

*Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*)*

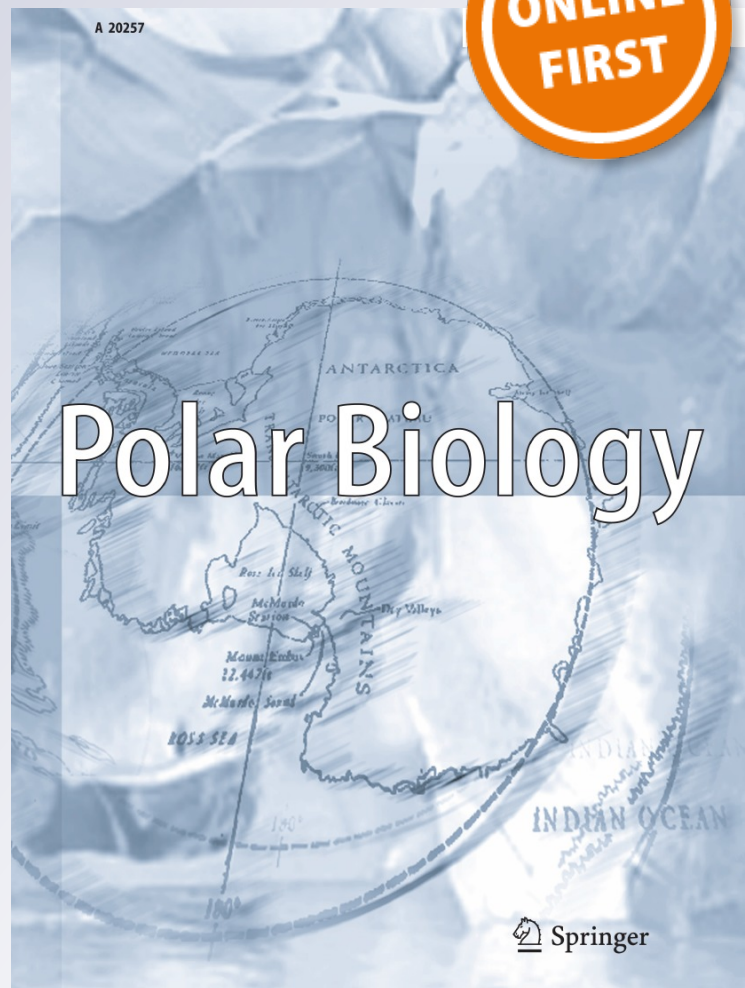
**Donna D. W. Hauser, Kristin L. Laidre,
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Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*)

Donna D. W. Hauser · Kristin L. Laidre ·
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Abstract Two populations of beluga whales (*Delphinapterus leucas*), the Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS), make extensive seasonal migrations into the Pacific Arctic. However, the extent to which these populations overlap in time and space is not known. We quantified distribution and migration patterns for BS and ECS belugas using daily locations from whales tracked with satellite-linked transmitters. Home ranges and core areas in summer (July and August) and in each month (July–November), daily displacement, dispersal from core areas, and autumn migration timing were estimated. Distinct summer and fall distribution patterns and staggered autumn migration timing were identified for BS and ECS whales. Summer home ranges for each population had less than 10 % overlap. Monthly home ranges were also relatively distinct between populations except in September (up to 88 % home range overlap). A distinct east–west shift in focal area use occurred in September that persisted into October, with the two populations essentially switching

longitudinal positions. Highest daily displacements occurred during the migratory period in September for BS whales and October for ECS whales, further indicating westward fall migration was offset between populations. Sexual segregation of males and females within a population also varied monthly. Autumn migration timing as well as differences in spatial and temporal segregation between BS and ECS beluga populations may be a result of maternally driven philopatry and population-specific adaptations to dynamically available resources. Our results contribute to the management of these populations by identifying seasonal area use and differences in migration patterns.

Keywords Arctic · Spatial and temporal variability · Habitat use · Home range · Seasonal migration · Sexual segregation · Beaufort Sea · Chukchi Sea

Introduction

Ecological theory predicts that co-occurring species limit competition by occupying different physical locations or focusing on unique prey species (Roughgarden 1976), yet most research on niche separation focuses on multi-species assemblages rather than considering intra-specific patterns of spatial or temporal segregation. Particularly for resource-limiting systems, spatial and temporal segregation in distribution patterns may result from competition between populations, age classes, or different sexes of individuals of the same species. Furthermore, social structure can reinforce intra-species site fidelity or movement patterns as described for a variety of taxa, including birds, turtles, and whales (e.g., Hawkes et al. 2007; Hoelzel et al. 2007; Harrison et al. 2010).

D. D. W. Hauser (✉) · K. L. Laidre
School of Aquatic and Fishery Sciences, University of
Washington, Box 355020, Seattle, WA 98195, USA
e-mail: dhauser@uw.edu

K. L. Laidre
Polar Science Center, Applied Physics Laboratory, University of
Washington, 1013 NE 40th Street, Seattle, WA 98195, USA

R. S. Suydam
North Slope Borough Department of Wildlife Management,
PO Box 69, Barrow, AK 99723, USA

P. R. Richard
Freshwater Institute, Fisheries and Ocean Canada, 501
University Crescent, Winnipeg, MB R3T 2N6, Canada

For top marine predators in Arctic environments, such as cetaceans, prey resource availability is constrained seasonally due to short periods of open water (Bluhm and Gradinger 2008). In response to this extreme seasonality, many Arctic cetaceans exhibit migratory life histories that presumably maximize accessibility to available resources (e.g., Dietz et al. 2008; Citta et al. 2012; Bailleul et al. 2012). One species, the beluga whale (*Delphinapterus leucas*), is a highly social, medium-sized cetacean that uses estuaries, continental shelves, slopes, and deep basins of the circumpolar Arctic (Stewart and Stewart 1989). Population-specific movement patterns are presumably driven by intrinsic factors (i.e., natal homing, predator avoidance, access to molting areas), and environmental forcing (i.e., seasonal presence of sea ice, resource availability) causing populations to become increasingly genetically differentiated due to inter-generational and maternally driven philopatry (O'Corry-Crowe 2008; Turgeon et al. 2012).

