukchi Sea stock.

Sex/Age	July	Aug	Sep	Oct
Males				
Adults	-1407 (260; 12)	-1695 (412; 10)	-1996 (412; 6)	-1641 (920; 3)
Immature	-979 (491; 5)	-573 (281; 4)	-1292 (437; 3)	
Females				
Adult	-98 (37; 3)	-739 (45; 2)	-2420 (631; 2)	-1237 (740; 2)
Immature	-690 (322; 4)	-423 (155; 4)	-1083 (196; 4)	-165 (25; 2)

Table 4-3. Average distance (km) traveled (SE; n) between average daily locations by month for adult and immature belugas from the eastern Chukchi Sea stock.

Sex/Age	July	Aug	Sep	Oct
Males				
Adults	53.1 (6.5; 12)	59.9 (9.7; 10)	66.6 (7.6; 6)	73.8 (21.9; 3)
Immature	37.0 (8.5; 5)	49.5 (8.3; 4)	43.8 (16.5; 3)	
Females				
Adult	46.9 (12.2; 3)	76.1 (8.9; 2)	115.3 (12.5; 2)	58.1 (3.9; 2)
Immature	42.0 (6.3; 4)	58.5 (8.9; 4)	58.7 (19.0; 4)	79.8 (6.6; 2)



Figure 4-1. Configurations of satellite data recorders deployed on beluga whales in the eastern Chukchi Sea in 1998, 1999, 2001, 2002, and 2007. Upper panel: saddle tag. Middle panel: side mount. Lower panel: spider tag.

