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Beluga whales in the western Beaufort Sea: Current state of knowledge on timing, distribution, habitat use and environmental drivers

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ABSTRACT

The seasonal and geographic patterns in the distribution, residency, and density of two populations (Chukchi and Beaufort) of beluga whales (*Delphinapterus leucas*) were examined using data from aerial surveys, passive acoustic recordings, and satellite telemetry to better understand this arctic species in the oceanographically complex and changing western Beaufort Sea. An aerial survey data-based model of beluga density highlights the Beaufort Sea slope as important habitat for belugas, with westerly regions becoming more important as summer progresses into fall. The Barrow Canyon region always had the highest relative densities of belugas from July–October. Passive acoustic data showed that beluga whales occupied the Beaufort slope and Beaufort Sea from early April until early November and passed each hydrophone location in three broad pulses during this time. These pulses likely represent the migrations of the two beluga populations: the first pulse in spring being from Beaufort animals, the second spring pulse Chukchi belugas, with the third, fall pulse a combination of both populations. Core-use and home range analyses of satellite-tagged belugas showed similar use of habitats as the aerial survey data, but also showed that it is predominantly the Chukchi population of belugas that uses the western Beaufort, with the exception of September when both populations overlap. Finally, an examination of these beluga datasets in the context of wind-driven changes in the local currents and water masses suggests that belugas are highly capable of adapting to oceanographic changes that may drive the distribution of their prey.

1. Introduction

That the Arctic is changing rapidly is indisputable. The most visible environmental changes are the reductions in summer sea ice extent and thickness (Frey et al., 2015; Kwok and Rothrock, 2009; Stroeve et al., 2012), but there are many other changes, including increasing wind strength and storms (Pickart et al., 2013; Spall et al., 2014), and changes in primary and possibly secondary productivity (Ardyna et al., 2014; Arrigo and van Dijken, 2015; Arrigo et al., 2008). In concert with this changing environment, human use of the Arctic is also changing.

There are increased interests in exploring for oil, gas and other mineral resources and in shipping through arctic waters (Reeves et al., 2014). Interest in commercial fishing, tourism and scientific research is also on the rise. Predictions about future impacts to marine mammals and other species are uncertain because of our limited understanding of future environmental and anthropogenic changes, how animals use the Arctic, and the linkages between habitat changes and population dynamics, among other factors (Laidre et al., 2015). How beluga whales (*Delphinapterus leucas*) will respond to rapid environmental changes is currently unknown but informed predictions could be made

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based on a better understanding of how belugas currently interact with their environment.

Belugas are a top predator in the Arctic. They help meet cultural and nutritional needs of Inuit residents in the Arctic and subarctic. Belugas feed on a wide variety of prey, including fishes, cephalopods and invertebrates (Huntington et al., 1999; Quakenbush et al., 2015; Seaman et al., 1982), but in the Beaufort and Chukchi seas, Arctic cod (*Boreogadus saida*) is thought to be their primary prey (Loseto et al., 2009). Belugas occupy a wide range of habitats, including inlets, glacier fronts, continental slopes, underwater canyons, and deep-water basins; each habitat having ice concentrations that vary spatially (within and across habitats) and temporally (e.g., on seasonal, annual, and longer time scales) (Lydersen et al., 2001; Moore et al., 2000; Suydam et al., 2001). Belugas are generally considered ice-associated, primarily because sea ice plays a critical role in structuring arctic ecosystems (Kovacs et al., 2010; Moore and Huntington, 2008).

Off northern Alaska, there are at least two populations of belugas: the Beaufort Sea stock (hereafter referred to as Beaufort belugas) and the eastern Chukchi Sea stock (hereafter referred to as Chukchi belugas)¹. These populations are genetically distinct and segregate in different summering areas in the Beaufort Sea, although they may overlap in time and space during the winter in the Bering Sea (Hauser et al., 2014; O'Corry-Crowe et al., 1997; Seaman et al., 1988). In the western Beaufort Sea (west of 140°W), their home ranges overlap during fall migration, although their migratory timing and core use areas differ somewhat by stock. Beaufort belugas migrate north from the Bering Sea in April and May through leads in the sea ice. This stock spends the summer in the Mackenzie Estuary, the eastern Beaufort Sea, Viscount Melville Sound, Amundsen Gulf and beyond, before migrating back to the Bering Sea (Harwood et al., 1996; Richard et al., 2001). Chukchi belugas appear to migrate from the Bering Sea to the Chukchi Sea in June and July before moving into the western Beaufort Sea for the summer and early autumn months (Suydam et al., 2001). The overall trends in abundance for these two populations are considered “unknown” based on a recent review of the status of Arctic marine mammals (Laidre et al., 2015) because there are no recent stock estimates. There is some evidence that the Beaufort stock is stable or possibly increasing (Harwood and Kingsley, 2013). There is a need to better understand how belugas use the western Beaufort Sea to predict impacts and prepare for and mitigate continuing changes in the Arctic. Such knowledge will be essential for adapting management strategies to conserve beluga populations and to ensure food security for many northern communities.

We synthesize what is known about the residency and distribution of beluga whales in this area by reviewing available aerial survey, passive acoustic, and satellite tracking data. The purpose of synthesizing these temporally and spatially diverse data sets (Table 1) is to gain a more holistic understanding of beluga distribution in the western Beaufort Sea and to develop testable hypotheses for future integrated studies of how and why belugas use this area. Previous analyses of telemetry data show that the migratory range of both beluga populations extends from the northern Bering Sea as far north as the Arctic Basin (Richard et al., 2001; Suydam et al., 2001; Hauser et al., 2014). However, our study focuses on belugas in the western Beaufort Sea from roughly 140°W to 159°W because this area has the most extensive overlap of data types, allowing constructive comparison of results from the different studies (Fig. 1). Interest in anthropogenic activities is also expanding within this region where baseline information is particularly needed (Reeves et al., 2014). In addition, the oceanography of the area around Barrow Canyon has been relatively well studied, allowing inference into ecological mechanisms that shape beluga distribution patterns in the western Beaufort Sea.

¹ These two populations are sometimes referred to as the EBS or BS (eastern Beaufort Sea or Beaufort Sea) and ECS (eastern Chukchi Sea) belugas. To avoid confusion with the eastern Bering Sea (also EBS) population of belugas, we prefer the nomenclature above.

Table 1
Temporal and spatial extent of the three data sources used in this synthesis with strengths and limitations of each.

Data Source	Geographic Extent	Sampling Period	Stock ID	Sex and Age Estimation	Calf Presence	Enable Population Density Estimation	Multi-species Sampling	Dive Data	Daylight or Weather Limitations
Tagging	Global, limited only by the whale's range	Tagging occurred in late June/early July, 1993–2012, deployments ranged 7 d ^a – 18 m	X	X	X ^b			X	
Acoustics	6 moorings, each with an effective radius of 20 km	Year-round, data from 2007–2014					X		
Aerial Surveys	67–72°N, 140–169°W	Daytime surveys, July – October 2000–2015			X	X	X		X

^a Tag deployments occurred in specific years, 1993–2012: 1993, 1995, 1997, 2004, 2005 (Beaufort belugas); 1998, 1999, 2001, 2002, 2007, 2010, 2012 (Chukchi belugas). Tag analyses were restricted to deployments ≥ 1 wk (see Hauser et al., 2014).

^b Calf presence and length was noted for the Beaufort population (see Richard et al., 2001).