In the Pacific Arctic, two beluga whale populations conduct northward migrations from the Bering Sea in spring to summering areas north of Alaska and western Canada where they molt, forage, and give birth (Frost and Lowry 1990). Traditional (Huntington et al. 1999) and scientific (Frost and Lowry 1990) knowledge confirmed by genetic analyses (O'Corry-Crowe et al. 1997) identified two main summering areas: the Eastern Chukchi Sea (ECS) population concentrated near northwest Alaska in the southeast Chukchi Sea and the Eastern Beaufort Sea (BS) population using the eastern Beaufort Sea near the Mackenzie River Delta. Minimum population estimates are based on surveys from the 1990s, but the BS population (39,258 whales) is approximately an order of magnitude larger than that of the ECS (3,710 whales) (summarized in Allen and Angliss 2013). While individuals from each population have been observed moving beyond the bounds of these summering areas (Suydam et al. 2001; Richard et al. 2001; Suydam 2009), to date no analyses have quantified their spatial and temporal overlap.

Aerial surveys of belugas in the Alaskan and Canadian Beaufort Sea indicate associations with slope and basin waters and moderate to heavy ice levels in spring–summer, with a shift to more shallow shelf waters in fall (Moore 2000; Moore et al. 2000; Asselin et al. 2011). Observations from aerial surveys, however, cannot be attributed to specific populations. Passive acoustic monitoring (i.e., recordings of underwater vocalizations) also indicates the importance of specific bathymetric and oceanographic features for beluga whales, such as Barrow Canyon north of Alaska (Stafford et al. 2013), but population identity of vocalizing individuals cannot be determined. While the geographic distributions of both populations encompass broad regions of the Pacific Arctic, population-specific spatial and temporal overlap and potential resource

partitioning are unknown. This information is vital for informed conservation and management, particularly in the context of changing Arctic ecosystems and as integral cultural and subsistence resources for Inupiat and Inuvialuit communities. Knowledge of population-specific spatial distribution is required when assessing impacts of dramatic physical changes in regional sea ice dynamics (e.g., Steele et al. 2010) as well as increasing anthropogenic interests in the region (e.g., marine shipping, oil and gas exploration and possible development, commercial fishing, and research or tourism activities).

The purpose of this study was to quantify summer and fall spatial and temporal overlap and segregation between males and females of two Pacific Arctic beluga whale populations using satellite telemetry over the period 1993–2008. We also distinguish autumn migration timing between sexes and populations. Using daily locations of satellite-tracked individual whales from both populations, we identify: (1) summer (encompassing July–August) population-specific core areas and home ranges; (2) specific July to November male and female monthly core areas and home ranges; and (3) sex-specific autumn migration timing.

Methods

Study region: Pacific Arctic physical environment

The waters of the Pacific Arctic continental shelf are made up of the Chukchi and Beaufort seas (Fig. 1). Situated off the northern and western coasts of Alaska, northeastern Russia, and northwestern Canada, the region provides a connection between the North Pacific and Arctic oceans for both biological and physical processes. The Chukchi Sea is shallow (mean depth = 58 m) and wide and contains a network of shoals and submarine canyons, while the Beaufort Sea to the east is a thin continental shelf (mean depth = 80 m) along the margins of the deep Canada Basin (Carmack and Wassman 2006). Seasonal sea ice cover is the dominant physical characteristic of this region, with minimum sea ice extent in September, ice coverage during winter, and the maximum in March before breakup. The Chukchi Sea, through Bering Strait, is a major inflow of Pacific water into the Arctic Ocean. Dynamic water properties of predominant circulation patterns in the region contribute to extreme productivity during spring and summer periods of ice retreat (Arrigo and van Dijken 2011).

Tagging procedures and location filtering

Beluga whales from the BS population were captured and tagged with satellite-linked transmitters in the Mackenzie

