# Beluga whale distribution, migration, and behavior in a changing Pacific Arctic

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A dissertation

submitted in partial fulfillment of the

requirements for the degree of

Doctor of Philosophy

University of Washington

2016

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## Abstract

# Beluga whale distribution, migration, and behavior in a changing Pacific Arctic

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Sea ice is disappearing at unprecedented rates in the Pacific Arctic with potential impacts to ice-associated marine predators that migrate to this seasonally accessible and productive ecosystem. In this dissertation I used satellite telemetry data spanning 1993-2012 collected from two migratory populations of beluga whales (*Delphinapterus leucas*) in the Pacific Arctic (i.e., Eastern Chukchi Sea and Eastern Beaufort Sea populations) to investigate how loss of sea ice and changes in other environmental factors affect distribution, movement, and behavior. I quantified fidelity to summer areas, sexual segregation, and migration timing as well as variations in diving behavior among regions. These analyses illustrate that population-scale patterns of philopatry, migration, and foraging are mediated by the combined effects of seasonal sea ice and oceanographic fluctuations, prey distribution, and social interactions. I also addressed the question of whether belugas would adjust their distribution, migration, and behavior to shifting sea ice conditions and to what extent matrilineally-learned behavior might supersede environmental forcing through the development of resource selection functions. Results indicate that sea ice is a contributing factor but not sole determinant of beluga habitat preferences. One population (Eastern Chukchi Sea) exhibits delayed fall migration in response to later sea ice freeze-up. Changing environmental conditions also seem to favor deeper, longer dives for this population. There were few overall differences in preferred habitat selection during 1990-2014, and summer distribution appears to be governed by philopatry rather than ice conditions. These results correspond to a conclusion that Eastern Chukchi Sea belugas are responding to a changing Pacific Arctic environment through behavioral plasticity in migration timing and foraging behavior. In contrast, there were few examples where migration timing or sea ice associations of Eastern Beaufort Sea belugas changed between the 1990s and 2000s. Taken as a whole, these results suggest population-specific responses by belugas in the face of fluctuating sea ice conditions. Across the circumpolar Arctic, some beluga populations may be more likely than others to adapt and persist in a changing climate.

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# ACKNOWLEDGEMENTS

As the adage goes, “it takes a village” and this is certainly the case for my dissertation – literally and figuratively. My dissertation rests on decades of data collected in collaboration with the communities of Point Lay, Alaska, and those dotting the coast of Canada’s Northwest Territories. These villages have facilitated studies of beluga whales, and the data used in my dissertation would not have been collected without their support. Interactions with hunters and families in these communities serve as reminders that my analyses have implications for their contemporary and future livelihoods. I am especially grateful to Robert Suydam and Pierre Richard for their confidence in me, demonstrated as access to the extensive telemetry datasets previously collected under their leadership. A small but important part of my dissertation involved participating in the most recent tagging efforts in Point Lay, which were highlights of my program and I particularly thank Robert and the North Slope Borough Department of Wildlife Management for supporting my engagement.

A number of additional individuals have been instrumental in the field efforts and data processing associated with tagging two populations of belugas over several years. For belugas from the Eastern Beaufort Sea population, I thank J. Orr, who was the lead for the field work, and A. Martin and B. Leblanc for data processing. I am also grateful to the Inuvialuit Hunter and Trapper Corporations of Inuvik, Aklavik, and Tuktoyaktuk, as well as the Polar Continental Shelf Project for their support and assistance. Resources were provided by Fisheries and Oceans Canada (DFO), the Fisheries Joint Management Committee, Environmental Studies Revolving Fund, and the National Marine Mammal Laboratory of the US National Marine Fisheries Service (NMFS). The village of Point Lay and many people facilitated tagging and data processing of belugas in the

Eastern Chukchi Sea population, including L. Lowry, K. Frost, G. O'Corry-Crowe, D. Pikok, R. Small, T. Romano, J. Tazruk, B. and M. Tracey, J. Rexford, J. Orr, A. Ashby, V. Dollarhide, L. Ferreira, L. Pierce, L. Stalker, H. Smith, R. Hobbs, R. Hoover, T. Nukapigak, M. Sparck, S. Speckman, D. Susook, C. Aniskette, J. Tuckfield, C. Rea, G. Marshall, N. Hank, L. Hansen, L. Hoberecht, L. Quakenbush, T. Robeck, A. Simon, G. and K. VanBlaricom, J. Taylor, J. Edwards, D. Ramey, B. Achootchook, and J. Citta. Resources were provided by the Alaska Beluga Whale Committee, North Slope Borough of Alaska, Village of Point Lay, NMFS, Alaska Department of Fish and Game, Minerals Management Service, and National Fish and Wildlife Foundation. Tagging was conducted under Marine Mammal Protection Act permits (nos. 14620, 782-1438, and 782-1719) for Chukchi whales and DFO obtained permits required for Canadian work.

My research would not have been possible or as broad in scope without the support of several key collaborators. In addition to data and organizational support contributed by Pierre Richard and Robert Suydam, I am grateful to additional co-authors of the papers that have or will result from my dissertation. Kristin Laidre provided expert direction and oversight in each case. Harry Stern was an incredible resource and collaborator for anything involving sea ice, which was invaluable to the development of chapters 4 to 6. Sandy Parker-Stetter was a superb collaborator on Chapter 3 who, along with John Horne, contributed useful data and insights on beluga prey in the Beaufort Sea. Sue Moore helped shape the objectives and define environmental characteristics explored in Chapter 4. Similarly, the inclusion of acoustic data and expertise from Kate Stafford to Chapter 5 substantially improved the strength of our results and conclusions we could draw.

I have been fortunate for the support of two fellowships: from the School of Aquatic and Fishery Sciences (SAFS) and from the University of Washington Integrative Graduate Education and Research Traineeship Program on Ocean Change (iPOC; funded by the National Science

Foundation). The SAFS faculty and graduate students have been a haven of intellectual inspiration, as well as comradery. I am grateful for the many friendships and support gained while at SAFS, including from the Laidre Lab. The iPOC was not only vital research funding for me, but also provided an outlet to attend an international course in species distribution modeling and develop interdisciplinary research, science communication skills, and an interesting and fun side project. I am particularly thankful for Terrie Klinger's interest and support as a result of my participation in iPOC. One additional quarter of support came from a NASA Climate Indicators Program Grant (NNX13AN28G), and I was also fortunate to receive various travel grants to attend conferences from the SAFS Fisheries Interdisciplinary Network of Students, Puget Sound Chapter of the American Cetacean Society, Alaska Sea Grant, and Society for Marine Mammalogy.

Several other individuals, both within and outside the University of Washington, have been instrumental at various stages of my graduate development. Thoughtful discussion improved my perspective and approaches, particularly from Kathy Frost, Lloyd Lowry, Lori Quakenbush, Lisa Loseto, Kate Stafford, John Citta, and several members of the Alaska Beluga Whale Committee. I gained particularly useful understanding of oceanographic processes in the Pacific Arctic via interactions with Steve Okkonen and Mike Steele. Jay Ver Hoef, Josh London, Cole Monnahan, Richard McGovern, Ryan Wilson, and Elie Gurarie were valued resources for various pieces of quantitative, spatial, and R coding advice.

I spent a lot of time deciding who should compose my dissertation committee, which has proven to be time well spent. Each member contributed useful suggestions and feedback along the way, and collectively they have substantially improved the quality and scope of my research. Daniel Schindler and Rod Hobbs provided fantastic editorial assistance as members of my reading committee. Daniel helped me think with a broader ecological lens, which is precisely what I hoped he would challenge me to do. Rod's insightful comments sharpened my analytical approaches and interpretation of results. Sue Moore provided a wealth of knowledge about belugas and the Pacific Arctic ecosystem, and helped bring an oceanographic perspective to beluga ecology. I also appreciate Miles Logsdon's enthusiasm, encouragement, and expertise in spatial analyses. He contributed far more than his role as Graduate Student Representative required.

Deciding to return to graduate school, after a five year hiatus, was not a decision I made lightly and identifying an ideal advisor was one key component. I cannot imagine a better mentor for my needs and interests than I found in Kristin Laidre, to whom I owe the greatest deal of gratitude. She boosted my confidence when needed but also allowed me to develop independently, bolstered my science, improved my analytical and writing skills, served as a role model and provided inspiration by example. I am immensely grateful she took a chance on me as her first student and then also had confidence in my ability to work remotely for the last two years. I have learned so much via our collaborations and hope we can continue to partner for the rest of my career.

Last, I want to thank my family and friends. So many people have kept me nourished in mind and body. Cindy helped keep my family operational and manage the chaos of our home, particularly in the early years. I am especially grateful to my dear friends Kristi, Pete, Kristin, and Eric who have offered so much more than just their homes and hearts. I am so lucky to have family who also support my aspirations. My parents' boundless faith in me and my endeavors built the foundation upon which I have been able to succeed. My husband, Peter, is the soundest support I can imagine, and I am certain that I would not have been able to do this without him. He inspires me every day. My son Finn was a wee 14 months old when I started. His growth, energy, and love have kept me centered as well as motivated throughout the process.

# DEDICATION

For Finn, who has simultaneously been my best distraction and motivation.

# Chapter 1. INTRODUCTION

## 1.1 ANIMAL MOVEMENTS IN A CHANGING WORLD

Climate change is now recognized as one of the greatest threats to global biodiversity (Sala et al. 2000, Thomas et al. 2004, Hoegh-Guldberg and Bruno 2010, Dawson et al. 2011). Anthropogenic climate change is producing a multitude of interacting physical changes (e.g., increasing temperatures, sea level rise, loss of polar ice cover, increasing ocean acidification, glacial melt) on a number of spatial and temporal scales (IPCC 2007, Hansen and Cramer 2015). Species responses to climate change are expected to also be quite variable across marine and terrestrial habitats, and may involve poleward range expansion or vertical movement in elevation or depth, shifts in community composition, increased disease exposure, and phenological changes (e.g., Parmesan 2006, Doney et al. 2012, Poloczanska et al. 2013). Furthermore, many of these changes are occurring rapidly and at unprecedented speeds (Loarie et al. 2009, Burrows et al. 2011). It is predicted that not all species will be able to track their changing habitats nor will responses be uniform among species or ecosystems (Schloss et al. 2012, Pinsky et al. 2013, Staudinger et al. 2013).

Whether individual species can respond promptly enough to accommodate these rapid physical changes is determined, at least in part, by species-specific movement ecology (Travis et al. 2013). Observations of animal movements have been used to address a variety of research questions regarding how and why animals use heterogeneous environments, making them critical to understanding specific life history strategies, physiological tolerances, and probabilities of population extinction and colonization. Locations from tracked animals indicate individuals interacting with their surrounding ecosystems at a single point, movements between locations indicate choices made by the individual either in response to the initial location or in anticipation of the destination. Movement choices made by individuals reflect proximate responses to intrinsic and extrinsic factors that ultimately translate to individual fitness and population persistence (Hanski and Gilpin 1997, Nathan et al. 2008, Visser 2008, Cagnacci et al. 2010).

Investigations of movement parameters have been useful to understanding species distribution, resource use, population processes, behavioral ecology, and spatially structured population dynamics as well as guiding conservation and management (e.g. Costa et al. 2012, Hays et al. 2016). Our understanding of animal movements are due, at least in part, to a recent surge in modeling techniques as well as advances in biotelemetry technology (Patterson et al. 2008, Cagnacci et al. 2010, Yackulic et al. 2011). Ultimately, movement data interface individuals, populations, and ecosystems to ultimately provide insight to species responses and persistence in changing conditions, yet population-scale demographic impacts resulting from movement-related responses to changing conditions are challenging to predict (Sydeman et al. 2015, Hays et al. 2016).

## 1.2 ARCTIC SEA ICE LOSS AND TRANSFORMING MARINE ECOSYSTEMS

Arctic marine ecosystems are at the epicenter of some of the most prominent physical signals of global climate change, particularly in the case of unprecedented rates of seasonal ice loss occurring over broad spatial scales. As atmospheric warming increases Arctic Ocean temperatures, sea ice extent and thickness has decreased (Kwok and Rothrock 2009, Stroeve et al. 2012, Overland and Wang 2013), largely shifted from multi-year pack to seasonal ice (Maslanik et al. 2007, Comiso 2012), and the open water season of most regions have significantly increased (Laidre et al. 2015, Barnhart et al. 2016). Severe Arctic weather systems and freshwater inputs have also increased (McPhee et al. 2009, Morison et al. 2012, Simmonds and Rudeva 2012), and snow cover has decreased (Derksen and Brown 2012). It is currently expected that the Arctic Ocean will be ice-free in summer within only a few decades (Overland and Wang 2013).

Simultaneous to altered physical and biological habitats of the Arctic, increasing anthropogenic pressures make it particularly timely to develop detailed information on the distribution and movements of vulnerable species in anticipation of the responses of Arctic species to changing conditions (Reeves et al. 2014, Laidre et al. 2015). There have been several biotic responses to physical changes in Arctic marine, yet efforts have been primarily focused on lower trophic levels (Wassmann et al. 2011). Ecosystem impacts are expected to translate to upper trophic level Arctic marine predators, such as marine mammals. While many Arctic marine mammals have persisted through prehistoric climate alternations (Harington 2008, Murray 2008), the rate and unidirectional intensity of physical changes in the Arctic are unprecedented and most populations are relatively poorly described (Laidre et al. 2015). Arctic marine mammals are long-lived with low reproductive rates and 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). Impacts of sea ice loss are palpable for species directly dependent on ice as a platform for specialized feeding, reproduction, or resting. However it less clear what changing environments mean for Arctic marine species, such as cetaceans, that indirectly use sea ice habitat (Moore and Huntington 2008, Kovacs et al. 2011). These ice-associated species will likely be most impacted by shifts in prey productivity and community structure that result from changes in sea ice cover. Furthermore, many Arctic species are long-lived and have a social structure and specific adaptations that have facilitated their persistence in harsh and seasonal Arctic environments such as seasonal migrations that maximize resource accessibility. In a changing Arctic, special adaptations that may have previously functioned well could make these species more susceptible to novel diseases and vulnerable to new levels of competition and predation as temperate species invade (Gilg et al. 2012). Thus, adaptation via natural selection is unlikely in such a swiftly changing system, although many species can and already exhibit responses in phenotypic plasticity on more immediate temporal scales (Gilg et al. 2012).

## 1.3 RESEARCH GOALS

The overarching goal of my dissertation is to understand how animal movements are affected by a combination of intrinsic and extrinsic factors at varying spatial and temporal scales and impacted by a broader ecosystem in flux. Using satellite telemetry data collected >2 decades from two populations of beluga whales (*Delphinapterus leucas*) in the Pacific Arctic, my dissertation specifically investigates distribution, migration, and behavioral responses of each population to their highly seasonal and patchy environment in the context of a rapidly transforming ecosystem. Chapter 2 quantifies seasonal population-specific distribution and migration timing of male and female belugas, which is relevant to the conservation and management of Eastern Chukchi Sea ('Chukchi') and Eastern Beaufort Sea ('Beaufort') populations. These results also established a benchmark against which to measure changes in distribution and migration. Chapter 3 examines the behavioral ecology and environmental drivers of foraging belugas, finding that both populations target similar depths within Pacific Arctic regions. A combination of benthic and pelagic foraging behavior occurred among regions, although oceanographic properties in Barrow Canyon and along the Beaufort Sea continental shelf likely function to aggregate prey like Arctic cod (*Boreogadus saida*). Chukchi belugas most frequently dove to the same depths that Arctic cod were most abundant in a 2008 hydroacoustic survey of the Beaufort Sea (Parker-Stetter et al. 2011). I further investigated environmental drivers of distribution in Chapter 4 by estimating monthly sea ice habitat selection for both sexes and populations. While not the primary predictor of preferred habitat, sea ice was one important determinant of beluga habitat selection.

Given ice associations, two additional chapters assessed potential changes in migration phenology, behavior, and distribution patterns relative to recent loss of sea ice cover and delayed fall freeze-up. In both chapters 5 and 6, I found distinct responses by Chukchi and Beaufort beluga whales to reduced regional ice. Chukchi belugas delayed migration from Beaufort and Chukchi sea foraging areas as freeze-up occurred later in recent years compared to no changes in migration timing or correlations with freeze-up timing for Beaufort belugas, other than at Bering Strait. In 2007-2012, Chukchi belugas were also associated with significantly lower ice concentrations, farther from the pack ice, and spent more time diving deeper than in 1998-2002. I did not detect similar differences in ice conditions used by Beaufort belugas between the 1990s and 2000s, and Chukchi belugas appear to be more tightly linked to sea ice conditions than Beaufort belugas. However, I estimated that summer-fall sea ice preferences and amount of optimal habitat did not change from 1990-2014 for either population. Overall, my results of chapters 5 and 6 suggest that changing sea ice conditions may favor more extensive beluga foraging opportunities, longer into the fall, or a combination of both, for Chukchi belugas. However, the divergent responses by each population indicate that the implications of changing sea ice will not be uniform for belugas across the Arctic. Belugas may be well equipped to adapt to changing conditions, yet distinct population-specific responses complicate predictions of how belugas will fare in a transforming Pacific Arctic marine ecosystem. I briefly synthesize my overall conclusions in Chapter 7.

Lastly, it is worth noting that all chapters have been written with the intention that each will constitute a stand-alone manuscript in the peer-reviewed literature. Indeed, chapters 2 and 3 are already published (Hauser et al. 2014, Hauser et al. 2015) and included here under copyright permission from the publishers. Chapters 4 to 6 are in manuscript preparation. My research has not been conducted in isolation and several co-authors contributed to each chapter; as a result, I have sometimes used the first person plural form (i.e. “we”) when describing research in the chapters included here with the intention that these chapters will be edited in the manuscript submission process.

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# Chapter 2. POPULATION-SPECIFIC HOME RANGES AND MIGRATION TIMING OF PACIFIC ARCTIC BELUGA WHALES (*DELPHINAPTERUS LEUCAS)*

(Hauser, D. D. W., K. L. Laidre, R. S. Suydam, and P. R. Richard. 2014. Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). Polar Biology 37:1171-1183. The final publication is available online from Springer-Verlag Berlin Heidelberg at http://link.springer.com/article/10.1007%2Fs00300-014-1510-1)

## 2.1 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 management of these populations by identifying seasonal area use and differences in migration patterns.

## 2.2 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).

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 & 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; Asselin et al. 2011; Moore et al. 2000). 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 is 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.

## 2.3 METHODS

### 2.3.1 *Study Region: Pacific Arctic physical environment*

The waters of the Pacific Arctic continental shelf are made up of the Chukchi and Beaufort seas (Figure 2-1). 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 break-up. 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).

### 2.3.2 *Tagging procedures and location filtering*

Beluga whales from the BS population were captured and tagged with satellite-linked transmitters in the Mackenzie River Delta, Northwest Territories, Canada primarily in early – mid July in 1993, 1995, 1997, 2004, and 2005 (n=40; see Table 2-1). 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 (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 2-1). 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 Team 2012) using the package ‘argosfilter’ (Freitas et al. 2008). Positions exceeding a maximum between-location travel velocity (6.4 km/hr for BS belugas; Richard et al. 2001) or 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 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 hours and 0000-0800 hours GMT for the BS and ECS, 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 (Figure 2-1), and data from all tagged individuals in each population were pooled among males or females for each month of July to November.

### 2.3.3 *Data Analysis*

Locations were plotted using a Polar Stereographic (WGS84 Horizontal Datum) projection with a central meridian of $155^0$W and reference latitude of $75^0$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; Duong 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 one 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 was 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.

## 2.4 RESULTS

### 2.4.1 *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 2-1). 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 2-1). 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 10-301 days (mean = 71.1 d) and 5-522 days (mean = 93 d) 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 13-274 daily locations (in November for BS females and August for ECS males, respectively; see Table 2-2). 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.

### 2.4.2 *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 (Figure 2-1). 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 km$^2$) north of the Mackenzie River Estuary/Delta and a smaller area (16,750 km$^2$) 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 (Figure 2-1). 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 7,374 km$^2$. 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).

### 2.4.3 *Monthly summer and autumn distribution patterns*

July to November monthly home ranges, home range overlap, and core areas were estimated for males and females of both populations (Table 2-3, Figure 2-2). 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 (Figure 2-2). There was no spatial overlap between populations (Table 2-3). 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 2-3, Figure 2-2). 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 2-3, Figure 2-2). 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 2-3, Figure 2-2). 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.

Both populations were primarily located in the southern Chukchi Sea in November, with BS whales generally distributed west of ECS whales (Figure 2-2). Male and female BS 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 2-3). 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.

### 2.4.4 *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 2-4). 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 (Figure 2-3). 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 2-4). For BS males, the greatest mean daily displacement occurred in July (55.2 km/d) and in September (51.6 km/d), whereas relatively small displacements occurred in November (9.9 km/d; Figure 2-3). A similar pattern was observed in BS females, with maximum displacements in September (57.4 km/d) and minimums in November (18.2 km/d). In contrast, the smallest daily displacements for ECS males and females occurred in July (33.3 and 38.4 km/d, respectively). Male ECS whales exerted their greatest daily displacements in October (71.2 km/d), while females' greatest displacements were achieved in both September (65.4 km/d) and October (64.8 km/d).

