ARCTIC
VOL. 70, NO. 3 (SEPTEMBER 2017) P. 273–286
https://doi.org/10.14430/arctic4667

Aerial Survey Estimates of Abundance of the Eastern Chukchi Sea Stock of Beluga Whales (*Delphinapterus leucas*) in 2012

Lloyd F. Lowry,[1] Michael C.S. Kingsley,[2] Donna D.W. Hauser,[3] Janet Clarke[4] and Robert Suydam[5]

(*Received 5 October 2016; accepted in revised form 1 May 2017*)

ABSTRACT. The eastern Chukchi Sea (ECS) stock of beluga whales is one of three stocks in western Alaska that are co-managed by the National Marine Fisheries Service and the Alaska Beluga Whale Committee. Abundance of this stock was estimated as 3710 in 1991 from incomplete data. Analysis of data from satellite-linked time-depth recorders (SDRs) attached to belugas in summer concentration areas of the ECS and Beaufort Sea (BS) stocks provided an overview of beluga distribution and movements and allowed the identification of an area (140˚ W to 157˚ W in the BS) and a time period (19 July–20 August) in which the distributions of the two stocks do not overlap. Aerial survey data were collected by the Aerial Surveys of Arctic Marine Mammals (ASAMM) project in that region and time period in 2012. We used those data in a line transect analysis that estimated there were 5547 (CV = 0.22) surface-visible belugas in the study area. Data from SDRs were used to develop correction factors to account for animals that were missed because they were either outside of the study area or diving too deep to be seen, resulting in a total abundance estimate of 20 752 (CV = 0.70). The average annual Alaska Native subsistence harvest from the ECS stock (57) is about 0.3% of the population estimate. Without data collected by the ASAMM project and from satellite-linked tags, this analysis would not have been possible. Additional surveys and tagging of ECS belugas are warranted.

Key words: Arctic; Alaska; Chukchi Sea; Beaufort Sea; beluga whales; *Delphinapterus leucas*; aerial surveys; line transect; abundance; survey correction factors; satellite-linked tags

RÉSUMÉ. Le stock de bélugas de l'est de la mer des Tchouktches (EMT) figure parmi les trois stocks de l'ouest de l'Alaska à être gérés conjointement par le National Marine Fisheries Service et l'Alaska Beluga Whale Committee. À partir de données incomplètes, l'abondance de ce stock a été estimée à 3 710 en 1991. L'analyse des données recueillies à l'aide d'enregistreurs de profondeur temporelle satellitaires (SDR) fixés aux bélugas dans les zones de concentration estivales de l'EMT et de la mer de Beaufort (MB) a permis d'obtenir un aperçu de la répartition et du déplacement des bélugas ainsi que de cerner une zone (de 140˚ O à 157˚ O dans la MB) et une période (du 19 juillet au 20 août) pour lesquelles la répartition des deux stocks ne se chevauchent pas. Le projet Aerial Surveys of Arctic Marine Mammals (ASAMM) a permis de recueillir des données à partir de levés aériens pour la région et la période concernées en 2012. Grâce à une analyse de lignes interceptées, ces données ont permis d'estimer qu'il y avait 5 547 (CV = 0,22) bélugas visibles à la surface dans la zone à l'étude. Les données en provenance de SDR ont servi à mettre au point des facteurs de correction pour tenir compte des bélugas qui n'ont pas été captés, soit parce qu'ils se trouvaient en dehors de la zone visée par l'étude, soit parce qu'ils plongeaient trop loin pour être vus, ce qui s'est traduit par une estimation totale d'abondance de 20 752 (CV = 0,70) bélugas. La prise de subsistance annuelle moyenne de stock (57) par les Autochtones de l'Alaska dans l'EMT correspond à environ à 0,3 % de l'estimation de la population. Cette analyse n'aurait pu être possible sans les données prélevées par le projet ASAMM et les SDR. D'autres levés et l'étiquetage des bélugas de l'EMT s'imposent.

Mots clés : Arctique; Alaska; mer des Tchouktches; mer de Beaufort; bélugas; *Delphinapterus leucas*; levés aériens; ligne interceptée; abondance; facteurs de correction de levés; étiquettes satellitaires

Traduit pour la revue *Arctic* par Nicole Giguère.

---

[1] University of Alaska Fairbanks, 73-4388 Paiaha Street, Kailua Kona, Hawaii 96740, USA; llowry@hawaii.rr.com
[2] Rua Principal 191, PO Box 3, 3300-357 Sao Martinho da Cortica, Portugal; deceased
[3] Polar Science Center, Applied Physics Laboratory, University of Washington, 1013 NE 40th Street, Seattle, Washington 98105, USA
[4] Leidos, Inc., 4001 N. Fairfax Drive, Arlington, Virginia 22203, USA
[5] North Slope Borough, Department of Wildlife Management, Box 69, Barrow, Alaska 99723, USA
© The Arctic Institute of North America

INTRODUCTION

At least four stocks of beluga whales (*Delphinapterus leucas*) occur in waters of northern and western Alaska. These stocks were initially identified on the basis of traditional summering areas (Frost and Lowry, 1990) and later confirmed with genetic analysis (O'Corry-Crowe et al., 1997, 2002) and satellite-linked telemetry (Hauser et al., 2014; Citta et al., 2016a, b; Alaska Beluga Whale Committee, unpubl. data). Whales from western and northern Alaska may migrate through Alaskan, Canadian, and Russian waters, including areas in Alaska and Canada that have been leased for oil and gas activities. Concerns about potential effects of offshore oil and gas exploration and development on beluga whales exist at local, national, and international levels (Suydam et al., 2005; Reeves et al., 2014). Potential effects of climate change are also of concern (Laidre et al., 2008, 2015; Kovacs et al., 2011).

Two of these beluga stocks, the Beaufort Sea (BS) and the eastern Chukchi Sea (ECS) stocks, occur seasonally in the Bering, Chukchi, and Beaufort Seas (Hauser et al., 2014). Beluga whales of the BS stock winter in the Bering Sea and migrate north and east through leads in the spring sea ice in April and May to their summering areas in and offshore of the Mackenzie River Delta. They return west through the BS in September and October (Richard et al., 2001). Beluga whales of the ECS stock also winter in the Bering Sea, are commonly seen in northwestern Alaska near Kasegaluk Lagoon in early summer (Frost and Lowry, 1990), then range widely in the CS and BS in later summer and fall (Suydam et al., 2001, 2005). The coastal congregation areas of these two stocks, along the CS coast near Kasegaluk Lagoon and in the Mackenzie Delta region of the BS, are separated by about 1000 km, but the areas used may overlap at other times of year (Hauser et al., 2014).

Until relatively recently, little information about the ECS stock was available. Whales apparently have been using the Kasegaluk Lagoon region during summer for many years, as Warren Neakok, an Inupiat elder, described hunting them there in about 1930 (Neakok et al., 1985). More recent local knowledge indicates continuing regular use of this part of the Alaska coast (Huntington et al., 1999; Suydam, 2009). Scientific studies did not begin in the area until the late 1970s, when concerns about offshore oil and gas development caused the Outer Continental Shelf Environmental Assessment Program (OCSEAP) and the Minerals Management Service (MMS—now referred to as the Bureau of Ocean Energy Management, BOEM) to sponsor research on beluga food habits (Seaman et al., 1982), reproduction (Burns and Seaman, 1986), and distribution and abundance (Frost and Lowry, 1990) in western Alaska. When it became clear that a large number of belugas appeared each summer near Kasegaluk Lagoon, specific studies began to target that region (Frost et al., 1993; Suydam, 2009).

The Alaska Beluga Whale Committee (ABWC) was formed in 1988 to conserve beluga whales and manage beluga subsistence hunting in western Alaska in cooperation with the National Oceanic and Atmospheric Administration (NOAA) (Adams et al., 1993; Fernandez-Gimenez et al., 2006). One of the ABWC's first scientific objectives was to estimate the abundance and trends of western Alaska beluga stocks. Population abundance has been estimated for the Bristol Bay and eastern Bering Sea stocks (Lowry et al., 2008, 2017; Allen and Angliss, 2014). Abundance of the BS stock is studied by Canadian researchers (e.g., Harwood and Kingsley, 2013). Determining abundance of the ECS stock, with early efforts centered on the known coastal concentration area near Kasegaluk Lagoon, has been problematic (Frost et al., 1993). Surveys conducted in 1996–98 found belugas in the nearshore areas previously surveyed, but also detected groups of whales farther offshore (Lowry et al., 1999). Subsequent survey efforts in 2002–03 included more offshore flight lines, but while belugas were occasionally sighted more than 50 km offshore, sightings were very infrequent (Lowry et al., 2002, 2003). Because of the high cost of aerial surveys and the lack of progress on population assessment, beluga-specific surveys in the CS were suspended by the ABWC after 2003.