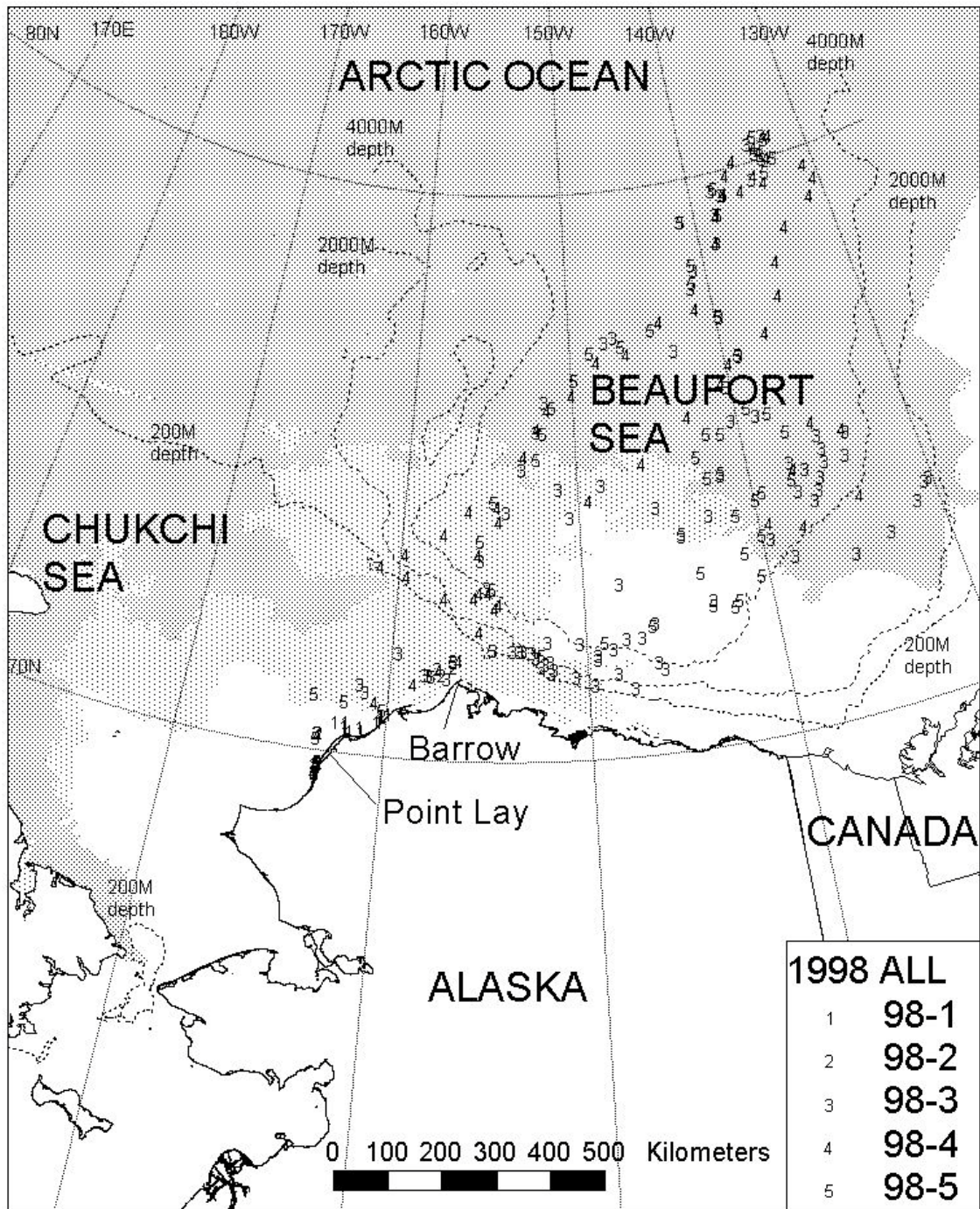


Figure 4-2. Locations of beluga whales satellite tagged at Point Lay, Alaska, 8 July-10 October 1998. Light stippling is $\geq 30\%$ ice cover on 16 July, dark stippling is $\geq 30\%$ ice cover on 4 September.

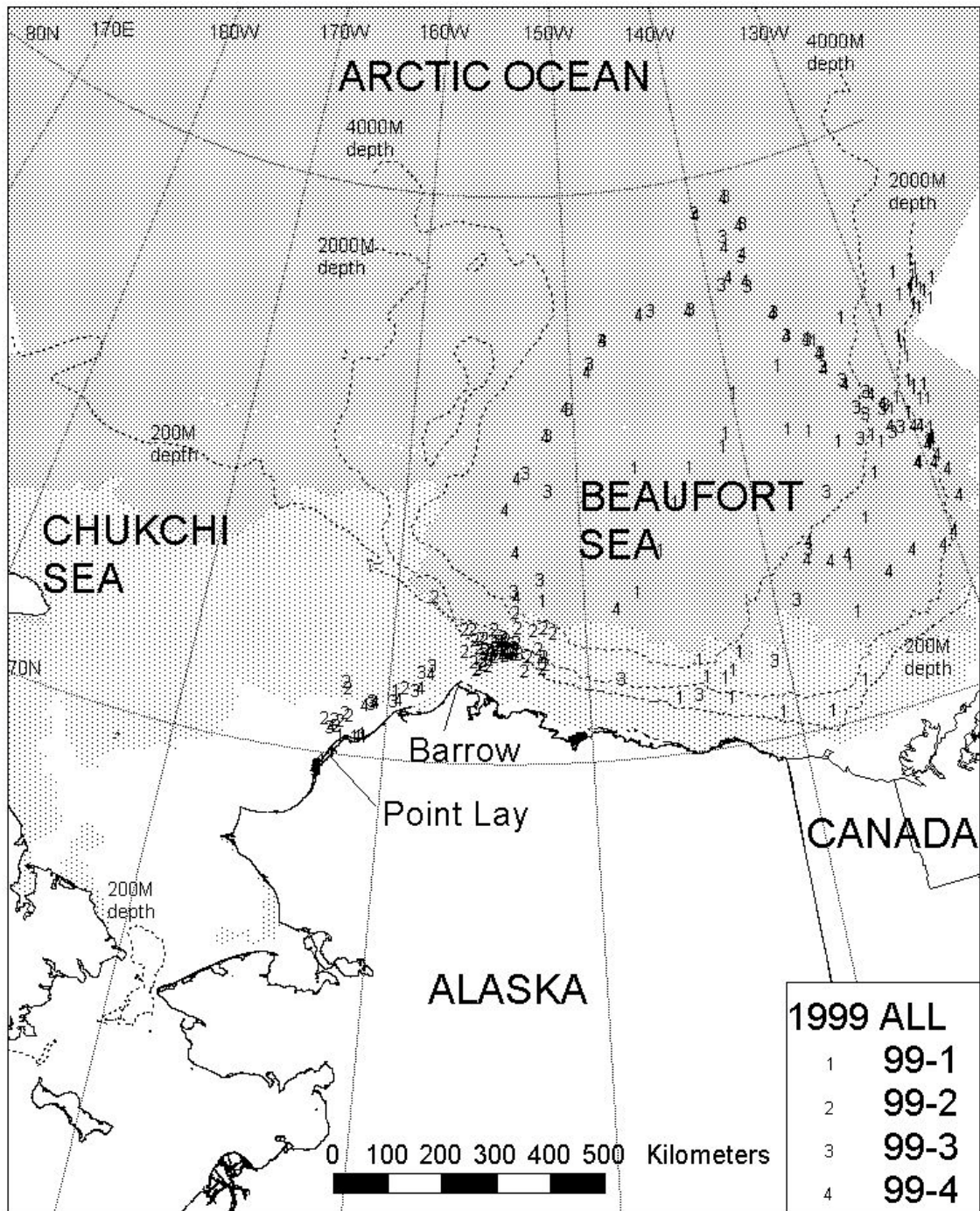


Figure 4-3. Locations of beluga whales satellite tagged at Point Lay, Alaska, 30 June-24 September 1999. Light stippling is $\geq 30\%$ ice cover on 16 July, dark stippling is $\geq 30\%$ ice cover on 4 September.