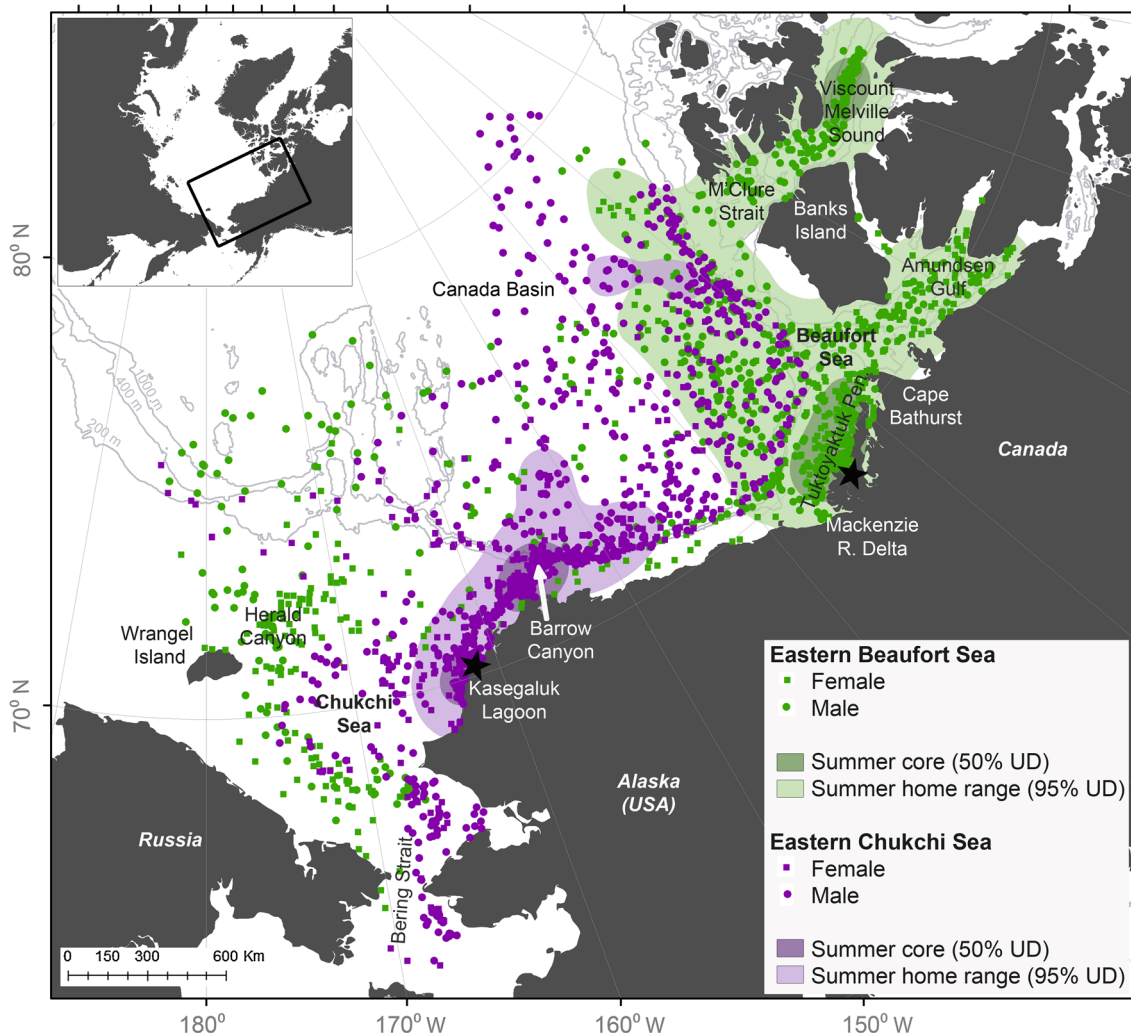


Fig. 1 Daily locations of BS and ECS satellite-tagged beluga whales ($n = 40$ and 24 , respectively), July–November, and place names mentioned in the text. *Shaded polygons* represent the summer (i.e.,

July and August) core areas [50 % probability contour of the utilization distribution (UD)] and home range (95 % probability). *Black stars* indicate approximate tagging locations

River Delta, Northwest Territories, Canada primarily in early–mid July in 1993, 1995, 1997, 2004, and 2005 ($n = 40$; see Table 1). Similarly, 24 beluga whales from the ECS population were tagged near Kasegaluk Lagoon, northwest Alaska, USA in late June–early July in 1998, 1999, 2001, 2002, and 2007. Capture and tagging protocols for each population are described in detail for the BS (Orr et al. 2001; Richard et al. 2001) and ECS whales (Suydam et al. 2001). Tag make and model and number of days of transmission varied slightly among years and between the two populations (see Table 1). Transmitters used in the BS were manufactured by either the Sea Mammal Research Unit (SMRU; University of St. Andrews) or Wildlife Computers Ltd. (WC; Redmond, WA), while all ECS transmitters were WC models.

Satellite tags transmitted location data to polar-orbiting satellites and were subsequently obtained from Service

ARGOS. As a result of variable experimental objectives, different duty cycles were used for BS tags in an effort to extend battery life or gather information from specific time periods (see Richard et al. 2001), while ECS tags were programmed to transmit continuously. Location qualities are assigned by ARGOS to each position, with location qualities of 0–3 estimated to have errors of 1.5 km or less and those categorized as ‘A,’ ‘B,’ or ‘Z’ have no predicted accuracy. Unrealistic and poor quality locations were removed using a speed and angle filter in R version 2.13.2 (R Development Core Team 2012) using the package ‘argosfilter’ (Freitas et al. 2008). Positions exceeding a maximum between location travel velocity (6.4 km/h for BS belugas; Richard et al. 2001) and angle (measured from the track between three successive locations; set to the default) were removed by the filtering algorithm. The resulting locations for each whale were next reduced to a

Table 1 Sample sizes, mean body lengths, and tagging periods for BS and ECS beluga whales by year

Population	Year	<i>n</i> (M, F)	Transmitter make/model	Mean length (cm) ± SD	Tagging period	Mean tag duration (days) ± SD
BS	1993	4 (3, 1)	All SMRU 1	406.25 ± 70.8	10–19 July	41 ± 35
	1995	15 (11, 4)	7 SMRU 1, 8 SMRU 2	390.56 ± 34.9	3–16 July	38 ± 19
	1997	9 (6, 3)	2 WC ST-10, 5 SMRU 3, 2 SMRU 2	387.4 ± 27.2	26 July–1 Aug	85 ± 25
	2004	9 (5, 4)	All WC SPOT	381.9 ± 37.9	3–8 July	136 ± 123
	2005	3 (1, 2)	All WC SPLASH	363.2 ± 66.3	4–10 July	168 ± 111
	Total	40 (26, 14)		386.9 ± 40.5	3 July–1 Aug	81 ± 79
	ECS	1998	5 (5, 0)	All WC ST-10	419.8 ± 16.5	26 June–1 July
1999		4 (3, 1)	All WC ST-16	394.6 ± 72.4	30 June	76.5 ± 14
2001		8 (5, 3)	All WC ST-16	343.5 ± 24.8	3–7 July	81 ± 60
2002		4 (3, 1)	3 WC ST-16, 1 WC SPOT	301.0 ± 42.9	7–8 July	70 ± 10
2007		3 (1, 2)	All WC SPLASH	404.7 ± 22.7	1–Jul	260.3 ± 225.8
Total		24 (17, 7)		366.9 ± 57.6	26 June–8 July	95 ± 100

Tag duration refers to the number of days from tagging until the last location

single position per day to reduce autocorrelation bias, standardize temporal sampling, and address the effects of variable duty cycling among the tags. To obtain a daily position for each tag, the first, best quality location within the period of peak satellite passage (0100–0900 and 0000–0800 hours GMT for the BS and ECS populations, respectively) was selected each day. Daily positions, after filtering and optimal daily position selection, only consisted of ARGOS qualities 0–3. Distances between successive daily positions were calculated as the great circle route and used to compute minimum daily displacements. Daily positions for each individual were categorized by sex and month (Fig. 1), and data from all tagged individuals in each population were pooled among males or females for each month of July–November.

Data analysis

Locations were plotted using a Polar Stereographic (WGS84 Horizontal Datum) projection with a central meridian of 155°W and reference latitude of 75°N, and spatial analyses were conducted with ArcGIS version 10.0 (ESRI, Redlands, CA) unless otherwise specified. Using a fixed kernel density approach (Worton 1989), we estimated the geographic areas characterized by a high probability of use by satellite-tagged male and female beluga whales of each population. Kernel density estimators provide a non-parametric probability of using a given point in space and are reliably used to define the utilization distribution, or home range, for marine and terrestrial wildlife (Kie et al. 2010). The ‘kde’ tool in the program Geospatial Modeling Environment (available online from spatialecology.com/gme), which relies on the ‘ks’ package in R (Duong 2004, 2014), was used to calculate quartic kernel density, with