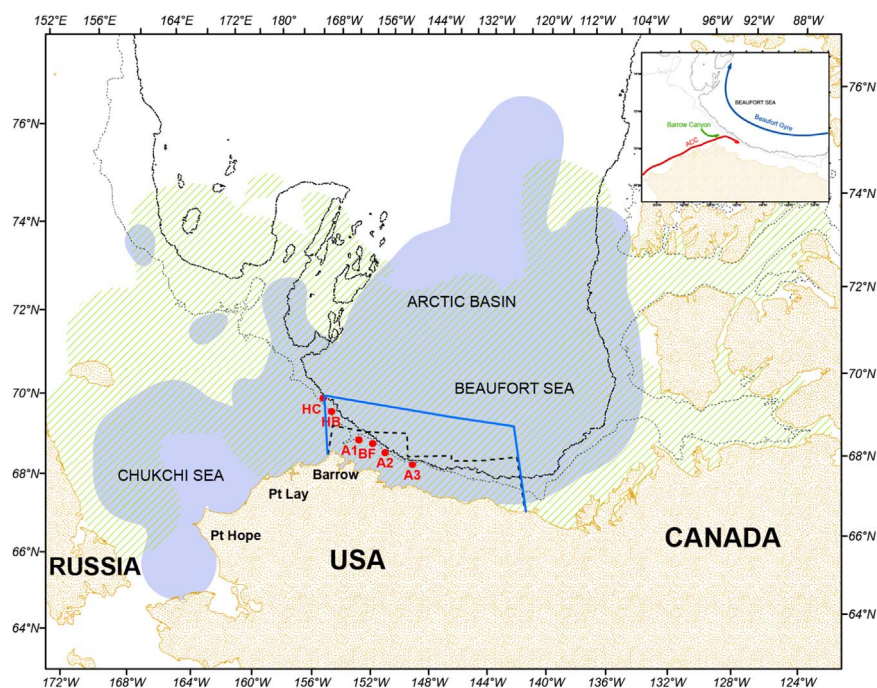


Fig. 1. Map of the Pacific Arctic, showing the geographic extent of available data used in this study. Aerial survey boundaries are shown as dashed lines, hydrophone locations as red circles, satellite telemetry home ranges as solid purple (Chukchi belugas) and hatched green (Beaufort belugas), and study area in the western Arctic outlined in blue. The inset shows predominant circulation patterns and bathymetry (200 m and 1000 m isobaths). The Alaskan Coastal Current (ACC) is shown as a red arrow, the southern limb of the Beaufort Gyre as a blue arrow, and the location of Barrow Canyon is denoted with a green arrow.

1.1. Overview of the oceanography of the western Beaufort Sea

The Beaufort Sea extends from Point Barrow, Alaska, in the west to the Canadian archipelago in the east (Fig. 1). In the western Beaufort Sea, a relatively narrow shelf (~50–100 km wide) delineates the southern extent of the sea, whereas the northern limb of the anticyclonic Beaufort Gyre roughly delineates the northern extent of the sea. The Beaufort shelf is incised by Barrow Canyon at its western end and by Mackenzie Canyon near its eastern end. Barrow Canyon is a conduit within and through which Pacific-origin water masses exhibiting different seasonal characteristics merge and enter the Arctic Basin (Gong and Pickart, 2015). The warmest and freshest of these water masses, Alaskan Coastal Water (ACW; $T > 3^{\circ}\text{C}$, $S > 30$), is carried northward along the Alaskan Chukchi coast during summer and early autumn by the Alaskan Coastal Current (ACC). In cross-section, ACW overlies somewhat cooler Chukchi Summer Water (CSW; $-1^{\circ}\text{C} < T < 3^{\circ}\text{C}$, $30 < S < 32.8$; Gong and Pickart, 2015) and denser, cold, salty Pacific Winter Water (PWW; $T < -1^{\circ}\text{C}$, $S > 31.5$; Coachman and Barnes, 1961; Roach et al., 1995). Upon exiting Barrow Canyon, these Pacific-origin waters spread out atop the dense Atlantic Water, which is a somewhat warmer layer (AW; $T > -1^{\circ}\text{C}$, $S > 34$; Gong and Pickart, 2015). The resulting mean structure of the water column overlying the continental slope in the western Beaufort Sea finds ACW near the shelfbreak (< 50 m depth), CSW between ~50 m and 100 m, PWW between ~100 m and 200 m, and AW below ~200 m. These depth regimes are approximate and shoal in response to upwelling-favorable, easterly winds and deepen under downwelling-favorable, westerly winds.

2. Data and methods

2.1. Aerial surveys

2.1.1. Aerial survey methods

The Aerial Surveys of Arctic Marine Mammals (ASAMM; formerly called the Bowhead Whale Aerial Survey Program—BWASP) project, co-managed by the Bureau of Ocean Energy Management (BOEM,

formerly Minerals Management Service, MMS) and the Marine Mammal Laboratory, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration (NOAA), conducted aerial surveys during summer and fall each year from 1989–2015, beginning as early as July or as late as September in some years, and continuing into late October in all years (Clarke et al., 2016). The entire ASAMM study area encompasses the eastern Chukchi Sea and western Beaufort Sea, extending from 67°N to 72°N and from 140°W to 169°W ; the western Beaufort Sea study area (140°W to 156°W) encompasses approximately $107,500\text{ km}^2$, or 44% of the total ASAMM study area (Fig. 1). Surveys were flown in de Havilland Twin Otter and Turbo Commander aircraft outfitted with bubble windows to allow complete visibility of the trackline. Both types of aircraft were flown in 2009–2011. Line-transect aerial surveys were flown at 305–460 m altitude, maintaining a speed of approximately 220 km/h. Transects were oriented perpendicular to shore to sample across isobaths, prevailing currents, across the prevailing direction of migration of marine mammals, and across their expected gradients in density. Transects originated at the shoreline or, when present, barrier islands. Areas inshore of barrier islands (e.g., lagoons or bays) were visible during transits between transect lines. Survey flights were conducted every day that conditions allowed, with the goal of surveying the entire area approximately every 10 days to two weeks. Allowable survey conditions generally included cloud ceilings > 335 m, visibility > 3 km, and Beaufort sea state less than or equal to Beaufort 5.

Two primary observers, one on each side of the aircraft, maintained a continuous watch for marine mammals while a third observer/data recorder entered data into a computer for each sighting, whenever survey conditions changed, or every 5 min. All marine mammals observed were recorded, regardless of species. Sighting data in this analysis were limited solely to those collected on transect because they were collected systematically over the 16-year span and represent the most consistent dataset. Data routinely logged when belugas were observed included time, altitude, position (latitude and longitude), sea state, sea-ice type and percent cover, visibility conditions, angle of declination from the horizon to the sighting (to determine distance

from the trackline), number of whales, number of calves, and the whales' initial heading and behavior. Additional details of survey protocol are provided in Clarke et al. (2016).

2.1.2. Beluga density modeling

The 2000–2015 ASAMM data were used to create a temporally- and spatially-explicit model of beluga density in the western Beaufort Sea (140°W–156°W) during summer and fall (July through October). This subset of the data was chosen because these years correspond to the “new Arctic” regime during which time sea ice loss has accelerated in summer in the Beaufort Sea and Canada Basin, driven by different atmospheric processes (Frey et al., 2015; Wood et al., 2013). This analysis involved a three-step process: 1) estimating the effective strip half-width (*ESW*) of aerial observer data collected from 1989–2015 to correct for the decreasing probability of detecting sightings with increasing distance from the trackline; 2) constructing a spatial model of beluga density, stratified by month, with data from each month pooled across years 2000–2015; and 3) applying the 2000–2015 spatial density model to predict the expected number of beluga whales in every grid cell overlying the study area. This three-step analysis used only on-transect beluga whale sightings made by primary observers, excluding sightings collected during a subset of ASAMM surveys conducted in a small area near Point Barrow during two weeks in 2015. The analysis was restricted to the portion of the ASAMM study area that was consistently surveyed in every year (140°W to 146°W, shore to 71.17°N; 146°W to 150°W, shore to 71.33°N; 150°W to 156°W, shore to 72°N; Fig. 2). This analysis did not account for trackline detection probability, and therefore represents estimates of relative densities that are undoubtedly lower than the actual density of belugas in the study area during the aerial surveys. For simplicity, we hereafter refer to density rather than relative density. The analysis was conducted in R version 3.2.4 (Core Team 2016) using packages *sp* (Bivand et al., 2013; Pebesma and Bivand, 2005), *mapproj* (Bivand and Lewin-Koh, 2015), *raster* (Hijmans 2015), *rgeos* (Bivand and Rundel, 2015), *rgdal* (Bivand et al., 2015), *mgcv* (Wood, 2006), *mrds* (Laake et al., 2015), and *gstat* (Pebesma, 2004).