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 (Figure 2-4, two-factor ANOVA, p=0.006, F= 8.521, df=1,38). The mean last day in summer core areas was Julian 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, but only by sex for ECS whales (Figure 2-4, Table 2-4). 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 day 200 (~late July) and 230 (~mid-August) (Figure 2-4). 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 (1102.9 km) was achieved by a male ECS whale in August. By late October, ECS males traveled back towards 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 2-4).

## 2.5 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 non-random effects of capture or changes in behavior as a result of tagging. Although fewer females were tagged than males in both populations (Table 2-1), 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 towards 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., Citta et al. 2012; Bailleul et al. 2012; Dietz et al. 2008). Generally, a minimum of 30 locations are 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., Stafford et al. 2013; Asselin et al. 2011; Moore 2000; Moore et al. 2000). 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, echiurids, 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 is 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 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 of competition for resources. Males of both populations generally ventured farther north, with the highest latitude for daily locations ~79$^0$ and 81$^0$N for BS and ECS males, respectively, in contrast to few individual females ranging as far as 77$^0$ and 75$^0$ 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 yr, 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 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 (Kovacs et al. 2011; Moore and Huntington 2008). 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.

## 2.6 ACKNOWLEDGEMENTS

A number of individuals have been instrumental in the field efforts and data processing associated with tagging two populations of belugas over several years. For the BS data, we thank J. Orr, who was the lead for the field work, and A. Martin and B. Leblanc for data processing. We are also grateful to the Inuvialuit Hunter and Trapper Corporations of Inuvik, Aklavik, and Tuktoyaktuk, as well as the Polar Continental Shelf Project for their support and assistance. Resources were provided by Fisheries and Oceans Canada (DFO), the Fisheries Joint Management Committee, Environmental Studies Revolving Fund, US Minerals Management Service, and the National Marine Mammal Laboratory of the US National Marine Fisheries Service (NMFS). The village of Point Lay and many people facilitated ECS tagging and data processing, including L. Lowry, K. Frost, G. O'Corry-Crowe, D. Pikok, R. Small, J. Tazruk, J. Orr, A. Ashby, V. Dollarhide, L. Ferreira, R. Hobbs, R. Hoover, T. Nukapigak, L. Pierce, T. Romano, M. Sparck, H. Smith, S. Speckman, D. Susook, C. Aniskette, N. Hank, L. Hansen, L. Hoberecht, L. Quakenbush, T. Robeck, A. Simon, G. and K. VanBlaricom, B. and M. Tracey, J. Rexford, J. Taylor, J. Edwards, D. Ramey, B. Achootchook, and J. Citta. Resources were provided by the Alaska Beluga Whale Committee, North Slope Borough of Alaska, NMFS, Alaska Department of Fish and Game, Minerals Management Service, and Village of Point Lay. D.D.W. Hauser was supported by the School of Aquatic and Fishery Sciences at the University of Washington and a National Science Foundation Integrative Graduate Education and Research Traineeship (University of Washington Program on Ocean Change). Thoughtful discussion and suggestions were greatly appreciated from S. Moore, C. Monnahan, E. Gurarie, K. Frost, L. Quakenbush, and J. Citta. This manuscript was also considerably improved by six anonymous reviewers. Tagging was conducted under Marine Mammal Protection Act permits issued to NMFS (Nos. 782-1438 and 782-1719) for ECS whales and all required permits for Canadian work were obtained through DFO.

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Table 2-1. Sample sizes, mean body lengths, and tagging periods for Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) beluga whales by year. Tag duration refers to the number of days from tagging until the last location.

| **Population** | **Year** | **n (M,F)** | **Transmitter make/model** | **Mean length (cm) +/- s.d.** | **Tagging period** | **Mean tag duration (days) +/- s.d.** |
|---|---|---|---|---|---|---|
| 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 | 55.8 +/- 42 |
| | 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** |

Table 2-2. Monthly sample sizes of daily locations and total number of tagged Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (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) |

Table 2-3. The proportion of home range overlap (HR) estimated for monthly (July-November) home ranges of Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) male and female belugas, based on Fieberg and Kochanny (2005).

| | **Proportion of Home Range Overlap (HR)** | | | | |
|---|---|---|---|---|---|
| | **July** | **August** | **September** | **October** | **November** |
| $HR_{\text{BS male, ECS male}}$ | 0.00 | 0.002 | 0.70 | 0.26 | 0.15 |
| $HR_{\text{BS male, ECS female}}$ | 0.00 | 0.00 | 0.88 | 0.41 | 0.18 |
| $HR_{\text{BS female, ECS male}}$ | 0.00 | 0.17 | 0.45 | 0.22 | 0.27 |
| $HR_{\text{BS female, ECS female}}$ | 0.00 | 0.00 | 0.59 | 0.28 | 0.35 |
| $HR_{\text{ECS male, BS male}}$ | 0.00 | 0.002 | 0.32 | 0.40 | 0.62 |
| $HR_{\text{ECS male, BS female}}$ | 0.00 | 0.22 | 0.27 | 0.46 | 0.54 |
| $HR_{\text{ECS female, BS male}}$ | 0.00 | 0.00 | 0.42 | 0.53 | 0.55 |
| $HR_{\text{ECS female, BS female}}$ | 0.00 | 0.00 | 0.37 | 0.49 | 0.52 |

Table 2-4. Results of mixed effect models of Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (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* |

* indicates significance at $p < 0.05$

… indicates covariate was not selected in final statistical model

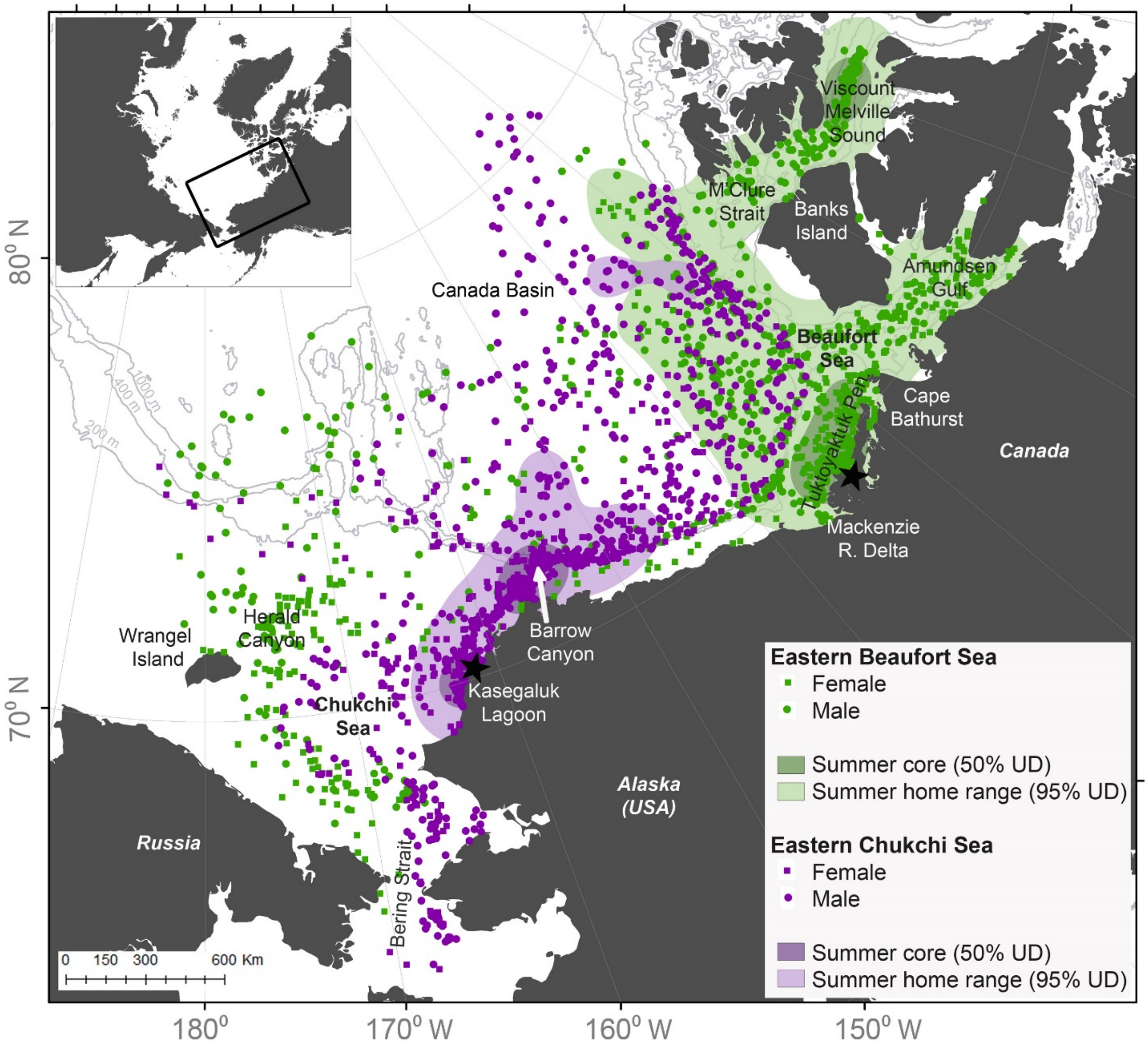

Figure 2-1. Daily locations of Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) satellite-tagged beluga whales (n=40 and 24, respectively), July-November, and place names mentioned in the text. Shaded polygons represent the summer (i.e., July and August) core areas (50% probability contour of the utilization distribution (UD)) and home range (95% probability). Black stars indicate approximate tagging locations.

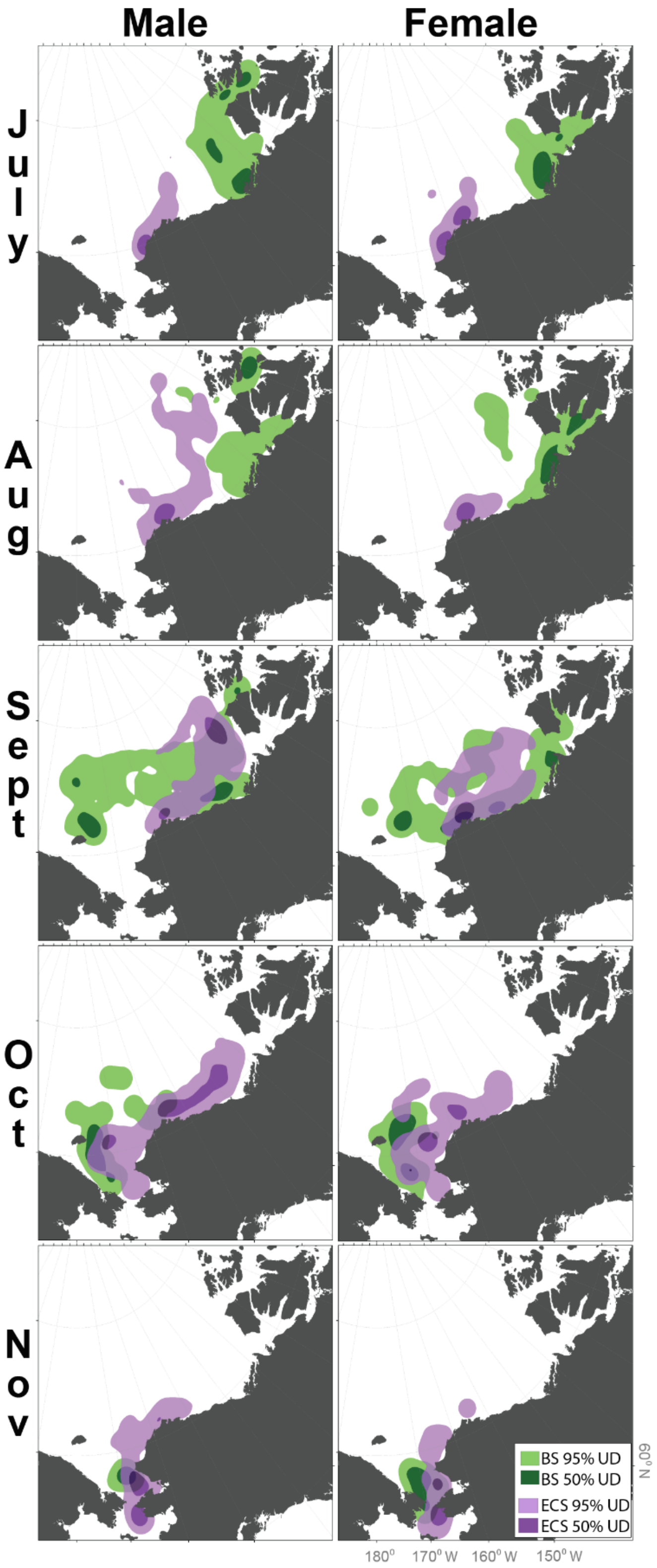

Figure 2-2. July to November home ranges (95% probability contour of the utilization distribution (UD)) and core areas (50% probability) for male and female Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) beluga whales, estimated using fixed kernel density.

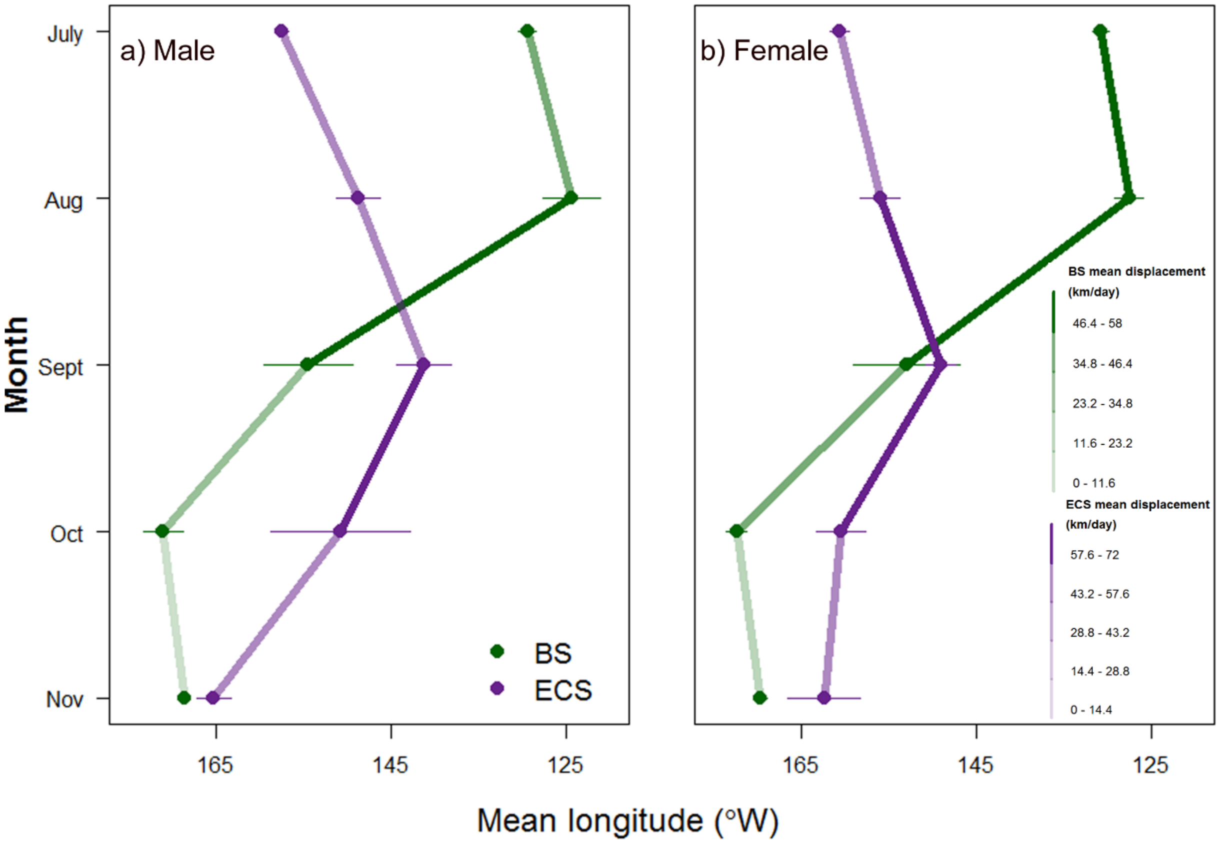

Figure 2-3. Summer and fall (July-November) migration timing, shown as monthly mean longitude (+/- 1 standard error) and relative daily displacement for satellite-tagged a) male and b) female Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) beluga whales in the Pacific Arctic (n=40 and 24, respectively). Lines represent relative monthly mean displacement, scaled by color shading.

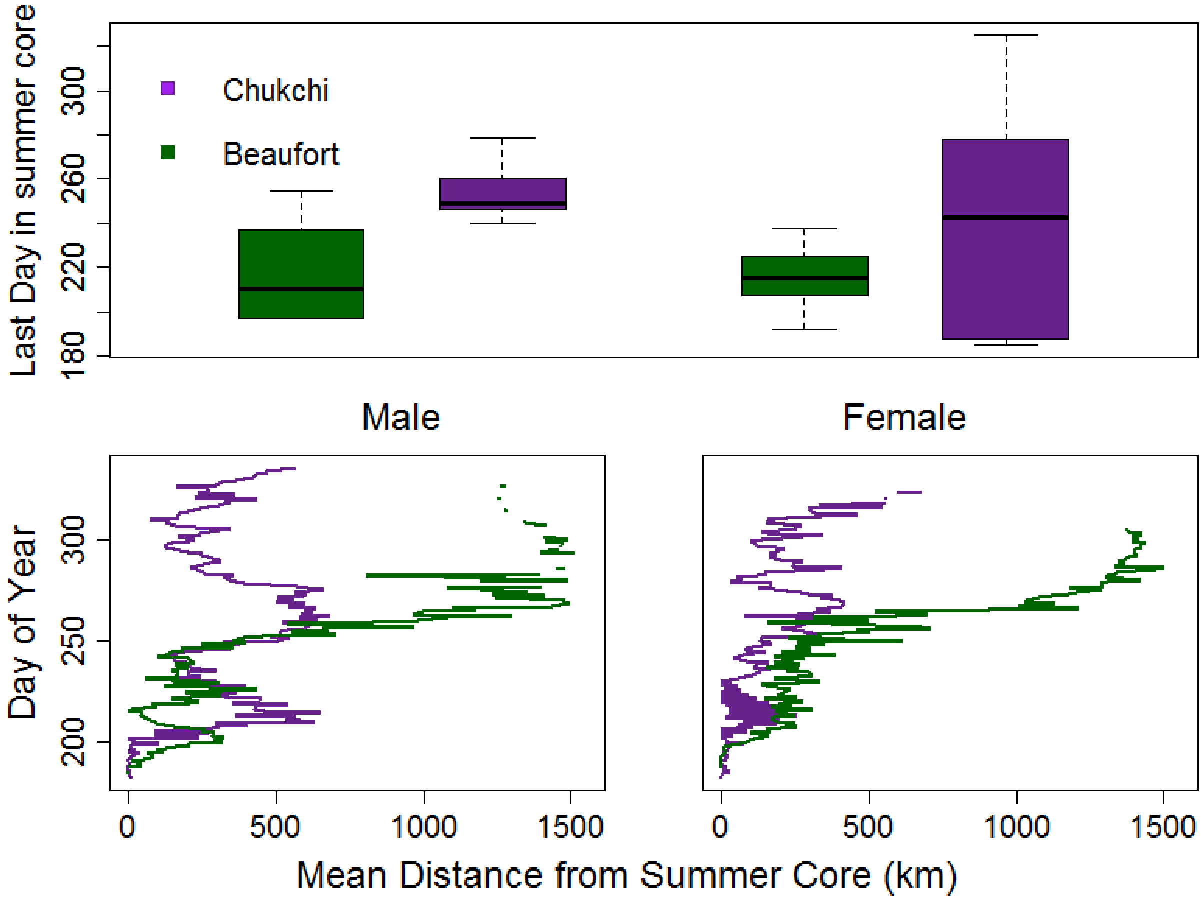

Figure 2-4. Timing of migration away from summer core areas by male (left) and female (right) Eastern Beaufort Sea (Beaufort) and Eastern Chukchi Sea (Chukchi) satellite-tagged beluga whales (n=40 and 24, respectively). The top panel provides boxplots of the last day of the year males and females of 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.

# Chapter 3. REGIONAL DIVING BEHAVIOR OF PACIFIC ARCTIC BELUGA WHALES (*DELPHINAPTERUS LEUCAS*) AND POSSIBLE ASSOCIATIONS WITH PREY

(Hauser, D. D. W., K. L. Laidre, S.L. Parker-Stetter, J.K. Horne, R. S. Suydam, and P. R. Richard. 2015. Regional diving behavior of Pacific Arctic beluga whales (*Delphinapterus leucas*) and possible associations with prey. Marine Ecology Progress Series 541: 245-264. The final publication is available online from Inter-Research at http://www.int-res.com/abstracts/meps/v541/p245-264/)

## 3.1 ABSTRACT

Two populations of beluga whales (*Delphinapterus leucas*) in the Pacific Arctic make seasonal migrations to regions characterized by diverse bathymetry and hydrography, yet there is limited information contrasting behavior and foraging across regions. We used satellite-linked time-depth recorders attached to 30 belugas from 1997-2012 to infer the depths at which belugas forage seasonally and regionally. We also examined the correspondence between patterns of beluga diving and the vertical distribution of a primary prey species, Arctic cod (*Boreogadus saida*), within the western Beaufort Sea. A suite of regional diving metrics revealed that beluga dive behavior varied among regions and sometimes between populations. Estimates of occupancy time at depth, in addition to maximum and modal dive depths for 6-h periods, suggested that Eastern Chukchi Sea and Eastern Beaufort Sea belugas were regularly diving to the seafloor in shallow shelf regions. Along slope margins and in the deep Canada Basin (>3,000 m), specific portions of the water column were more frequently targeted. The greatest maximum daily dive depths were >900 m in Canada Basin. Arctic cod were most abundant at 200-300 m in the western Beaufort

Sea, and beluga dives within the survey area also most frequently targeted these depths. These results are consistent with a hypothesis that Arctic cod are a primary prey item for Pacific Arctic belugas and suggest foraging belugas dive to depths that maximize prey encounters. In the context of a rapidly transforming Arctic ecosystem increasingly exposed to anthropogenic activities, our results quantify the ecological importance of key regions for these two populations.