cell size set to 500 m and bandwidth set to 146.9 km. Cell size determines the smoothness of the resulting prediction, but has minimal impact on kernel density estimation relative to bandwidth selection. The bandwidth controls the width of the estimated kernel thereby determining how much regional variation is emphasized. Here, bandwidth selection was based on biologically relevant parameters measured from BS whales as the maximum daily travel distance, calculated from the documented maximum daily speed for beluga whales (Richard et al. 2001). Overlapping land was removed, and kernel densities were then rescaled relative to the maximum value to facilitate comparisons among sexes, populations, and months. Male and female BS and ECS home ranges (defined as the 95 % probability) and core areas (defined as the 50 % probability) were estimated for each month (July–November), while BS and ECS home ranges and core areas were estimated for pooled male and female locations for the summer period (July–August, Richard et al. 2001). The overall area was calculated for each resulting home range estimate using the ‘addarea’ tool in Geospatial Modeling Environment, and the ‘intersect’ tool in ArcGIS was used to identify overlapping home ranges between populations. The proportion of home range overlap (Feiberg and Kochanny 2005) was also calculated as:

$$HR_{i,j} = A_{i,j}/A_i$$

where $HR_{i,j}$ is the proportion of population i 's (or sex-population group) home range that is overlapped by population j 's home range, such that A_i is the total home range area of population i , and $A_{i,j}$ is the area of overlap between the two population's home ranges. Inter-annual variation in summer home range estimation was also assessed for both populations by successively removing 1 year, re-estimating

the summer home range, and then calculating the proportion of summer home range overlap relative to the home range estimated for pooled years.

Several measures were used to assess spatial segregation and autumn migration timing for BS and ECS populations. Monthly spatial separation and overlap were estimated by calculating mean daily longitudes for each individual whale between July and November. Mean daily displacements (km/day) were also calculated for each month, where higher relative displacements were assumed to correspond to directed migration through an area. Two measures of movement away from the population-specific summer core areas were estimated: (1) the mean last day of the year that an individual was observed within their population's summer core areas and (2) the mean monthly distance individuals traveled away from their population's summer core area, measured as the shortest linear distance from the closest summer core area edge. To account for repeated measures of individual tagged whales, a series of mixed effect models with Gaussian error were used for each population to compare mean responses in monthly longitude, daily displacements, and daily distances from summer core areas between sexes using the 'nlme' package in R (Pinheiro et al. 2013). In each case, model specification followed procedures outlined in Zuur et al. (2009) for model selection with fixed (month and sex, in this case) and random effects (individual whales). Two-factor analysis of variance was used to assess differences in mean departure dates from summer core areas between populations and sexes.

Results

Tagging

Sixty-four beluga whales were captured, tagged with satellite transmitters, and used in these analyses, including 40 and 24 from the BS and ECS populations, respectively (Table 1). In total, 17,883 ARGOS locations were received for BS whales and 20,755 for ECS whales over the entire data set (tagging years 1993–2007, see Table 1). Filtering reduced the datasets to 12,193 (68.2 % acceptance) and 13,713 locations (66.1 % acceptance), respectively. Selecting daily locations resulted in a final dataset of 1,131 BS and 1,595 ECS locations. Tagging durations for filtered daily locations ranged from 10 to 301 days (mean = 71.1 days) and 5–522 days (mean = 93 days) for BS and ECS whales, respectively. For all subsequent analyses, locations were restricted to July–November for a total of 1,082 BS and 1,396 ECS locations. Monthly sample sizes for kernel density analyses averaged 108.2 and 139.6 daily locations for BS and ECS whales, respectively, and ranged from 13 to 274 daily

Table 2 Monthly sample sizes of daily locations and total number of tagged BS and ECS beluga whales (in parentheses) used for kernel density analyses

	July	August	September	October	November
Male					
BS	225 (22)	230 (21)	132 (11)	27 (8)	15 (4)
ECS	240 (17)	274 (14)	173 (9)	119 (4)	101 (3)
Female					
BS	123 (10)	134 (10)	98 (6)	85 (5)	13 (3)
ECS	126 (7)	150 (6)	115 (6)	70 (4)	28 (3)

locations (in November for BS females and August for ECS males, respectively, see Table 2). Inter-annual variation in summer home range estimation was minimal, with proportions of home range overlap when each year was successively removed ranged from 0.92–0.99 and 0.85–0.98 in BS and ECS whales, respectively.

Summer core areas

Summer home ranges of tracked BS and ECS whales were spatially distinct, such that there was only 3 and 8 % overlap of summer home ranges with the total ECS and BS summer home ranges, respectively (Fig. 1). The entire BS summer home range included Amundsen Gulf, the eastern Beaufort Sea shelf, shelf and slope regions west and north of Banks Island into M'Clure Strait and Viscount Melville Sound. Summer core areas for BS whales consisted of a large area (36,349 km²) north of the Mackenzie River Estuary/Delta and a smaller area (16,750 km²) in Viscount Melville Sound. The larger Mackenzie River Delta core area is recognized as a BS summering area and extended along Tuktoyaktuk Peninsula to the entrance of Liverpool Bay. This is a shallow (<80 m) and turbid water body where belugas are traditionally harvested by local Inuvialuit communities (Harwood et al. 2002). The smaller BS summer core area centered over a deep trench area (100–600 m) in Viscount Melville Sound and was only used by male BS belugas tagged in 1993, 1995, and 2004. No whales tracked in 1997 or 2005 used Viscount Melville Sound, although tag durations and duty cycling for males in 2005 may have precluded detection in the northern core area.

The ECS summer home range was ~65 % smaller in area than that of the BS and primarily restricted to the continental shelf and slope north of Alaska in the northeast Chukchi and western Beaufort seas (Fig. 1). A small separate portion of the ECS summer home range overlapped with the BS summer home range and was located over the slope and deep Canada Basin west of Banks Island. Similar to BS whales, there were also two summer core areas estimated for ECS whales, comprising a total of 23,638 and

Table 3 Proportion of home range overlap (HR) estimated for monthly (July–November) home ranges of BS and ECS male and female belugas, based on Fieberg and Kochanny (2005)

	Proportion of home range overlap (HR)				
	July	August	September	October	November
HR _{BS male, ECS male}	0.00	0.002	0.70	0.26	0.15
HR _{BS male, ECS female}	0.00	0.00	0.88	0.41	0.18
HR _{BS female, ECS male}	0.00	0.17	0.45	0.22	0.27
HR _{BS female, ECS female}	0.00	0.00	0.59	0.28	0.35
HR _{ECS male, BS male}	0.00	0.002	0.32	0.40	0.62
HR _{ECS male, BS female}	0.00	0.22	0.27	0.46	0.54
HR _{ECS female, BS male}	0.00	0.00	0.42	0.53	0.55
HR _{ECS female, BS female}	0.00	0.00	0.37	0.49	0.52

7,374 km². The larger summer core area was north of Point Barrow, Alaska, centered directly over Barrow Canyon. A smaller summer core area was located ~152 km southwest just offshore of a series of barrier islands that create a complex lagoon system, centered on Kasegaluk Lagoon, where beluga whales are known to congregate in June and July and are subsistence harvested annually (Huntington et al. 1999).