To begin, *ESW* was estimated for beluga data collected throughout ASAMM's entire study area (encompassing the eastern Chukchi and western Beaufort seas) since 1989 using multiple covariates distance sampling (MCDS) methods, following the methods of Ferguson and Clarke (2013), which are reviewed briefly here. Detection probability can vary during visual line-transect surveys due to a variety of factors, including distance of the sighting from the aircraft and weather. Therefore, during a survey the number of animals sighted is often less than the number of animals at the surface of the water and available to be seen. During visual scans, ASAMM observers focus effort close to the aircraft, but their scanning range extends to the horizon. The *ESW* is the distance on one side of the trackline that would contain the same number of sightings if detection probability were equal to 1.0 as were actually detected during the survey. *ESW* is equal to the integral (equivalently, the area under) of the detection function over the range of the distance surveyed on each side of the trackline (Buckland et al., 2001). In MCDS, covariates relating to the environment, sighting, observer, or survey platform can be included in the estimation of *ESW*, thereby affecting the width of the detection function (Marques and Buckland, 2003). The covariates considered for inclusion in the detection function models related to depth where the sighting was located (*log10z* and *catZ*), Beaufort sea state (*iBeauf* and *f4Beauf*), longitude of the sighting (*long100* and *catLong*), ice percent (*catIcePct*), and observer (*obs0*) (Table 2). Depth data were from the IBCAO Version 3.0 database, which has a resolution of 500 m × 500 m (Jakobsson et al., 2012). Separate detection functions were fit to three data subsets: Twin Otter data collected from 1989–2007, Twin Otter data collected from 2008–2011, and Turbo Commander data collected from 2009–2015. Only sightings collected in sea states less than Beaufort 4 were included. The data from the Twin Otter collected after

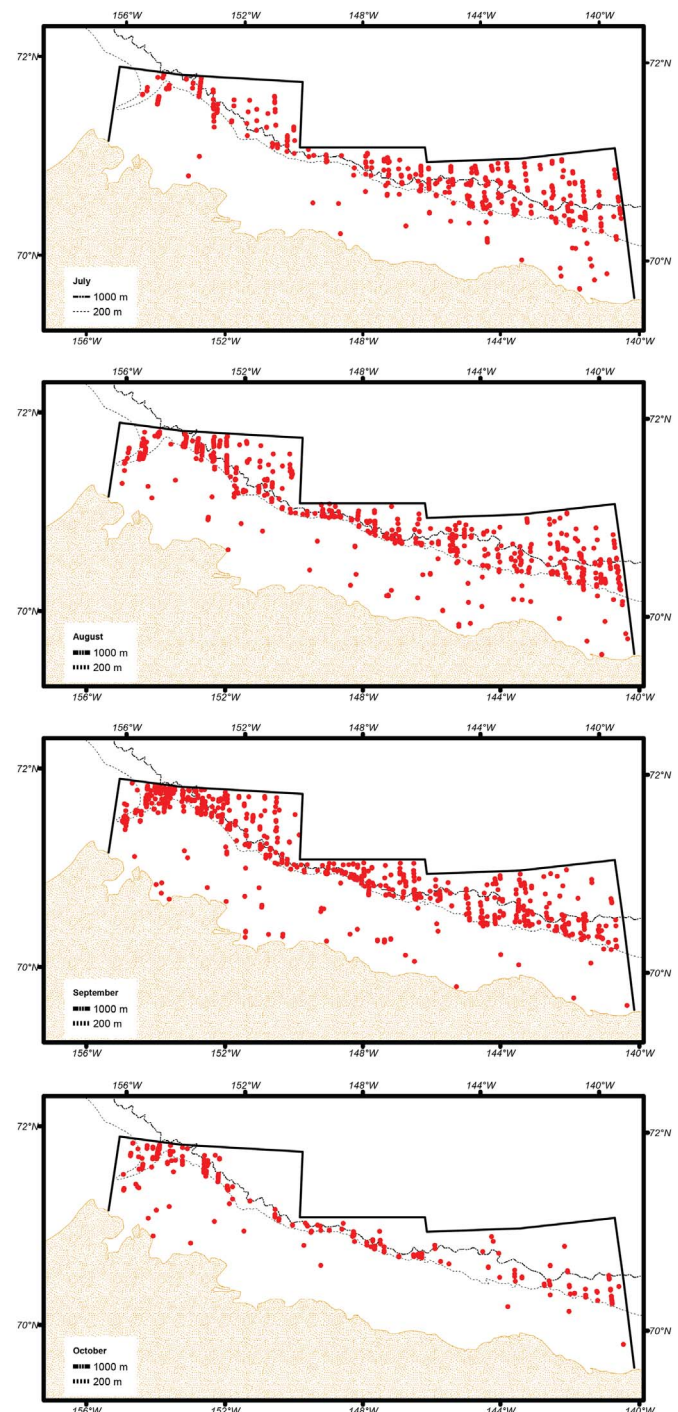


Fig. 2. Aerial survey sightings of beluga whales by month made by primary observers while on transect, July–October 2000–2015. The thick black lines show the region used for the analysis of aerial survey data shown in Fig. 3.

2007 and all of the Turbo Commander data were left-truncated by 150 m to omit a strip with lower sighting rates, likely due to the relatively short period of time objects near the trackline were in the observers' field of view. There was no apparent reduction in sighting rates near the trackline in the earlier Twin Otter data set. The farthest 5% of sightings from each data set were omitted from the detection function model construction, and only sightings collected when lateral visibility was 1.5 km or greater were included in the analyses. The detection function models were created using binned data, with bin widths of 185 m for the early Twin Otter data, 150 m for the later Twin Otter data, and 125 m for the Turbo Commander data. Model selection

Table 2

Definition of covariates considered for inclusion in detection function models.

Covariate Name	Definition	Categories
<i>log10z</i>	$\log_{10}$ of the depth of the ocean floor at the location of the sighting	
<i>catZ</i>	categorical variable for depth	{0–20 m, 20–50 m, 50–200 m, 200–2000 m, > 2000 m}
<i>iBeauf</i>	Beaufort sea state, as an integer-valued numeric variable	
<i>f4Beauf</i>	Beaufort sea state, as a categorical variable	{0–2, 3–4}
<i>Long100</i>	longitude of the sighting, scaled by $-1/100$	
<i>catLong</i>	categorical variable for longitude	{140°W–148°W, 148°W–154°W, 154°W–157°W, 157°W–169°W}
<i>catIcePct</i>	categorical variable for percent sea ice cover	{0–10%, > 10%}
<i>obs0</i>	categorical variable for "Observer Zero"	<i>obs0</i> =0 for sightings made by observer who focused search heavily on the trackline

involved forward selection of covariates, and the final models were selected based on Akaike's Information Criterion (AIC) and visual examination of the model fit to the data.

To construct the spatial model of beluga density from 2000–2015 ASAMM data, the western Beaufort Sea study area was partitioned into a 5 km × 5 km grid. This grid resolution was chosen as a compromise between having adequate survey effort and sightings in each cell in order to construct models, versus maximizing the spatial resolution of the data. Sample units were defined as unique combinations of cell (*i*), month (*j*), and aircraft (*k*). Samples having total survey effort in the 5th quantile were omitted from the analysis to remove outliers that could result in deceptively high density estimates due to minimal survey effort. All geospatial data were projected into an Equidistant Conic projection with the following parameterization: first standard parallel 69.5°; second standard parallel 71.5°; latitude of origin 70.5°; central meridian −148.0°; false easting 0.0; and false northing 0.0. Data extracted for each cell included the total number of whales sighted, the projected *X* and *Y* coordinates of the midpoint of each cell, and all relevant covariates from the MCDS models that were necessary to compute an overall estimate of *ESW* for each sample unit. Median values of the temporally dynamic covariates *catIcePct*, *iBeauf*, and *f4Beauf* were used to estimate *ESW* for each sample unit. The values of *long100*, *catLong*, and *catZ* were based on the location of the cell midpoints. The values of *log10z* represent the mean depth for each cell.