## 3.2 INTRODUCTION

Optimal foraging theory predicts that predators aim to maximize energy intake through prey consumption while simultaneously minimizing the time and energy required to obtain that prey (Schoener 1971). For air-breathing marine predators, an additional constraint is imposed by oxygen demands limiting foraging time. Accordingly, predators minimize their transit time to optimize foraging before surfacing and recovering from oxygen depletion (Boyd 1997). In addition to physiological limits, other factors such as quality and distribution of prey affect dive duration (Thompson & Fedak 2001, Thums et al. 2013). Animals that frequently dive deep trade-off foraging needs over the physiological demands of diving deeply (Davis 2014). As a result, depth layers of the water column where divers frequently visit or spend extended periods of time can indicate where foraging is focused (Laidre et al. 2003, Robinson et al. 2012).

Marine environments also present a complex suite of factors that may influence the dive behavior of marine predators. Dive depths can vary according to prey density at depth, as well as the habitat characteristics (e.g., bathymetry, hydrography, presence of sea ice) encountered. Indices of dive depth relative to ocean depth can indicate pelagic or benthic foraging (Jessop et al. 2013, Watt et al. 2015), and maximum dive depth may identify specific foraging depths (Photopoulou et al. 2013). Understanding patterns of prey within the water column provides additional context for interpreting diving behavior where estimates of prey distribution, abundance, or density can inform a mechanistic understanding of marine mammal diving, foraging at depth, and habitat use (e.g., Palacios et al. 2013, Witteveen et al. 2015).

Beluga whales (*Delphinapterus leucas*) are a generalist predator, occurring in a number of habitat types and feeding on diverse prey (Laidre et al. 2008). In the Pacific Arctic, some belugas migrate thousands of kilometers seasonally as the annual sea ice recedes and advances (Richard et al. 2001, Suydam et al. 2001, Suydam 2009). Two beluga populations, the Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS), winter in the northern Bering Sea before migrating during spring into the Beaufort and Chukchi seas (Frost & Lowry 1990) as well as the deep (>3,000 m) Canada Basin where they are generally spatially and temporally segregated during summer to fall (Hauser et al. 2014). Managed as separate stocks with distinct mitochondrial DNA signatures (O'Corry-Crowe et al. 1997, Allen & Angliss 2014), spatial overlap between populations is greatest in fall when BS belugas initiate westward migration to the Chukchi Sea ahead of the ECS westward migration (Hauser et al. 2014). Both populations commence southward passage through Bering Strait in November. These belugas use different habitats over the range of their seasonal migrations, and each region is characterized by complex hydrography, diverse topography, seasonal sea ice fluctuations, and freshwater input that presumably influence prey distributions and foraging arenas for diving belugas (Weingartner et al. 1998, Day et al. 2013).

The limited information on BS beluga diving behavior suggests most dives were ‘square-shaped’ to the seafloor in Beaufort Sea waters 15-600 m or ‘V-shaped’ dives to 700-900 m in deep (>600 m) areas over Canada Basin (Richard et al. 1997). Recent analyses of ECS beluga diving suggest that regional differences exist in the proportion of time spent at depth, modal depths, and dive durations (Citta et al. 2013). Looking across inshore shelf (<75 m), slope (75 – 400 m), basin (>400 m), and Barrow Canyon regions, Citta et al. (2013) found that ECS shallow-type diving (<50 m) most often occurred in shelf waters compared to deep diving (a mode <50 m and another >400 m) in the Canada Basin. However, intermediate diving (a mode <50 m and another near 250 m) was found in all but shelf regions. ECS beluga diving in slope areas and Barrow Canyon tended to coincide with depths where regional hydrographic conditions are commonly assumed to concentrate prey such as Arctic cod (*Boreogadus saida*). Available stomach content and fatty acid diet information suggest that adult Arctic cod are a primary prey item of both BS and ECS belugas, although other fish (e.g., Saffron cod, *Eleginus gracilis*), cephalopods (primarily octopus), and benthic invertebrates (primarily Crangonid shrimp or echiurid worms) have been recorded (Seaman et al. 1982, Loseto et al. 2009, Quakenbush et al. 2015). Arctic cod make up the bulk of surveyed fish biomass in the Pacific Arctic, yet have only been surveyed in the nearshore shelf, and more recently, slope waters of the Chukchi and Beaufort seas (Parker-Stetter et al. 2011, Norcross et al. 2013, Logerwell et al. 2015).

Both BS and ECS populations are considered to be stable (Allen & Angliss 2014); though recent evidence suggests a decline in BS growth rates (Harwood et al. 2014). This decline is coincident with downward trends in body condition or reproduction of other Beaufort Sea marine predators that also primarily consume Arctic cod (Harwood et al. 2015). Harwood et al. (2014, 2015) suggest these shifts in life history parameters are possibly related to recent Pacific Arctic ecosystem changes (e.g., Grebmeier 2012) affecting prey, further indicating the importance of understanding foraging behavior and beluga relationships with prey.

Little work has been done to investigate inter-population differences in dive behavior for BS and ECS belugas, or to quantify how diving is related to foraging at depth. We used diving information from 30 beluga whales tagged with satellite transmitters linked to time-depth recorders to quantify differences in underwater behavior between populations and among regions. Our goal was to identify the depths and portions of the water column targeted by belugas within diverse oceanographic and bathymetric regions of the Pacific Arctic. We inferred foraging behavior for BS and ECS belugas based on the depths where belugas exhibited prolonged time at depth after accounting for the time spent traveling to and from each depth as well as modal and maximum dive depths. We then estimated whether diving was in close proximity to the seafloor or pelagic portions of the water column to indicate potential demersal or water column foraging. Additionally, we examined patterns of ECS beluga diving relative to the vertical distribution of a primary prey item, Arctic cod, in the western Beaufort Sea. We compared a subset of ECS beluga diving data to the vertically-integrated densities of Arctic cod from a fisheries acoustic survey (Parker-Stetter et al. 2011) and hypothesized that the number of beluga dives to target depths is positively related to the density of Arctic cod at the same depths. Although limited in spatial and temporal resolution, this analysis allowed us to explore the relationship between beluga diving behavior and prey abundance as well as evaluate the use of our diving parameters as indicators of foraging behavior.

## 3.3 METHODS

### 3.3.1 *Study area and region definition*

The regions of the Pacific Arctic are characterized by complex hydrography and diverse bathymetry affecting habitat and ecosystem structure (Carmack & Wassman 2006; Figure 3-1). The northern Bering Sea is comprised of shallow Chirikov Basin (<75 m) and connected to the Chukchi Sea via the narrow (~80 km wide) Bering Strait. The Chukchi Sea has complex, but shallow (<75 m everywhere but the northern perimeter), bathymetry characterized by several canyons and distinct water masses that can be strongly affected by wind-driven circulation (Danielson et al. 2014). The Alaska Coastal Current (ACC) flows from the northeast Chukchi Sea into the narrow, steeply sloped Alaska Beaufort Sea through Barrow Canyon (Pickart 2004) where wind forcing affects the presence of belugas and presumed foraging opportunities (Stafford et al. 2013). The warm, fresh ACC joins a shelfbreak jet along the Beaufort Sea slope, sometimes reaching the Canada Beaufort Sea (von Appen & Pickart 2012). Eddies spin off the shelfbreak jet into the deep, offshore Canada Basin (Spall et al. 2008) and upwelling along the slope is common (Pickart et al. 2013). Outflow from the Mackenzie River joins the shelfbreak jet and typically flows eastward over the shallow and wide Canada Beaufort sea shelf, forming a turbid plume over the Mackenzie Estuary (Carmack & Macdonald 2002). The plume continues into the steep-sloped Amundsen Gulf where wind-forced upwelling occurs near Cape Bathurst and a thermohalocline forms in mid-water depths.

We collected movement and diving behavior from BS and ECS belugas throughout the Pacific Arctic. To assess diving by belugas across the range of habitats in the Pacific Arctic, we designated eleven regions based on variable habitat types in the Pacific Arctic, previous descriptions of BS and ECS beluga distribution (Richard et al. 2001, Suydam et al. 2001, Suydam 2009), summer core areas (Hauser et al. 2014), and the 400 m isobath (Figure 3-1). The 400 m isobath has been used in previous assessments of beluga diving (Citta et al. 2013) and was the maximum depth sampled by beluga tags in some years (Appendix 3-1). Bathymetry and hydrography affects habitat type (i.e., ‘shallow shelf’, ‘slope’, and ‘deep pelagic’) for each region, and belugas use each region at different times during seasonal migrations (Table 3-1).

### 3.3.2 *Beluga whale telemetry data*

Belugas were captured and tagged near the Mackenzie River Estuary (BS in 1997 and 2005) and Point Lay, Alaska (ECS in 1998, 1999, 2001, 2002, 2007, 2010, and 2012) in association with local subsistence harvests (cf. Orr et al. 2001, Richard et al. 2001, Suydam et al. 2001, Hauser et al. 2014). All tags were manufactured by Wildlife Computers (Redmond, WA, USA) and consisted of ST-10, ST-16, SPLASH, and MK10 transmitters. Most tags were deployed in early July, with tag duration varying by individual (Table 3-2). All tags transmitted continuously except two BS tags in 2005, which were programmed to transmit every 4 days to conserve battery life.

We obtained location data, associated error classes, and binned dive histograms from the Argos data system. The first 24 h of location and dive data post-tag deployment were excluded to eliminate any potential behavioral effects resulting from capture and tagging. Speed (maximum 6.4 km/h, Richard et al. 2001) and angle filters were used to eliminate unlikely locations (Freitas et al. 2008). The tags contained pressure transducers which sampled whale depths at a resolution of 0.5 (2005-2012 tags), 2 (1997 tags), or 4 m (1998-2002 tags). Satellite data transmission limitations required diving data to be compressed into four 6-h histograms per day. Dive data were comprised of three types of histograms: the number of dives to maximum depth layers (‘maximum depth’ histogram periods), the proportional time within each depth layer (‘time at depth’ histogram periods), and number of dives to dive duration categories (‘duration’ histogram periods). We pre-specified depth layers (or ‘bins’) for each histogram type before deployment, but different bin thresholds were used among histogram types, populations, and tagging years (see Appendix 3-1) as tag technology improved and for different research purposes (e.g., see Richard et al. 1997, Citta et al. 2013). For analysis, we consolidated bins to the finest resolution available among all years and populations: 0-10, 10-50, 50-100, 100-200, 200-300, 300-400, >400 m for maximum depth 6-h periods; 0-10, 10-50, 50-100, 100-200, 200-400, >400 m for time at depth 6-h periods; and 0-1, 1-3, 3-6, 6-9, 9-20, >20 min for duration 6-h periods. We sampled time at depth layers differently than maximum depth layers in one year (2005), so slightly coarser time at depth layers were necessary when consolidated for analysis (Appendix 3-1). A depth of at least 2 or 4 m (for 2007-

2012 tags and 1997-2005 tags, respectively) was required before a dive was registered on the tag. We used a correlated random walk model to estimate geographic locations at the beginning of each 6-h period based on observed locations and associated Argos spatial error (Johnson et al. 2008). Six ECS tags from 2007, 2010, and 2012 also provided maximum daily dive depth (to a maximum of 1000 m), recorded as the maximum absolute depth measured by the tag within the previous 24 hr. Thus, maximum daily dive depths were point estimates for a 24-h period measured with higher resolution than the dive data summarized in 6-h maximum depth periods. We assigned the daily location from Hauser et al. (2014) to each maximum daily dive depth.

### 3.3.3 *Mapping beluga whale dive behavior*

Beluga dive characteristics, including deepest (‘maximum’) and modal depth and longest dive duration, were identified for each 6-h period and mapped using ArcGIS 10.1 (ESRI, Redlands, CA, USA). Prey searching and capture may occur throughout the water column, but we examined the deepest and modal depths in each 6-h period as indicators of where diving was focused as presumed foraging effort, both extracted from the maximum depth histograms. Maximum dive depth has been used as a proxy for specific foraging depth in other marine mammals (e.g., Photopoulou et al. 2013), and we also examined modal depths to consider which depths were most frequently used. We assumed the longest dive durations, extracted from the duration histograms for each 6-h period, were associated with deeper dives indicative of foraging effort (e.g., Davis et al. 2013). However, dive depth and duration were not directly linked, and we cannot verify that longer dives were also deeper dives (Citta et al. 2013).

The maximum daily dive depths from the 2007-2012 ECS whales were also mapped to describe deep diving at a higher resolution than previously available or available from the histogram data. We presumed that maximum daily depth also provided an indicator of the deepest depths foraging may occur. We compared maximum daily dive depth among regions using linear mixed effects (LME) models fit with maximum likelihood methods in the ‘nlme’ package (Pinheiro et al. 2013) in R (R Development Core Team 2012). Individual whales were treated as a random effect to account for repeated measures, and regions were considered a fixed effect. We excluded the Canada Basin eastern slope region from the LME due to small sample size.

The depth associated with each 6-h period’s location was extracted from the 500 m resolution International Bathymetric Chart for the Arctic Ocean (IBCAO; Jakobsson et al. 2012). Some dive locations (n=74, 1%) occurred south of the IBCAO extent in the northern Bering Sea, where we used the 1 arc-minute ETOPO1 global relief map (Amante & Eakins 2009). We also recorded whether the deepest and modal depths in a 6-h period overlapped with the depth of the seafloor (categorical yes/no), the proximity to the seafloor as a ratio of the modal depth in a 6-h period relative to seafloor depth (ranged 0-1), as well as the ratio of maximum daily dive depth to seafloor depth. In rare occasions, dives could be deeper than seafloor depth because of the matching of whale location, diving depth, and seafloor depth at different spatial and temporal scales. A ratio of 1 was assigned when the beluga dive depth equaled or exceeded the ocean depth for a given location. We assumed ratios >0.9 represented benthic diving that targeted the seafloor. Close proximity to the seafloor, measured by dive to seafloor depth ratios, has previously been used to indicate benthic foraging for seals and the closely-related narwhal (*Monodon monoceros*) (Jessop et al. 2013, Watt et al. 2015). We assumed ratios <0.9 corresponded to pelagic dives targeting other depths in the water column.

### 3.3.4 *Regional daily diving time budget model*

A daily diving time budget model was used to assess how individual belugas allocated time among depth layers within each region. We followed the approach developed for narwhals in Laidre et al.

(2003) to estimate time spent both transiting through (i.e., transit time) and within (i.e., occupancy time) each depth layer. We tested differences in regional occupancy time at depth, after eliminating estimated time transiting to and from each depth, to assess population, sex, and age class differences. We presumed extended occupancy time at deeper depths is related to foraging (Laidre et al. 2003). The model was based on scaling 6-h dive periods up to a 24-h period and used all three histogram types (i.e., maximum depth, time at depth, and duration histograms). Since transmission of dive data were sometimes fragmented by poor satellite reception, analyses were restricted to 6-h periods when there were complete records of all three histogram types. Similar to above, we used a consolidated depth layer classification scheme that matched both maximum depth and time at depth histogram types across all years (see Appendix 3-1): 0-10, 10-50, 50-100, 100-200, 200-400, and >400 m.

The time budget model required estimation of several parameters within each region for each tagged whale. Each parameter will be described briefly, using the same nomenclature as Laidre et al. (2003). First, region-specific vertical transit time ($\text{TransitTime}_j$) was estimated as the average time spent transiting through each depth layer (*j*) per day. Vertical transit time included time spent ascending and descending through each depth layer and relied on first estimating a population- and depth-specific vertical transit speed ($S_j$) for each region (Heide-Jørgensen et al. 1998).

We estimated depth-specific vertical speeds for each population and region to account for potential behavioral differences among regions and between populations. Estimating a depth-specific vertical speed required a depth layer (*j*) to be isolated such that dives were counted in the previous (*j*-1) and next (*j*+2) depth layers to estimate the speed through layer *j*. Sample size for vertical speed estimation was thus smaller than for the other daily time budget model parameters because there are fewer histograms that fit the constraint for isolated depth layers, particularly at each depth for all regions and both populations. This requirement limited the inclusion of regions for which a small number of samples were acquired, so we consolidated regions for vertical speed estimation for each population based on similar habitat types and used bootstrapping. The estimated population- and depth-specific vertical speeds for each habitat type were sampled with replacement 1000 times.

To estimate $\text{TransitTime}_j$ for each of the main regions, we applied the vertical speeds from the respective population and habitat type. Occupancy time ($\text{OT}_j$) within each depth layer was estimated by subtracting $\text{TransitTime}_j$ from the total time spent within each depth layer *j* each day. Resulting $\text{OT}_j$ values were the mean number of minutes a whale spent within each depth layer per day after removing transit time to and from that depth. To estimate occupancy time on a per dive basis ($\text{AOTdive}_j$), $\text{OT}_j$ was divided by the average number of dives per day to depth layer *j*.

For each region, we compared mean population responses of individual differences in average occupancy time per dive ($\text{AOT}_{\text{dive}j}$) using two-way ANOVA. Factors included depth layers (i.e., 0-10, 10-50, 50-100, 100-200, 200-400, and >400 m), population (BS and ECS), and their interaction. Limited sample size of BS whales precluded analysis of differences between sex or age classes, but we also tested differences in $\text{AOT}_{\text{dive}j}$ between ECS sexes and between ages (i.e., adult and immature ECS whales) in additional ANOVAs. We applied a square-root transformation to each test of $\text{AOT}_{\text{dive}j}$, and evaluated model structure using Akaike's Information Criterion (AIC). Applying the Bonferroni correction for multiple comparisons, statistical significance of ANOVAs was considered at the 0.002 alpha level.

### 3.3.5 *Estimation of the vertical distribution of Arctic cod density in the Beaufort Sea*

We estimated densities of age 1+ Arctic cod within each beluga whale depth layer from 38 kHz data collected during an acoustic-trawl survey in the western Beaufort Sea during 16-21 August

2008 (Parker-Stetter et al. 2011; see trackline in Figure 3-1). Age 1+ Arctic cod (hereafter simply 'cod') constituted >99% of the Marinovich trawl (fishing dimensions 3-4 m vertical by 6 m horizontal) catches used to verify the species and size composition of fish within the midwater acoustic backscatter (n=14, Parker-Stetter et al. 2011), and cod was the dominant fish species across several recent surveys in the Beaufort Sea (Logerwell et al. 2015). The relatively small number of detections of age-0 Arctic cod (i.e., young-of-the-year) or other species were not analyzed here, and are not considered part of BS or ECS diets (Quakenbush et al. 2015). Integrated volume backscatter (area backscattering coefficient; $s_a$ in $m^2/m^2$) of cod was exported in 10 m vertical depth bins, between 9.0 m below the surface and 0.5 m above the bottom, at a 500 m horizontal resolution.  Density (no. fish/$m^2$) was then calculated for each 10 m bin by dividing the integrated backscatter by a target strength of -52.7 dB re 1 $m^2$, estimated in Parker-Stetter et al. (2011). Cod densities in 10 m bins were then summed to vertical depth layers (i.e., 0-10, 10-50, 50-100, 100-200, 200-300, 300-400, >400 m) matching those used to identify the number of beluga dives made during 6-h periods (i.e., the 6-h maximum depth histograms). Cod densities along the survey trackline were next interpolated to create a smoothed surface of cod density for each beluga depth layer. We used ordinary kriging in the Geostatistical Analyst extension of ArcGIS 10.1, fitting a spherical model with no trend removal for each depth layer. Interpolation of cod density for each depth layer was limited to the bounds of the cod survey area other than the landward limit, which was set by the 100 m isobath used in Parker-Stetter et al. (2011) when estimating cod target strength. This landward limit was supported by beluga biology, since belugas detected by aerial surveys were most frequently located offshore of the 100 m isobath in the Alaska Beaufort Sea (e.g., Moore et al. 2000). We limited seaward interpolation of cod densities to the minimum depth threshold of each depth layer (e.g., the minimum isobath of the 200-300 m depth layer was 200 m) when interpolating densities of cod in the deeper depth layers (i.e., 200-300, 300-400, and >400 m), and we refer to these as the >200, >300, and >400 m cod 'survey areas', respectively.