Monthly summer and autumn distribution patterns

July–November monthly home ranges, home range overlap, and core areas were estimated for males and females of both populations (Table 3; Fig. 2). In July, the two populations were segregated to their respective summer home ranges, with BS whales east of ECS whales and using Canadian shelf regions (Fig. 2). There was no spatial overlap between populations (Table 3). However, within a population, male and female whales exhibited distinct home range patterns. Male BS whales used several core areas in July, the largest of which was centered near the Mackenzie Delta and overlapping with the primary BS female July core area. The July home range of female BS whales was more condensed in the eastern Beaufort Sea than that of BS males. Male and female ECS whales had relatively similar home ranges in July. While both ECS males and females used a single core area just offshore of the Kasegaluk Lagoon system, ECS females additionally used a Barrow Canyon core area.

In August, the home ranges of both populations were more extensive than in July yet still distinct (Table 3; Fig. 2). The male BS home range was large, yet featured a single core area in Viscount Melville Sound. Female BS whales, in contrast, ranged more broadly than in July. There were two female BS core areas, focused in the Mackenzie Delta and Amundsen Gulf. Male ECS whales had a single core area over Barrow Canyon, but their home range extended from Kasegaluk Lagoon to the eastern Canada Basin slope, overlapping the female BS home

range (22 and 17 % of overlap of the BS female and ECS male home ranges, respectively). Only a small area overlapped along the eastern slope of Canada Basin northwest of Banks Island between BS and ECS males (2 % of each's home range). The female ECS home range and core area were constrained to Barrow Canyon and directly adjacent to western Beaufort Sea shelf and slope areas.

In September, the spatial separation of the populations eroded resulting in the greatest home range overlap (Table 3; Fig. 2). While the home ranges of ECS whales shifted east, those of BS whales transferred west. The September BS male home range covered over 2,000 km from east to west, with 70 and 88 % overlapping with ECS male and female home ranges, respectively. The September BS female home range was also large, extending from Prince of Wales Strait to the east and the northeastern Chukchi Sea to the west. Several core areas were used by BS males and females in September, including portions of the eastern and western Beaufort Sea and the Chukchi Sea near Herald Canyon. The BS female home range overlapped 45 and 59 % with ECS male and female home ranges, respectively. In September, home ranges of both male and female ECS whales were farther north and east, using the southern Canada Basin as well as the Beaufort Sea shelf and slope. While both maintained a small core area over Barrow Canyon, ECS males also had a larger core area located over the eastern Canada Basin slope.

The home ranges of BS whales shifted predominantly west of whales in the ECS population in October, although home range overlap of ECS males constituted 40 and 46 % of BS male and female home ranges, respectively (Table 3; Fig. 2). Home range overlap of ECS females was 53 and 49 % of BS male and female home ranges, respectively. Male and female ECS whales shifted their home ranges south and west in October, although not as far west as BS whales. Male ECS whales had a core area extending over the Beaufort Sea slope into Barrow Canyon and another over Herald Shoal in the Chukchi Sea. Female ECS whales used the western Beaufort and Chukchi seas in October.

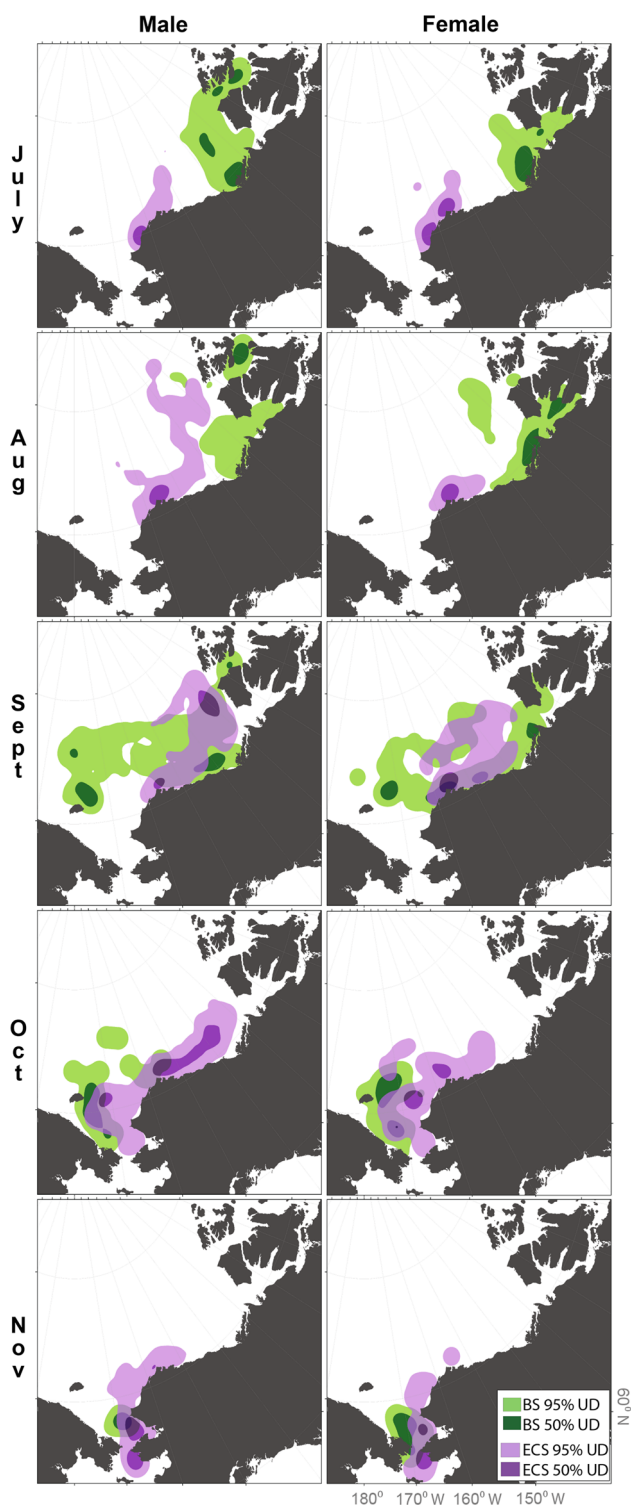


Fig. 2 July–November home ranges [95 % probability contour of the utilized distribution (UD)] and core areas (50 % probability) for male and female BS and ECS beluga whales estimated using fixed kernel density