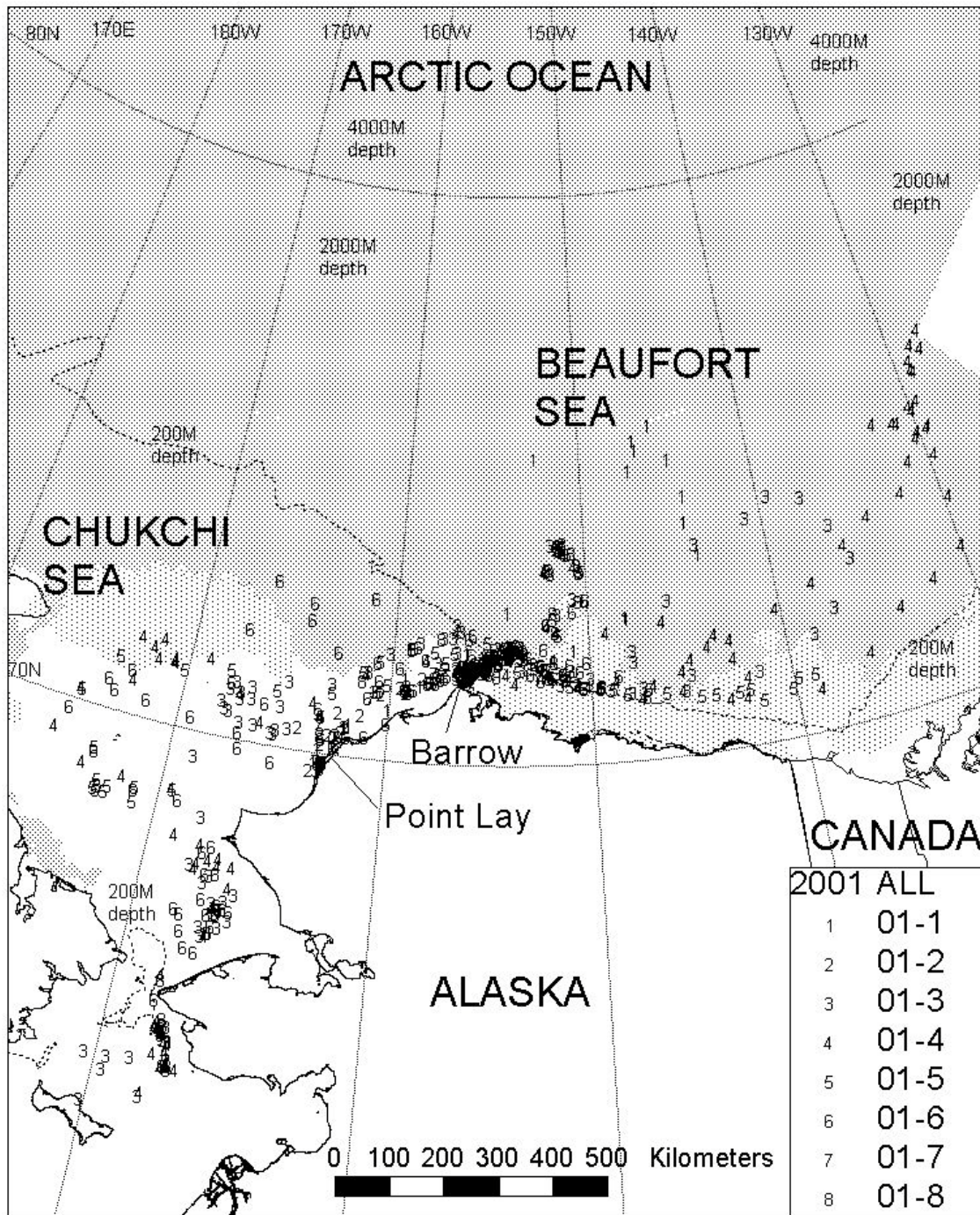


Figure 4-4. Locations of beluga whales satellite tagged at Point Lay, Alaska, 3 July-5 December 2001. Light stippling is $\geq 30\%$ ice cover on 13 July, dark stippling is $\geq 30\%$ ice cover on 10 September.