### 3.3.6 *Statistical analysis of ECS beluga dive behavior relative to Arctic cod density*

We compared the pattern of beluga dive behavior to the depth-specific estimates of cod density within the cod survey area. A subset of 192 ECS beluga dive records that occurred within the survey area were used in this analysis. Few (n=4) BS 6-h dive periods occurred in the cod survey area, which precluded similar comparisons. We were particularly interested in diving activity targeting the 100-200, 200-300, and 300-400 m depth layers, because we inferred foraging likely occurred at these depths. Specifically, ECS belugas had prolonged occupancy time as well as maximum and mode dives to these depths in Barrow Canyon and the Alaska Beaufort Sea regions coinciding with the survey area (see Results). These 'target' depths also match depths where fronts and upwelling occur in this area and promote the concentration of zooplankton, thereby presumably attracting beluga prey (Pickart et al. 2013, Stafford et al. 2013). Our goal was to examine whether the number of dives to these target depth layers corresponded with the depth layers at which cod were most abundant, indicating a relationship between inferred foraging dive depths and presumed prey patterns.

We used ECS beluga 6-h dive period locations that occurred within the cod survey area during July – October, when ECS belugas use Barrow Canyon and the Alaska Beaufort Sea (Hauser et al. 2014) and representing the period that is characteristic of when belugas dive to these target depth layers. We intersected the locations for each 6-h dive period within the >200 and >300 m cod survey areas with each interpolated cod density depth layer. Generalized linear mixed models (GLMMs) were used to model the number of dives to specific target depth layers (i.e., 100-200, 200-300, and 300-400 m) using the 'lme4' package in R (Bates et al. 2014). The number of dives to target depth layers was modeled using a Poisson error distribution and log link. Individual whales were considered a random effect to account for repeated measures and individual variation. We tested dive rates to 100-200 and 200-300 m depth layers in the >200 m survey area and also modeled dive rates to 200-300 and 300-400 m in the >300 m survey area. Explanatory variables for each GLMM included additive effects of cod densities in 10-50, 50-100, 100-200, and 200-300 m depth layers and log-transformed seafloor depth. We also included two additional predictor variables when modeling within the >300 m survey area that were not appropriate for models in the >200 m survey area: cod density in the 300-400 m depth layer, and a categorical variable identifying which depth layer contained the maximum cod density.  Final model structure was determined via AIC model selection.

## 3.4 RESULTS

Four BS and 26 ECS beluga whales were tagged, resulting in 1,600 and 7,923 maximum depth 6-h histogram periods, respectively, within 10 Pacific Arctic regions (Tables 3-1, 3-2). For the BS whales, 1,561 time at depth and 1,610 duration 6-h histogram periods were also collected. We collected 8,075 6-h time at depth and 7,823 duration 6-h histogram periods for ECS whales. Belugas from both populations ranged across all but one of the Pacific Arctic regions (Table 3-1, Figure 3-2). No dive data were collected in the Viscount Melville Sound BS summer core area, although it is typically used by BS males in July and August (Hauser et al. 2014). The majority of BS 6-h dive periods were obtained from the Chukchi Sea shelf (34%) while the greatest percentage (31%) of ECS 6-h dive periods were collected from the deep Canada Basin, Barrow Canyon slope (24%), and Chukchi Sea shelf (21%; Table 3-1). Seasonal presence varied among regions, and we are the first to document winter (November-April) and spring (May-June) behavior and locations of tagged belugas in the Bering Sea (Table 3-1, Figure 3-2).

### 3.4.1 *Spatial patterns of dive behavior*

Geographically-referenced dive data revealed differences in dive behavior among regions and between populations (Figure 3-2). Maximum dive depth in 6-h periods was similar between populations for each region, ranging >400 m in deep pelagic habitats (i.e., Canada Basin) where maximum diving depth never reached the seafloor. In slope areas, maximum dive depths were often >400 m and typically (63% and 65% of 6-h periods for BS and ECS, respectively) reached the seafloor (Figure 3-3). However, ECS belugas typically dove to mid-water depth layers (100-200 and 200-300 m) in the Barrow Canyon and Alaska Beaufort slope regions (Figure 3-2). BS belugas also often dove to mid-water depths (200-300 m) in certain slope regions like Amundsen Gulf. Maximum dive depth in shelf areas was most frequently to 10-50 m (62% of 6-h periods) and to the seafloor (91% of 6-h periods) for ECS belugas. BS beluga shelf maximum dive depth was more frequently to 50-100 m (60% of 6-h periods) to typically reach the seafloor (89% of 6-h periods).

Modal depth of 6-h periods were most frequently in the <10 and 10-50 m depth layers for both populations, regardless of habitat type (see Appendix 3-2). Dives <10 m represented surface-oriented dives (Citta et al. 2013), so we excluded 6-h periods with <10 m modal depths in subsequent modal dive depth analyses (resulting in n=962 and n=2,808 BS and ECS 6-h periods, respectively). We most often observed modal dives in the 10-50 m depth layers for both populations in all habitat types (Figure 3-3), but deeper dive depths were also common in some regions (Figure 3-2). ECS modal depths in the 10-50 m depth layer (95% of 6-h periods) were typically benthic dives (90% of 6-h periods) within shallow shelf habitats (Figure 3-3). BS modal depths in shelf habitats were common in the 10-50 and 50-100 m depth layers (50% and 43% of 6-h periods, respectively), and were less frequently benthic (70% of 6-h periods) than those of

ECS belugas in shelf habitats. BS modal dive to seafloor depth ratios were typically pelagic in the northern and northwestern Chukchi Sea (Figure 3-2). In slope and deep pelagic habitats, modal depths for both populations were typically not benthic for BS (63% and 100% of 6-h periods, respectively) or ECS belugas (59% and 100% of 6-h periods, respectively), occurring most often in the 10-50 m depth layer but also in deeper depths (Figure 3-3). Deeper modal depths were common in 100-200 and 200-300 m depth layers for ECS belugas in slope (22% and 9% of 6-h periods, respectively) and basin (10% and 4%, respectively) habitats, especially in the Barrow Canyon and Alaska Beaufort Sea (Figure 3-2). Additional modal depths for BS belugas were in the 50-100 and 300-400 m depth layers (23% and 8% of 6-h periods, respectively) in slope habitat, and >400 m in deep pelagic habitat (20% of 6-h periods).

Maximum dive durations within a 6-h duration period were greater for ECS than BS whales (Figure 3-2). Maximum dive duration was frequently >20 min for ECS whales while BS maximum dive durations were often 6-9 min throughout the Beaufort and Chukchi seas and the Amundsen Gulf, compared to 9-20 min in Canada Basin and the Bering Sea. Dive depth and duration histograms were not directly linked within a 6-h period, so it was not possible to examine whether longer dives were also deeper dives.

Maximum daily depths recorded for six ECS tags deployed in 2007-2012 also varied regionally (LME, F=375.4, df=6,16, $p<0.0001$) and never exceeded the 1,000 m limit of their tags (Figure 3-4). The deepest maximum daily depth recorded was 956 m for an adult male, although two adult females also attained maximum daily depths >900 m. The ratio of the maximum daily dive depth to ocean depth indicated that these whales were diving to the seafloor at least daily in all regions but Canada Basin where seafloor depths ranged >3,000 m. Within Canada Basin, ECS belugas generally dove in excess of 600 m at least once daily (mean=741.4 m).

### 3.4.2 *Occupancy time at depth*

Depth-specific vertical speeds ($S_j$) increased with depth for both populations in each habitat type (Figure 3-5) and were similar in magnitude to those estimated for High Arctic belugas and narwhals (Heide-Jørgensen et al. 1998, Laidre et al. 2003). There were no significant differences in average occupancy time per dive ($AOT_{divej}$) between populations within any region, but there were significant differences in $AOT_{divej}$ among depth bins in all but the shallow shelf regions (i.e., the Bering and Chukchi seas; Table 3-3, Figure 3-6). Similarly, no significant differences between ECS male and female or immature and adult whales occurred in any region except Canada Basin where adult whales spent significantly more time at 200-400 and >400 m depth bins than immature whales, presumably because adult whales have larger oxygen stores and aerobic capacity than smaller-bodied immature whales (Schreer & Kovacs 1997, Noren & Williams 2000). Occupancy times were greatest in the 200-400 m depth layer in the deep pelagic basin and some slope regions (Figure 3-6). However, whales also spent more time in the 100-200 m depth layer in the Barrow Canyon and Alaska Beaufort slope regions.

### 3.4.3 *Vertical distribution of Arctic cod and beluga diving in the Alaska Beaufort Sea*

Age 1+ Arctic cod occurred throughout the water column during the fish survey, but the 200-300 m depth layer contained the highest cod densities of all depth layers regardless of water depth (see Appendix 3-3). This supports suggestions by Parker-Stetter et al. (2011) that cod aggregations extend into Canada Basin in a horizontal pelagic layer as the seafloor drops steeply along the continental slope. Coincident with depth layers where cod were most dense, the greatest number of ECS beluga dives occurring within the cod survey area also targeted the 200-300 m depth layer other than dives closer to the surface in 10-50 m (Figure 3-7). Maximum and modal dive depths also most frequently occurred in the 200-300 m depth layer, in addition to a mode near the surface at 10-50 m.

The number of ECS beluga dives to 100-200, 200-300, and 300-400 m target depth layers was significantly related to the vertical distribution of cod density (Table 3-4). Cod density in 200-300 m was a consistently significant predictor for dive rates to each target depth, but cod density at other depths and seafloor depth were also related to dive rate for some models. Dive rate to a specific target depth was always negatively correlated with cod density in that same depth.

## 3.5 DISCUSSION

For marine mammals, targeted diving depths or extended occupancy at depth are often assumed to indicate foraging or the presence of predictable prey resources that may vary regionally or seasonally (Laidre et al. 2003, Aguilar Soto et al. 2008, Robinson et al. 2012). In this study spatial variation in diving behavior for BS and ECS beluga whales suggested different foraging strategies among regions and, in some cases, between populations. In the absence of high-resolution dive data, lower-resolution satellite-relayed data loggers, such as used in this study, can still reliably estimate foraging behavior (e.g., Heerah et al. 2015). We determined foraging based on the maximum duration of dives, maximum (at 6-h and daily time scales) and modal dive depths, the proximity of dives to the seafloor, and the time spent within each depth layer. In studies where foraging can be confirmed, the deepest and longest maximum dive depths and durations are often associated with dives that have prey captures (e.g., Davis et al. 2013). The higher vertical speeds estimated here for deeper depths also support the assumption that foraging occurs at deeper depths. For example, high speeds at depth for some odontocetes coincide with foraging buzzes for particular prey types and the deepest parts of a dive (Aguilar Soto et al. 2008). Similarly, maximum dive depth serves as an indicator of foraging depth for benthic foragers (Photopoulou et al. 2013), and close proximity to the seafloor (or not) can be confirmed by comparing dive depth to water depth (Jessop et al. 2013, Watt et al. 2015). Extended time at target depths has also been used to identify depth layers where foraging is expected to occur (Laidre et al. 2003). Our depth and duration histogram data could not be directly compared to indicate whether deeper dives were also longer dives, but our estimates of depths with prolonged occupancy time corresponded well with maximum dive depths. Lastly, we estimated modal dive depths to identify the most common depths used by belugas.

### 3.5.1 *Non-foraging diving behavior*

Analysis of modal dive depths was complicated by the high frequency of shallow dives in the 0-10 and 10-50 m depth layers (e.g., see Appendix 3-2). Citta et al. (2013) found that ECS belugas typically had a mode at the surface and another in a deeper layer. Bimodal distributions of maximum dive histograms were still common after excluding dives <10 m, and the deeper of the two modes were used in analyses. We considered all depths in estimating modal dive depths, but we focused on modal dives >10 m since we assumed dives in the upper 10 m were associated with surfacing behavior as in Citta et al. (2013). The 10-50 m depth layer was still often a primary mode, even when there may have been a second deeper mode. We assumed dives in the 10-50 m depth layer likely included surface-oriented behavior such as travel or recovery diving. Richard et al. (1997) provided evidence that shallower dives represent dive recovery or migration, reporting that BS belugas in areas 15-600 m deep and >600 m would dive deeply followed by long periods with dives <50 m. Histograms and dive records from other deep-diving predators also indicate concentrated and prolonged periods in shallow depths consistent with travel and dive recovery following deep foraging dives (e.g., Laidre et al. 2003, Arranz et al. 2011). However, we cannot exclude the possibility that foraging occurred <50 m, especially in shallow shelf habitats where water depths are often ≤50 m, yet a deeper secondary mode is presumably associated with foraging in slope and deep pelagic habitats.

The coastal and shallow summer core areas of Kasegaluk Lagoon (mean depth ~7 m) and the Mackenzie River Estuary (mean depth ~25 m), are used by ECS and BS belugas, respectively, in spring-early summer during annual migrations (Hauser et al. 2014). Stomachs of belugas harvested during subsistence hunts near these regions are typically empty (Harwood & Smith 2002, Quakenbush et al. 2015), although intestines were not examined. Histological studies of liver and kidney tissues from whales harvested in the areas also indicate fasting (Woshner et al. 2002). It seems unlikely that belugas forage in these coastal core areas and rather use them for an annual spring-summer molt where warmer and fresher water, such as near estuaries, accelerates epidermal regrowth (St. Aubin et al. 1990). Calving also occurs in spring, and shallow areas may provide thermal benefit to calves or provide additional protection from killer whale (*Orcinus orca*) predation (Finley 1982).

In contrast, Canada Basin is a uniquely deep (>3,000), pelagic, and historically ice-covered habitat where both populations had maximum dive depths >400 m (see Figures 3-2 and 3-3) and extended occupancy time at 200-400 and >400 m (see Figure 3-6). The average depth of maximum daily dives by ECS belugas (741 m) also suggested deep, pelagic diving (see Figure 3-4). Richard et al. (1997) reported male BS dives in Canada Basin were typically 'V-shaped' to 700-900 m for 15-20 min and accompanied by many dives <50 m, suggesting that these deep dives involved a whale reaching its maximum depth before immediately heading to the surface without searching for prey at depth. They hypothesized that whales may have used these dives to locate small breathing holes in the dense pack ice during ascent from depth and noted that V-shaped dives were not detected elsewhere. In addition to maximum dives >400 m in Canada Basin, we found a secondary mode

>400 m for BS belugas (see Figure 3-3) that would support the description by Richard et al. (1997). ECS belugas may also have V-shaped dives based on their maximum dive depths, but ECS whales had additional modes at 100-200 m and 200-300 m in Canada Basin (see Figure 3-3) that may be associated with foraging. Relatively little is known about the distribution or abundance of potential prey in Canada Basin, but boundary currents along the Chukchi and Beaufort shelves create mesoscale eddies that infuse nutrients and zooplankton into the region that could fuel higher trophic levels (Llinas et al. 2009). There is a stratified front located ~200-250 m between cold, dense Pacific water (PW) and warmer Atlantic water (AW; Pickart 2004, Nikolopoulos et al. 2009) that could aggregate zooplankton thereby attracting forage fish like Arctic cod (Logerwell et al. 2011). A dense layer of Arctic cod likely extends off the Beaufort Sea slope into Canada Basin around ~250 m depth (Appendix 3-3; Parker-Stetter et al. 2011). There is another front between ~600-1,000 m as the AW transitions to Deep Arctic water (McLaughlin et al. 1996). Ultimately, the functional importance of Canada Basin remains somewhat unclear and may differ between BS and ECS belugas.

### 3.5.2 *Benthic diving behavior*

Our results indicated that both beluga populations primarily targeted either benthic or pelagic portions of the water column depending on the geographic region. Both maximum and modal dive depths suggested both populations usually make benthic dives in shallow shelf habitats like the Chukchi and northern Bering seas, but pelagic diving was more common in the deep Canada Basin (e.g., see Figure 3-3). Stable isotope values from BS and ECS belugas suggest reliance on both benthic and pelagic prey (Dehn et al. 2006, Horstmann-Dehn et al. 2012), which fits the mixed pattern of benthic and pelagic diving among regions in our results. Benthic invertebrates (e.g., shrimp and echiurid worms) also dominated stomach contents of BS and ECS belugas sampled in spring and early summer when whales would have most recently been in the northern Bering or eastern Chukchi seas (Quakenbush et al. 2015), further supporting a conclusion that benthic foraging occurs in these shallow shelf habitats. The northern Bering and Chukchi seas are considered productive benthos-dominated systems, with abundant and diverse benthic macrofauna (Grebmeier et al. 2006, Day et al. 2013) and benthic age 1+ Arctic (Norcross et al. 2013) that are potential beluga prey.

A small proportion of 6-h periods were characterized by non-benthic diving in the Chukchi and Bering seas for BS belugas (see Figure 3-2), which coincided with the deeper northern portions of the Chukchi Plateau and Herald Canyon. Although Herald Canyon is less affected by wind-driven fronts than Barrow Canyon in the eastern Chukchi Sea, easterly winds contribute to continental shelf waves over the western Chukchi Sea that can affect the transport of zooplankton and may have important effects on benthos as well as forage fish (Danielson et al. 2014). Relatively little is known about the distribution and abundance of potential beluga prey in the western Chukchi Sea. Similarly, circulation in the northwest Bering Sea fluctuates depending on wind stress, which is also a dynamic marginal sea ice zone in winter when BS belugas were present (Danielson et al. 2014). Few tags continued transmitting during winter in the Bering Sea and additional work is needed to identify habitat use and foraging within this period.

In slope habitats, diving generally appeared to target the seafloor but also portions of the water column in certain regions. Maximum dive depths typically reached the seafloor (see Figure 3-3), but varied depending on finer regions for the two populations (see Figure 3-2). BS beluga diving focused on the seafloor in the Alaska Beaufort Sea and Barrow Canyon while ECS belugas had more pelagic 6-h maximum and modal depths that corresponded to a frontal transition zone between PW and AW (Pickart 2004, Nikolopoulos et al. 2009) along the steep continental slope where age 1+ Arctic cod are most abundant (Parker-Stetter et al. 2011, Crawford et al. 2012). Both beluga populations made deeper dives in the Canada Beaufort slope region than in the Alaska Beaufort Sea, but rarely to the seafloor. Prolonged occupancy time at depth (see Figure 3-6) as well as pelagic maximum and modal dive depths corresponded to the same depths of dense Arctic cod schools surveyed during summer and fall of 2006-2012 in the Canada Beaufort Sea and Amundsen Gulf (Geoffroy et al. In Review, Majewski et al. In Review). However, Richard et al. (1997) reported 10-20 min 'square-shaped' dives to the seafloor by BS belugas in waters 15-600 m deep and assumed these were demersal foraging dives. These dives would typically be followed by several minutes at shallow depths or were conducted in batches trailed by multiple hours <50 m. Nearly 37% of the modal dives we observed for BS belugas in slope waters reached the seafloor and may have represented similar square-shaped foraging dives. Our slightly different categorization of slope habitat as well as our sample of tagged whales may account for the apparent differences in our results. Of note, the sample of whales included in the Richard et al. (1997) study was largely male and focused on use of the 600-m deep BS core area in Viscount Melville Sound compared to our largely female (and one immature male) sample that remained in Amundsen Gulf and the Canada Beaufort Sea before migrating west.

### 3.5.3 *Maximum dive duration*

ECS belugas almost universally had greater maximum dive durations than BS whales (see Figure 3-2). The general similarities in diving behavior between populations is suggestive of comparable foraging patterns at depth within a given region. Rather, spatiotemporal differences in BS and ECS movements (Hauser et al. 2014) would limit overlap and potential competition for prey at depth. Whales from the BS population are comparably sized to ECS whales (Suydam 2009), but our sample of BS tagged whales was biased toward females, with the only male being immature. Thus the difference in population-specific dive duration was likely due to the small sample of tagged BS whales. Additional tagging is needed to further compare dive durations between populations.

### 3.5.4 *Beluga dive patterns relative to the vertical distribution of cod*

Even with temporal mismatch between predator and prey sampling, significant relationships between predator diving and prey abundance can be detected (Kuhn et al. 2015). Despite asynchronous sampling between ECS beluga diving and cod density data, we assumed that observed patterns were representative of typical conditions. Several aspects of beluga behavior, diet, and regional hydrography support this assumption. Belugas are long-lived, social cetaceans with matrilineally-derived migration routes and philopatry (O'Corry-Crowe 2008, Turgeon et al. 2012), suggesting that the same regions are used each summer by related social groups. ECS belugas exhibit strong interannual philopatry for areas in the Barrow Canyon and Alaska Beaufort Sea, areas which overlap with the fish survey area (Hauser et al. 2014). Beluga diving in the area targeted depths where fronts occur (e.g., occupancy time, maximum dive depth, dive rates to target depths, Citta et al. 2013). These persistent stratified fronts function to concentrate secondary production that likely attracts prey like Arctic cod and thus likely promote foraging opportunities for belugas in this area (Stafford et al. 2013). A simultaneously-occurring benthic trawl survey supported the high biomass of cod found here and also indicated an association between Arctic cod and fronts (Logerwell et al. 2011). However, there have been few systematic surveys of cod in the Alaska Beaufort Sea for comparison to the distribution we observed (e.g., Lowry & Frost 1981), and the area surveyed in this study likely did not fully sample the offshore extent of cod schools (Parker-Stetter et al. 2011). Yet age 1+ Arctic cod have dominated catches elsewhere in the eastern Chukchi and Beaufort seas, especially on continental slopes that were consistently sampled in numerous years (e.g., Norcross et al. 2010, Crawford et al. 2012). Collectively, both pelagic and benthic surveys support our assumptions of cod density, suggesting a persistent pattern of high Arctic cod biomass in our survey area and throughout the Pacific Arctic (see also Logerwell et al. 2015).