Both populations were primarily located in the southern Chukchi Sea in November, with BS whales generally distributed west of ECS whales (Fig. 2). Male and female BS

Table 4 Results of mixed effect models of BS and ECS beluga mean longitude, daily displacement, and distance from summer core area (km) for each month (July–November) and sex

	Eastern Beaufort Sea (BS)			Eastern Chukchi Sea (ECS)		
	F value	df	p value	F value	df	p value
Mean longitude						
Month	84.514	4,58	<0.0001*	18.233	4,45	<0.0001*
Sex	–			5.288	1,22	0.0313*
Mean daily displacement (km/day)						
Month	7.54097	4,52	0.0001*	6.5512	4,43	0.0003*
Sex	–			–		
Mean distance from summer core area (km)						
Month	81.07068	4,58	<0.0001*	4.95058	4,45	0.0022*
Sex	–			5.47239	1,22	0.0288*

* Significance at $p < 0.05$

– Covariate was not selected in final statistical model

home ranges and core areas were smaller than those of ECS whales in November and reached south through Bering Strait along the Russian coast. Home ranges overlapped up to 62 % in November (for ECS male overlap with the BS male home range; Table 3). The home ranges of both male and female ECS whales extended from Barrow Canyon, along the northwest Alaska coast in the southeast Chukchi Sea, south through Bering Strait, to the northern Bering Sea north of St. Lawrence Island.

Autumn migration timing

Mixed effect models, accounting for random effects of individual tagged whales, revealed differences in movement variables for each population. A randomly varying intercept model was selected in each case, and none of the final models included interaction terms. Mean longitude varied significantly by month for both populations, but sex was only a significant predictor for ECS whales (Table 4). Mean longitude followed patterns similar to monthly home ranges, where BS and ECS whales were spatially distinct in July, shifted east in August (although ECS females less so than males), and BS whales switched to the west in September (Fig. 3). This east–west partitioning in the Chukchi Sea between animals from the two populations persisted into November.

Mean daily displacement varied significantly by month for both populations, but sex was not a significant predictor (Table 4). For BS males, the greatest mean daily displacement occurred in July (55.2 km/day) and in September (51.6 km/day), whereas relatively small displacements occurred in November (9.9 km/day; Fig. 3). A similar pattern was observed in BS females, with maximum displacements in September (57.4 km/day) and minimums in

Fig. 3 Summer and fall (July–November) migration timing shown as monthly mean longitude (± 1 SE) and relative daily displacement for satellite-tagged **a** male and **b** female BS and ECS beluga whales in the Pacific Arctic ($n = 40$ and 24 , respectively). Lines represent relative monthly mean displacement, scaled by color shading

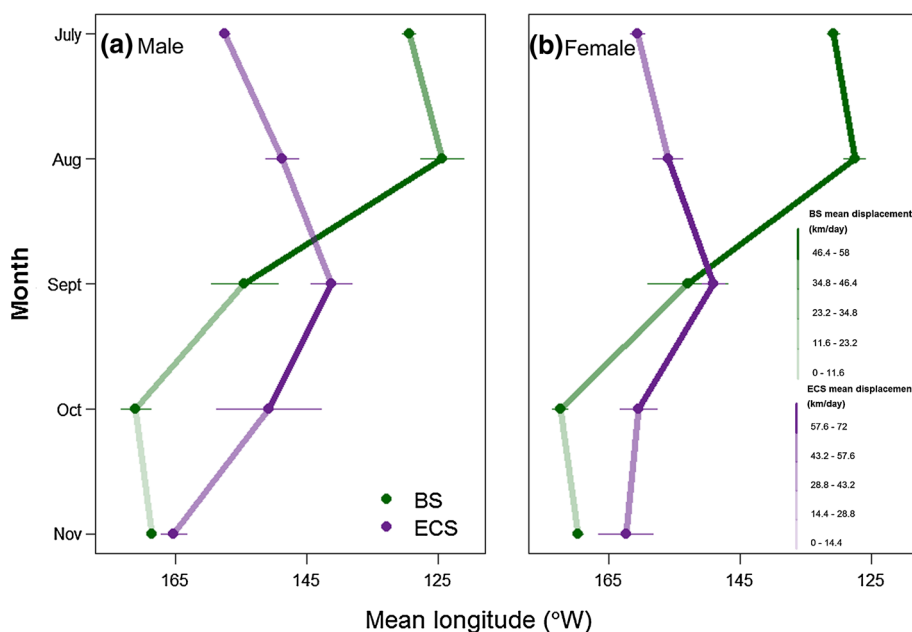
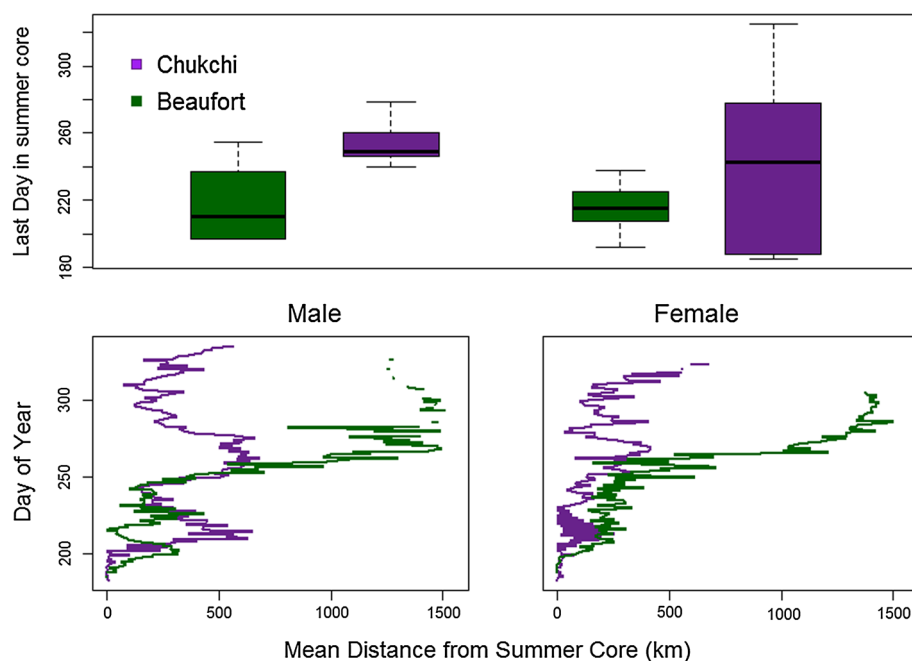


Fig. 4 Timing of migration away from summer core areas by male (left) and female (right) BS and ECS satellite-tagged beluga whales ($n = 40$ and 24 , respectively). The top panel provides boxplots of the last day of the year males and females of both populations were observed within their summer core area, while the bottom panel provides mean distances traveled away from summer core areas by day of year for males (left) and females (right) of both populations



November (18.2 km/day). In contrast, the smallest daily displacements for ECS males and females occurred in July (33.3 and 38.4 km/day, respectively). Male ECS whales exerted their greatest daily displacements in October (71.2 km/day), while females' greatest displacements were achieved in both September (65.4 km/day) and October (64.8 km/day).