In 1998, the ABWC, in conjunction with the village of Point Lay and the North Slope Borough Department of Wildlife Management, began capturing belugas at Kasegaluk Lagoon and instrumenting them with satellite-linked time-depth recorders (SDRs) (Suydam et al., 2001, 2005; Suydam, 2009). Between 1998 and 2012, 27 belugas were tracked as they left the Lagoon and moved about in the CS and BS. Results showed that while ECS belugas used relatively large areas in the summer and fall, their core use areas did not overlap with those of the BS stock in July and August (Hauser et al., 2014).

Aerial surveys, focused particularly on bowhead whales (*Balaena mysticetus*) but including other marine mammals, have been flown in northern Alaska for decades, initially with support provided by OCSEAP and MMS. Since 2008, systematic surveys (now called Aerial Surveys of Arctic Marine Mammals, ASAMM) supported by BOEM and operated by NOAA, have covered both the northeastern CS and most of the western BS, including much of the area used by ECS belugas, each year during July–October. In this paper we use data collected during the ASAMM surveys in 2012 (Clarke et al., 2013) to develop an abundance estimate for the ECS beluga stock.

METHODS

Study Design and Execution

As noted above, ABWC aerial survey efforts in 1996–98 and 2001–03 focused on the CS during the time when ECS belugas were using nearshore areas, but those efforts

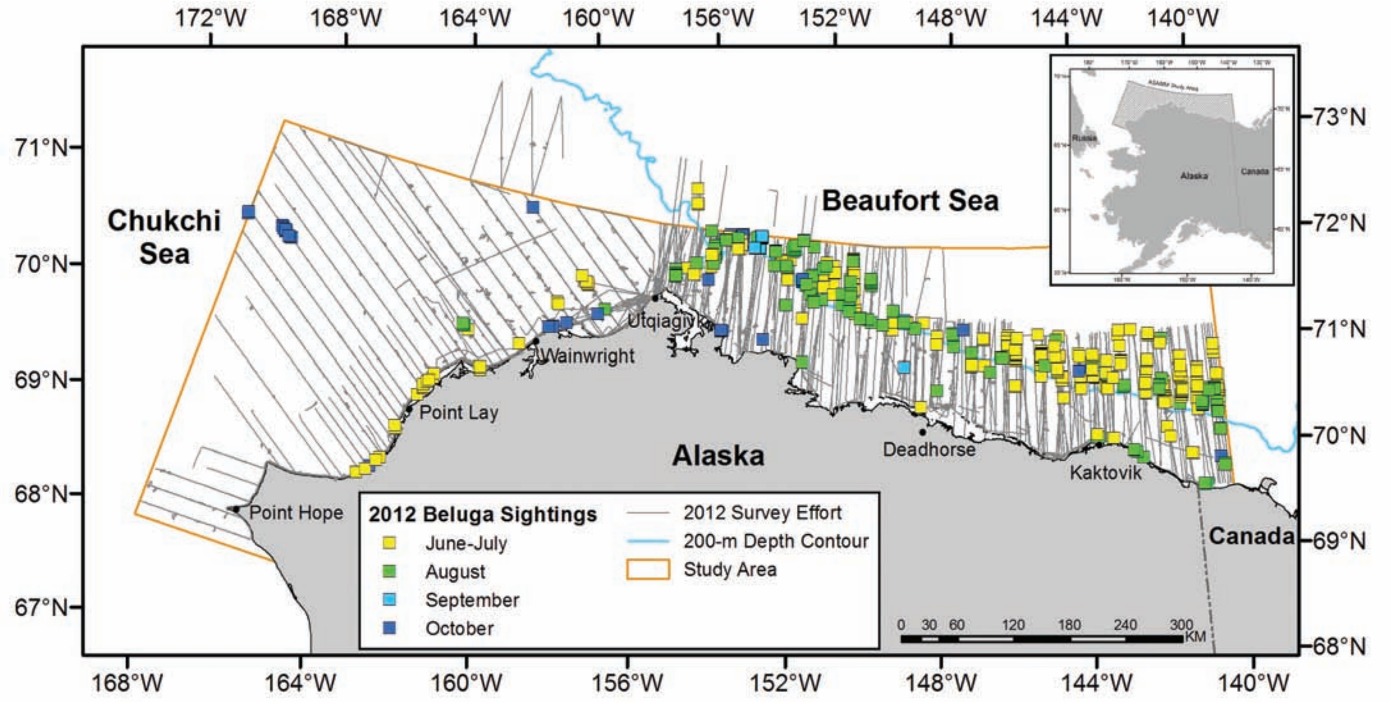

FIG. 1. ASAMM beluga sightings plotted by month, including transect, search, and circling effort, June–October 2012.

were not successful at covering the offshore distribution indicated by the satellite-linked tags. However, ASAMM surveys flown in 2008–11 in the CS (previously called Chukchi Offshore Monitoring in Drilling Area) and BS (previously called Bowhead Whale Aerial Survey Project) made numerous sightings of belugas in the region used by the ECS stock (Clarke et al., 2012). An agreement was made between the ABWC, ASAMM investigators, and their funding sources (BOEM and NOAA) to use a subset of ASAMM data collected in 2012 to investigate its utility for estimating ECS beluga stock abundance. Anticipating that many belugas might be offshore in the CS early in the survey period, the ABWC provided funding for the ASAMM research team to fly additional survey lines in that area (Clarke et al., 2013).

The survey was a visual transect survey with onshore-offshore transects covering a study area of approximately 230 000 km^2, between 68˚ and 72˚ N latitude and from 140˚ W to 169˚ W longitude (Fig. 1). Transects were placed perpendicular to the coastline to cross major bathymetric features, such as Barrow Canyon, the BS shelf and slope, and bowhead and beluga whale migration paths. Transects were spaced one per every one-half degree of longitude (BS) or every 19 km (CS), with randomly generated transect endpoints for each flight (BS) or for the year (CS). Transects extended 68–176 km northwards from the Alaskan coast. Given the independent placement of transects on the different flights, the area is considered sampled with replacement. To estimate numbers of surface-visible belugas, circling effort and its associated sightings were removed from the data, and only passing-mode effort and sightings were analyzed. The area to be covered by a survey flight was non-random, dependent on reported or observed weather conditions, avoidance of recently surveyed areas, other aerial operations, and subsistence use areas.

The aircraft used was a high-wing Rockwell Aero Commander 690A twin turboprop equipped with bubble windows. Target survey altitude was 365–457 m above sea level. Target airspeed was 204–213 km/h. Single-observer line-transect methods were used, including the recording of sighting angles by hand-held clinometer. All marine mammals sighted were recorded. Transect flying was interrupted by closing-mode circling to confirm sightings or group sizes; the times and positions of starting and ending the circling were recorded. Survey conditions that were recorded at the start of transects and when conditions changed included sea state, cloud cover, impediments to visibility, range (km) in visibility perpendicular to the aircraft, glare, and ice cover. Visibility and glare were recorded separately for the two sides of the aircraft (Clarke et al., 2013).

Data Selection

Prior to data analysis, we made decisions regarding what subset of ASAMM data to use. It is particularly important that belugas from the BS stock are also known to occur sometimes in the area covered by ASAMM, particularly during their September–October fall migration (Richard et al., 2001). However, while there is broad geographic overlap in area use, analysis of locations and movements of 64 belugas from the two stocks monitored with satellite telemetry indicated little temporal overlap. Within the