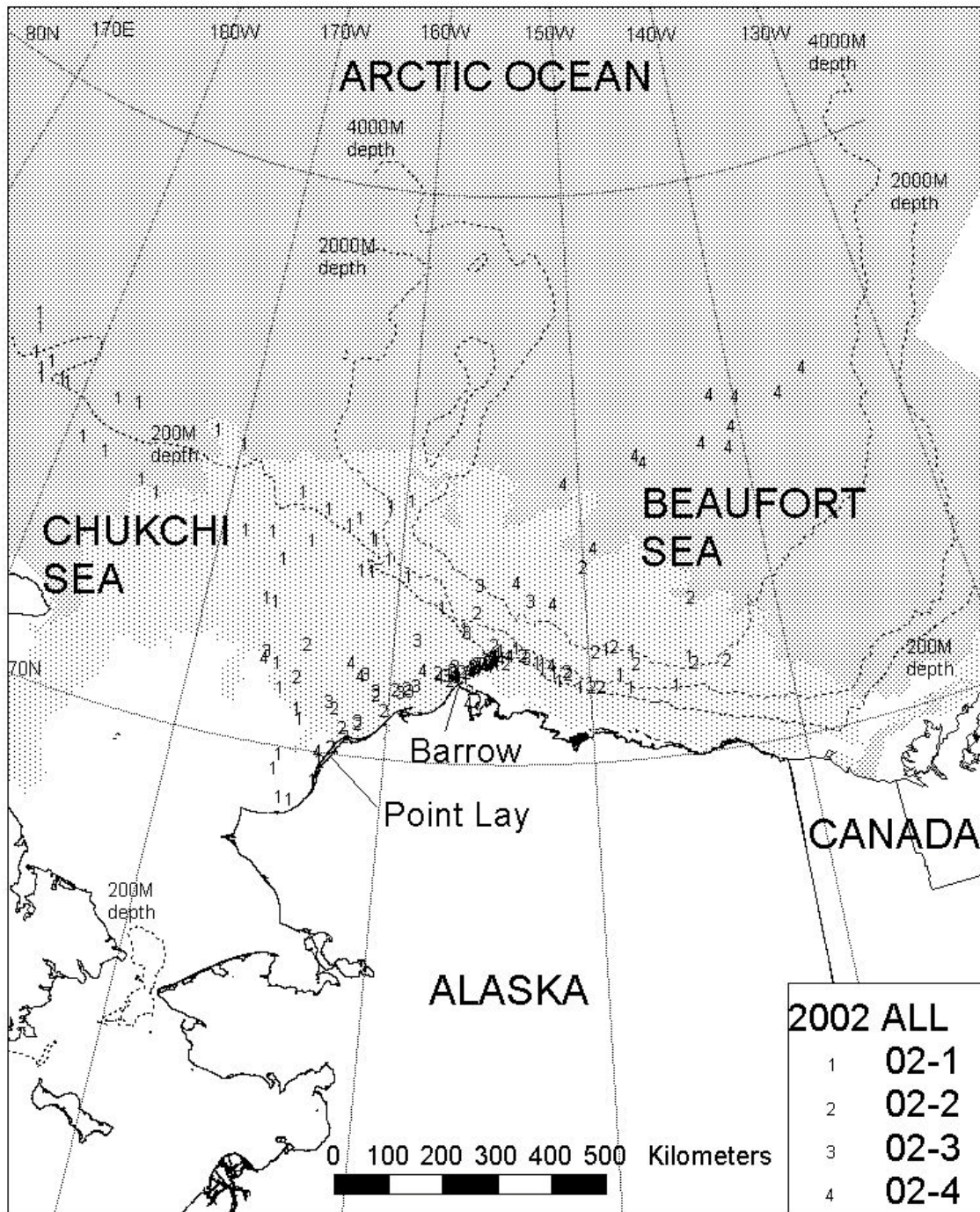


Figure 4-5. Locations of beluga whales satellite tagged at Point Lay, Alaska, 7 July-29 September 2002. Light stippling is $\geq 30\%$ ice cover on 15 July, dark stippling is $\geq 30\%$ ice cover on 2 September.