Beluga density was modeled as a generalized additive model (GAM), parameterized by a negative binomial distribution with a natural logarithmic link function. Quasi-Poisson and Tweedie (Tweedie, 1984; Dunn and Smith, 2005) models were also considered, but examination of model residuals (Ver Hoef and Boveng, 2007) suggested that the negative binomial distribution provided a better fit to the data. The model formula can be represented as

$$\ln(E(W_{i,j,k})) = \ln(\mu_{i,j,k}) = \alpha + s_j(X_i, Y_i) + month_j + offset(\ln(L_{i,j,k}) + \ln(ESW_{i,j,k}))$$

where

$W_{i,j,k}$: random variable for the number of individual beluga whales in grid cell *i* during month *j* that was flown by aircraft *k*, with *W* referring to the associated observations and $E(W)$ the expected value (mean) of *W*;

$\mu_{i,j,k}$: number of individual beluga whales expected to be observed from aircraft *k* in cell *i* during month *j*;

α : intercept;

X_i : projected (Equidistant Conic) longitude of the midpoint of grid cell *i*;

Y_i : projected (Equidistant Conic) latitude of the midpoint of grid cell *i*;

$s_j(\cdot)$: smooth function (Wood et al., 2008) of location covariates used to describe beluga whale density in month *j*; this function is parameterized in the model-fitting process;

month_j: month during which sightings were made;

$L_{i,j,k}$: length (km) of transect effort in cell *i* during month *j* that was

flown by aircraft *k*, which was incorporated into the model as a constant (an "offset") in order to account for spatially heterogeneous survey effort throughout the study area;

$ESW_{i,j,k}$: estimated effective strip width for aircraft *k* in cell *i* during month *j*, incorporated into the model as an offset in order to account for temporally and spatially heterogeneous detection probabilities throughout the surveys.

The smooth function was defined by a thin plate regression spline, with a modification to the smoothing penalty that allowed the term to shrink to zero. Furthermore, *month* was included as a factor in the smooth function, generating a varying-coefficient model that essentially defined a different smooth function for each month. Beluga whale density was estimated using the spatial model to predict the number of individuals likely to be observed in each cell during each month after a uniform amount of transect effort (a constant L_i for all *i*) was covered.

2.2. Passive acoustic data

Hydrophone packages were moored at six locations in the Beaufort Sea (BF, HB, HC, A1, A2, A3; Fig. 1) to detect marine mammal presence, including beluga whale vocalizations, at remote locations throughout the entire year. Two of these locations (HB and HC) had High-frequency Acoustic Recording Packages (HARPs; Wiggins and Hildebrand, 2007) developed, deployed and maintained by the Scripps Institution of Oceanography (SIO). The other four locations (BF, A1, A2 and A3) had Multi-electronique Aural M2 recording packages deployed and maintained by the Applied Physics Laboratory of the University of Washington and the Alaska Fisheries Science Center Marine Mammal Laboratory (Table 3).

The HARP hydrophones (HB and HC) were located 10 m off the bottom in 235 and 335 m of water, respectively, and recorded at a sample rate of 32 kHz. A recording schedule of seven minutes on and seven minutes off (50% duty cycle) was used from 2007 through 2009. The instruments recorded continuously from September 2009 through August 2010. Analysts used the Matlab-based program *Triton* to determine the acoustic presence of beluga whales. This program calculated and displayed Long-Term Spectral Averages (LTSA) and spectrograms of acoustic data, performed audio playback, and allowed analysts to log call detections (Wiggins and Hildebrand, 2007). Half-hour LTSA windows (10 s time avg, 5 Hz freq bins) were visually scanned for the presence of beluga whale calls. Analysts zoomed in on 60-s spectrogram windows (Hanning window, Fast Fourier Transform (FFT) 500 points, 70% overlap) in the corresponding sound files to confirm the identity of all calls and log them. All hours of acoustic data were scanned and one detection was logged for each hour containing beluga whale calls. In the final step of call detection, an experienced independent analyst reviewed all detections to check for identification errors and delete any misidentifications from the detection database.

The hydrophones at sites BF, A1, A2 and A3 were located ~5 m off the bottom in 40 m–120 m water depth. These instruments recorded on a 30% (9 min/30 min) or 45% (9 min/20 min) duty cycle at a sample rate of 8192 Hz or 16,384 Hz (2-byte resolution). At sites A1,

A2, and A3, each 9-min file was converted to a spectrogram (Hanning window, FFT 2048 points, 50% overlap) in the program *Ishmael* (Mellinger, 2001) and visually scanned for the presence of beluga whale calls. This resulted in a time series indicating whether at least one beluga whale call was recorded every half hour for the duration of the mooring.

For the BF site, spectrograms were analyzed as image files using an in-house MATLAB-based program (Hamming window, FFT 1024 points, 85% overlap, see Garland et al., 2015a). These image files displayed 180 s of data from 0 to 4 kHz. Beluga presence was noted for each image file at each site by an experienced analyst (ECG). As above, all acoustic data (100%) were analyzed to provide a robust data set.

When multiple years of data were available (for all locations except A3 and BF, Table 3), these were averaged by week over all years and presented as average number of hours per week with call detections to provide an overall climatological view of beluga whale occurrence. To determine if the different duty cycles of the locations (30% to continuous) might affect the weekly average detections, we compared both the total hours by week for March–June (as there was a July–September gap in recording in all three years) with detections and the average hours by week with detections for site HB. This was a site where the duty cycle was 50% from 2007–2009 and continuous from 2009–2010. There were more calls per week on average detected during continuous recording, but the overall seasonal pattern was similar among years with a 50% duty cycle (2008 and 2009) and continuous recording (2010). We did not have enough data to determine if this discrepancy could have been due to interannual variability.

2.3. Satellite telemetry

Movement and dive behavior data from satellite telemetry have been presented in a number of peer-reviewed publications including Richard et al. (2001), Suydam et al. (2001), Suydam (2009), Citta et al. (2013), and Hauser et al. (2014, 2015). Detailed methods are provided in the references noted above. In this study, monthly utilization distributions were estimated from tagged Chukchi and Beaufort belugas by modifying the approach in Hauser et al. (2014) in two ways. First, to provide a more synthetic representation of population-specific distribution, July–October utilization distributions were estimated using locations from male and female belugas combined whereas Hauser et al. (2014) estimated monthly home ranges separately for each sex. Second, the present study included more recently tagged Chukchi belugas from 2010 ($n=2$) and 2012 ($n=1$), which increased sample size. To briefly summarize methods from Hauser et al. (2014), 65 belugas (27 Chukchi and 38 Beaufort whales) were fitted with satellite-linked transmitters that provided locations through the Argos satellite system with varying spatial accuracy. Land-based and unrealistic locations were removed using a speed and angle filter (Freitas et al., 2008). The single best daily location occurring during peak transmission hours (see Hauser et al., 2014) was used to estimate monthly (July–October) home ranges (95% probability contour) and

core areas (50% probability contour). Home ranges and core areas used quartic kernel density estimation of the utilization distribution, where bandwidth was based on the maximum daily displacement (153.6 km) estimated from displacement rates in Richard et al., (2001). Tag longevity ranged from 7–521 d, but sample size was small after November; therefore, the most detailed movement analyses of whales are focused on summer and fall. Data presented here encompass only those locations and months during which belugas at least partially occupied the western Beaufort Sea.

2.4. Sea ice concentration

Sea ice concentration data (AMSR-E Aqua 12.5- and 25-km resolution) used in this study were obtained from the National Snow and Ice Data Center (Cavalieri et al., 2014a, 2014b). Daily sea ice concentrations were extracted from within a circular (20-km radius) region centered on each mooring location to provide an overall climatological view of sea ice concentration relative to beluga whale acoustic occurrence. Weekly averages of mean daily sea ice were computed for each location using the zonal statistics toolbox in ArcMap 10.0 (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute).

3. Results

3.1. Aerial surveys

Aerial survey coverage avoided areas with unsuitable weather and sea state, thus varied both inter- and intra-annually. Survey coverage in the western Beaufort Sea was greatest in September and early October, and least in July and late October (Table 4). Despite the temporal variation in ASAMM aerial survey effort, patterns in beluga distribution in the western Beaufort Sea were evident. Beluga sightings in every month primarily ranged from the continental slope to deeper waters of the basin, and in Barrow Canyon (Fig. 2). Some belugas were sighted on the continental shelf, but those sightings were relatively few and generally of single animals or small groups (< 10 whales per sighting).

Summary statistics for the beluga whale detection function models for the early (1989–2007) and late (2008–2011) surveys on the Twin Otter and the 2009–2015 surveys on the Turbo Commander are presented in Table 5. The analysis of the early Twin Otter surveys incorporated 744 beluga sightings; the best model was a half-normal model with *catLong*, *iBeauf*, and *catIcePct*, resulting in an average ESW of 632 m. The analysis of the late Twin Otter surveys incorporated 68 beluga sightings; the best model was a hazard-rate model with *log10z* and *f4Beauf*, resulting in an average ESW of 512 m. The Turbo Commander analysis incorporated 1896 beluga sightings; the best model was a half-normal model with *catIcePct*, *Long100*, and *catZ*, resulting in an average ESW of 583 m. The longitude and depth covariates are likely indirect measures of variability in beluga behavior or environmental conditions throughout the study area that affect detectability.