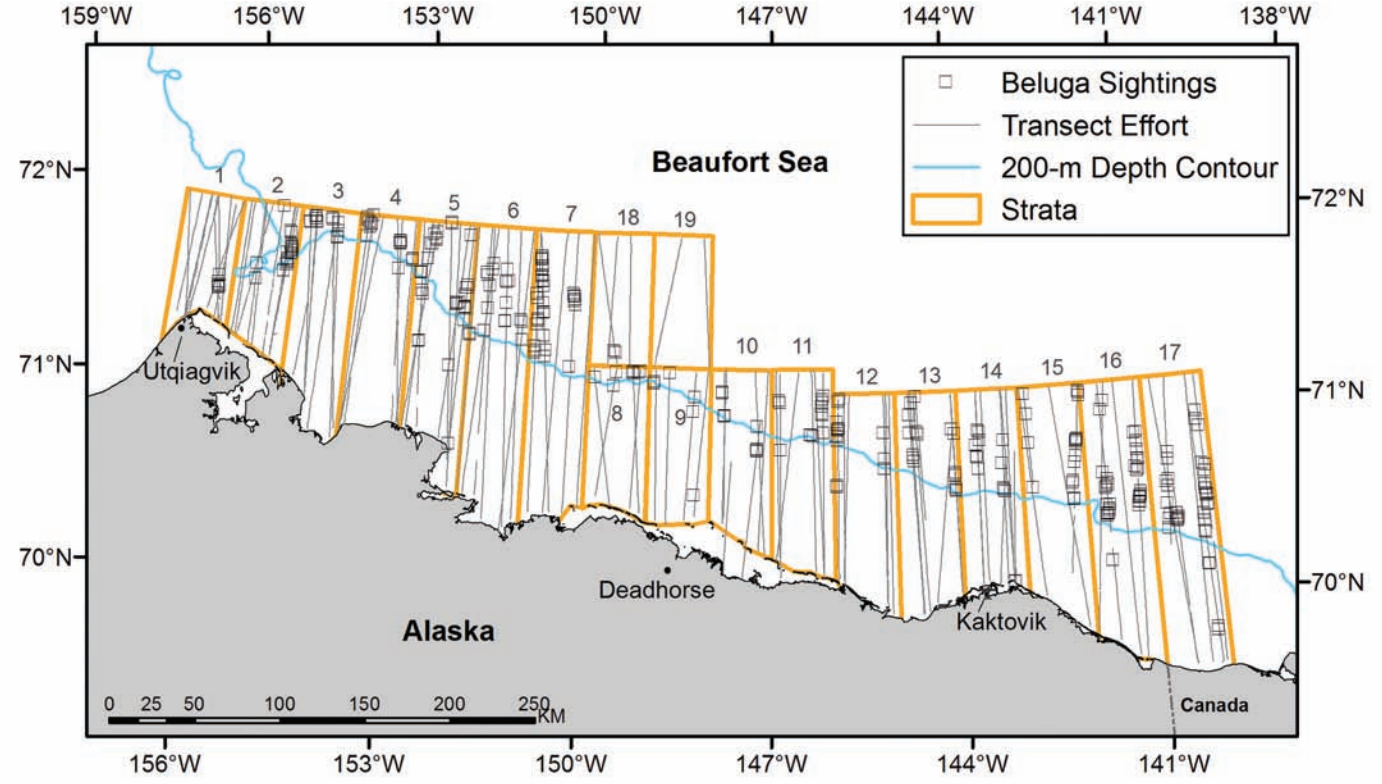

FIG. 2. Strata, transects flown, and locations of beluga sightings in the Alaskan Beaufort Sea in July–August 2012 that were used for the eastern Chukchi Sea abundance analysis.

survey area, there was no overlap between the home ranges (defined as the 95% probability contour of the utilization distributions) of the ECS and BS stocks in the months of July and August (Hauser et al., 2014). The easternmost boundary of the ASAMM survey area at 140˚ W longitude coincided well with the break in summer distribution of the two stocks and was used as the eastern boundary for this study. Satellite telemetry data indicated few movements of BS belugas west of this boundary prior to 1 September (Richard et al., 2001; D.D.W. Hauser, unpubl. data), but to ensure that BS belugas were excluded from our counts, we included only survey data collected prior to 20 August.

In 2012, ASAMM surveys began on 30 June, but flights were mostly confined to the CS until 19 July (Clarke et al., 2013). Belugas were seen on 10 of 19 flights during that period (Fig. 1). On seven flights, all sightings were close to a coastal area where ECS belugas are known to congregate while migrating through the region in early summer (Frost et al., 1993; Suydam et al., 2005). The coastal flights were not part of the systematic survey grid and thus are not useful for this analysis. There was only one on-transect sighting of six belugas in the CS during this period. We therefore included only ASAMM data from 19 July on, when the area of emphasis shifted to include the Beaufort Sea.

Transect coverage was uneven, with more intense coverage of the western part of the study area, and because beluga density was not uniform, we used a stratified analysis to reduce the coefficient of variation (CV) of the overall abundance estimate as recommended by Thomas et al. (2007). For the analysis of encounter rates, the study area was divided into one-degree-of-longitude strata (Fig. 2). The northern boundary, based on transect survey effort during this time period, was at 71˚10′ N between 140˚ W and 146˚ W, 71˚18′ N between 146˚ W and 148˚ W, and 72˚ N between 148˚ W and 157˚ W. Two strata were identified: one between 148˚ W and 149˚ W and the second between 149˚ W and 150˚ W. They were separated at 71˚18′ N because in allocating and laying out transects for the survey flying, those areas had been sampled independently of one another. To measure the areas of strata, a southern boundary for the survey area was defined by joining the southern ends of transects that ended at or near the coastline.

Sighting data were analyzed using line transect (distance sampling) methods (Buckland et al., 2001). A number of factors may affect counts made during line transect sampling, and it is necessary to take those factors into account (Quang and Becker, 1996). The approach we chose was to specify a range of acceptable survey conditions and to analyze only sighting data collected under those conditions. Because this survey targeted all marine mammal species in the area, there was no prior specification of acceptable conditions for counting belugas, and observations were recorded under a wide range of conditions. We evaluated thresholds for acceptable conditions by checking beluga sighting rates (sightings per transect km) under different conditions and deciding on limiting values.

It was also necessary to decide on selection of group sightings to be used for analysis. Two situations required this decision. One was a single group of 100 belugas that was sighted in stratum 1. This group was omitted from the detection function analysis because the fitted sighting curve would have to apply to all strata, including those with lower densities of belugas, where such large groups would be unlikely. The group was included in the encounter-rate analysis for the stratum where it was seen and to which it was uniquely relevant.

The other occurrence comprised four sightings totaling 1100 belugas made on the same day, within a short time, at the northern ends of two consecutive, and close together, transects in stratum 3. These groups did not appear to belong to the same statistical population as the generally much smaller groups that composed most of the sightings farther south. They were omitted from the detection function analysis, three of the four having in any case no sighting angle recorded; encounter rate analyses for the stratum were carried out both with and without these sightings.

Detection Function Analysis

As is normal line-transect practice (Buckland et al., 2001), the data were truncated, and groups with recorded distances greater than 1500 m from the centerline were omitted from both the detection function and the encounter rate analyses. The 1500 m truncation distance was selected as it included approximately 95% of the sightings. For a small number of groups, sighting angles were not recorded and therefore distance from the transect centerline was unknown. Because 96% of recorded distances were inside the 1500 m limit, we considered it likely that groups without recorded distances also were inside the limit, and we included all of them in the encounter rate analysis.

In spite of the bubble windows, there was evidently a loss of sightings close to the platform, also noted in Ferguson and Clarke (2013). This loss might be due to the smaller size of the Aero Commander bubble windows compared to bubble windows in larger survey aircraft (e.g., DeHavilland Twin Otter), which makes it more difficult for observers to see directly under the aircraft. A two-part sighting curve was fitted to the data (cf. Kingsley and Reeves, 1998; Kingsley, 2000). The near-side sighting curve was a quasi-half-normal with two parameters:

$$f\left(x\right) = \exp\left(\frac{-\left(\mu - x\right)^2}{2\sigma^2}\right), 0 \le x \le \mu$$

where μ is the abscissa at the peak of the curve and σ is a breadth parameter. This function guarantees a non-zero sighting probability on the trackline, appropriate for the deep bubble windows used in this survey.

The far-side sighting curve was a three-parameter sigmoidal hazard-rate curve defined by

$$g\left(x\right) = 1 - \exp\left(-\frac{1+c}{c}\left(\frac{x_{\max} - x_0}{x - x_0}\right)^c\right)$$

where

$$x_0 = x_{\max} - \frac{1+c}{g'_{\max}}\exp\left(-\frac{1+c}{c}\right)$$

and x_0 is the abscissa at the origin of the hazard-rate function, $x_{\max}$ is the abscissa at its point of inflection with maximum slope $g'_{\max}$, and c is a shape parameter. When x_0 was less than μ, i.e., the range of the hazard-rate curve overlapped the quasi-normal lefthand limb, the two curves were fused by defining

$$f\left(x\right) = \frac{g\left(x\right)}{g\left(\mu\right)}, x \ge \mu$$

to ensure no discontinuity in ordinate, and by constraining $g(\mu)$ to be greater than 0.999 to ensure a small slope of the hazard-rate curve at μ and therefore a minimum discontinuity in slope. When x_0 was greater than μ, the two curves were joined by defining

$$f\left(x\right) = 1,\ \ x_0 \ge x \ge \mu \text{ and } f\left(x\right) = g\left(x\right),\ \ x \ge x_0$$

The compound sighting curve was fitted to densities of individual belugas out to a maximum distance of 1500 m by maximum likelihood using Excel Solver. The function maximized was:

$$\ln\left(L\right) = \sum_i \left(n_i \cdot \ln\left(\frac{f\left(x_i\right)}{\int_{x=0}^{1500} f\left(x\right)dx}\right)\right)$$

where n_i is the number of belugas in the i^{th} group, recorded at distance x_i. The compound sighting curve was integrated numerically over 1000 intervals. With the sighting curve defined to have a maximum ordinate of 1, its integral is the "effective strip width" (ESW). The reciprocal of the ESW was defined as the "lateral density."

A bias-reduced estimate of the ESW was obtained by resampling. Sighting curves were fitted to, and lateral densities calculated for, one thousand joint resamplings (joint means that group size and sighting distance were sampled together) of the observations. A bias-reduced estimate of the lateral density was calculated from the bootstrap results, and its reciprocal was taken as a bias-reduced estimate of the ESW.

Group size appeared not to be independent of sighting distance. Larger groups appeared to be clustered in a small range of distances from the platform. To investigate this relationship, sighting distance and group size were resampled independently. That is, sightings were constructed, to the same number as in the data, by separately resampling group size and sighting distance from the observations. Sighting curves were fitted and lateral densities calculated, and the lateral density from the observed data was placed on the distribution of lateral densities from this independent (double) bootstrap.