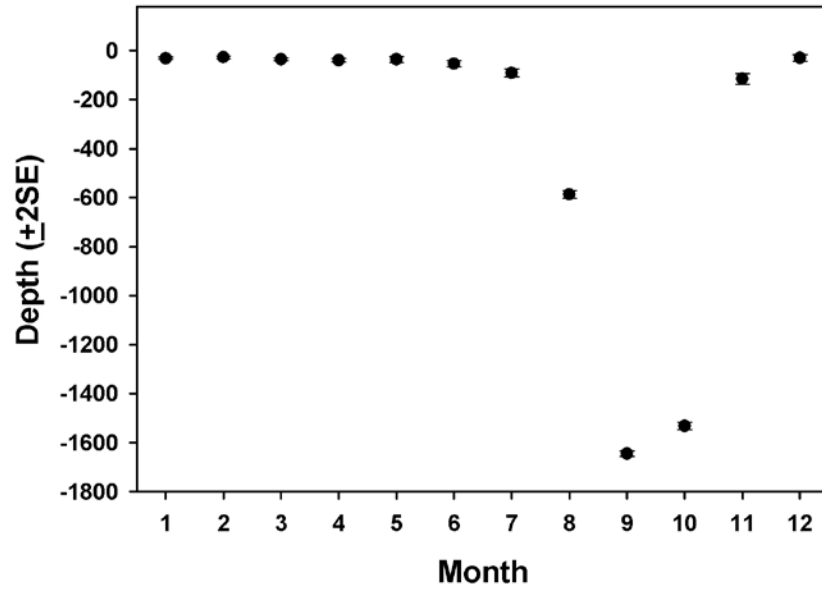


Figure 4-6. Average water depth (m) at average daily location, by month, for beluga 07-1.

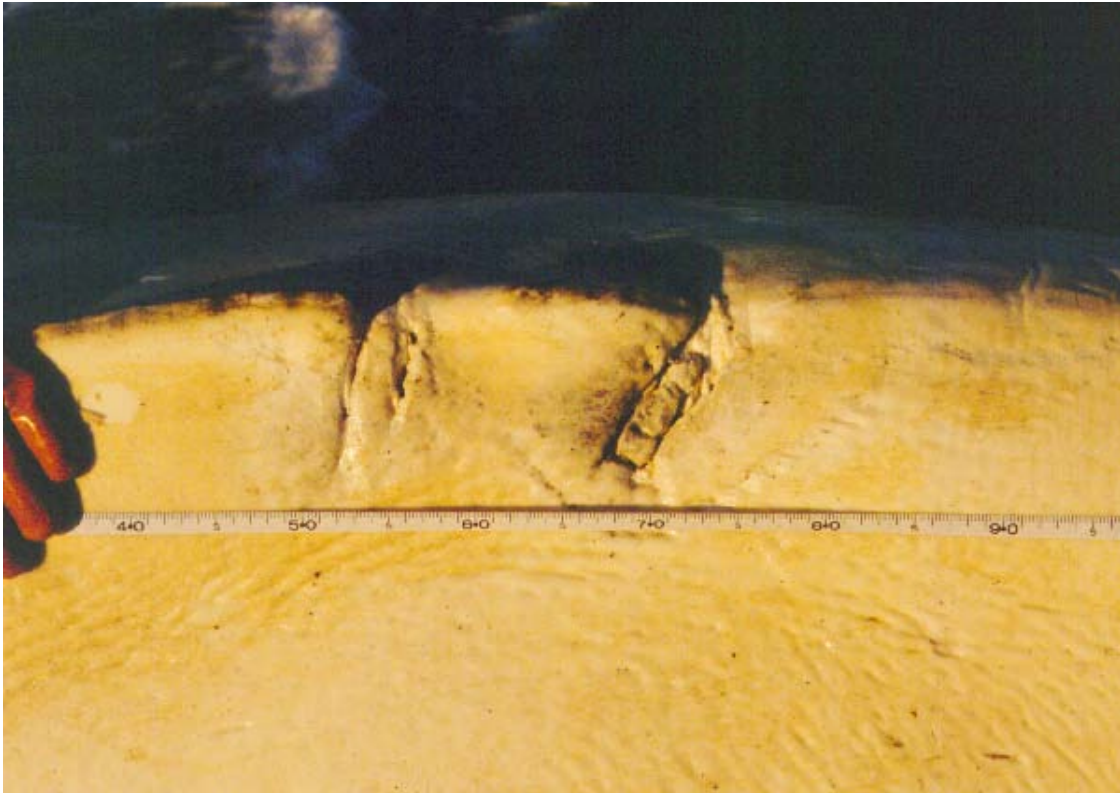


Figure 4-7. Scars on the dorsum of a beluga at a transmitter attachment site. The head is toward the left in the photo and the tail to the right. This animal was taken in a subsistence hunt at Point Lay, Alaska on 30 June 1999 and had been tagged on 29 June 1998.

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