Table 3

Deployment information for hydrophones used in acoustic data analysis. “cont” = continuous sampling.

Name	Type	Latitude (°N)	Longitude (°W)	Water depth (m)	Dates (mo/yr)	Sample Rate (kHz)	Duty Cycle (min on/min off)
HC	HARP	72.8	–158.4	340	3/2010–8/2010 9/2010–8/2011	32	cont
HB	HARP	72.46	–157.4	235	9/2007–6/2008 9/2008–6/2009 9/2009–7/2010	32	7/14 7/14 cont
BF	Aural	71.7	153.2	105	9/2010–8/2011	8	9/20
A1	Aural	71.75	154.48	95	8/2008–8/2010	8	9/30
A2	Aural	71.45	152.0	165	8/2008–7/2014	8 or 16	9/30
A3	Aural	71.1	149.46	50	8/2008–7/2009	8	9/30

The spatial model of beluga density incorporated approximately 2000 beluga whale sightings, involving 6150 total whales, 164,500 km of transect effort, and nearly 15,000 sample units from 2000–2015 (Table 4). The total number of beluga sightings included in the models ranged from a low of approximately 260 in October, to 420 in July, 600 in August, and over 700 in September. Monthly variability was also evident in the total number of belugas sighted, ranging from 947 in July to 2259 in September (Table 4). The maximum number of belugas sighted per cell was highest in August (140 whales) and lowest in July (45 whales) (Table 6). Total transect effort varied across months, with July having the least (~12,500 km) and September the most (~86,000 km) (Table 4). The distribution of transect effort varied across cells both within and across months, with October having the least and September the most transect effort (Table 6). The final model of beluga density explained 46.1% of the deviance, requiring 96.9 effective degrees of freedom.

Beluga density varied spatially in the study area in all months, with an overall tendency for the highest densities to be over the continental slope (Fig. 3). In July (Fig. 3A), high densities were predicted to occur over Barrow Canyon and over the continental slope between 140°W and 142°W. Maximum predicted densities in August (Fig. 3B) were located over Barrow Canyon, with moderately high densities over slope waters throughout the study area. Predicted densities decreased in October (Fig. 3D), with considerably lower densities in the eastern portion of the study area compared to the summer months, although high predicted densities remained over Barrow Canyon.

3.2. Passive acoustic data

Beluga whale calls were recorded seasonally at all sites and plotted with sea ice concentration (Fig. 4). Using currently available techniques, it is not possible to differentiate the Beaufort Sea stock from the Chukchi Sea stock based on signal characteristics in the acoustic data. However, using migratory timing and results from satellite telemetry (Hauser et al., 2014) that show some differences in the core use areas of the two populations, we can speculate about the population identity of recorded animals.

At all sites along the shelf break in spring, beluga call detections began in early April when sea ice concentration was over 90%. All locations also exhibited three distinct acoustic detection periods, with the first from mid-April to mid-June, the second from late June to late August, and third from late September through early November (Fig. 4). The temporal gap in acoustic detections during the third week of June, which was consistent across recorders, may be indicative of the gap between the migration timing of the Beaufort (first period) and Chukchi (second period) belugas. Unlike the spring and early summer detections, there was no site-wide hiatus in calling in fall. Presumably, during the fall west- and southbound migration, the two populations overlap somewhat in space and time. Unlike the spring detections, which seemed uninfluenced by sea ice, fall detections declined as sea ice increased. During the spring migration, the number of weeks with calls during which ice concentration was greater than 75% ranged from

Table 4

Overview of ASAMM aerial survey data, 2000–2015, used to build the spatial model of beluga density. Numbers reflect monthly totals for the number of whales, transect effort covered in Beaufort sea state 4 or less, and number of sample units included in the model. One sample unit is defined as a unique combination of cell, month, and aircraft.

Month	Total Number of Belugas Sighted	Total Transect Effort (km)	Total Sample Units
July	947	12473.3	1582
August	1900	28012.8	2721
September	2259	85667.7	6246
October	1044	38347.8	4314
Total	6150	164501.6	14863

Table 5

Summary of detection function models for ASAMM beluga whale sightings made by observers flying on the Twin Otter (1989–2007; 2008–2011) and Turbo Commander aircraft. *ESW* = effective strip half-width.

	Twin Otter 1989–2007	Twin Otter 2008–2011	Turbo Commander
Number of Sightings	744	68	1896
Range (km)	0.000–1.295	0.150–1.350	0.150–1.400
Bin Width (m)	185	150	125
Key Function	half-normal	hazard-rate	half-normal
Scale	intercept, <i>catLong</i> ,	intercept,	intercept, <i>catIcePct</i> ,
Parameters	<i>iBeauf</i> , <i>catIcePct</i>	<i>log10z</i> , <i>f4Beauf</i>	<i>Long100</i> , <i>catZ</i>
Shape	NA	intercept	NA
Parameters			
Average <i>ESW</i> (km)	0.632	0.512	0.583
CV(<i>ESW</i>)	0.03	0.237	0.018

6 (site A2) to 12 (HC and HB), while there were no calls recorded at any site when sea ice concentration was over 75% in fall (Fig. 4).

The greatest numbers of overall hours per day with beluga detections were recorded at sites HC, HB and A1 (Fig. 4). The first two of these sites had instruments for which there was 100% duty cycle in some years (Table 3); therefore, some of the increase in detections could be due to a greater detection probability.

Site A3 was located on the outer shelf in only 50 m of water, unlike the other sites that were all in water >100 m deep. There were relatively few beluga whale detections (likely Beaufort whales) in spring and these occurred only from late April to late May. Detections of beluga whales occurred consistently and at high levels throughout July but dropped off by the end of the deployment in mid-August. In fall, whales were again heard from October into early November but at relatively low levels.

3.3. Satellite telemetry

The range of tagged Chukchi Sea belugas was centered on the western Beaufort Sea during July – October; in contrast, Beaufort Sea belugas used this area only in September (Hauser et al., 2014). Similar to previous analyses, the monthly home ranges and core areas clearly indicated that Chukchi whales were the dominant population found in the western Beaufort Sea in all summer months except September, when the two populations overlapped (Fig. 5). Beaufort belugas migrate through the Alaskan Arctic in April and May but their home range extended only into the eastern edge of the western Beaufort Sea in July and August. In July and August, a Chukchi core area was centered over Barrow Canyon, and belugas ranged eastward along the Beaufort Sea slope. Barrow Canyon remained a core area for Chukchi belugas in September, but tagged whales were distributed farther north and east than earlier in the summer. Chukchi belugas also ranged north into the Arctic Basin in all months of the study. By November, few tagged whales of either population remained in the Beaufort Sea and were instead distributed farther south in the western Chukchi Sea and Bering Strait (Hauser et al., 2014).

4. Discussion

This synthesis brings together data from aerial surveys, passive acoustic recordings, and satellite-tagged beluga whales to examine seasonal and geographic patterns in the distribution, residency, and density of this arctic species in the oceanographically complex, and changing, western Beaufort Sea. Consideration of these beluga data sets in conjunction with oceanographic (currents and hydrography), wind, and prey (e.g., Arctic cod) fields is beginning to provide insights into beluga usage of complex ocean habitats, which may ultimately provide

Table 6

Summary statistics for ASAMM aerial survey data, 2000–2015, used to build the spatial model of beluga density. Numbers reflect monthly minima, medians, means, and maxima, by cell, for the number of whales and transect effort covered in Beaufort sea state 4 or less.