In this study depths of maximum and modal beluga dives were similar to depths with maximum and high mean cod densities (see Figure 3-7). While recognizing beluga dive behavior and cod distribution were not sampled concurrently, these results add weight to the use of our dive parameters as indicators of foraging behavior. The depth layer with the highest cod density (200-300 m) was a consistent, significant predictor of the number of ECS beluga dives (see Table 3-4) and suggested an overlap between beluga dive depths and high densities of Arctic cod, at least for ECS belugas in the survey area. Even though Arctic cod density consistently predicted the number of dives to target depths, we cannot exclude the possibility that other prey are pursued in this area. For example, belugas also dove to the seafloor and depth layers deeper than 200-300 m, although with much lower frequency.

We hypothesized that the number of beluga dives would increase with the density of cod, but we found that there was a negative correlation between beluga dive rate to a target depth and cod density in that target or shallower depths. In contrast, there was a positive correlation with cod density in depths deeper than the target depth. This result suggests that belugas dive less frequently when cod are abundant because foraging is efficient at high prey densities, consistent with marginal value theorem predictions of optimal foraging (Charnov 1976). Empirical tests have demonstrated that other marine predators reduce foraging time in high quality prey patches (e.g., Thums et al. 2013), and higher prey abundance improves foraging efficiency for deep-divers (Goundie et al. 2015). For Pacific Arctic belugas, additional data are needed that incorporate simultaneous sampling of beluga behavior, cod distribution, and other potential prey to quantify the costs and benefits of beluga foraging on cod prey.

### 3.5.5 *Conclusions*

We used satellite-linked time-depth recorders to infer depths at which BS and ECS beluga whales forage throughout diverse regions of the Pacific Arctic. Maximum and modal dive depths suggested demersal foraging on shallow shelves like the Chukchi and northern Bering seas in contrast to pelagic diving in the deep Canada Basin for both populations. While maximum dive depths often reached the seafloor in slope habitats, portions of the water column were more frequently targeted in certain regions. We also found that patterns of ECS beluga diving coincided with the depths at which Arctic cod were most abundant during a fisheries acoustic survey in the western Beaufort Sea, thereby providing additional support for our classification of foraging dives. Our regional and population-specific estimates of foraging behavior provide important baseline information in the context of a rapidly transforming Arctic ecosystem that is increasingly exposed to anthropogenic activities (Grebmeier 2012). Industrial and other human activities (e.g., shipping and other vessels, mining, fishing, and tourism) are expanding and can potentially affect belugas directly (e.g., hearing impairment or stress response) or indirectly alter behavior (Reeves et al. 2014). Although both populations are considered stable stocks (Allen & Angliss 2014), recent evidence for declining growth, body condition, and blubber thickness suggests that ecosystem changes may be affecting belugas through reduced availability or quality of prey (Harwood et al. 2014, Harwood et al. 2015). Thus, understanding the behavioral use in each region offers a baseline for which changes in beluga behavior can be assessed, as well as information to identify ecologically significant areas that may warrant protection.

## 3.6 ACKNOWLEDGEMENTS

Tagging would not have been possible without the support of the Inuvialuit Hunter and Trapper Corporations of Inuvik, Aklavik, and Tuktoyaktuk, and Polar Continental Shelf Project for BS belugas or the village of Point Lay for ECS belugas. We are grateful to a multitude of people and organizations who were instrumental in tagging operations and data processing: J. Orr, A. Martin, B. LeBlanc (BS whales); L. Lowry, K. Frost, G. O'Corry-Crowe, D. Pikok, R. Small, J. Tazruk, J. Orr, A. Ashby, V. Dollarhide, L. Ferreira, R. Hobbs, R. Hoover, T. Nukapigak, L. Pierce, T. Romano, M. Sparck, H. Smith, S. Speckman, D. Susook, C. Aniskette, N. Hank, L. Hansen, L. Hoberecht, L. Quakenbush, T. Robeck, A. Simon, G. and K. VanBlaricom, B. and M. Tracey, J. Rexford, J. Taylor, J. Edwards, D. Ramey, B. Achootchook (ECS whales). Funding for tagging was provided by the Alaska Beluga Whale Committee, Alaska Department of Fish and Game, Environmental Studies Revolving Fund, Fisheries and Oceans Canada (DFO), Fisheries Joint Management Committee, U.S. Minerals Management Service (now U.S. Bureau of Ocean Energy Management), National Marine Fisheries Service (NMFS), North Slope Borough of Alaska, North Slope Borough School District, and Village of Point Lay. Several people and organizations also supported the fish survey (see Parker-Stetter et al. 2011). We appreciate statistical advice from J. Ver Hoef. J. Nomura assisted with analysis of cod vertical distributions. Discussions with S. Moore and R. Hobbs helped develop this project, and J. Citta provided valuable feedback. Four anonymous reviewers contributed suggestions that greatly improved this manuscript. D.D.W. Hauser was supported by a fellowship from the University of Washington's Integrative Graduate Education and Research Traineeship Program on Ocean Change (National Science Foundation). All required permits for capture and tagging were approved by DFO for BS whales and NMFS (Nos. 14610, 782-1438, and 782-1719) for ECS whales.

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Table 3-1. Study regions (see Figure 3-1) and number of tagged Eastern Beaufort Sea (BS; total n = 4) and Eastern Chukchi Sea (ECS; total n=26) beluga whales in each region, including the number of 6-h maximum depth periods. Habitat types vary according to bathymetry and hydrography. Median (range) depths measured by the location of 6-h dive periods are also shown for each region. The first to last day of the year and season (summer=July-August, fall=September-October, winter=November-April, spring=May-June) when a tagged whale was located in each region are indicated.

| | **ECS** | | | **BS** | | |
|---|---|---|---|---|---|---|
| **Region (habitat type)** | **No. tagged whales in region (no. 6-h dive periods)** | **Median (range)[1] depth (m)** | **First-last day of year (season)** | **No. tagged whales in region (no. 6-h dive periods)** | **Median (range)[1] depth (m)** | **First-last day of year (season)[2]** |
| a. Bering Sea (shallow shelf) | 6 (1078) | 34 (1-56) | 311-142 (winter, spring) | 2 (123) | 75 (15-123) | 335-107[3] (winter) |
| b. Chukchi Sea (shallow shelf) | 26 (1612) | 45 (0-1004) | 142-354 (year-round) | 4 (541) | 54 (0-995) | 253-335 (fall, winter) |
| c. ECS core: Kasegaluk Lagoon (shallow shelf) | 23 (465) | 3 (0-30) | 178-317 (spring-fall) | - | - | - |
| d. ECS core: Barrow Canyon (slope) | 24 (1874) | 150.5 (0-2429) | 170-325 (spring-fall) | 3 (32) | 145.5 (28-1702) | 250-270 (fall) |
| e. AK Beaufort Sea (slope) | 15 (221) | 335 (0-999) | 194-310 (summer, fall) | 3 (62) | 48.5 (0-943) | 240-266 (fall) |
| f. Canada Beaufort Sea (slope) | 6 (86) | 630.5 (189-987) | 239-305 (fall) | 4 (140) | 353 (0-967) | 193-261 (summer, fall) |
| g. BS core: Mackenzie Estuary (shallow shelf) | - | - | - | 4 (137) | 17 (0-66) | 189-239 (summer) |
| h. Amundsen Gulf (slope) | - | - | - | 3 (238) | 314 (1-644) | 201-251 (summer) |
| i. east slope Canada Basin (slope) | 6 (118) | 636 (373-985) | 214-271 (summer, fall) | - | - | - |
| j. BS core: Viscount Melville Sound (slope) | - | - | - | - | - | - |
| k. Canada Basin (pelagic deep) | 22 (2417) | 3248 (993-3907) | 191-308 (summer, fall) | 2 (274) | 3108 (1025-3918) | 210-260 (summer, fall) |
| **Total** | **26 (7923)** | **147 (0-3907)** | | **4 (1600)** | **84.5 (0-3918)** | |

[1] Minimum depths of 0 m correspond to locations very close to shore, based on a Mean High Water vertical datum (Jakobsson et al. 2012).
[2] There were no year-round tag deployments available for BS beluga whales. Deployments ranged from day 189 (early July) to 107 (mid-April).
[3] Date of last tag transmission, last date in region is unknown.
- No tagged whales occurred in the region.

Table 3-2. Beluga whales tagged in the Eastern Beaufort Sea (BS, n = 4) and Eastern Chukchi Sea (ECS, n = 26) populations near the Mackenzie River Estuary, Canada, and Point Lay, AK, USA, respectively. Adult (ADU) or immature (IMM) reproductive status was visually assessed based on size, coloration, and presence of a calf if possible. Tag duration refers to the number of days dive data were collected and used in the present study.

| Population | Year | Tag ID | Sex | Length (cm) | Reproductive status | Capture date | Tag duration (days) |
|---|---|---|---|---|---|---|---|
| **BS** | 1997 | 97-2118 | F | 374 | ADU | 26-Jul | 127 |
| | | 97-25846 | M | 374 | IMM | 29-Jul | 83 |
| | 2005 | 05-57591 | F | 275 | IMM | 5-Jul | 283 |
| | | 05-57593 | F | 350 | ADU | 10-Jul | 157 |
| **ECS** | 1998 | 98-11035 | M | 440 | ADU | 26-Jun | 11 |
| | | 98-2284 | M | 432 | ADU | 28-Jun | 13 |
| | | 98-11036 | M | 398 | ADU | 29-Jun | 98 |
| | | 98-2285 | M | 415 | ADU | 29-Jun | 89 |
| | | 98-2282 | M | 414 | ADU | 1-Jul | 58 |
| | 1999 | 99-11035 | M | 418 | ADU | 30-Jun | 85 |
| | | 99-11036 | F | 266 | IMM | 30-Jun | 73 |
| | | 99-11037 | M | 424 | ADU | 30-Jun | 55 |
| | | 99-11041 | M | 424 | ADU | 30-Jun | 84 |
| | 2001 | 01-2093 | M | 381 | ADU | 3-Jul | 36 |
| | | 01-2094 | F | 359 | ADU | 3-Jul | 17 |
| | | 01-11038 | F | 316 | IMM | 5-Jul | 145 |
| | | 01-11041 | M | 324 | IMM | 5-Jul | 145 |
| | | 01-2280 | F | 335 | IMM | 5-Jul | 107 |
| | | 01-11037 | M | 340 | ADU | 7-Jul | 131 |
| | | 01-228 | M | 320 | IMM | 7-Jul | 15 |
| | | 01-2282 | M | 373 | ADU | 7-Jul | 35 |
| | 2002 | 02-11036 | F | 320 | IMM | 7-Jul | 66 |
| | | 02-11044 | M | 276 | IMM | 7-Jul | 80 |
| | | 02-2088 | M | 267 | IMM | 8-Jul | 62 |
| | 2007 | 07-77015 | F | 386 | ADU | 1-Jul | 132 |
| | | 07-36516 | F | 398 | ADU | 1-Jul | 125 |
| | | 07-22149 | M | 430 | ADU | 1-Jul | 520 |
| | 2010 | 10-22117 | M | 305 | IMM | 30-Jun | 157 |
| | | 10-36517 | M | 345 | ADU | 30-Jun | 99 |
| | 2012 | 12-108772 | F | 328 | ADU | 9-Jul | 303 |

Table 3-3. Results of ANOVAS comparing regional average occupancy time per dive ($\text{AOT}_{\text{dive}j}$) among depth layers and between Eastern Chukchi Sea (ECS) males and females (left section), ECS adult and immature whales (middle section), and Eastern Beaufort Sea (BS) and ECS populations (right section). For each regional comparison, sample size is indicated as well as whether depth layers, sex (or age, or population, respectively), or interactions between depth and sex were significantly different. Significant factors, assessed at *p*<0.002, are highlighted in bold. Regions correspond to those in Table 3-1and Figure 3-1.

| **Region** | **ECS sexes** | | | | **ECS age classes** | | | | **Populations** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **No. tagged whales (M,F)** | **Depth layer p-value** | **Sex p-value** | **Depth x sex p-value** | **No. tagged whales (adult, immature)** | **Depth layer p-value** | **Age class p-value** | **Depth x age p-value** | **No. tagged whales (BS, ECS)** | **Depth layer p-value** | **Population p-value** | **Depth x population p-value** |
| Bering Sea | 4,2 | 0.038 | - | - | 3,3 | 0.030 | 0.605 | 0.121 | 2,6 | 0.012 | 0.324 | - |
| Chukchi Sea | 16,6 | - | 0.383 | - | 16,9 | - | 0.024 | - | 3,25 | - | 0.066 | - |
| ECS core: Kasegaluk Lagoon | 16,6 | 0.039 | - | - | 15,7 | 0.038 | 0.098 | - | 0,22 | 0.040 | NT | NT |
| ECS core: Barrow Canyon | 15,8 | **<0.001** | - | - | 14,9 | **<0.001** | 0.197 | | 3,23 | **<0.001** | 0.260 | - |
| AK Beaufort Sea | 9,6 | **<0.001** | - | - | 9,6 | **<0.001** | - | - | 3,15 | **<0.001** | 0.054 | - |
| Canada Beaufort Sea | 4,2 | **<0.001** | - | - | 5,1 | | | | 4,6 | **<0.001** | 0.090 | - |
| BS core: Mackenzie Estuary | 0,0 | | | | 0,0 | | | | 4,0 | 0.054 | NT | NT |
| Amundsen Gulf | 0,0 | | | | 0,0 | | | | 3,0 | 0.011 | NT | NT |
| E. slope Canada Basin | 4,2 | **<0.001** | - | - | 5,1 | | | | 0,6 | **<0.001** | NT | NT |
| Canada Basin | 14,7 | **<0.001** | 0.474 | **<0.001** | 13,8 | **<0.001** | **<0.001** | 0.087 | 2,21 | **<0.001** | 0.200 | - |

'NT' indicates a factor was not tested.

- Factor not included in final model.

Table 3-4. Parameter estimates of the fixed effects of generalized linear mixed models for number of Eastern Chukchi Sea beluga whale dives to target depths. Analyses were restricted to 6-h maximum depth periods within either the >200 m Arctic cod survey area (n = 192 6-h periods, from 20 whales) or >300 m Arctic cod survey area (n = 68 6-h periods, from 16 whales) (see Appendix 3-4). The categorical explanatory variable 'depth layer with the maximum density of Arctic cod' (reference level = 100-200 m depth) was only included for models using the >300 m survey area.

| **Response** | **Factor** | **Estimate** | **SE** | ***P*** |
|---|---|---|---|---|
| No. beluga dives to 100-200 m (>200 m area) | Intercept | 2.591 | 0.543 | <0.001* |
| | Cod density 100-200 m | -0.095 | 0.043 | 0.029* |
| | Cod density 200-300 m | 0.032 | 0.014 | 0.021* |
| | log(depth) | -0.189 | 0.088 | 0.032* |
| No. beluga dives to 200-300 m (>200 m area) | Intercept | 4.595 | 0.555 | <0.001* |
| | log(depth) | -0.484 | 0.094 | <0.001* |
| | Cod density 200-300 m | -0.048 | 0.017 | 0.004* |
| No. beluga dives to 200-300 m (>300 m area) | Intercept | 1.120 | 0.440 | 0.006* |
| | Cod density 50-100 m | -19.938 | 5.795 | <0.001* |
| | Cod density 100-200 m | -0.245 | 0.141 | 0.084 |
| | Cod density 200-300 m | -0.241 | 0.094 | 0.010* |
| | Cod density 300-400 m | 0.441 | 0.169 | 0.009* |
| | Depth of maximum cod density | | | |
| | 200-300 m | 0.344 | 0.282 | 0.223 |
| | 300-400 m | -0.420 | 0.316 | 0.183 |
| No. beluga dives to 300-400 m (>300 m area) | Intercept | 1.439 | 1.005 | 0.152 |
| | Cod density 10-50 m | -5.341 | 2.124 | 0.012* |
| | Cod density 50-100 m | -16.846 | 12.087 | 0.163 |
| | Cod density 100-200 m | 1.114 | 0.221 | <0.001* |
| | Cod density 200-300 m | 1.133 | 0.258 | <0.001* |
| | Cod density 300-400 m | -1.191 | 0.431 | <0.001* |
| | Depth of maximum cod density | | | |
| | 200-300 m | -1.028 | 0.497 | 0.039* |
| | 300-400 m | 0.574 | 0.508 | 0.259 |

*Significant at $p<0.05$

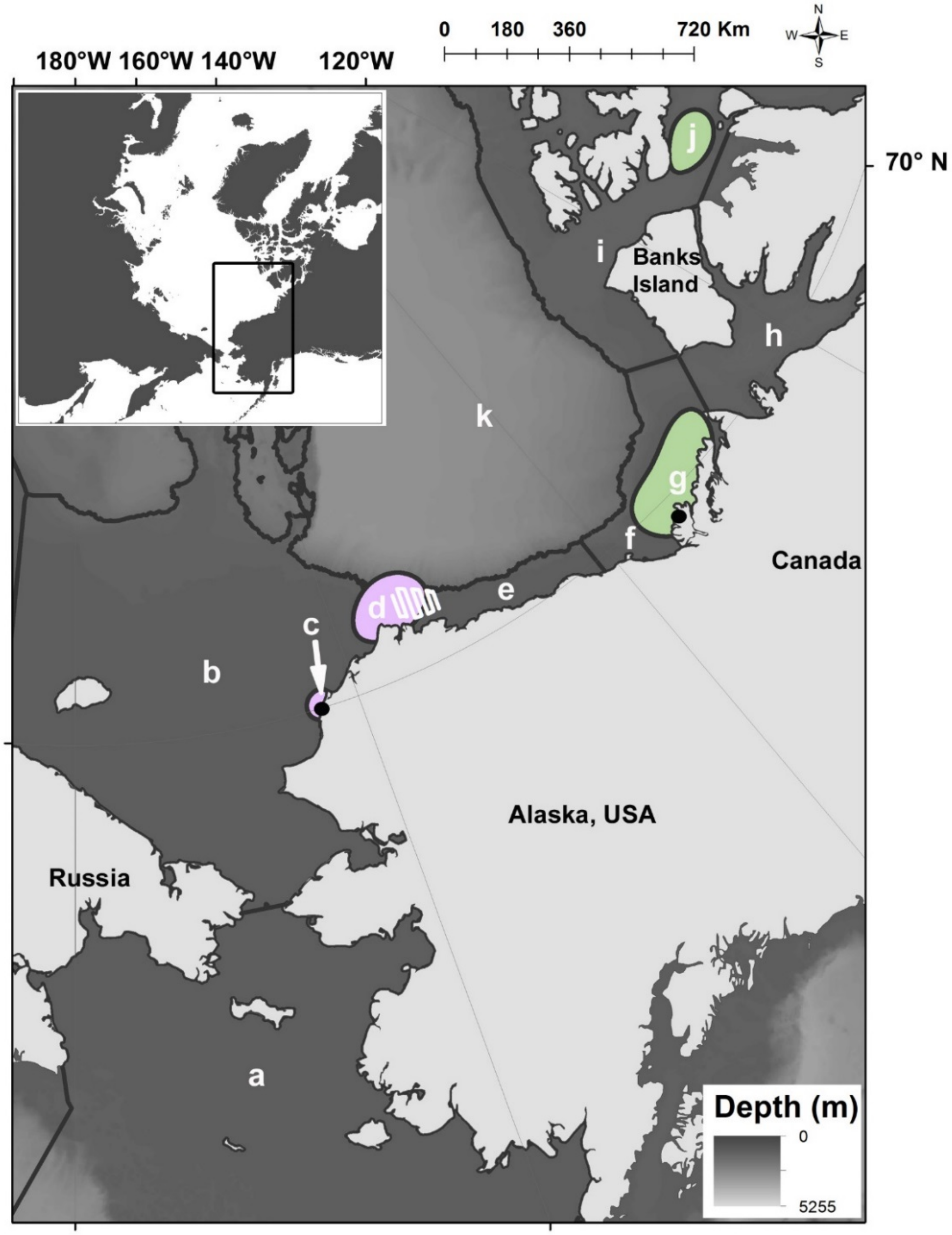


Figure 3-1. Eleven regions (and habitat type) of the Pacific Arctic used to examine regional diving behavior of Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) beluga whales: a) northern Bering Sea (shallow shelf), b) Chukchi Sea (shallow shelf), c) Kasegaluk Lagoon ECS summer core area (shallow shelf), d) Barrow Canyon ECS summer core area (slope), e) Alaska Beaufort Sea (slope), f) Canada Beaufort Sea (slope), g) Mackenzie Estuary BS summer core area (shallow shelf), h) Amundsen Gulf (slope), i) east slope of Canada Basin (slope), j) Viscount Melville Sound BS summer core area (slope), and k) Canada Basin (pelagic deep). Summer core areas follow Hauser et al. (2014); green and purple areas correspond to BS and ECS core areas, respectively. Black circles indicate approximate tagging locations, including Point Lay, Alaska, USA (ECS population, west circle) and the Mackenzie River Estuary, Canada (BS population, east circle). The location of a 2008 survey for Arctic cod (Parker-Stetter et al. 2011) is shown as the white trackline.