Encounter Rate Analysis

For each stratum, a mean encounter rate (number of individuals per unit distance) was calculated as

$$\hat{E}_s = \frac{\sum_t n_t}{\sum_i l_t},$$

and its error coefficient of variation as

$$\mathrm{CV}\left(\hat{E}_s\right) = \sqrt{\frac{\sum_t \left(\frac{n_t^2}{l_t}\right) \cdot \frac{\sum_t l_t}{\left(\sum_t n_t\right)^2} - 1}{\left(T_s - 1\right)}}$$

(Cochran, 1977; Kingsley, 2000), where n_t was the number of belugas counted on transect t, of T_s in stratum s, and l_t was its length. An estimate for the number of belugas in the stratum was calculated as

$\hat{N}_s = \hat{E}_s A_s \hat{D}$ and its error CV as $\mathrm{CV}\left(\hat{N}_s\right) = \sqrt{\left(\mathrm{CV}\left(\hat{E}_s\right)\right)^2 + \left(\mathrm{CV}\left(\hat{D}\right)\right)^2}$

where A_s is the stratum area, $\hat{D}$ is the estimated two-sided lateral density, and CV($\hat{D}$) its error coefficient of variation. Total number for the entire survey area was then estimated by $\sum_S \hat{N}_S$ and its CV by

$$\sqrt{\left(CV\left(\hat{D}\right)\right)^2 + \frac{\sum_s A_s^2 \hat{E}_s^2 \left(CV\left(\hat{E}_s\right)\right)^2}{\left(\sum_s A_s \hat{E}_s\right)^2}}$$

Correction for Animals Missed during the Survey

In spite of their extensive nature, the ASAMM surveys did not cover all of the July-August home range of ECS belugas. Previous studies describe the capture and tagging of ECS belugas (Suydam et al., 2001, 2005; Suydam, 2009). In total, 25 instruments provided locations on dates corresponding to the survey period (but not during the study year) and were used to derive corrections for animals located outside the survey area. The tags were programmed to transmit continuously and provided locations of varying spatial accuracy via the ARGOS satellite service. Locations were passed through a speed and angle filter (Freitas et al., 2008) to eliminate unrealistic and poor-quality locations. A single daily location was selected as the first, best quality location (among ARGOS classes 1–3, with predicted spatial errors ≤ 1.5 km) occurring within peak satellite transmission hours (0000–0800 GMT; Hauser et al., 2014).

Daily locations were used to estimate the average fraction of time a beluga would be in the study area during the survey period. Daily locations occurring during dates corresponding to the survey period were selected and mapped using ArcGIS version 10.2 (ESRI, Redlands, CA). Those occurring within the survey area were used to determine how many of the total survey days an individual whale was inside the survey area. Several beluga populations migrating to Arctic regions exhibit sexual segregation (Barber et al., 2001; Loseto et al., 2006). Males in the ECS stock occur farther north and offshore in deeper water more frequently than females (Suydam et al., 2001; Hauser et al., 2014). ECS males also select steeper slopes and heavier ice concentrations (Hauser et al., 2017). Given this sexual segregation, we calculated the average fraction of time spent in the survey area separately for tagged male and female whales.

Dive data were collected from 19 tagged ECS belugas on dates corresponding to the survey period and were used to estimate the proportion of whales visible to observers during the survey. Dive data are compressed into four 6 h periods each day, and a correlated random walk state-space model (Johnson et al., 2008; see Hauser et al., 2015) was used to assign a location for the beginning of each 6 h period. Dive data that occurred within the survey area and on dates corresponding to the survey period were selected for analysis. Three types of dive data are summarized into 6 h histograms by SDRs (number of dives in pre-specified depth bins or duration bins, and percentage of time in depth bins), but these analyses used only the percentage of time spent in pre-specified depth bins. Tags applied in different years had different dive bin configuration (see Hauser et al., 2015), so bins were consolidated for analysis to calculate the percentage of time belugas spent in either the 0–4 m or 0–10 m depth bin for each 6 h period. These two depth bins represent ranges at which belugas were assumed to be visible in the water column, although visibility likely depends on several factors including sea state, glare, turbidity, animal coloration and behavior, sea ice, and angle to the sighting. Bin values were averaged to estimate the overall percentage of time spent in those two portions of the water column (i.e., 0–4 m or 0–10 m). As a result of dive bin configuration, only data from SDRs attached in 1998–2002 could be used to estimate the percent of time in 0–4 m. All SDR data could be used to estimate the percent of time in 0–10 m. Note that a depth of at least 2 or 4 m was required before a tag registered a dive in 2007–12 and 1998–2002, respectively. There is limited evidence of sex-based differences in ECS beluga dive behavior (Citta et al., 2013), particularly in the Alaskan BS (Hauser et al., 2015), and we therefore did not estimate the percentage of time spent in surface waters separately for males and females.

The number of observed animals in the study area can be corrected to account for animals missed using the formula:

$$N = y / \left(mav + \left(1 - m\right) bw \right)$$

where N is true total population, y is the estimated number of surface-visible belugas in the study area, m is the proportion of males in the population, a is the probability of a male being in the study area, b is the probability of a female being in the study area, v is the probability of males being visible during the survey, and w is the probability of females being visible during the survey. Since we assumed no sex-based differences in dive behavior, $v = w$. The CV was calculated by pooling variances of each component:

$$\mathrm{CV}(N) = \sqrt{\left(\mathrm{CV}\left(y\right)\right)^2 + \left(\mathrm{CV}\left(v\right)\right)^2 + \left(\mathrm{CV}\left(a\right)/2\right)^2 + \left(\mathrm{CV}\left(b\right)/2\right)^2}$$

RESULTS

Study Area Coverage

Coverage of the survey area between the limiting dates was uneven, with mean spacing of retained transects ranging from 3.8 to 17.7 km (Fig. 2, Table 1). Coverage was generally higher in the more densely populated strata except for the three easternmost strata, which had fairly high densities but low coverage.

A plot of transect longitude against date showed that the survey did not tend to progress either eastward or westward during the time period covered by the data.

Selected Data

Because survey flights were conducted in a variety of conditions that may have affected counts even at the distance where visibility was at its highest, we considered the possible influence of sea state, obstructions to visibility, visibility range, glare, and ice cover before conducting the line-transect analysis.

An effect of Beaufort state on beluga sightings has been previously reported (DeMaster et al., 2001), and precedents exist for restricting visual surveys for belugas (Harwood and Kingsley, 2013) and other small cetaceans (Kingsley and Reeves, 1998) to Beaufort state 3 (defined as wind speed 13–19 km/h; large wavelets, crests begin to break, scattered whitecaps) or less. In our dataset, sighting rates for sea states up to Beaufort state 4 ranged from 20.6 to 35.5 per 1000 km with an average of 29.3, but at Beaufort 5 and 6 there were on average only 6.2 sightings per 1000 km. Flights in Beaufort state 4 accounted for only 5% the effort in sea states corresponding to Beaufort 0–4. We therefore retained transect segments and sightings only for sea states corresponding to Beaufort 0–3.

When visibility was recorded as less than 2 km there were on average 8.7 sightings per 1000 km, compared to 14.3 with visibility over 2 km. Therefore, for the detection function analysis we retained data with visibility at least 2 km on the sighting side, and for encounter rate analysis, we retained transect segments and sightings for which visibility was at least 2 km on both sides.

Glare, recorded as present or absent, was frequently recorded as an impediment to visibility: flights with glare on one side of the aircraft or the other accounted for 40% of effort, and a further 20% had glare on both sides. Sighting rates were 33% lower with glare than without it. Sighting curves were fitted to glare and non-glare data; the ESW was 21% less with glare. The residual ratio of the sighting rates at the peak of the sighting curve was therefore estimated at (100–33)/(100–21) or 85%, i.e., a difference of 15%. Not wishing to reject the large proportion of effort and sightings made with glare, we retained the data with glare in the analysis.

There were fewer beluga sightings in ice cover over 80%. Ice cover over 80% was recorded only seldom and only at the western end of the survey area. Of various possibilities—belugas present but not surfaced because of the ice, present and surfaced but not seen because of the ice, or not present but moved elsewhere—we considered the third the most likely. Therefore, we included data collected in heavy ice conditions in the encounter rate analysis in order to average its lower densities with the higher densities elsewhere that might have resulted from belugas moving into lighter ice conditions.

For detection function analysis, we retained 298 sightings comprising 729 belugas, not including the group of 100 in stratum 1 mentioned earlier. For encounter rate analysis, we retained 10 608 km of transect and 301 sightings comprising 841 belugas. We also analyzed encounter rates including the four groups (totaling 1100 belugas) that were recorded close together on the same day at the northern end of stratum 3, giving an overall total of 1941 belugas in that analysis.