The last day of the year observed within summer core areas was significantly earlier for BS whales than ECS whales, but did not vary significantly between sexes

(Fig. 4, two-factor ANOVA, $p = 0.006$, $F = 8.521$, $df = 1,38$). The mean last day in summer core areas was day 216.1 (4 August) and 243.4 (29 August) for BS and ECS whales, respectively. However, individual whales would enter and exit a summer core area multiple times, so we examined the relationship between mean distance traveled away from summer core and month. Mean daily distance traveled away from summer core areas varied significantly among months, and by sex only for ECS whales (Fig. 4; Table 4). Male and female BS whales made

directed movements away from their summer core areas in September, while movements away from summer core areas were less directed for ECS whales. Two peaks in travel away from summer core areas are apparent from male BS whales around days 200 (~late July) and 230 (~mid-August) (Fig. 4). These likely correspond to movements between the two BS summer core areas, each peak indicating approximately mid-distance between the two summer core areas: first, when whales moved from the Mackenzie Delta to the Viscount Melville Sound core area and second, when whales left the summer core areas and were near the west side of Banks Island. Unidirectional travel away from summer core areas commenced around day 245 (early September) for male BS whales, while this appears to occur slightly later for BS females (~day 255). Male ECS whales moved farthest from summer core areas in August, September, and October when they moved east and north away from the easterly Barrow Canyon core area. The maximum travel distance from summer core areas (1,102.9 km) was achieved by a male ECS whale in August. By late October, ECS males traveled back toward and through their summer core areas on the way to the southern Chukchi Sea and wintering regions in the northern Bering Sea by November. As seen in the home range analyses, ECS females generally remained closer to their summer core areas and mean monthly distance traveled away from summer core areas varied little among months. The mixed effects model confirmed that ECS males moved significantly farther from summer core areas than females (Table 4).

Discussion

The most striking components of our results were the identification of distinct summer and fall distribution patterns and staggered autumn migration timing for BS and ECS beluga whales before both populations reached their wintering areas in the Bering Sea. This behavior led to a distinct east–west shift in focal area between populations in September that persisted into October, with the two populations essentially switching positions. While both populations were located in what is typically considered their summering regions in July and August, they overlapped extensively in September as BS whales relocated west of ECS whales. The BS whales used the southern and western Chukchi Sea in October and November as ECS whales used the central, eastern, and southeastern Chukchi Sea in October and November. Autumn migration timing and movements underscore the differences in spatial and temporal segregation between populations.

Our results rely on assumptions that tagged whales are representative of the larger populations, population

distribution patterns do not vary among years, and sample sizes are adequate. Sampling bias may exist if there are nonrandom effects of capture or changes in behavior as a result of tagging. Although fewer females were tagged than males in both populations (Table 1), capture techniques were standard among years and generally occurred at approximately the same date and locations. Tagging operations coincided with subsistence harvests that are biased toward adult males, at least for ECS whales (Suydam 2009), and avoid capturing females with neonates, which accounts for sex differences in sampling. Age or reproductive status of whales is not well established in the field, but body length and coloration patterns suggest that mostly adults were captured. Thus, there is limited reason to assume that tagged whales are not representative of at least adult belugas within each population. Behavioral changes as a result of capture could also impact inferences on movement or habitat use. In the case of beluga whales, satellite tagging procedures appear to have limited impact on behavior in the days following capture or over the longer term (Orr et al. 2001). Similarly, we found little inter-annual variation in the locations and areas of home range estimates, which suggests that pooling among years is appropriate for our analyses. Belugas, similar to other cetaceans, also migrate together in groups of related individuals along established migratory routes (Colbeck et al. 2012), suggesting relatively few tagged whales could be illustrative of population-level spatial patterns. Despite extensive field efforts, it is frequently the case where only small numbers of whales can be captured and a balanced sampling design cannot be achieved for home range and movement analyses, particularly for both sexes of Arctic cetaceans (e.g., Dietz et al. 2008; Citta et al. 2012; Bailleul et al. 2012). Generally, a minimum of 30 locations is recommended for kernel density home range estimation (Seaman et al. 1999), and use of fewer locations may overestimate home range size (Seaman and Powell 1996). We achieved appropriate sample sizes of locations for nearly all months, and limited sample sizes precluded additional analyses beyond November. However, it is possible that home ranges were overestimated for some sex-population groups (e.g., BS whales in November), given the smaller sample sizes as tags tended to fail in the later months of our study.

Our analyses support earlier conclusions that beluga whales concentrate near Barrow Canyon, slope regions of the western and eastern Beaufort Sea, and near the Mackenzie Delta (e.g., Moore 2000; Moore et al. 2000; Asselin et al. 2011; Stafford et al. 2013). However, previous observations are based on aerial surveys and passive acoustics that cannot distinguish population identity. In this study, the Beaufort Sea slope was important for both populations, although BS and ECS whales segregated