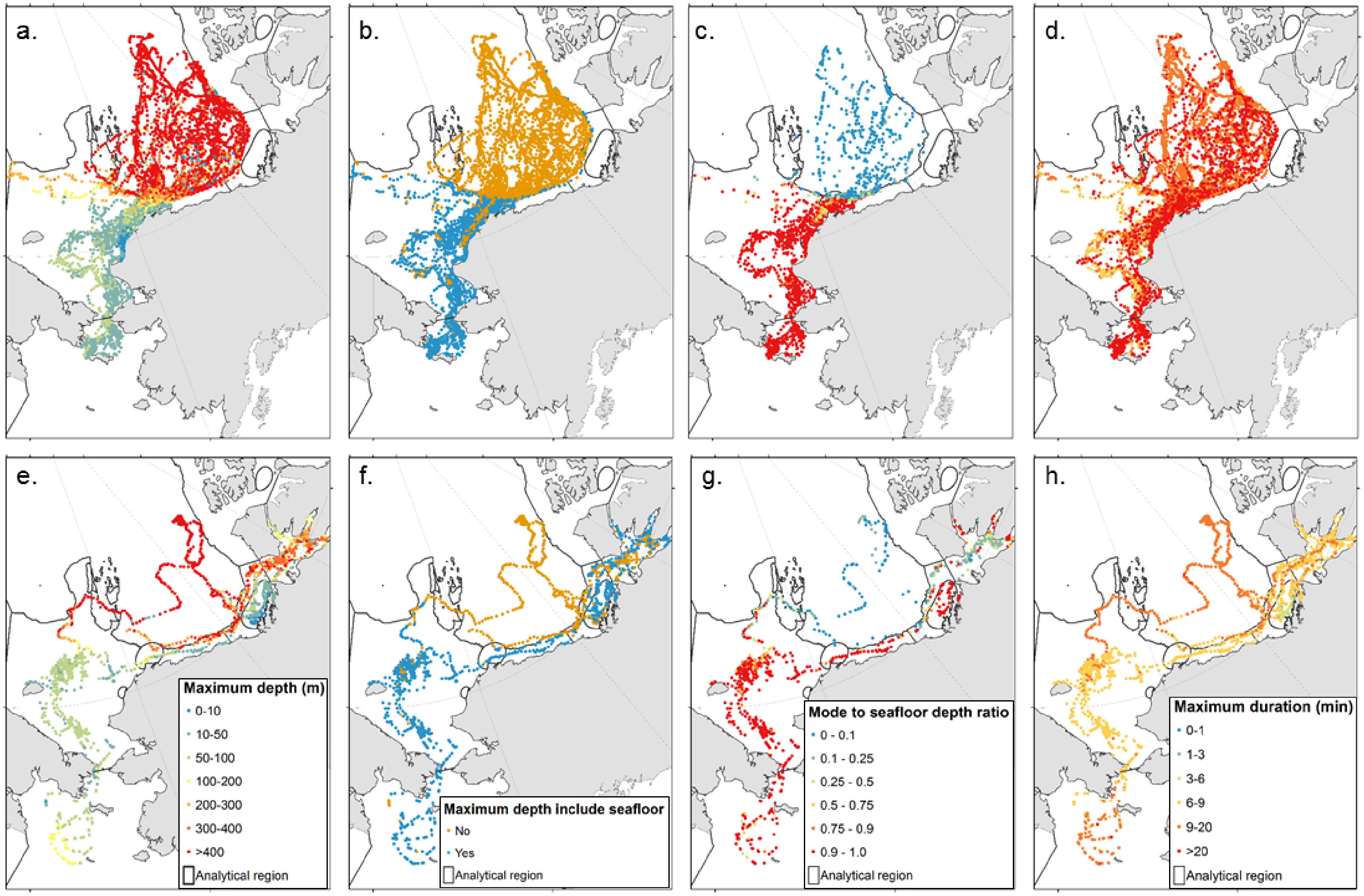


Figure 3-2. Locations corresponding to each 6-h period for Eastern Chukchi Sea belugas (panels a-d) and Eastern Beaufort Sea belugas (panels e-h). Colors represent maximum dive depth (a, e), if the maximum depth coincided with the seafloor (b, f), the ratio of the most common (mode) depth to seafloor depth (excluding modal depths <10 m; c, g), and categories of maximum dive durations (d, h). Ratios >0.9 were considered benthic dives. Black lines delineate each region (see Figure 3-1).

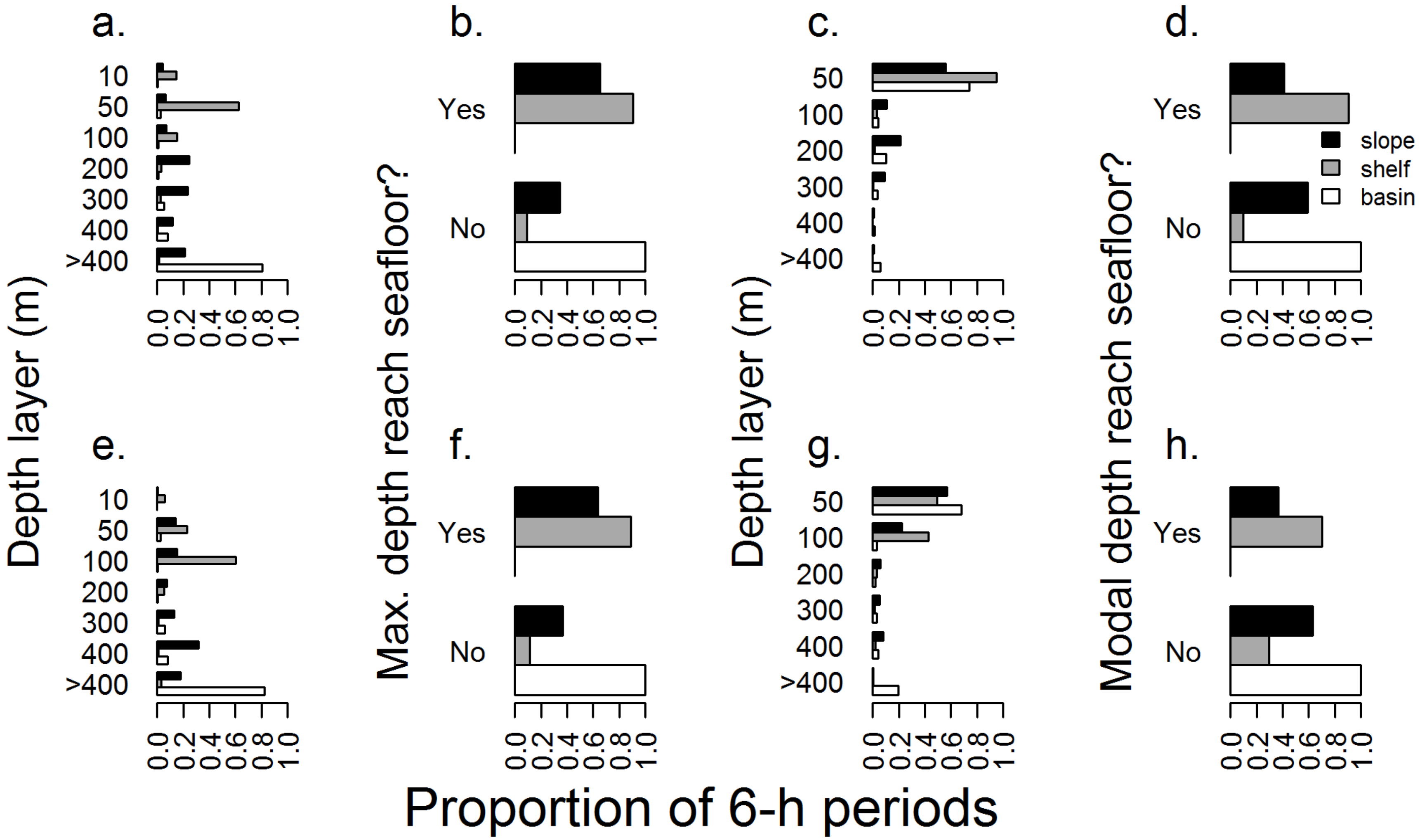


Figure 3-3. Proportion of 6-h periods summarizing diving behavior to each depth layer by Eastern Chukchi Sea (ECS; panels a-d) and Eastern Beaufort Sea (BS; panels e-h) beluga whales in slope (black), shelf (grey), and deep pelagic 'basin' (white) habitat types (see Table 3-1; Figure 3-1): maximum dive depth (a, e); whether maximum dive depth reached the seafloor (b, f); modal dive depth (c, g); and whether modal dive depth reached the seafloor (d, h).

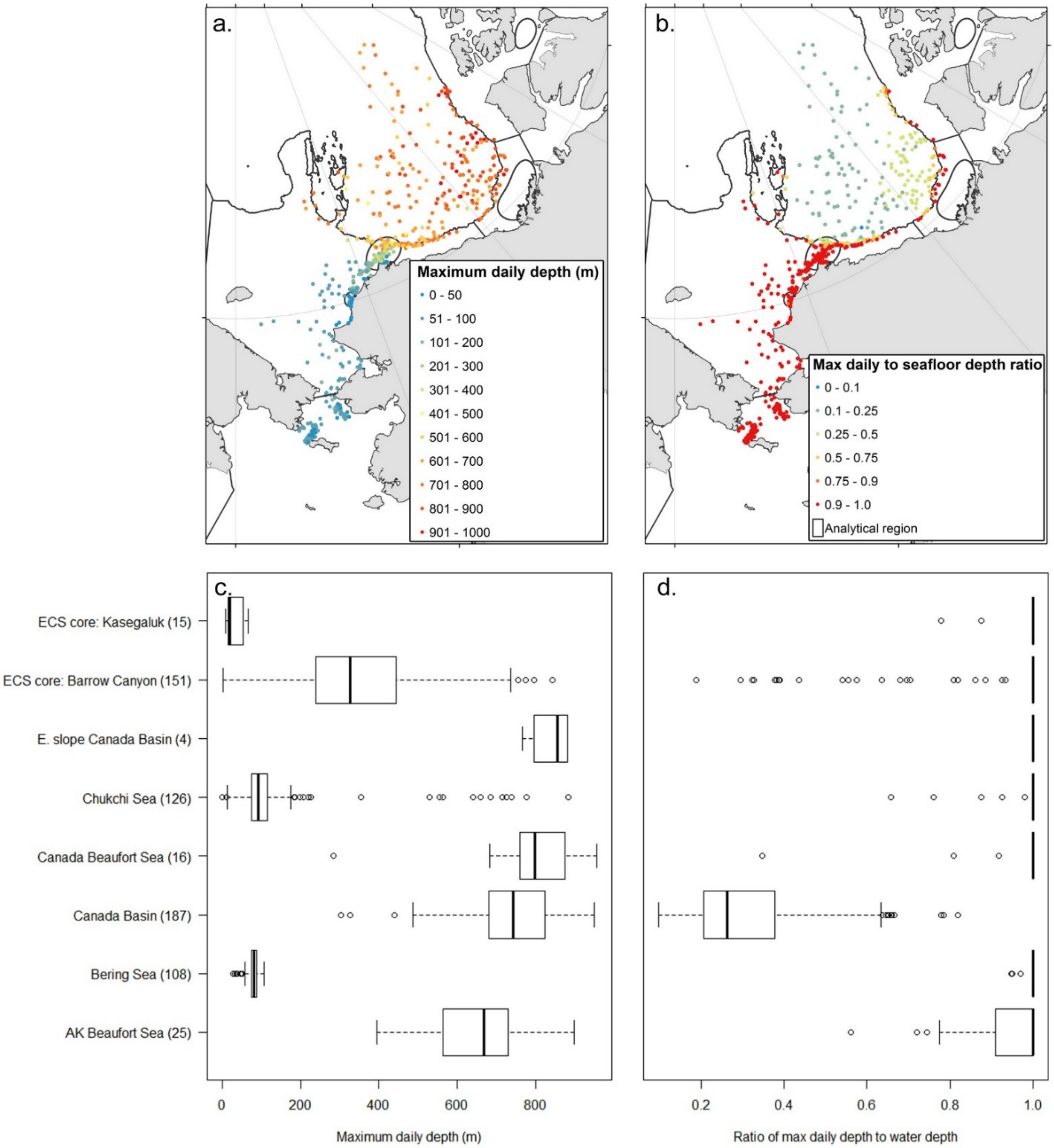


Figure 3-4. Maps of maximum daily dive depth (a) and the ratio of maximum daily dive depth to ocean depth (b) for six Eastern Chukchi Sea belugas tagged in 2007, 2010, and 2012. Regions are outlined in black lines in a and b (see Figure 3-1). Boxplots indicate regional maximum daily dive depth (c) and ratios (d). The number of maximum daily dive depth records for each region is shown in parentheses. Ratios >0.9 were considered benthic dives in close proximity to the seafloor.

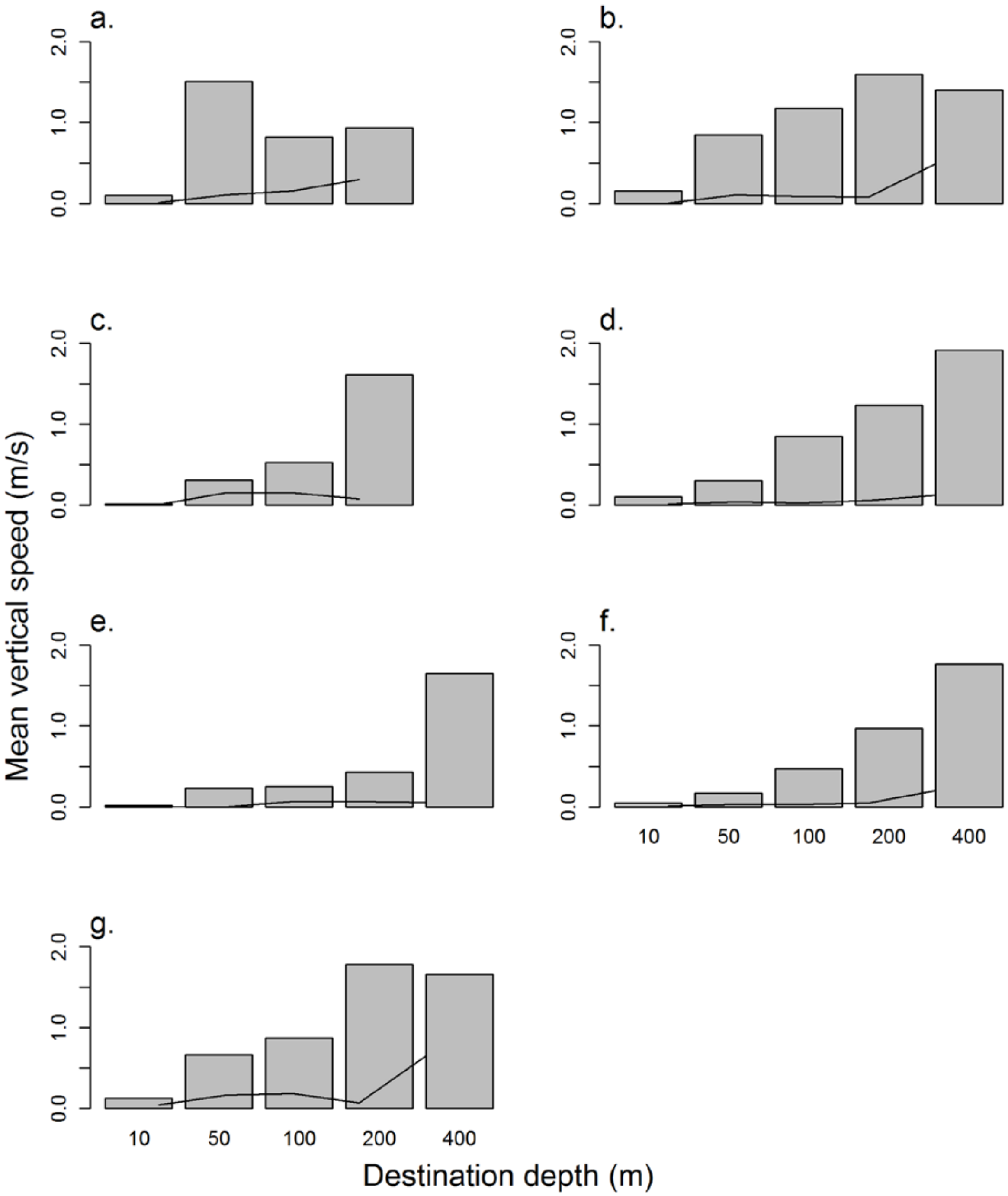


Figure 3-5. Estimated mean vertical transit speed ($S_j$; bars) among depth layers (shown as the maximum depth threshold) for Eastern Beaufort Sea (BS; panels a, c, e, g) and Eastern Chukchi Sea (ECS; panels b, d, f) beluga whales in the Chukchi and Bering seas shallow shelf (a, b), slope (c, d), deep pelagic Canada Basin (e, f), and Mackenzie Estuary and Amundsen shelf and slope (g) habitat types. Lines indicate the standard deviation of vertical transit speed. No ECS belugas occurred in the Mackenzie Estuary or Amundsen Gulf. No samples of Sj were obtained for BS belugas in the 200-400 m depth layer in the Chukchi and Bering seas shallow shelf (a) or slope (c) habitats, so the corresponding estimates from ECS whales were applied to the estimation of average occupancy time per dive (AOTdivej) in these cases.

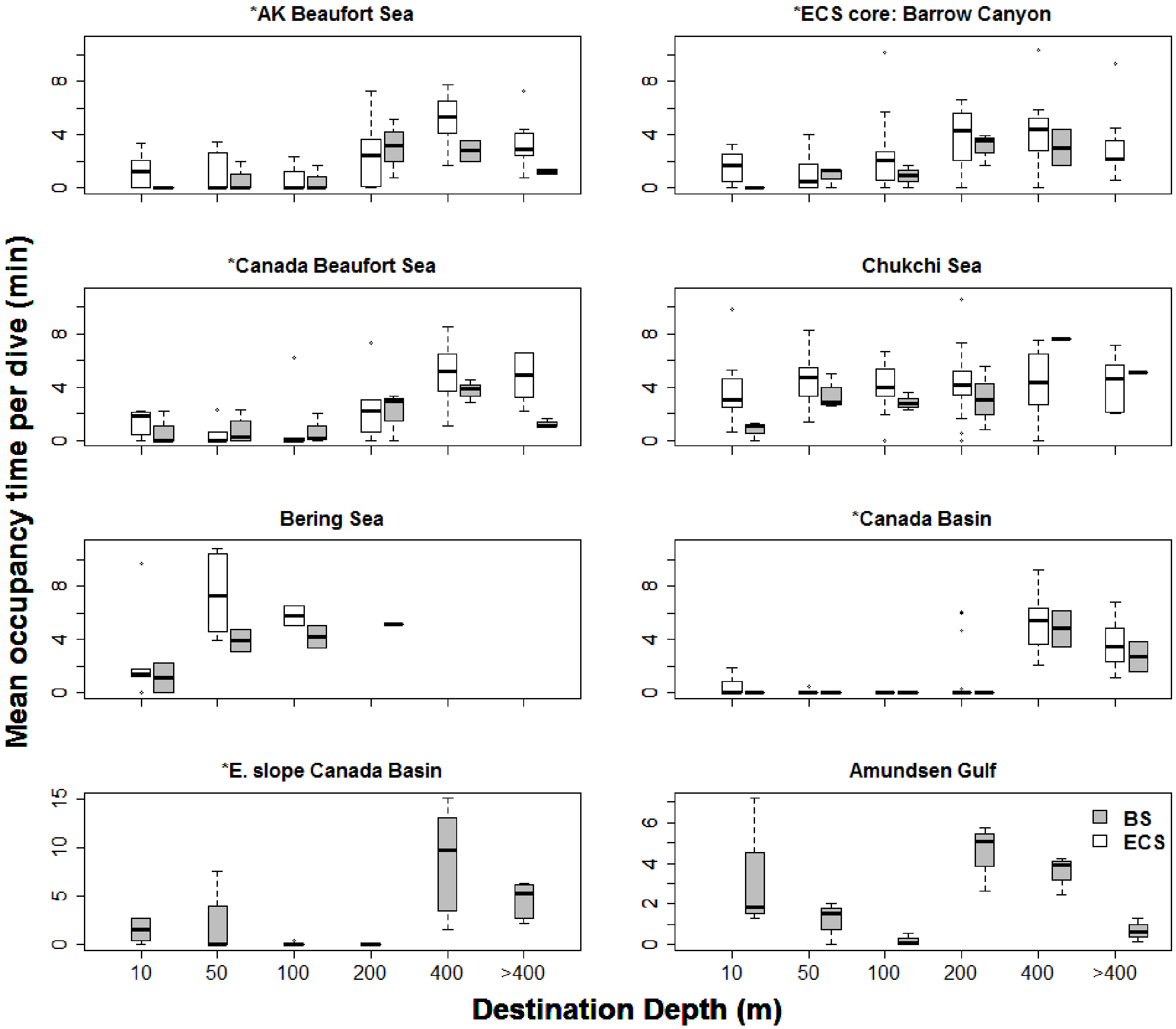


Figure 3-6. Estimated average occupancy time per dive ($AOT_{divej}$) among depth layers (shown as the maximum depth threshold) in Pacific Arctic regions (see Figure 3-1) for Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) populations of beluga whales. Regions with significant differences ($p<0.002$) in $AOT_{divej}$ among depths are indicated by asterisks (see Table 3-3).