Detection Function Analysis

The compound sighting curve fitted easily and closely to the observations (Fig. 3, Table 2). There was some deviation of the cumulative distribution of observed distances from the fitted sighting curve between about 700 m and 1050 m, apparently because of an overweight in the data of sighting angles recorded between 26° and 31° and associated depopulation of neighboring regions in the data spectrum. The sighting curve had no plateau, but a sharp peak instead. The maximum likelihood estimate of the (one-sided) ESW was 560 m, i.e., a lateral density of 1.785/km. The bootstrap-bias-reduced lateral density was 1.752/km (CV = 0.15) and a corresponding ESW of 571 m.

The maximum likelihood estimate of lateral density given by the observations was, as expected, near the median of the distribution obtained by single bootstrap of the data. However, on the distribution of lateral density obtained by double bootstrap—i.e., a distribution that assumes group size and sighting distance are independent—it was in the upper tail of the distribution at the 7.5% point.

TABLE 1. Estimate of numbers of ECS belugas visible on the surface during aerial surveys flown in the Beaufort Sea between 19 July and 20 August 2012.

Stratum	Area (km^2)	Number of transects	Mean transect spacing (km)	Retained total belugas	Estimated number of belugas	CV of estimate
1	2544	10	3.81	113	378	112.9
2	3013	11	5.17	62	281	68.4
3	4107	7	6.53	24	137	81.7
4	4301	8	6.29	36	198	54.8
5	4611	8	5.77	68	344	32.7
6	5994	8	6.12	48	258	39.2
7	5877	5	9.56	70	586	37.6
8	2951	4	9.24	15	121	30.8
9	3232	4	9.62	19	160	46.8
10	3981	6	7.43	27	176	75.0
11	4366	6	6.37	30	167	48.1
12	4342	6	7.72	26	176	69.0
13	4616	7	7.20	42	265	48.3
14	4209	9	7.37	37	239	55.4
15	4837	4	13.55	48	570	69.3
16	5845	4	10.91	78	746	48.5
17	6308	7	8.56	95	712	49.2
18	2724	3	12.60	3	33	103.0
19	2724	2	17.67	0	0	
			2-sided ESW = 1.141 km			
Sum of strata					5547	0.22

TABLE 2. Parameters of a compound (normal plus hazard-rate) sighting curve fitted to ECS beluga sightings in the Beaufort Sea, 2012.

Parameter	Value
μ Normal curve peak	341 m
σ Normal curve breadth	218 m
x_{max} Hazard-rate inflection	409 m
x_0 Hazard-rate origin	317 m
g'_{max} Hazard-rate max. slope	3.85 × E–3 /m
C Hazard-rate shape parameter	1.207
Lateral density (one side of platform, maximum likelihood estimate)	1.785/km
Lateral density (one side of platform, bootstrap-bias-reduced)	1.753/km
Effective strip width (one side of platform, bootstrap-bias-reduced)	570.6 m
Effective strip width, bootstrap error CV	15.67 %

This estimate of ESW omitted one sighting of a large group of 100 belugas in stratum 1 because we considered that groups of that size would probably not occur in more sparsely populated strata. Like several other large groups, this sighting was recorded near the middle of the range of sighting distances. When the large group was included in the detection function analysis, it gave a maximum likelihood estimate of the ESW of 426 m, i.e., 76% of that without it, and therefore increased the estimate of numbers by close to one-third. It doubled the CV of the ESW, increasing the CV of the estimate of numbers by about 50%.

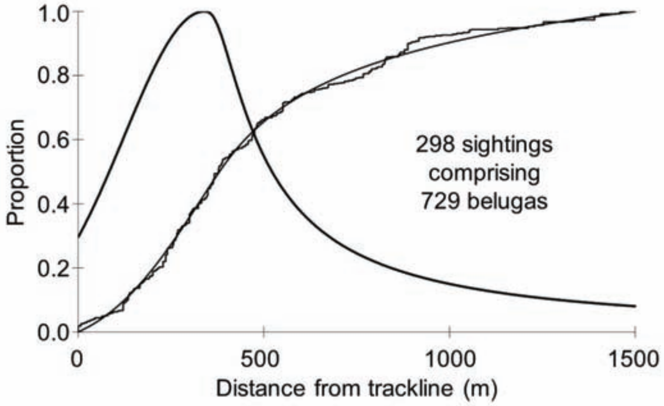

FIG. 3. Compound (normal plus hazard-rate) sighting curve (bold black line) fitted to line-transect observations of belugas in the western Beaufort Sea in 2012. The cumulant (rough line) and the cumulated (smooth line) distributions of sighting distances to individual belugas are also shown.

Encounter Rate Analysis

The stratified analysis of the selected data produced an estimate of 5547 (CV = 0.22) surface-visible belugas (Table 1). The uncertainty in the ESW, and that in the mean encounter rate, contributed about equally to the overall uncertainty.

When the four large groups sighted in stratum 3 on 20 August were included in the encounter rate analysis, the estimate of numbers became 11 703 (CV = 0.36). Of those individuals, 6432 were calculated to be in stratum 3.

TABLE 3. Information on 25 ECS belugas tagged with satellite-linked transmitters near Point Lay, Alaska, 1998–2012. The last three columns show number of locations in the survey area on days corresponding to the survey period, total number of days in the survey period, and percentage of total days each beluga spent in the survey area.

Sex	Year	Tag ID	Date of capture	Date of last transmission	Days in survey area	Total survey days	Days in area/ total survey days
Females:							
	1999	B99-2	July 1 1999	12 September 1999	20	23	0.87
	2001	B01-2	July 4 2001	22 July 2001	1	3	0.33
		B01-3	July 6 2001	29 November 2001	20	25	0.80
		B01-5	July 7 2001	23 October 2001	16	23	0.70
	2002	B02-1	July 8 2002	14 September 2002	0	16	0.00
	2007	B07-2	July 2 2007	13 November 2007	26	33	0.79
		B07-3	July 3 2007	6 November 2007	25	33	0.76
	2012	B12-1	July 2 2012	11 May 2013	28	32	0.88
Mean (CV)							0.64 (0.49)
Males:							
	2001	B01-1	July 5 2001	10 August 2001	6	13	0.46
		B01-4	July 6 2001	6 December 2001	20	26	0.77
		B01-6	July 8 2001	17 November 2001	10	26	0.38
		B01-7	July 8 2001	24 July 2001	4	5	0.80
		B01-8	July 8 2001	13 August 2001	16	25	0.64
	2002	B02-2	July 8 2002	28 September 2002	6	14	0.43
		B02-3	July 10 2002	25 August 2002	2	11	0.18
		B02-4	July 9 2002	11 September 2002	3	17	0.18
	2007	B07-1	July 2 2007	4 December 2008	25	65	0.38
	2010	B10-1	June 25 2010	6 December 2010	20	32	0.63
		B10-2	June 30 2010	9 October 2010	24	33	0.73
	1998	B98-3	June 30 1998	7 October 1998	8	26	0.31
		B98-4	July 1 1998	29 September 1998	0	26	0.00
		B98-5	July 2 1998	30 August 1998	0	30	0.00
	1999	B99-1	July 1 1999	25 September 1999	0	25	0.00
		B99-3	July 1 1999	26 August 1999	2	33	0.06
		B99-4	July 1 1999	23 September 1999	0	22	0.00
Mean (CV)							0.35 (0.83)

TABLE 4. Proportions of time spent in 0–10 and 0–4 m water depths by SDR-tagged ECS belugas in the study area on dates corresponding to the survey period. N is the number of dive histograms available for each individual whale.

	Proportion in 0–10 m depth			Proportion in 0–4 m depth		
Tag ID	Mean	SD	n	Mean	SD	n
B98-3	0.68	0.13	34	0.46	0.14	34
B99-2	0.52	0.17	77	0.42	0.16	77
B99-3	0.78	0.22	7	0.76	0.22	7
B01-1	0.71	0.19	12	0.54	0.17	12
B01-2	0.83	0.13	7	0.79	0.14	7
B01-3	0.32	0.13	68	0.24	0.07	68
B01-4	0.34	0.18	52	0.27	0.15	52
B01-5	0.48	0.25	64	0.39	0.21	64
B01-6	0.53	0.29	36	0.43	0.27	36
B01-7	0.83	0.11	16	0.78	0.13	16
B01-8	0.67	0.19	57	0.51	0.18	57
B02-2	0.45	0.13	29	0.32	0.07	29
B02-4	0.34	0.10	13	0.29	0.09	13
B07-1	0.52	0.18	84			
B07-2	0.62	0.27	92			
B07-3	0.53	0.22	87			
B10-1	0.58	0.32	74			
B10-2	0.57	0.26	77			
Overall	0.54	0.24 (CV 0.45)		0.41	0.21 (CV 0.52)	

Correction for Animals Missed during the Survey

Daily locations on dates corresponding to the survey period were provided by 25 tagged ECS belugas, eight females and 17 males (Table 3). The average proportion of those days that tagged belugas were located within the study area was 0.64 (CV = 0.49) for females and 0.35 (CV = 0.83) for males.