along east–west gradients depending on month. Both populations also made extensive use of canyons or trenches: Viscount Melville Sound (BS males in July and August), Herald Canyon (BS whales in September and October), and Barrow Canyon (ECS males in August–October and females in July–October). Recent analyses of aerial survey and passive acoustic data, in addition to results presented here, strongly suggest the importance of Barrow Canyon in particular for aggregating prey and promoting beluga foraging. Stafford et al. (2013) showed that beluga whales appeared to use Barrow Canyon more frequently during conditions of southwest winds, which facilitate the Alaska Coastal Current (ACC) forming a stratified front along the Beaufort slope (Pickart 2004). In contrast, fewer whales were detected when strong to moderate winds from the northeast caused a reversal of flow in Barrow Canyon. The typical front system near Barrow Canyon and the western Beaufort Sea slope likely aggregates prey, and it is assumed that belugas are foraging extensively near Barrow Canyon. Although beluga detections in Stafford et al. (2013) could not be identified to population, our results strongly suggest it is ECS belugas that use Barrow Canyon. New evidence further suggests diving by ECS belugas is focused at depths typical of fronts in Barrow Canyon (Citta et al. 2013). Arctic cod (*Boreogadus saida*) are considered to be primary prey item of BS and ECS belugas (Seaman et al. 1982; Loseto et al. 2009), in addition to saffron cod (*Eleginus gracilis*), shrimp, echinurids, and smoothskin octopus (*Benthoctopus leioderma*), at least as sampled in stomachs from whales harvested in northwest Alaska in spring (Quakenbush et al. in press). Large numbers of adult Arctic cod and benthic invertebrates have been observed along the Alaskan Beaufort shelf break and associated with the ACC through Barrow Canyon (Logerwell et al. 2011; Parker-Stetter et al. 2011), as well as along the Chukchi and Beaufort seas continental slope in waters 250–350 m deep (Crawford et al. 2012). Our results generally support the hypothesis that BS and ECS distributions are linked to the dynamic oceanographic and bathymetric features impacting their prey distribution, yet more focused habitat selection modeling and analysis of diving behavior are needed.

Our results could also contribute to population assessment and harvest management of these populations by identifying when and where each population is centered each month. For example, we confirm that ECS belugas, in particular, extensively use Barrow Canyon and the western Beaufort Sea slope in summer. Whales from the BS population also transit near these features, but mainly during September. This suggests that aerial surveys conducted in the western Beaufort Sea during July and August are primarily of ECS whales. The populations cross-paths in September, but BS whales are transiting through the area

rapidly and in a directed fashion westward. In contrast, ECS whales monthly home ranges did not extend into the BS summer core areas other than ECS males, and only marginally in September when most BS whales had already shifted their home ranges to the west. The core area along the Kasegaluk Lagoon system is used extensively in summer (particularly July), and ECS philopatry to this region is well known to nearby Alaska Native villages that harvest ECS whales annually for subsistence. Local knowledge suggested that whales forage here, but the stomachs of harvested whales frequently have few prey remains suggesting limited foraging (Huntington et al. 1999; Quakenbush et al. in press). Rather, whales may be using the nearshore for their annual molt, which may be a strong motivator of spring and early summer distribution. Similarly, BS whales found in nearshore areas of the Mackenzie Delta are likely molting, as fresher and warmer estuarine waters accelerate epidermal cell regrowth for belugas (St. Aubin et al. 1990).

Our results also support previous results indicating sexual segregation of male and female belugas (Loseto et al. 2006; Barber et al. 2001). Varying sex, size, and reproductive stage of belugas will affect spatial segregation within a population, reflecting different energy requirements and survival strategies or the reduction in competition for resources. Males of both populations generally ventured farther north, with the highest latitude for daily locations $\sim 79^\circ$ and 81°N for BS and ECS males, respectively, in contrast to few individual females ranging as far as 77° and 75°N . Indeed, only BS males used the Viscount Melville Sound core area, which was never occupied by females. Belugas are sexually dimorphic, with males larger than females on average, so presumably have higher energetic demands or utilize different prey resources. Nursing females would also have high energetic demands, but may choose habitat that reduces predation or ice entrapment risk. Calves remain with their mothers ~ 2 years, and BS females with calves appear to use ice edge habitat or shallow nearshore areas (Loseto et al. 2006).

Our analyses found differences in autumn migration patterns between BS and ECS populations. Migration is a critical life history strategy for many Arctic marine species, reflecting the extreme seasonality of available resources or exclusion of certain habitats by sea ice formation, yet it can be challenging to distinguish daily movements from those more characteristic of migration. Migratory movements are considered to be persistent, somewhat oriented or unidirectional, feature displacement between distinct regions, and more rapid than movement characteristic of focused concentration in a restricted area (Dingle 1996; Stern 2002). Our analyses revealed large spatial displacements and movements from summer core

areas indicative of migratory behavior of both populations, although BS migration was particularly pronounced relative to ECS whales. Their extensive use of productive high Arctic regions during summer was punctuated with a departure likely prior to or coincident with autumn sea ice formation, which is at a minimum in September. Reports from the earliest BS and ECS tagging efforts revealed that whales ranged into regions of more than 90 % ice cover (Richard et al. 2001; Suydam et al. 2001) where they are able to exploit leads and flaws in the pack ice. Indeed, both populations exhibit extensive July–September home ranges that contract with the typical timing of sea ice advancement in October when entrapment risk increases. Migration was initiated earlier by BS whales, resulting in earlier arrival in Chukchi Sea habitats, and could be related to the greater distances they needed to travel from summer core areas to avoid autumn ice formation. However, ECS males remained east of Canada Basin into October. Acoustic detections of beluga whales near Barrow Canyon in 2008 and 2009 confirmed a similar departure pattern from the Beaufort Sea, consistent with ice formation, with the last vocalizations detected in mid-late November (Stafford et al. 2013).

Understanding spatial distribution and migration patterns are also vital for predicting potential effects of changing environmental conditions (Stern 2002). While many marine species have persisted through prehistoric climate alternations, the rate and intensity of physical changes in the Arctic are unprecedented and particularly pronounced in the Chukchi and Beaufort seas (Walsh et al. 2011). Arctic marine mammals have life histories, behaviors, and foraging strategies matched temporally to sea ice conditions that can make them particularly susceptible to broad-scale, sudden, and unidirectional changes (Laidre et al. 2008). Changes in prey abundance and composition will likely result from summer sea ice retreat, yet the impacts to foraging belugas are challenging to predict (Moore and Huntington 2008; Kovacs et al. 2011). As more generalist feeders with a broad pan-Arctic distribution, beluga whales are predicted to be more able to compensate for changing Arctic ecosystems than more specialist species with restricted ranges (Laidre et al. 2008). However, it remains to be seen if beluga whales can track changes in prey and ice over the appropriate spatial and temporal scales. Fall migration timing, in particular, seems to be linked to sea ice cover, a relationship that warrants additional research. Beyond predictions of future beluga habitat use in a changing environment, assessments of the potential impacts of anthropogenic activities in newly available Arctic regions increasingly rely on information of beluga core areas and movement patterns. Here, we have identified seasonally important areas for two beluga whale populations poised to have escalating interactions with shipping, oil and gas activities, and possibly commercial

fisheries in addition to potential ecological implications of a changing physical environment.

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