	Summary Statistics	Number of Belugas Sighted Per Cell	Transect Effort Per Cell (km)
July	Minimum	0.0	2.4
	Median	0.0	5.2
	Mean	0.6	7.9
	Maximum	45.0	83.2
August	Minimum	0.0	2.4
	Median	0.0	10.1
	Mean	0.8	12.1
	Maximum	140.0	75.0
September	Minimum	0.0	2.5
	Median	0.0	26.0
	Mean	0.8	29.3
	Maximum	95.0	111.7
October	Minimum	0.0	2.4
	Median	0.0	12.8
	Mean	0.4	15.5
	Maximum	95.0	69.4

a mechanistic understanding of how and why that usage varies in time and space. Each of the data sets presented here has strengths and weaknesses, but collectively they represent complementary information about beluga whales in the western Beaufort Sea. All three data sets emphasize the importance of the Barrow Canyon region to beluga whales. Overall, the different methods were in good agreement regarding beluga occurrence, although the passive acoustic data expand this to earlier in the year than either aerial survey or telemetry data. The only seeming discrepancy among the datasets occurred in July when both the acoustic and aerial survey data showed belugas east of 154° W, west to the study area boundary but the core use area from telemetry data did not encompass this region (Fig. 6). Nevertheless, in July all three data sources identified the Barrow Canyon region as important. Indeed, although the different data sets had different spatial and temporal scales in the coverage, the effect of combining the three methods provided greater insight into *which* population of belugas uses the western Beaufort Sea, and when, as well as highlighting when both populations might overlap in space and time.

4.1. Beluga whale use of the western Beaufort Sea

All three data sources show that beluga whales occupy the western Beaufort Sea throughout the summer and fall, and that the Barrow Canyon and shelf break habitats are particularly important to belugas during the summer and fall months when they are resident in the western Beaufort Sea (Fig. 6). Our spatial density model predictions confirm these habitat preferences have been persistent over the past two decades despite changes in the environment due to decreased seasonal sea ice. Past analyses of aerial survey data established that beluga whales show a clear preference for slope/shelf break habitat (Clarke et al., 1993; Kuletz et al., 2015; Moore, 2000; Moore et al., 2000). Satellite tracking data also confirmed that the shelf break and Barrow Canyon are areas used extensively by Chukchi Sea belugas, both populations used the deep basin (Hauser et al., 2014; Suydam et al., 2001), and Beaufort Sea belugas showed preferences for the eastern Beaufort shelf break (Richard et al., 2001).

Satellite tracking data provide some insight into the population identity of beluga sightings collected during aerial surveys and acoustic monitoring in the western Beaufort Sea. Tag data suggest that belugas observed in July and August likely represent Chukchi whales (Hauser et al., 2014). It is conceivable, then, that the aerial survey data from

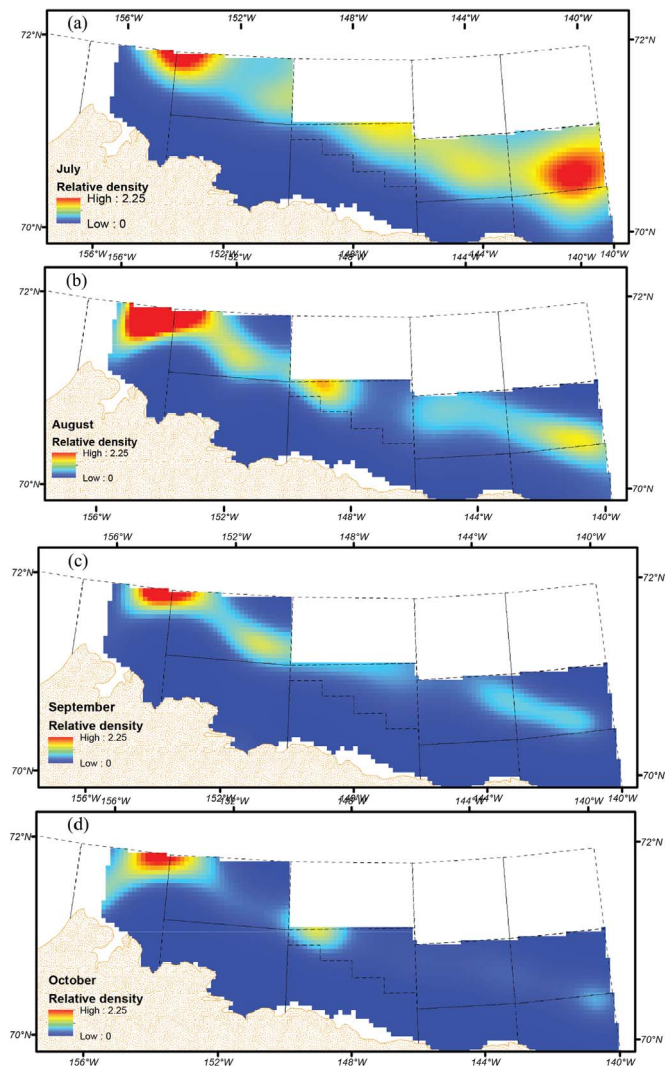


Fig. 3. Predicted density (# whales per km²) of beluga whales in the western Beaufort Sea in July (a), August (b), September (c), and October (d). Predicted densities were derived from a spatially-explicit generalized additive model, created using ASAMM 2000–2015 data, that accounted for spatial and temporal variability in effective strip width, but not for trackline detection probability.

these months might be used to derive population estimates and long-term trends for Chukchi whales, information that is critical to proper management of the population.

Tagged whales from both populations occurred throughout the study area in September, and the home range of tagged Beaufort belugas in October suggested few whales remained in the western portion of the study area in October. Belugas observed during aerial surveys conducted in September and into October likely represent animals from both the Chukchi Sea and Beaufort Sea stocks (Fig. 6). Similarly, acoustic detections in July, August and October are likely vocalizations of Chukchi belugas, while those from September could be either population (Fig. 6, Garland et al., 2015a). Such data could be useful in examining if there are population-specific vocalizations that could be used to identify which population was present at locations and times when this is uncertain, such as the Chukchi Plateau (Garland et al., 2015b; Moore et al., 2012), or in the Bering Sea.

Chukchi and Beaufort belugas exhibit sexual segregation (Hauser et al., 2014; Loseto et al., 2006), and telemetry data additionally elucidate which segments of the population are likely to be present for aerial surveys and acoustic detection within the western Beaufort Sea during July–October. Beaufort females with calves and juvenile whales select areas closer to shore, with lighter sea ice and shallower water

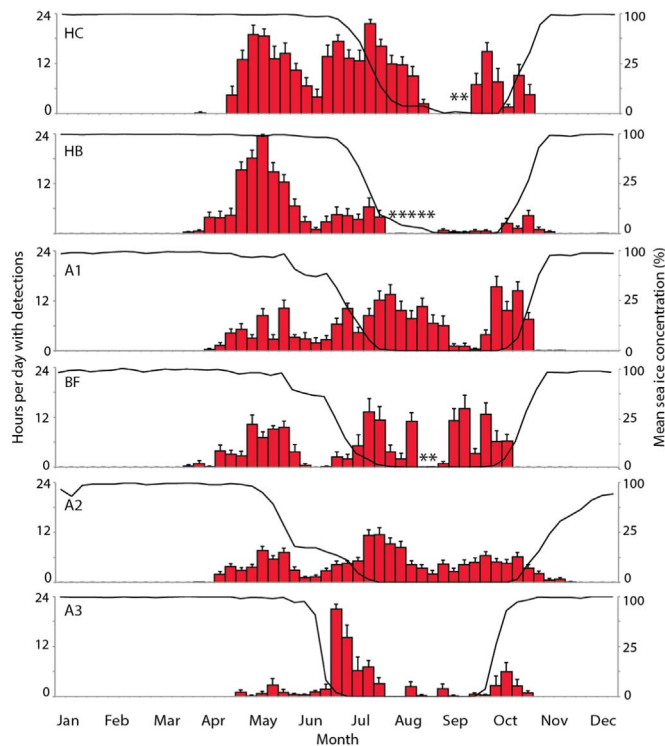


Fig. 4. Histograms of acoustic detections of beluga whale calls at mooring locations in the Alaskan Arctic (left y-axis), represented as average number of hours per week, pooled across years. Lines represent the average sea ice concentrations around each mooring location (right y-axis). Mooring locations correspond to those in Fig. 1. **indicates missing data.

than adult males in the eastern Beaufort Sea (Loseto et al., 2006), but both sexes transit the western Beaufort Sea in September (Hauser et al., 2014). Both male and female Chukchi belugas use the Barrow Canyon region as a core area from July through October, but males tend to range farther north into the Arctic Basin than females (Hauser et al., 2014). Thus, the use of the western Beaufort Sea in July and August as determined by aerial surveys and passive acoustics is likely to be biased towards females (and possibly those with calves or younger whales) of the Chukchi population.