Dive data were collected from 19 of the SDR-tagged whales that were within the study area on dates corresponding to the survey period. Those tagged belugas spent an average of 0.54 (CV = 0.45) of their time in

0–10 m depths and 0.41 (CV= 0.52) of their time in 0–4 m depths (Table 4).

Using the formula shown in methods and the numbers above, we estimated N for the stratified analysis of the selected data. The estimate is 27 332 (CV = 0.74) if it is assumed that whales are visible for counting by aerial observers only in the upper 4 m of the water column and 20 752 (CV = 0.70) if whales are visible down to 10 m deep. Including the four large groups on 20 August yields estimates of 57 664 (CV = 0.80) assuming whales are visible in the upper 4 m only and 43 782 (CV = 0.75) assuming whales are visible in the 10 m depth zone.

DISCUSSION

Determining abundance of Arctic cetacean populations, especially those that range widely like ECS belugas, can be difficult. Of the 19 beluga stocks listed by Laidre et al. (2015), abundance is unknown for three, and five of the available estimates have no measure of uncertainty. Eight of the available estimates are 10 or more years old, and the trend is unknown for 15 of the stocks. Laidre et al. (2015) and the NOAA stock assessment reports (Allen and Angliss, 2014) give a point estimate of abundance for ECS belugas (3710) based on 1989–91 data (Frost et al., 1993), and the trend is indicated as unknown.

Prior to the development of satellite-linked tags and methods for attaching them to belugas, little was known about the whereabouts of these animals except when they occurred near shore, which was usually during summer. Their summer concentration areas commonly corresponded with locations where indigenous communities harvested belugas, and several of those areas became the focus of targeted scientific studies (e.g., Fraker et al., 1979; Born et al., 1994; Heide-Jørgensen and Wiig, 2002; Suydam, 2009). For some stocks, including for the ECS (Seaman et al., 1988; Frost and Lowry, 1990) and BS (Fraker et al., 1979) stocks, initial abundance estimates were based on the number of animals seen in nearshore concentration areas (Kasegaluk Lagoon in western Alaska and the Mackenzie River Delta in western Canada). In the Canadian BS region, aerial surveys conducted primarily for bowhead whales detected many belugas scattered in offshore waters (Norton and Harwood, 1985), which led to efforts to quantify BS beluga population abundance more completely that were based on the assumption that offshore whales belonged to the BS stock (Harwood et al., 1994; Harwood and Kingsley, 2013). A similar situation occurred with ECS belugas. Initial population estimates were based on counts at the summer coastal aggregation site (Seaman et al., 1998; Frost et al., 1993). While it was suspected that additional whales were distributed offshore at the same time, efforts to count them were not successful (Lowry et al., 2002, 2003). Furthermore, extensive summer-fall aerial surveys, again primarily directed at bowhead whales, detected numerous belugas in the ECS and the BS regions (Ljungblad et. al., 1986; Moore, 2000). However, because it was not possible to know which stock those belugas belonged to, the survey data were not used for estimating beluga abundance.

In the 1990s, researchers working with local communities began attaching SDRs to belugas at the coastal concentration areas of both the ECS and BS beluga populations. Twenty-seven whales were successfully tagged at Kasegaluk Lagoon and 40 in the Mackenzie Delta (Hauser, 2016). Initial analyses of those data (Suydam et al., 2001, 2005; Suydam, 2009; Richard et al., 2001) showed wide-ranging offshore movements with considerable overlap of the areas used by the two groups. However, when the data for the two stocks were considered together in a more detailed analysis, it became evident that for a substantial period of time there was no overlap between the core use areas (Hauser et al., 2014). With this knowledge, it became possible to use ASAMM aerial survey data for a range of dates when the populations did not overlap in a line-transect analysis to estimate the number of ECS belugas in the surveyed area.

While the ASAMM surveys were not specifically designed for beluga whales, we were able to access a dataset of 119 transects covering 10 608 km in the BS that were flown on appropriate dates under acceptable survey conditions. Using all these data, we estimated the number of surface visible belugas in the study area during the survey period as 11 703. However, when some statistically anomalous sightings that occurred on one day at the northern ends of two neighboring transects were removed from the dataset, the estimate was reduced to 5547 surface-visible belugas. Although four anomalous groups were recorded, this appeared to be a single event, not four independent events. The group sizes recorded, and as a result the combined group size, were inconsistent with the statistical distribution of group sizes among the other sightings. At this time we believe that the estimate of 5547 gives a more accurate measure of the average number of surface-visible belugas in this study area within the survey period.

Although the study area covered a large portion of the BS (80 585 km^2), it did not include the entire area used by ECS belugas that had been SDR tagged and tracked in previous years. We calculated that the time tagged whales spent in the survey area on dates corresponding to the survey period was 64% of tracking days for females and 34% for males. While we cannot be certain that the tagged whales provide an unbiased sample of the population as a whole, and we acknowledge that it would have been better if the whale tracking and the survey had been contemporaneous, we believe that these are reasonable estimates that can be used to account for animals missed during the 2012 survey because they were not in the survey area. In 2016, ASAMM survey lines were extended farther offshore in the BS, and belugas were commonly seen beyond the area included in this study (J. Clarke, pers. obs.).

We used data from SDR-tagged whales on time spent at depth to account for whales that were too deep to be seen from the survey aircraft when it passed over. Citta et al. (2013) found that in this region ECS belugas commonly dove to depths of 400 m or more, with some dives lasting longer than 20 minutes, so clearly many whales were not visible to surveyors. Because of the likelihood that many diving whales are missed during aerial surveys, considerable effort has been devoted to developing an availability correction factor (e.g., Martin and Smith, 1992; Kingsley et al., 2001). Models that simulated whales have been used to measure how far below the surface submerged animals can be detected. For monodontids (beluga and narwhal, *Monodon monoceros*) adult-sized models could be detected visually or photographically from directly above when they were as much as 10–11 m below the surface. Young gray juveniles could be seen to only half (or less) of that depth (Richard et al., 1994; Gauthier, 1999). However, because sightings made during transect visual surveys are made at an oblique angle, the distance through water at which animals are seen can be much greater than their vertical depth (Kingsley et al., 2001). For a beluga survey in Hudson Bay, Kingsley et al. (2001) used SDR data on dive depth and a visibility threshold of 7 m to calculate an availability correction factor of 1.85. This value is identical to what we calculated using ECS beluga SDR data for a visibility threshold of 10 m and somewhat less than the 2.17 from the 4 m cutoff.

Belugas are born dark gray and gradually become white as they near sexual and physical maturity (Suydam, 2009). Brodie (1971) concluded that dark-colored neonates and yearlings are not counted during aerial surveys, and Richard et al. (1994) and Gauthier (1999) found that gray juveniles could be seen to only half or less of the depth for white animals. While it is clear that more juvenile whales than adults were missed during BS aerial surveys, we did not apply a separate correction factor to account for that bias.

As is commonly the case in wildlife surveys, there is uncertainty associated with our abundance estimates. We have dealt with statistical uncertainty by calculating CVs for all the parameters that were used in abundance calculations and pooling them. The CV for our estimate of surface-visible belugas, 0.22, is similar to the 0.2 considered by Wade (1998) to be a low CV for cetacean abundance estimates. But when variability of the data used to develop correction factors is accounted for, the CV of the overall abundance estimate rose to 0.70. This result is largely due to the relatively small number of SDR-tagged whales and individual variability in their movements and dive behavior.

To select the most appropriate estimate of abundance, we had to make two major decisions. The first of those was whether or not to include the four unexpectedly large groups of belugas seen on 20 August. We did not include those sightings, but we note that if they had been included, our estimates of abundance would have been 2.1 times as large. The second decision was what cutoff to use for the depth at which belugas were not detectable to the observers. This is a complex question that cannot be answered satisfactorily with current data and knowledge. Because of the way the SDRs we used were programmed, we are limited to examining cutoff values of 4 m and 10 m. Given all the factors that affect beluga sightability (e.g., sea state, glare, distance and angle from the observer, color of the whale, turbidity of the water), we are certain that many belugas submerged at depths of 4–10 m were not counted during the surveys we analyzed. Nonetheless, at this time we recommend that 20 752, the estimate incorporating the 10 m threshold, be used as the estimated size of the ECS beluga stock, recognizing that this number is likely to underestimate the actual total abundance by a substantial amount.

The ABWC co-manages beluga whale stocks in western Alaska with NOAA, and two of the agreed-upon objectives of the management plan are to “conserve the Western Alaska beluga whale population” and to “protect Alaska Native beluga whale subsistence hunting traditions and culture” (ABWC, 1999). Knowledge of harvest levels and population size are obviously needed to attain these objectives. The average annual harvest of belugas from the ECS stock during 2007–16 was 57 (ABWC, unpubl. data). Prior to this study, the “most reliable” abundance estimate available for the ECS stock was 3710 derived from a count of whales nearshore with correction factors applied (Allen and Angliss, 2014). The removal of 57 whales per year from a population of 3710 would be a harvest level of nearly 2%. With an estimated population size of 20 752, the annual harvest amounts to 0.3% of the population, which should be well within sustainable limits. For perspective, during 1993–2005, the stock of belugas in Bristol Bay, Alaska, numbering about 2000 animals (Angliss and Lodge, 2002) increased at an average rate of 4.8% per year (Lowry et al., 2008) while sustaining a subsistence harvest of 17 animals per year (Frost and Suydam, 2010).