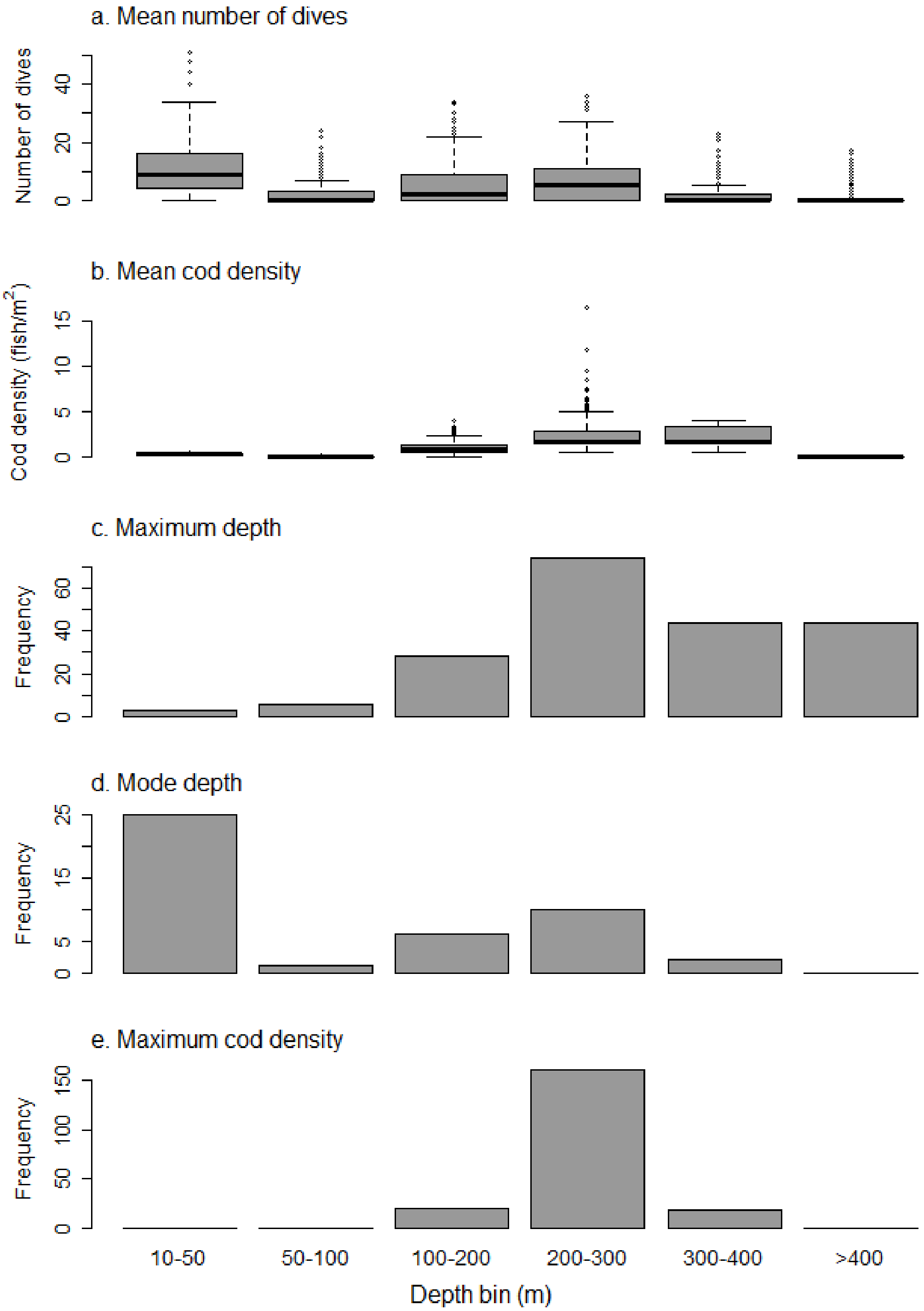
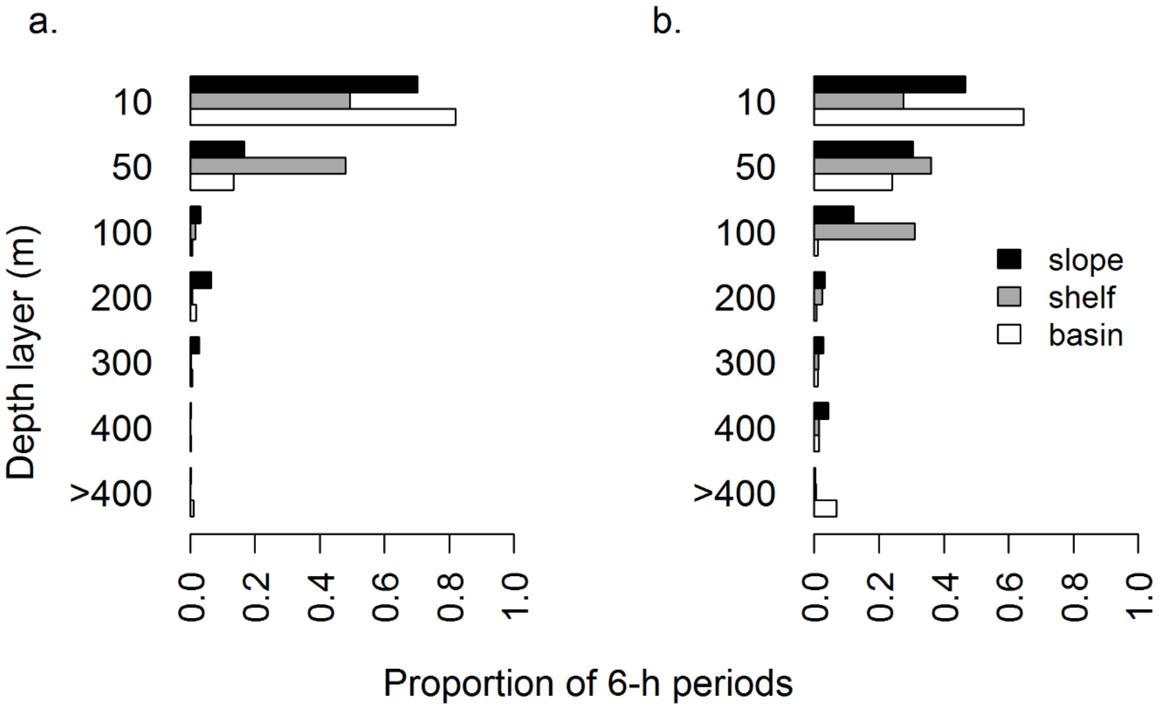


Figure 3-7. The (a) mean number of Eastern Chukchi Sea (ECS) beluga dives, (b) mean Arctic cod density, (c) frequency distribution of ECS maximum dive depth, (d) frequency distribution of ECS modal dive depth, and (e) frequency distribution of which depth layer contained the maximum Arctic cod density among depth layers (or ‘bins’), based on 6-h maximum depth periods within the Arctic cod >200 m survey area (n=192 6-h periods). Arctic cod densities are based on intersecting beluga locations with interpolated surfaces of Arctic cod density (see Appendix 3-4).

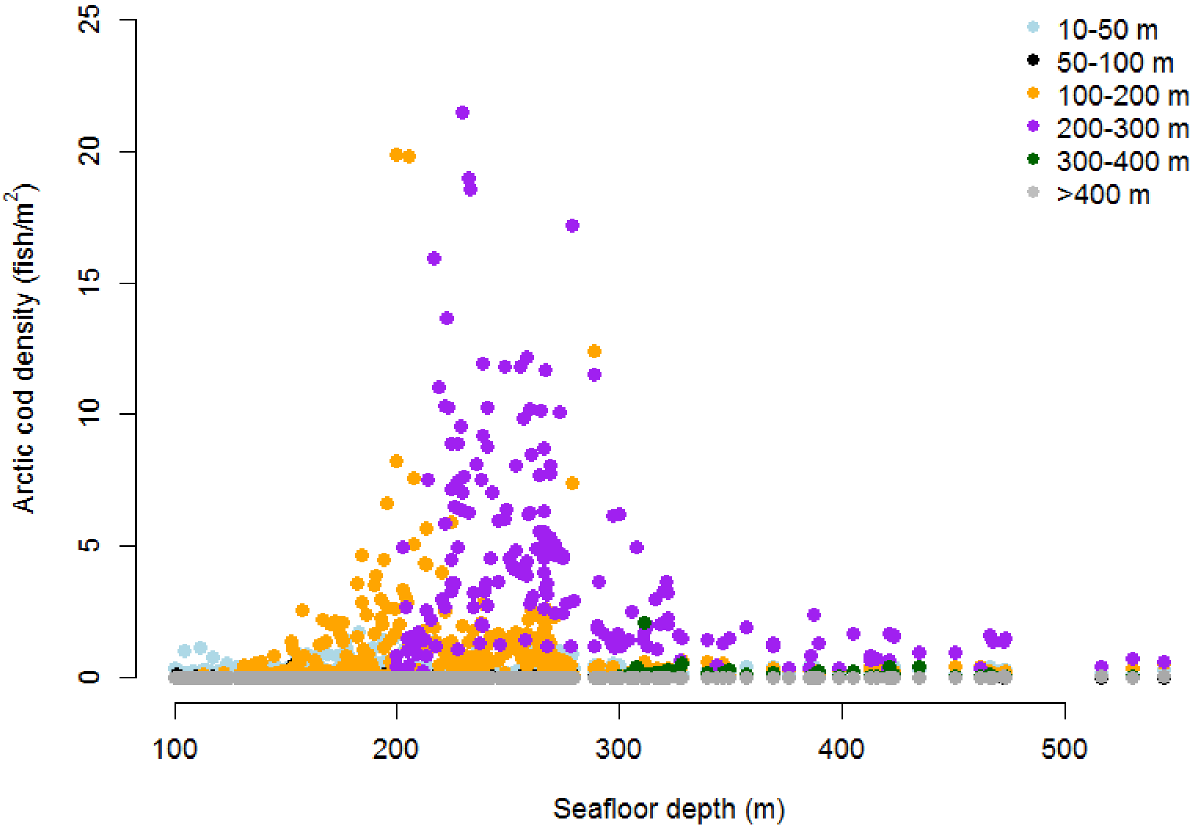
## 3.8 APPENDICES: SUPPLEMENTARY TABLES AND FIGURES

Appendix 3-1. Maximum depth, time at depth, and duration bins used in each year of tagging Eastern Beaufort Sea (BS) and Eastern Chukchi Sea (ECS) belugas. For analyses, we consolidated maximum depth, time at depth, and duration bins to the finest resolution possible to accommodate analyses of dive behavior (see 3.3 Methods).

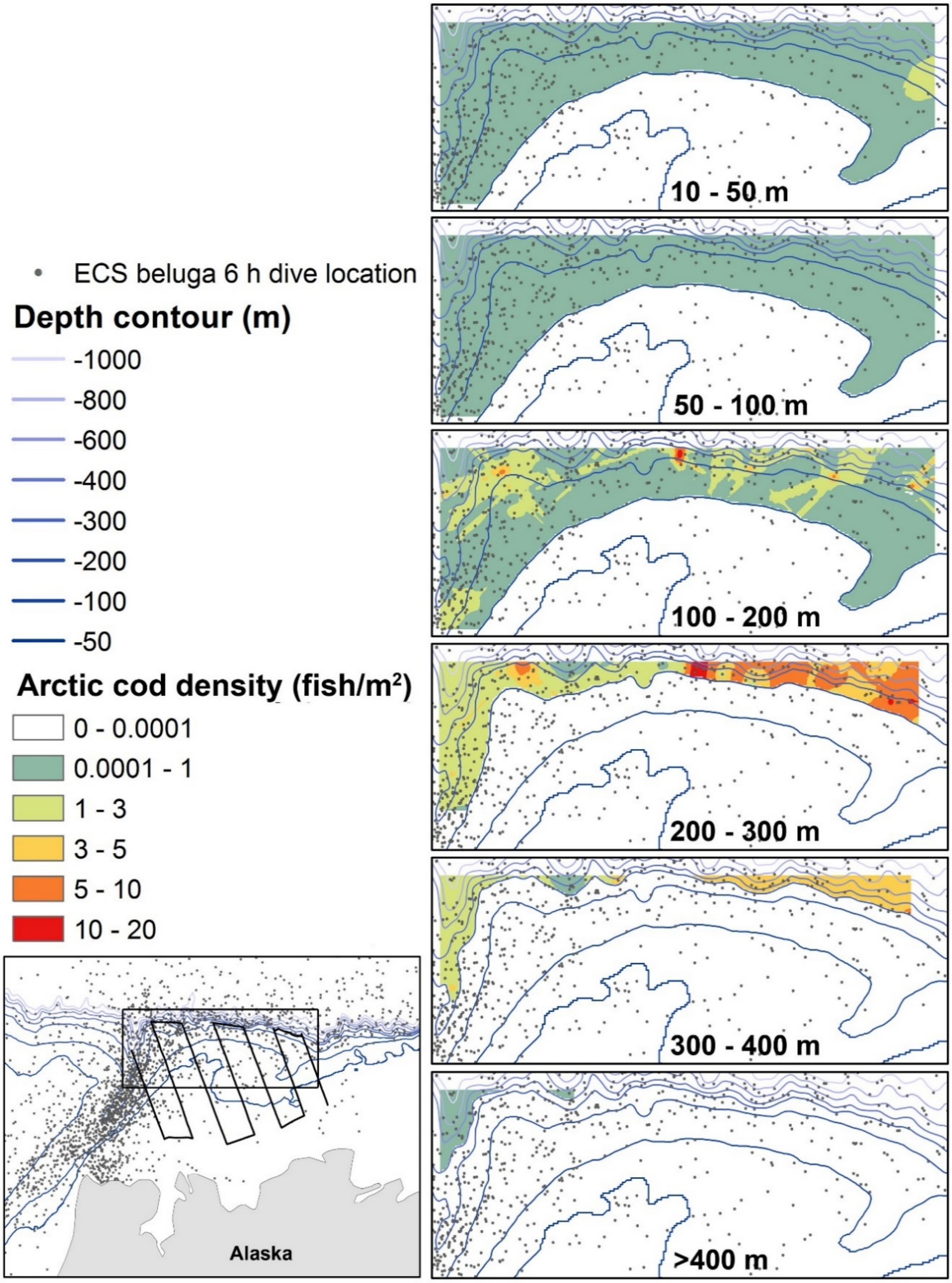
| Bin | Number of dives to maximum depth (m) | | | | | | | Time at depth (m) | | | | | | | Duration (min) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **ECS years** | | | | | **BS years** | | **ECS years** | | | | | **BS years** | | **ECS years** | | | **BS years** |
| | ‘98 | ‘99-‘02 | ‘07 | ‘10 | ‘12 | ‘97 | ‘05 | ‘98 | ‘99-‘02 | ‘07 | ‘10 | ‘12 | ‘97 | ‘05 | ‘98-‘02 | ‘07, ‘10 | ‘12 | ‘97, ‘05 |
| 1 | 2 | 4 | 0 | 0 | 10 | 2 | 10 | 2 | 4 | 0 | 0 | 0 | 2 | 0 | 1 | 0.5 | 1 | 1 |
| 2 | 4 | 8 | 10 | 10 | 20 | 4 | 25 | 4 | 8 | 10 | 10 | 2 | 4 | 1 | 3 | 1 | 2 | 3 |
| 3 | 6 | 12 | 50 | 20 | 50 | 6 | 50 | 6 | 12 | 50 | 20 | 10 | 6 | 2 | 6 | 1.5 | 3 | 6 |
| 4 | 10 | 28 | 100 | 50 | 100 | 10 | 75 | 10 | 28 | 100 | 50 | 20 | 10 | 3 | 9 | 2 | 4 | 9 |
| 5 | 26 | 52 | 200 | 100 | 150 | 26 | 100 | 26 | 52 | 200 | 100 | 50 | 26 | 4 | 12 | 3 | 5 | 12 |
| 6 | 50 | 100 | 300 | 150 | 200 | 50 | 150 | 50 | 100 | 300 | 150 | 100 | 50 | 5 | 15 | 4 | 10 | 15 |
| 7 | 100 | 152 | 400 | 200 | 300 | 100 | 200 | 100 | 152 | 400 | 200 | 150 | 100 | 10 | 18 | 5 | 15 | 18 |
| 8 | 150 | 200 | 500 | 300 | 400 | 150 | 300 | 150 | 200 | 500 | 300 | 200 | 150 | 50 | 21 | 6 | 20 | 21 |
| 9 | 200 | 252 | 600 | 400 | 500 | 200 | 400 | 200 | 252 | 600 | 400 | 300 | 200 | 100 | 24 | 7 | 25 | 24 |
| 10 | 250 | 300 | 700 | 500 | 600 | 250 | 500 | 250 | 300 | 700 | 500 | 400 | 250 | 200 | 24+ | 8 | 30 | 24+ |
| 11 | 300 | 352 | 800 | 600 | 700 | 300 | 600 | 300 | 352 | 800 | 600 | 500 | 300 | 400 | | 9 | 40 | |
| 12 | 350 | 400 | 900 | 700 | 700+ | 350 | 700 | 350 | 400 | 900 | 700 | 600 | 350 | 600 | | 10 | 50 | |
| 13 | 400 | 452 | 1000 | 800 | | 400 | 800 | 400 | 452 | 1000 | 800 | 700 | 400 | 800 | | 20 | 60 | |
| 14 | 400+ | 452+ | 1000+ | 800+ | | 400 | 800+ | 400+ | 452+ | 1000+ | 800+ | 700+ | 400+ | 800+ | | 20+ | 60+ | |



Appendix 3-2. Proportion of modal dive depths made to each depth layer in slope (black), shelf (grey), and deep pelagic ‘basin’ (white) habitat types for a) Eastern Chukchi Sea (ECS) and b) Beaufort Sea (BS) beluga whales.



Appendix 3-3. Densities of age 1+ Arctic cod in each beluga whale depth layer relative to seafloor depth, estimated from the Parker-Stetter et al. (2011) acoustic survey and along the trackline shown in Figure 3-1.



Appendix 3-4. Kriging results of Arctic cod densities within each vertical depth layer. Black dots indicate the locations of Eastern Chukchi Sea beluga 6-h maximum dive periods occurring within the survey area. The fish survey trackline, completed in 2008 (Parker-Stetter et al. 2008), is shown in the inset map and corresponds to the survey line in Figure 3-1.

# Chapter 4. HABITAT SELECTION IN SEA ICE BY TWO BELUGA WHALE POPULATIONS IN THE PACIFIC ARCTIC

## 4.1 ABSTRACT

There has been profound sea ice loss in the Pacific Arctic over the past two decades, especially in areas in which two beluga whale (*Delphinapterus leucas*) populations occur between July-November. To date no studies have investigated population-specific habitat selection in the context of changing sea ice conditions. We developed habitat selection models that incorporated daily sea ice measures (sea ice concentration, proximity to ice edge and dense ice) and bathymetric features (slope, depth, proximity to the continental slope, Barrow Canyon, and shore) to establish quantitative estimates of preferred habitat for the Eastern Chukchi Sea ('Chukchi') and Eastern Beaufort Sea ('Beaufort') populations. We applied used-available resource selection functions to locations of 65 whales (M=44, F=21) tagged from 1993-2012. Our models revealed large variations in seasonal habitat selection that were distinct among sex and population groups. Chukchi whales of both sexes used areas close in proximity to Barrow Canyon (typically <200 km) as well as the continental slope in summer, though males generally selected higher sea ice concentrations (20-60%) and steeper slopes (15-25%). There were larger differences in habitat selection between sexes for Beaufort belugas, with males selecting higher ice concentrations (40% or greater) and deeper water than females (>1500 m) in July-August. Close proximity to shore (<200 m) was an important predictor for summer habitat of Beaufort females while distance to the ice edge was a strong factor in the habitat selection of males, especially during westward migration in September. Habitat choices in seasonal Arctic environments can indicate features important to the foraging distribution of top predators as well as influences of sexual resource partitioning. Our results provide a benchmark on which to assess future changes in beluga habitat.

## 4.2 INTRODUCTION

Arctic marine ecosystems are influenced by the annual growth and retreat of seasonal sea ice from maximum-minimum extent in March and September, respectively. Sea ice is a key physical factor affecting the distribution and movements of marine mammal predators in the Arctic, because life history and movements are tightly coupled with sea ice conditions (Laidre et al. 2008). Some species like Pacific walruses (*Odobenus rosmarus*) and polar bears (*Ursus maritimus*) use sea ice as a platform for foraging, reproduction, and resting (e.g. Regehr et al. 2010, Jay et al. 2012), while the distribution and movements of Arctic cetaceans are indirectly linked to seasonal sea ice cycles that affect access and localized productivity (Moore and Huntington 2008).