Satellite tracking data provided valuable information about the use of the regions north of the area covered by aerial surveys. Satellite tagged belugas consistently used the Arctic Basin, with some animals reaching 80°N or 81°N (Richard et al., 2001; Suydam et al., 2001). From July–November, individuals from both populations were located in a domain from the eastern Beaufort Sea to the western Chukchi Sea and north into the deep (>3000 m) Arctic Basin. Although the two populations use similar regions of the Arctic Basin, Beaufort Sea, and Chukchi Sea, their timing is generally different and overlap is primarily limited to September (Hauser et al., 2014).

Analyses of dive data from tagged Chukchi and Beaufort belugas suggest that a combination of pelagic and benthic diving is common among the Chukchi and Beaufort seas, Barrow Canyon, and Arctic Basin regions (Citta et al., 2013; Hauser et al., 2015). Few Beaufort belugas ($n=4$) have provided diving information within the western Beaufort Sea, and these animals rapidly transited the study area (Hauser et al., 2015). Inferences about beluga diving behavior in the western Beaufort Sea are based mostly on Chukchi belugas. Citta et al. (2013) found two modal dive depths for Chukchi belugas in slope regions (75–400 m): a shallow depth stratum <50 m (presumably associated with surface-based recovery dives) and a deeper stratum centered at 250 m. There was little evidence that diving depths varied by sex or age class. Hauser et al. (2015) estimated that Chukchi belugas spent prolonged time at 200–400 m depths in Barrow Canyon and

along the western Beaufort slope, and modal dive depths were typically pelagic to 200–300 m. Beaufort belugas targeted similar depths in the study area. In addition, they also targeted 100–200 m, especially when migrating over the shelf rather than the continental slope. Although maximum dive depths of Chukchi belugas often reached the seafloor, maximum dive depths in Barrow Canyon and along the Beaufort slope margin were more commonly to a pelagic depth layer. Both analyses suggest that the depths to which Chukchi belugas typically dove in our study area (~200–300 m) corresponded to the stratified region where colder Pacific water is layered on top of warmer Atlantic water. This presumably promotes aggregation of zooplankton, thereby attracting pelagic consumers, including Arctic cod (Geoffroy et al., 2011; Majewski et al., 2016).

Our findings are consistent with earlier analyses of aerial survey and acoustic data relative to oceanographic properties in the western Beaufort Sea. Stafford et al. (2013) compared vocalizations and aerial observations of belugas with wind-driven changes to circulation and hydrography in Barrow Canyon to show that the numbers of belugas, average beluga group size, and inferred feeding behavior increased when winds strengthened the ACC and its associated frontal structure. Also in the western Beaufort Sea, Hauser et al. (2015) showed that Chukchi belugas most frequently dove to depths where a 2008 hydroacoustic survey found abundant Arctic cod (Parker-Stetter et al., 2011). Most recently, Stafford et al. (2016) showed that beluga dive behavior and inferred foraging behavior shifted proportionately from the shallow stratum to the deep stratum as upwelling-favorable, easterly winds increased.

4.2. Data sources – strengths and shortcomings

Aerial surveys for arctic marine mammals have occurred in the western Beaufort Sea every year since 1979. These surveys, conducted over nearly four decades, represent the longest-term data set presented here, encompassing more than 4800 beluga sightings ranging in group size from 1 to 750 whales. Aerial surveys are currently the only practical means to collect real-time information on beluga distribution and density over large study areas in the Arctic. Nevertheless, the aerial survey data are geographically restricted due to logistical and financial constraints, and mostly exclude the deep-water beluga habitat over some portions of the continental slope and basin. The aerial survey data are also temporally restricted by weather, daylight, and financial constraints. Furthermore, aerial survey data, like passive acoustic data, do not explicitly distinguish between the two beluga populations that use this region.

Passive acoustic data provide the best year-round information on the seasonal presence of belugas in the western Beaufort Sea. The strength of passive acoustic data is that animals can be detected year-round, even in heavy ice cover, darkness, and poor visibility, and some effort has been devoted to characterizing the acoustic repertoire of Beaufort belugas (Garland et al., 2015b). Thus, acoustic data provide an annual pattern of detections that can be correlated with environmental factors (Garland et al., 2015a; Stafford et al., 2013), extending the observation period covered by aerial surveys. In addition, efforts from industry, academia, and governmental organizations have resulted in an extensive array of acoustic moorings in the Bering, Beaufort, and Chukchi seas. Acoustic data do not, however, account for silent animals nor do they currently provide estimates of the number of animals.

Finally, the satellite telemetry data bridge some of the limitations of the aerial and acoustic data in that the population identity and sex of tagged animals are known, and age class can be estimated, allowing intra- and inter-population space use patterns (in and out of the western Beaufort Sea) to be ascertained (Hauser et al., 2014; Richard et al., 2001; Suydam et al., 2001). There are no bounds on the spatial extent of these data, and home ranges from tagged whales illustrate the areas used beyond the western Beaufort Sea. These data, however, are

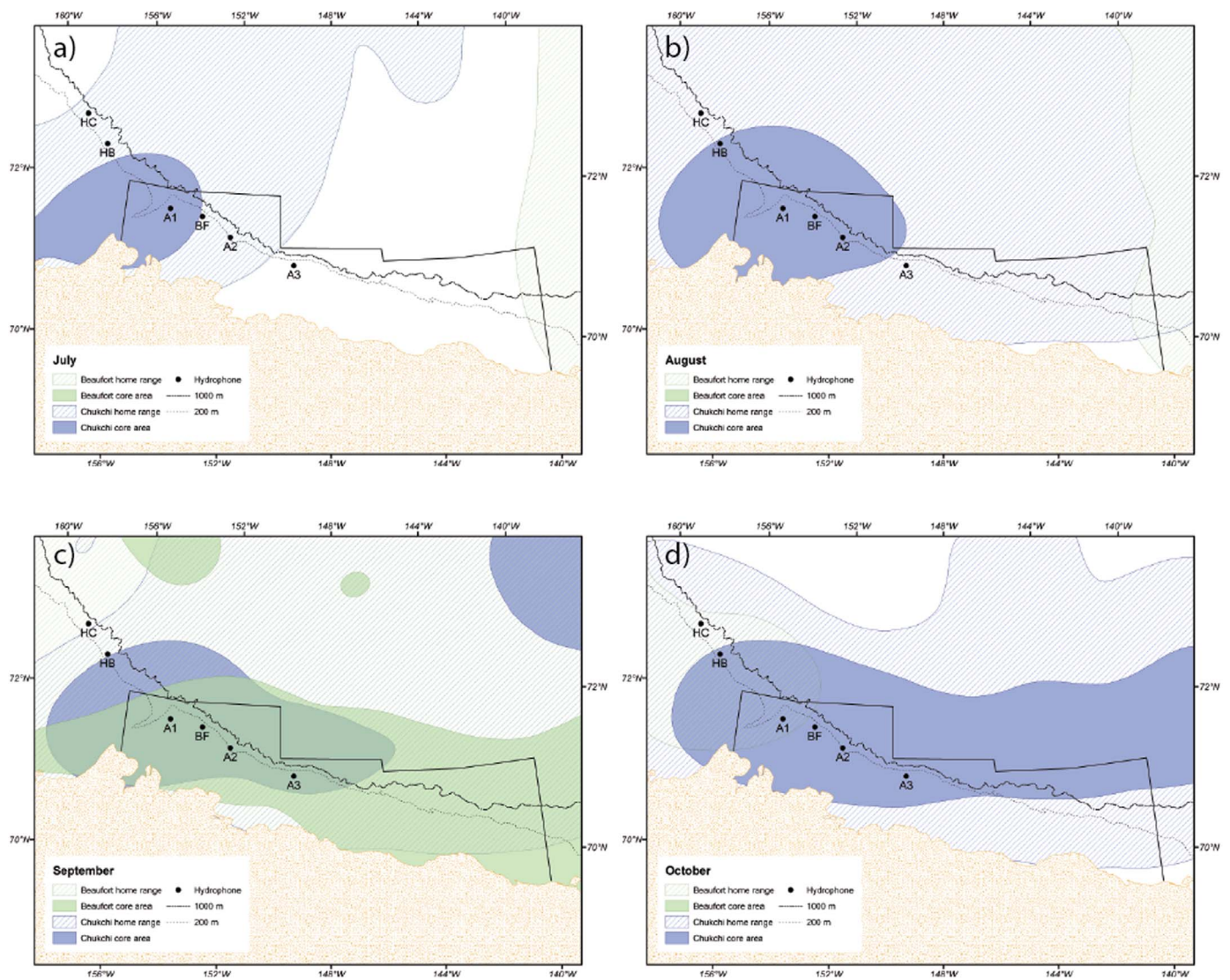


Fig. 5. Map of a) July, b) August, c) September, and d) October home ranges (lighter shading; 95% utilization distribution probability contour) and core areas (darker shading; 50% utilization distribution probability contour) of the Chukchi (purple) and Beaufort (green) beluga populations, based on telemetry data (modified from Hauser et al., 2014). Utilization distributions were based on 36, 33, 19, and 16, tagged Beaufort belugas in July–October, respectively, and 27, 23, 18, and 11 tagged Chukchi belugas in July–October, respectively. Region used for the aerial survey analysis is outlined with the solid black line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

based on relatively small sample sizes compared to population sizes, and come from animals instrumented during different years. Therefore, it is implicitly assumed that the movements of these animals are generally representative of overall population movements.