We emphasize the importance of data from SDR-tagged whales in allowing us to estimate abundance of ECS belugas. Substantial datasets from aerial surveys in the CS and BS have been available for many years, but until we learned enough about the whereabouts of ECS belugas and found a period when their distribution did not overlap with BS whales, the survey data could not be used for population estimation. Now the rich ASAMM dataset can be further explored with regard to ECS beluga abundance. Data from the SDRs also provided crucial information for developing availability correction factors to allow estimation of total abundance of this stock. Attaching additional SDRs to ECS belugas is warranted to increase our confidence in the correction factors that we apply. ASAMM surveys should be continued to improve our abundance estimates and determine trends in abundance for the ECS beluga stock.

ACKNOWLEDGEMENTS

This work was supported by BOEM, NOAA, and ABWC, and we particularly thank Jeff Denton (BOEM) Phil Clapham

(NOAA), and Malissa Langley (North Slope Borough) for their administrative help. We thank all the ASAMM project staff, and especially Megan Ferguson, Amelia Brower, and Cynthia Christman, for collecting and managing the data without which this study would not have been possible. Surveys were flown by Clearwater Air under direction of Andy Harcombe; pilots for the surveys were Stan Churches, Jim Kopczyski, Alex Shibakov, and Baine Thorn. Megan Ferguson, Rod Hobbs, Doug DeMaster, Paul Wade, Jeff Laake, Brian Taras, and Goef Givens provided helpful comments on preliminary data analyses. Jay Ver Hoef provided advice on applying correction factors. We particularly appreciate the beluga tagging efforts of our colleagues in Alaska and Canada, and especially those people in local communities without whose help the work could not have been done. We thank Kathy Frost and four peer reviewers for helpful comments on the draft manuscript. The principal analyst on this paper, Michael C.S. Kingsley, passed away on 22 December 2016 while the manuscript was in review. This made it particularly difficult to respond to some peer reviewers' comments, and the surviving authors especially thank reviewers Megan Ferguson and Doug Demaster, and *Arctic* Editor Karen McCullough, for being helpful and understanding during the revision process. Any errors or omissions that may remain are the sole responsibility of the senior author. This paper, the eighth that he published in *Arctic*, will likely be the last of Michael's many direct contributions to Arctic science.

REFERENCES

Adams, M., Frost, K.J., and Harwood, L.A. 1993. Alaska and Inuvialuit Beluga Whale Committee (AIBWC) – An initiative in "at home management." Arctic 46(2):134 – 137. https://doi.org/10.14430/arctic1334

Alaska Beluga Whale Committee. 1999. Agreement between the National Marine Fisheries Service and the Alaska Beluga Whale Committee for co-management of the western Alaska beluga whale population. Available from North Slope Borough, Department of Wildlife Management, Box 69, Barrow, Alaska 99723, USA. https://alaskafisheries.noaa.gov/sites/default/files/abwcagrefinal.pdf

Allen, B.M., and Angliss, R.P. 2014. Alaska marine mammal stock assessments, 2013. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-277. http://www.nmfs.noaa.gov/pr/sars/pdf/ak2013_final.pdf

Angliss, R.P., and Lodge, K.L. 2002. Alaska marine mammal stock assessments, 2002. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-133. http://www.nmfs.noaa.gov/pr/pdfs/sars/ak2002.pdf

Barber, D.G., Saczuk, E., and Richard, P.R. 2001. Examination of beluga-habitat relationships through the use of telemetry and a geographic information system. Arctic 54(3):305 – 316. https://doi.org/10.14430/arctic790

Born, E.W., Dietz, R., and Reeves, R.R., eds. 1994. Studies of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Greenland and adjacent waters. Meddelelser om Grønland, Bioscience 39.

Brodie, P.F. 1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas)*, with reference to the Cumberland Sound, Baffin Island, population. Journal of the Fisheries Research Board of Canada 28(9):1309 – 1318. https://doi.org/10.1139/f71-198

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., and Thomas L. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford: Oxford University Press.

Burns, J.J., and Seaman, G.A. 1986. Investigation of belukha whales in coastal waters of western and northern Alaska. II. Biology and ecology. U.S. Department of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program. Final Report 56:221 – 357.

Citta, J.J., Suydam, R.S., Quakenbush, L.T., Frost, K.J., and O'Corry-Crowe, G.M. 2013. Dive behavior of eastern Chukchi beluga whales (*Delphinapterus leucas*), 1998 – 2008. Arctic 66(4):389 – 406. https://doi.org/10.14430/arctic4326

Citta, J.J., Quakenbush, L.T., Frost, K.J., Lowry, L., Hobbs, R.C., and Aderman, H. 2016a. Movements of beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. Marine Mammal Science 32(4):1272 – 1298. https://doi.org/10.1111/mms.12337

Citta, J.J., Richard, P., Lowry, L.F., O'Corry Crowe, G., Marcoux, M., Suydam, R., Quakenbush, L.T., et al. 2016b. Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. Marine Mammal Science 33(1):236 – 250. https://doi.org/10.1111/mms.12357

Clarke, J.T., Christman, C.L., Brower, A.A., and Ferguson, M.C. 2012. Distribution and relative abundance of marine mammals in the Alaskan Chukchi and Beaufort Seas, 2011. Annual report OCS-BOEM-2012-009. Anchorage: Alaska OCS Region, U.S. Bureau of Ocean Energy Management.

———. 2013. Distribution and relative abundance of marine mammals in the northeastern Chukchi and western Beaufort Seas, 2012. Annual report OCS-BOEM-2013-00117. Anchorage: Alaska OCS Region, U.S. Bureau of Ocean Energy Management.

Cochran, W.G. 1977. Sampling techniques, 3rd ed. New York: John Wiley & Sons.

DeMaster, D.P., Lowry, L.F., Frost, K.J., and Bengtson, R.A. 2001. The effect of sea state on estimates of abundance for beluga whales (*Delphinapterus leucas*) in Norton Sound, Alaska. Fishery Bulletin 99(1):197 – 201.

Ferguson, M.C., and Clarke, J.T. 2013. Estimates of detection probability for BWASP bowhead whale, gray whale, and beluga sightings collected from Twin Otter and Aero Commander aircraft, 1989 to 2007 and 2008 to 2011. NOAA Technical Memorandum NMFS-AFSC-261. U.S. Department of Commerce.

Fernandez-Gimenez, M.E., Huntington, H.P., and Frost, K.J. 2006. Integration or co-optation? Traditional knowledge and science in the Alaska Beluga Whale Committee. Environmental Conservation 33(4):306 – 315. https://doi.org/10.1017/S0376892906003420

Fraker, M.A., Gordon, C.D., McDonald, J.W., Ford, J.K.B., and Cambers, G. 1979. White whale (*Delphinapterus leucas*) distribution and abundance and the relationship to physical and chemical characteristics of the Mackenzie estuary. Fisheries & Marine Service Technical Report No. 863. Winnipeg, Manitoba: Department of Fisheries and the Environment.

Freitas, C., Lydersen, C., Fedak, M.A., and Kovacs, K.M. 2008. A simple new algorithm to filter marine mammal Argos locations. Marine Mammal Science 24(2):315–325. https://doi.org/10.1111/j.1748-7692.2007.00180.x

Frost, K.J., and Lowry, L.F. 1990. Distribution, abundance, and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. In: Smith, T.G., St. Aubin, D.J., and Geraci, J.R., eds. Advances in research on the beluga whale, *Delphinapterus leucas*. Canadian Bulletin of Fisheries and Aquatic Sciences No. 224. 39–57.

Frost, K.J., and Suydam, R.S. 2010. Subsistence harvest of beluga or white whales (*Delphinapterus leucas*) in northern and western Alaska, 1987–2006. Journal of Cetacean Research and Management 11(3):293–299.

Frost, K.J., Lowry, L.F., and Carroll, G. 1993. Beluga whale and spotted seal use of a coastal lagoon system in the northeastern Chukchi Sea. Arctic 46(1):8–16. https://doi.org/10.14430/arctic1316

Gauthier, I. 1999. Estimation de la visibilité aérienne des bélugas du Saint-Laurent et les conséquences pour l'évaluation des effectifs. MSc thesis, Université du Québec à Rimouski, Québec.

Harwood, L.A., and Kingsley, M.C.S. 2013. Trends in the offshore distribution and relative abundance of Beaufort Sea belugas, 1982–85 vs 2007–09. Arctic 66(3):247–256. https://doi.org/10.14430/arctic4304

Harwood, L.A., Innes, S., Norton, P., and Kingsley, M.C.S. 1994. Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea, and west Amundsen Gulf during late July 1992. Canadian Journal of Fisheries and Aquatic Sciences 53(10):2262–2273. https://doi.org/10.1139/f96-180

Hauser, D.D.W. 2016. Beluga whale distribution, migration, and behavior in a changing Pacific Arctic. PhD thesis, University of Washington, Seattle.

Hauser, D.D.W., Laidre, K.L., Suydam, R.S., and Richard, P.R. 2014. Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). Polar Biology 37(8):1171–1183. https://doi.org/10.1007/s00300-014-1510-1

Hauser, D.D.W., Laidre, K.L., Parker-Stetter, S.L., Horne, J.K., Suydam, R.S., and Richard, P.R. 2015. Regional diving behavior of Pacific Arctic beluga whales *Delphinapterus leucas* and possible associations with prey. Marine Ecology Progress Series 541:245–264. https://doi.org/10.3354/meps11530

Hauser, D.D.W., Laidre, K.L., Stern, H.L., Moore, S.E., Suydam, R.S., and Richard, P.R. 2017. Habitat selection by two beluga whale populations in the Chukchi and Beaufort Seas. PLoS ONE 12(2): e0172755. https://doi.org/10.1371/journal.pone.0172755

Heide-Jørgensen, M.P., and Wiig, Ø., eds. 2002. Belugas in the North Atlantic and the Russian Arctic. NAMMCO Scientific Publications Vol. 4. Tromsø, Norway: North Atlantic Marine Mammal Commission.

Huntington, H.P., and the communities of Buckland, Elim, Koyuk, Point Lay and Shaktoolik. 1999. Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the eastern Chukchi and northern Bering Seas, Alaska. Arctic 52(1):49–61. https://doi.org/10.14430/arctic909

Johnson, D.S., London, J.M., Lea, M.-A., and Durban, J.W. 2008. Continuous-time correlated random walk model for animal telemetry data. Ecology 89(5):1208–1215. https://doi.org/10.1890/07-1032.1

Kingsley, M.C.S. 2000. Numbers and distribution of beluga whales, *Delphinapterus leucas*, in James Bay, eastern Hudson Bay, and Ungava Bay in Canada during the summer of 1993. Fishery Bulletin 98(4):736–747.

Kingsley, M.C.S., and Reeves, R.R. 1998. Aerial surveys of cetaceans in the Gulf of St. Lawrence in 1995 and 1996. Canadian Journal of Zoology 76(8):1529–1550. https://doi.org/10.1139/z98-054

Kingsley, M.C.S., Gosselin, S., and Sleno, G.A. 2001. Movements and dive behaviour of belugas in northern Quebec. Arctic 54(3):262–275. https://doi.org/10.14430/arctic786

Kovacs, K.M., Lydersen, C., Overland, J.E., and Moore, S. 2011. Impacts of changing sea ice conditions on Arctic marine mammals. Marine Biodiversity 41(1):181–194. https://doi.org/10.1007/s12526-010-0061-0

Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P., and Ferguson, S. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecological Applications 18(sp2):S97–S125. https://doi.org/10.1890/06-0546.1

Laidre, K.L., Stern, H., Kovacs, K.M., Lowry, L., Moore, S.E., Regehr, E.V., Ferguson, S.H., et al. 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conservation Biology 29(3):724–737. https://doi.org/10.1111/cobi.12474

Ljungblad, D.K., Moore, S.E., Clarke, J.T., and Bennett, J.C. 1986. Aerial surveys of endangered whales in the northern Bering, eastern Chukchi, and Alaskan Beaufort Seas, 1985: With a seven year review 1979–85. Technical Report 1111. San Diego, California: Naval Ocean Systems Center.

Loseto, L.L., Richard, P., Stern, G.A., Orr, J.R., and Ferguson, S.H. 2006. Segregation of Beaufort Sea beluga whales during the open-water season. Canadian Journal of Zoology 84(12):1743–1751. https://doi.org/10.1139/z06-160

Lowry, L., and Frost, K. 2002. Beluga whale surveys in the Chukchi Sea, July 2002. Alaska Beluga Whale Committee Report 02-2. Available from North Slope Borough, Department of Wildlife Management, Box 69, Barrow, Alaska 99723, USA.

———. 2003. Beluga whale surveys in the eastern Chukchi Sea, July 2003. Alaska Beluga Whale Committee Report 03-1. Available from North Slope Borough, Department of Wildlife Management, Box 69, Barrow, Alaska 99723, USA.

Lowry, L.F., DeMaster, D.P., Frost, K.J., and Perryman, W. 1999. Alaska Beluga Whale Committee surveys of beluga whales in the eastern Chukchi Sea, 1996–1998. Report to the International Whaling Commission's Scientific Committee SC/51/SM33.

Lowry, L.F., Frost, K.J., Zerbini, A., DeMaster, D., and Reeves, R.R. 2008. Trend in aerial counts of beluga or white whales (*Delphinapterus leucas*) in Bristol Bay, Alaska, 1993–2005. Journal of Cetacean Research and Management 10(3):201–207.

Lowry, L.F., Zerbini, A., Frost, K.J., DeMaster, D.P., and Hobbs, R.C. In press. Development of an abundance estimate for the eastern Bering Sea stock of beluga whales (*Delphinapterus leucas*). Journal of Cetacean Research and Management.

Martin, A.R., and Smith, T.G. 1992. Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. Canadian Journal of Fisheries and Aquatic Sciences 49(3):462–466. https://doi.org/10.1139/f92-055

Moore, S.E. 2000. Variability of cetacean distribution and habitat selection in the Alaskan Arctic, autumn 1982–91. Arctic 53(4):448–460. https://doi.org/10.14430/arctic874

Neakok, W., Neakok, D., Bodfish, W., Libbey, D., Hall, E.S., Jr., and the Point Lay Elders. 1985. To keep the past alive: The Point Lay cultural resource site survey. Barrow, Alaska: North Slope Borough.

Norton, P., and Harwood, L.A. 1985. White whale use of the southeastern Beaufort Sea, July–September 1984. Canadian Technical Report of Fisheries and Aquatic Sciences 1401. Winnipeg, Manitoba: Department of Fisheries and Oceans.

O'Corry-Crowe, G.M., Suydam, R.S., Rosenberg, A., Frost, K.J., and Dizon, A.E. 1997. Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. Molecular Ecology 6(1):955–970. https://doi.org/10.1046/j.1365-294X.1997.00267.x

O'Corry-Crowe, G.M., Dizon, A.E., Suydam, R.S., and Lowry, L.F. 2002. Molecular genetic studies of population structure and movement patterns in a migratory species: The beluga whale, *Delphinapterus leucas*, in the western Nearctic. In: Pfeiffer, C.J., ed. Molecular and cell biology of marine mammals. Malabar, Florida: Krieger Publishing Co. 53–64.

Quang, P.X., and Becker, E.F. 1996. Line transect sampling under varying conditions with application to aerial surveys. Ecology 77(4):1297–1302. https://doi.org/10.2307/2265601

Reeves, R.R., Ewins, P.J., Agbayani, S., Heide-Jørgensen, M.P., Kovacs, K.M., Lydersen, C., Suydam, R., et al. 2014. Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. Marine Policy 44:375–389. https://doi.org/10.1016/j.marpol.2013.10.005

Richard, P.R., Weaver, P.A., Dueck, L., and Barber, D.G. 1994. Distribution and numbers of Canadian High Arctic narwhals (*Monodon monoceros*) in August 1984. Meddelelser om Grønland, Bioscience 39:41–50.

Richard, P.R., Martin, A.R., and Orr, J.R. 2001. Summer and autumn movements of belugas of the Eastern Beaufort Sea stock. Arctic 54(3):223–236. https://doi.org/10.14430/arctic783

Seaman, G.A., Lowry, L.F., and Frost, K.J. 1982. Foods of belukha whales (*Delphinapterus leucas*) in western Alaska. Cetology 44:1–19.

Seaman, G.A., Frost, K.J., and Lowry, L.F. 1988. Investigations of belukha whales in coastal waters of western and northern Alaska. I. Distribution, abundance, and movements. U.S. Department of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program. Final Report 56:153–220.

Suydam, R.S. 2009. Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*) from the eastern Chukchi Sea. PhD thesis, University of Washington, Seattle.

Suydam, R.S., Lowry, L.F., Frost, K.J., O'Corry-Crowe, G.M., and Pikok, D., Jr. 2001. Satellite tracking of eastern Chukchi Sea beluga whales into the Arctic Ocean. Arctic 54(3):237–243. https://doi.org/10.14430/arctic784

Suydam, R.S., Lowry, L.F., and Frost, K.J. 2005. Distribution and movements of beluga whales from the eastern Chukchi Sea stock during summer and early autumn. Final report to Coastal Marine Institute, University of Alaska, Fairbanks. OCS Study MMS 2005-035. Available from North Slope Borough, Department of Wildlife Management, Box 69, Barrow, Alaska 99723, USA.

Thomas, L., Williams, R., and Sandilands, D. 2007. Designing line transect surveys for complex survey regions. Journal of Cetacean Research and Management 9(1):1–13.

Wade, P.R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Marine Mammal Science 14(1):1–37. https://doi.org/10.1111/j.1748-7692.1998.tb00688.x