5. Beluga whales in a changing western Beaufort Sea

Our synthesis of multiple datasets spanning the 1990s to the present provides a consistent benchmark in describing beluga use of the western Beaufort Sea. This study reinforces previous studies indicating that belugas are present in the western Beaufort Sea from April through early November and are concentrated along the continental slope with a persistent hotspot in the Barrow Canyon region. Although this region is undergoing extreme environmental changes, including seasonal decreases in sea ice cover, increasing east winds and decreased transport along the Beaufort shelf break, the overall spatial distribution of belugas in the Beaufort Sea does not appear to have changed from reports from the late 1970s and early 1980s (Clarke et al., 1993; Harwood and Kingsley, 2013; Moore et al., 1993, 2000a,b,c).

We have few data on how beluga prey may have changed during this time, although a long-term study of black guillemots (*Cephus grylle mandtii*) documented a sharp decrease in use of Arctic cod as prey in the Beaufort Sea from the 1970s and 1980s to the present, likely because cod became less available (Divoky et al., 2015). Beluga whales, however, have a catholic diet overall, likely feeding on larger size cod (Quakenbush et al., 2015), and are deeper divers than guillemots (maximum recorded dive depth 40 m, Madsen et al., 2013). Recent studies have determined that Arctic cod are widely distributed and abundant in the western Beaufort Sea (Logerwell et al., 2015; Parker-Stetter et al., 2011). Comparisons of acoustic and satellite telemetry data with physical oceanography and wind suggests that belugas change their dive behavior as environmental conditions change, likely because these conditions influence the distribution of their prey. Beluga distribution is well correlated with oceanographic features that help aggregate prey, such as Arctic cod (Hauser, 2016; Hauser et al., 2015; Stafford et al., 2013, 2016). While stomach content analysis indicates that most belugas in the Chukchi and Beaufort seas consume shrimp (*Crangon* spp) and cephalopods (octopus and squid, Quakenbush et al., 2015; Seaman et al., 1982), fatty acid analysis

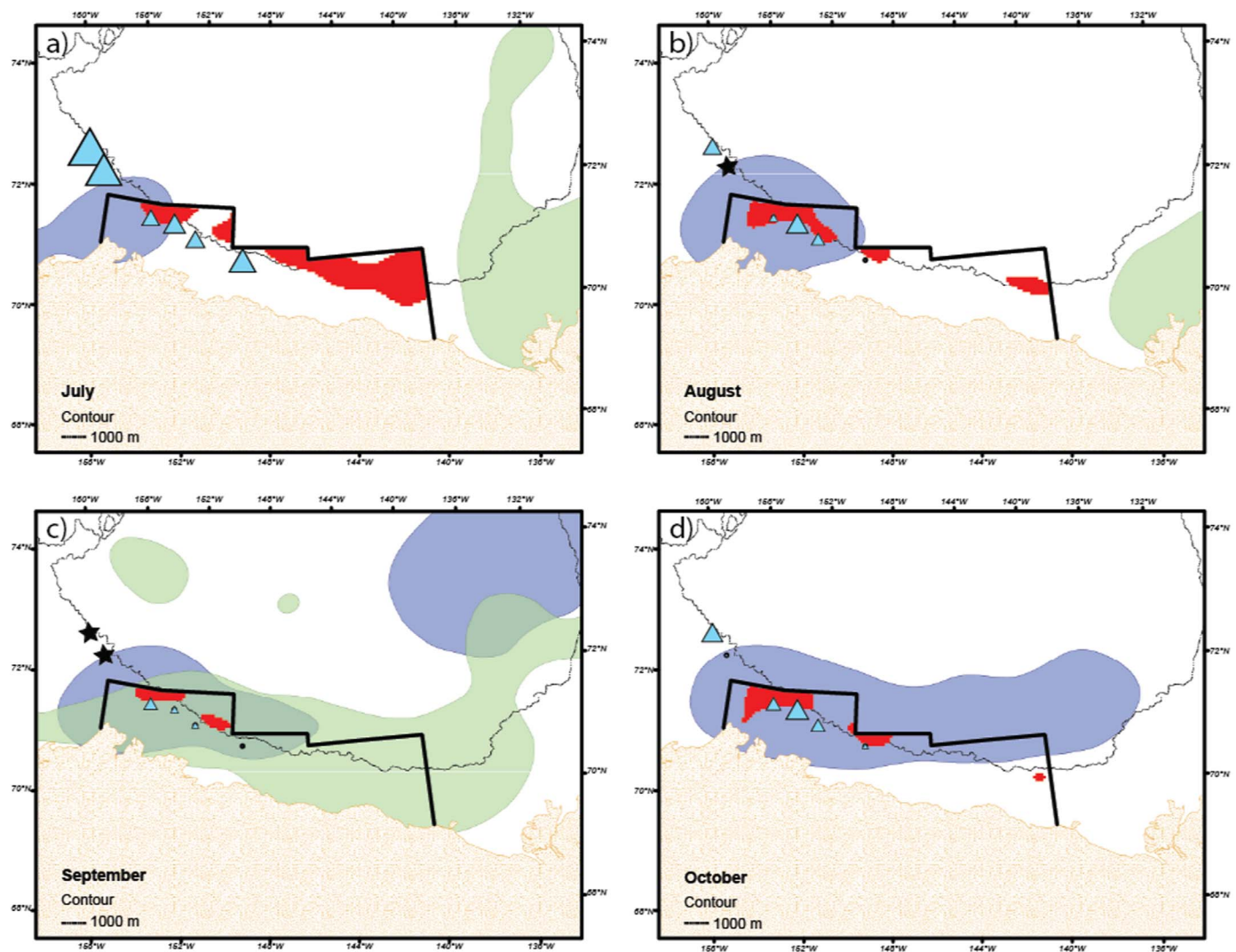


Fig. 6. Synthesis of three data sources used to examine beluga occurrence in the western Beaufort Sea by month. a) July; b) August; c) September; d) October. Total number of hours of acoustic detections of beluga whales at each hydrophone location shown as blue triangles (triangle size scaled by month, black stars indicate no data available, small black circles show no calls); Regions with greater than 0.25 whales/km² from aerial survey data (red shading); Core use areas from satellite telemetry shown for Chukchi (purple shading) and Beaufort (green shading) belugas. Region used for aerial survey analysis is outlined with solid black line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

indicates that Arctic cod are the major prey of belugas in the northern Chukchi and Beaufort seas (Loseto et al., 2006). Clearly, additional work is needed to further investigate predator-prey dynamics, preferably through programs that can simultaneously sample belugas, Arctic cod, other potential prey, and the environment in which they live.

Finally, although the spatial distribution of belugas in the western Beaufort Sea has been consistent over decades, the question arises as to whether the temporal distribution has changed in response to regional changes, particularly in sea ice extent. Recent analyses comparing the Chukchi and Beaufort beluga telemetry data between the 1990s and 2010s suggest habitat selection in the western Beaufort Sea has not changed (Hauser, 2016), although Chukchi belugas appear to have extended their occupancy of the western Beaufort Sea in October as sea ice advance has occurred later in recent years (Hauser et al., 2016). Passive acoustic detections of beluga whale calls may be a robust way to examine this going forward. Unfortunately, the earliest year-round acoustic data records of belugas were collected only a decade ago. Nevertheless, such data could be used to test if belugas are migrating earlier and spending more time in the western Beaufort Sea in the fall as the open water season continues to expand.

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The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service.

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