Beluga whales (*Delphinapterus leucas*) are an ice-associated cetacean comprised of >20 populations across the Arctic and sub-Arctic. Beluga whales have broad habitat preferences and can use open water, loose annual pack ice, the sea ice edge, and multiyear pack ice (Laidre et al. 2008). Some populations, such as the genetically-distinct Eastern Chukchi Sea (‘Chukchi’) and Eastern Beaufort Sea (‘Beaufort’) populations in the Pacific Arctic, seasonally migrate thousands of kilometers and range to ~80° N into areas of dense pack ice (Richard et al. 2001, Suydam et al. 2001) while also exhibiting philopatry to summering areas (O'Corry-Crowe et al. 1997). Foraging occurs on a combination of epi-benthic and pelagic prey (e.g. Arctic cod, *Boreogadus saida*) in shelf and continental slope regions, respectively, and deep diving (>900 m) occurs in basin habitat (Hauser et al. 2015, Quakenbush et al. 2015). Belugas detected by hydrophones and aerial observers during summer-fall in the Alaska Beaufort Sea are associated with the continental slope in moderate to heavy ice conditions and also in association with oceanographic features that could enhance foraging opportunities (e.g. a strong Alaska Coastal Current, ACC;

Moore 2000, Moore et al. 2000, Stafford et al. 2013). Previous studies have been unable to differentiate between Chukchi and Beaufort beluga populations, which overlap in distribution in the Alaska Beaufort Sea and primarily during September (Hauser et al. 2014). In addition to population-specific seasonal movements there are also intra-population patterns of sexual segregation with males tending to be distributed farther north and in deeper water (Loseto et al. 2006, Hauser et al. 2014).

Arctic regions are also experiencing unprecedented rates of change characterized as substantial reductions in sea ice extent, volume, and duration of seasonal cover (Stroeve et al. 2012, Frey et al. 2015). Arctic marine ecosystems are being transformed in response to shifting physical conditions (Grebmeier 2012), concomitant with increasing anthropogenic pressures throughout the range of belugas (Reeves et al. 2014). Questions remain about how sea ice influences seasonal foraging habitat for each population, especially in conjunction with other habitat features. There is a need to understand spatial and temporal variability in the use of sea ice habitat to guide aspects of population management. Improved understanding of seasonal habitat use by beluga populations could help predict future responses to ice loss as well as guide conservation of critical habitats potentially exposed to climate or anthropogenic impacts (Laidre et al. 2015b). In this paper, we quantify monthly shifts in sea ice habitat selection for both sexes of two populations of beluga whales in the Pacific Arctic, from July-November. Our primary goal is to use resource selection modeling applied to location data from 65 belugas tagged with satellite-linked transmitters to quantify population-specific seasonal habitat selection. We also contrasted sea ice habitat selected by male and female beluga whales of each population.

## 4.3 METHODS

### 4.3.1 *Study area*

The Pacific Arctic provides a connection between the North Pacific and Arctic oceans for both biological and physical processes (Figure 4-1). The Chukchi Sea is shallow (~50 m mean depth) and broad. The Beaufort Sea to the east is comprised of a narrow continental shelf north of Alaska and western Canada that borders the steep continental slope margins transitioning into the deep (>3,000 m) Canada Basin. The major inflow of Pacific water transits from Bering Strait across the Chukchi Sea and into the Arctic Ocean, bathymetrically channeled via a network of shoals and submarine canyons, including the Barrow Canyon (Woodgate et al. 2005). Advection from Bering Strait flows through Barrow Canyon as the ACC and continues along the Beaufort Sea continental slope as a shelfbreak jet with persistent upwelling (Pickart et al. 2013). These predominant circulation patterns contribute to an extremely productive region during periods of seasonal ice retreat, and the increased open-water season during the last decade may also be resulting in secondary plankton blooms that further enhances regional productivity into the fall (Ardyna et al. 2014, Arrigo and van Dijken 2015). Thus, a suite of physical factors related to sea ice and underwater topography influence regional productivity and prey availability that in turn presumably impact beluga habitat selection in the Pacific Arctic.

### 4.3.2 *Beluga capture and monitoring*

We captured and tagged Beaufort beluga whales in the Mackenzie River Estuary in July 1993-2005 (Figure 4-1, Table 4-1). We tagged Chukchi beluga whales near the village of Point Lay, Alaska in late June to early July 1998-2012. We affixed satellite-linked transmitters (Wildlife Computers, Redmond, WA or Sea Mammal Research Unit, University of St. Andrews) to the dorsal ridge of belugas, following procedures described in Orr et al. (2001). The tags transmitted locations via the Argos satellite system with varying levels of spatial accuracy, so we removed unrealistic locations using the ‘argosfilter’ package in R (R Development Team 2012; Freitas et al. 2008) by setting default turn angles and a maximum travel velocity of 6.4 km/h (Richard et al. 2001). To standardize sampling, we selected the best quality daily location similar to Hauser et al. (2014), including Argos position qualities 0-3 (error >1.5km to <250 m), A, and B (estimated as ~15 and 21 km, Douglas et al. 2012).

### 4.3.3 *Habitat variables*

We established a suite of spatially-explicit environmental variables based on beluga ecology to estimate habitat selection. Specifically, we compiled polar projections of spatial layers for predictors of daily sea ice concentration, seafloor slope, and water depth as well as distance to the daily sea ice edge (15% concentration), dense pack ice (90% concentration), shoreline, continental slope, and the Barrow Canyon region using ArcGIS 10.2 (ESRI, Redlands, CA). Beaufort beluga whale habitat selection is affected by ice type Loseto et al. (2006), and sea ice cover may affect access to the Beaufort and Chukchi seas during the open water season (Garland et al. 2015a). We obtained daily sea ice concentration values estimated from satellite passive microwave data (SSM/I), available at a nominal grid resolution of 25 km (Cavalieri et al. 1996). The sea ice edge, defined here as 15% sea ice concentration, is a dynamic and productive region presumed to be important foraging habitat for many Arctic marine predators (Bluhm and Gradinger 2008). Additionally, beluga whales may seek the ice edge or nearshore regions for protection from predators such as killer whales (*Orcinus orca*) (e.g. Laidre et al. 2006, Higdon et al. 2012). Use of coastal regions, particularly in early summer, may also be associated with molting and provide thermal benefits or predator avoidance for neonates (Finley 1982, St. Aubin et al. 1990). A layer of the 15% sea ice edge was created from each daily concentration grid, and we determined the distance of each location to the center of the nearest ice edge pixel. We also calculated the closest Euclidean distance of each location to shore. Similarly, we considered the daily distance to dense pack ice (i.e. 90% sea ice concentration). Although whales can navigate through dense pack ice (Richard et al. 2001, Suydam et al. 2001), we found few locations positioned in sea ice concentrations >90% (0.6% and 2.5% of Chukchi and Beaufort locations, respectively). Rather, the risk of entrapment increases in heavy ice and belugas may avoid dense pack ice.

Presumed foraging depths of Chukchi and Beaufort belugas, as well as habitat use, are affected by regional bathymetry (Loseto et al. 2006, Hauser et al. 2015). Barrow Canyon and the Beaufort Sea continental slope, as well as other trenches to the east in Viscount Melville Sound and Amundsen Gulf, represent some of the complex regional bathymetry that influence currents, advection, and localized productivity (Weingartner et al. 2005, Grebmeier et al. 2006). The abundance of key prey items like Arctic cod is affected by regional water properties and greatest in continental slope regions of the Beaufort Sea >100 m (e.g. Parker-Stetter et al. 2011, Majewski et al. 2015). We included variables for water depth and percent slope as well as proximity to the continental slope and Barrow Canyon to account for the potential influence of regional underwater terrain and oceanographic features. We also investigated potential sea ice and ice edge interactions with slope and oceanographic features that could affect beluga distribution (e.g. Moore et al. 2000) by including interaction factors between variables when constructing candidate models. We extracted depth at each location from the 1 arc-minute resolution ETOPO1 global relief map (Amante and Eakins 2009) and calculated percent slope from ETOPO1 water depths using ArcGIS Spatial Analyst tools. We created a slope edge feature by extracting the 400-1000 m isobaths as well as a Barrow Canyon feature by clipping the 75 m isobath to the seaward boundary, similar to Citta et al. (2013) (see Figure 4-1). We measured distance to each feature, as well as to the shoreline, using the ‘Near’ tool in ArcGIS 10.2.

We controlled for collinearity among habitat variables by calculating variance inflation factors (VIF) with the ‘corvif’ function in the ‘AED’ package in R. Variance inflation factors >3 indicated correlated covariates, which were sequentially removed until all covariate had VIFs <3 (Zuur et al. 2009). Due to collinearity, the distance to shore predictor variable was eliminated from Chukchi male habitat models.

### 4.3.4 *Habitat modeling*

We examined monthly (July – November) habitat selection for both sexes in each of the two populations, based on previously described differences in monthly distribution and sexual segregation (Loseto et al. 2006, Hauser et al. 2014). We applied “used versus available” resource selection functions to understand the environmental factors affecting habitat of beluga month-population-sex groups (Johnson 1980). We established habitat availability for each observed beluga location based on a set of random locations within a circular buffer representing plausible daily movement trajectories. The radius of each buffer was estimated as the 95th percentile of daily displacement rates for each month and population (Table 4-2). Northrup et al. (2013) suggested using >20 random locations to achieve accurate habitat selection estimates, and in our study we selected 25 random locations for each observed position. We used this set of random (i.e. ‘control’) locations to represent habitat availability for each observed (i.e. ‘case’) location. We estimated case-control multivariate conditional logistic regression models to predict the strength of association for habitat variables across summer – fall months, sexes, and populations by applying the ‘clogit’ function in the ‘survival’ package of R that includes a robust variance estimator to control for repeated measures of tagged whales.

We defined a set of 16 candidate models to estimate habitat selection for each month-sex-population group (Table 4-3). Each model included at least one sea ice variable given we were interested in how seasonal sea ice habitat affected beluga habitat. The variable of squared sea ice concentration has improved model fit for other ice-dependent species like polar bears by emphasizing variation in dense ice over variation in low ice cover (e.g. Wilson et al. 2014, Laidre et al. 2015a). This squared term was included in some candidate models. We used model selection to select the most parsimonious monthly habitat model for both sexes and populations. For each model, we found Akaike Information Criterion values that were corrected for small sample size (AICc) and used model averaging if multiple models had <2 $\Delta AIC_c$ (Burnham and Anderson 2002).

To assess the predictive capacity of monthly models for each group, we applied k-folds cross-validation techniques for case-control habitat selection models (Fortin et al. 2009). We withheld 20% of our matched observed-random locations to test against the remaining 80% used as a training set for each iteration (k=5). We calculated the mean Spearman’s Rank correlation to consider the frequency of observed locations for each final selected model.

Finally, we mapped predictions of monthly habitat selection for each population using the logistic function to transform coefficients to predicted use (Manly et al. 2002), scaled for comparison so the maximum prediction was 1.0 (DeCesare et al. 2012). We used monthly composite sea ice layers from the same SSM/I sea ice data (Cavalieri et al. 1996) for monthly-scale mapping and derived layers for the 15% and 90% sea ice edges from the monthly composite. Based on locations of tagged whales, we defined the spatial extent of monthly (July – November) population and sex-specific predicted habitat as the minimum convex polygons (MCPs) describing the entire range of tagged whale locations each month (Harris et al. 1990). In addition, we limited spatial predictions to years in which specific sex/population groups were tagged to remain within our scope of inference (see Table 4-1).

## 4.4 RESULTS

We acquired 2047 and 1776 daily locations from Chukchi and Beaufort belugas during July – November, respectively. The best resource selection models indicated that several different factors affect habitat selection for Pacific Arctic belugas (Table 4-4). A single best model was identified for each month-sex-population combination, except in October for Chukchi males and in November for Beaufort males, when multi-model inference was applied to two top models with <2 $\Delta AIC_c$. There were a few cases where additional models were within <2 $\Delta AIC_c$, but were essentially the same models other than a squared ice term or an interaction factor between ice concentration and bathymetry (e.g. models 5 and 7, Table 4-3), and the top model was used in these cases. Each monthly model was highly predictive of habitat selection with significant Spearman Rank correlations, other than for Beaufort females in September – November and Beaufort males in October – November when sample sizes of tagged whales were smallest (Table 4-5).

Sex-specific final models were identified for Chukchi whales in all months but August, although relationships with habitat variables were similar between sexes (Table 4-4, Figure 4-2). Proximity to Barrow Canyon and the continental slope region were included in nearly all monthly models for both females and males and one of these covariates was often the strongest predictor of habitat selection in a given month (Table 4-4). Sea ice concentration, and sometimes proximity to the ice edge, was a significant predictor in early summer and fall when selected ice concentrations were 20-40% rather than no strong selection for a particular ice concentration in August-September when sea ice typically recedes to its annual minimum extent (Table 4-4, Figure 4-2). Percent slope and depth, or an interaction with ice variables, were also strong predictors of habitat selection for both sexes in several months. Proximity to the coast was the strongest predictor of habitat selection for females in June. These habitat preferences resulted in predictions for a high probability of use near Barrow Canyon for Chukchi females from July to October, and for males from July to September and in November (Figure 4-3). The continental slope regions bordering Canada Basin were also predicted as high use areas for Chukchi males in August to October. West and southward migration regions were predicted in October and November.

Final habitat selection models between male and female Beaufort belugas were more distinct than for Chukchi belugas (Table 4-4, Figure 4-2). Proximity to Barrow Canyon was not included in top models for Beaufort belugas in any month, nor was the distance to dense ice. For Beaufort females, sea ice concentration was a strong predictor of habitat selection in July and August when predictive capacity was best (Tables 4-4, 4-5). Beaufort females selected ice concentrations <40% in summer (Figure 4-2), and maps of predicted probability of use reflect a preference for the Mackenzie River Estuary and Amundsen Gulf (Figure 4-3). Close proximity to shore was also a strong predictor from July – September, as well as interactions of distance to shore with ice concentration in September when Beaufort belugas migrate across the western Beaufort Sea (Table 4-4). Beaufort males had a strong relationship with deeper water in July and August (Table 4-4, Figures 4-2 and 4-3). Sea ice concentration, and especially nearness to the ice edge, were strong predictors of Beaufort male habitat selection in August when males selected ~40% ice concentrations, far from the ice edge yet close to slope regions, such as in Viscount Melville Sound where there is a male core area centered over a deep trench (Hauser et al. 2014). In September, Beaufort males especially selected areas near the ice edge, although there were also significant interactions of high percent slope with both ice concentration and distance to the ice edge. There were no significant predictors for either sex in October or November when predictive capacity of the final models was relatively poor (Tables 4-4, 4-5).

## 4.5 DISCUSSION

Beluga whales, like many migratory marine predators, are confronted by dynamic environmental conditions that influence resource availability over a range of spatial and temporal scales (e.g. Moore et al. 2000, Goetz et al. 2007). Habitat choices in seasonal Arctic environments can thus indicate important features affecting the foraging distribution of these populations, but may also reflect influences of social or sexual resource partitioning (Barber et al. 2001, Loseto et al. 2006). We developed highly predictive monthly models that revealed large variations in seasonal habitat selection distinct among sex and population groups within a remote marine region experiencing rapid environmental change.

### 4.5.1 *Seasonal foraging habitat*

We found that depth, slope, and proximity to key features (e.g. Barrow Canyon and the continental slope) influenced seasonal habitat selection of both populations, likely because the complex regional terrain influences currents, nutrient pathways, and localized productivity which affect foraging opportunities (Weingartner et al. 2005, Grebmeier et al. 2006, Pickart et al. 2013). Chukchi and Beaufort belugas forage on a combination of benthic invertebrates as well as fish like Arctic cod (Quakenbush et al. 2015) and dive depths presumably associated with foraging vary depth among bathymetric regions (Citta et al. 2013, Hauser et al. 2015). Fronts in

Barrow Canyon and upwelling events along the Beaufort slope can entrain zooplankton and thus attract prey of belugas, such as Arctic cod. Arctic cod abundance is greatest along the continental slope in the Beaufort Sea at depths that coincide with hydrographic fronts (e.g. Parker-Stetter et al. 2011, Majewski et al. 2015). In the Western Beaufort Sea, Chukchi belugas most frequently dive to pelagic depth layers (e.g., 200-400 m) at which Arctic cod are most abundant (Hauser et al. 2015). Our models predicted high use in areas that would be expected to also have high prey biomass because habitat variables like slope, depth, and proximity to Barrow Canyon and the continental slope were the strongest predictors of habitat selection. The Barrow Canyon region is recognized as a particularly important hotspot for several marine predators in summer (Grebmeier et al. 2015, Kuletz et al. 2015). Our models predicted high use in Barrow Canyon and the Beaufort Sea slope, which coincides with persistent summer core areas for Chukchi belugas (Hauser et al. 2014). Bathymetric features, like deep trenches, also contributed to predictions of preferred habitat for Beaufort belugas in Viscount Melville Sound (males) and Amundsen Gulf (females) where summer core areas have also previously been identified. Resource selection models are powerful tools to examine the factors affecting the habitat whales used relative to what was available, yet predictions are strongest in the most used areas. While our models predicted shelf and slope habitat well, we had less data in the deep (>3000 m) offshore Canada Basin. Belugas from both populations can regularly dive >900 m and focus dives to deeper layers of Atlantic Water origin (200-1000 m) possibly to feed in the Canada Basin (Richard et al. 1997, Citta et al. 2013, Hauser et al. 2015). Summer home ranges extend into the region (Hauser et al. 2014), and our models underestimated use by Chukchi males and females in August and September while overestimating use by Beaufort males in July and August compared to home range estimates. The ecology of this deep portion of the Arctic Basin is not well-known because it is sparsely sampled, and we expect other factors besides sea ice and topography affect beluga habitat choice in the region. For example, belugas may track eddies that shed from the slope and potentially entrain beluga prey (Llinas et al. 2009).

Our results suggest Pacific Arctic belugas select habitat that is predominantly driven by topography that promotes regional productivity and presumably foraging opportunities. Our models could potentially be improved by integrating more dynamic oceanographic predictors, such as mixed layer depth or eddy tracks, but would require the use of ocean models. Regional ocean models are developing for the Pacific Arctic, and there are promising signs that they can be used to accurately predict cetacean habitat in well-studied regions like the California Current (Becker et al. 2016). Alternatively wind parameters may be particularly important for structuring the Pacific Arctic ecosystem, and increasingly so, since wind-forcing impacts hydrography, localized productivity, and sea ice conditions throughout much of the Chukchi and Beaufort seas (Rainville et al. 2011, Schulze and Pickart 2012, Danielson et al. 2014, Wood et al. 2015). In a sub-Arctic Alaskan estuarine system, beluga habitat models also incorporated information on nearshore river flow, showing an association with mudflats and high flow accumulation that could impact foraging or other behaviors (Goetz et al. 2007). The inclusion of variables on turbidity or freshwater flow may also improve our models, particularly in July when all models predicted close proximity to shore and molting may occur in fresher, warmer nearshore conditions (St. Aubin et al. 1990, Smith et al. 1992). Freshwater flow from the Mackenzie River, in particular, peaks in June (Carmack and Macdonald 2002) and likely affects the aggregation of Beaufort belugas near the Estuary in spring-early summer (Hornby et al. 2016).

### 4.5.2 *Population-specific habitat models*

Our seasonal habitat models reinforced previous descriptions of environmental characteristics affecting Chukchi or Beaufort beluga habitat use, but we were able to describe population-specific associations that could not be examined previously. Summer and fall aerial survey data from 1982-1991 emphasized the importance of the continental slope (specified as 201-2000 m) in a range of moderate to heavy ice conditions for beluga whales in the Alaska Beaufort Sea (Moore 2000, Moore et al. 2000). Selection for slope habitat was related to transport of water from the Pacific via the ACC and onward to the Beaufort Sea, similar to our results. Stafford et al. (2013) incorporated additional aerial survey data and acoustic detections, suggesting hydrographic fronts that establish near Barrow Canyon and western Beaufort slope under wind-forced reversals of the ACC create foraging opportunities for belugas. A challenge with aerial survey or acoustic data, however, is the inability to identify which population or sex is being observed (although there is emerging suggestions of population-specific acoustic dialects; Garland et al. 2015b). Our results enabled us to differentiate populations and develop population-specific habitat models from July – November, underscoring differences among populations and sexes that could help guide managers in assessment of climate or anthropogenic changes for each population (Laidre et al. 2015b).

Our models helped elucidate population-specific use of the Chukchi Plateau. Moore et al. (2000) noted that beluga distribution from aerial surveys split near the mouth of Barrow Canyon and extended north towards the Chukchi Plateau in years when there was low transport through Bering Strait, and Beaufort belugas transit the region during westward migration in September (Hauser et al. 2014). Belugas are also detected acoustically on the Chukchi Plateau, predominantly from May-August (Moore et al. 2011). We predicted relatively high use by males (both populations) in August-September and Chukchi females in October based on a strong selection for steep slopes, since some of the steepest slopes of the Pacific Arctic occur along the continental slope edge of the Chukchi Plateau.

Our interpretation of habitat selection rests on the assumption that our sample of tagged whales was representative of each sex-population group in a given month, but our sample sizes decreased in the fall because tags fail with time (e.g. batteries wane, antennae break, or tags detach). Smaller sample size in later months could affect our interpretation in a few ways. First, the relatively poor predictive capacity of our Beaufort beluga fall models (September-November and October-November for females and males, respectively) could be a reflection of small samples of whale locations to estimate habitat selection in those months, especially when compared to sample sizes for Chukchi whales (see Table 4-1). There were also no significant predictors from top models for either Beaufort sex group in October and November, which could be related to sample size or may suggest there are other important predictors omitted from our candidate models. Second, our use of MCPs as the area of inference for predictive habitat mapping included all locations used by belugas in a given month, and MCPs tend to include unused or rarely-used areas (i.e. Harris et al. 1990). In our case a single tagged whale with tracks deviating from others could affect what regions are modeled, such as when a single Beaufort male (‘1993-17002’) departed the Canada Beaufort Sea ahead of all other Beaufort whales in early August (Richard et al. 2001) and used the Chukchi Plateau, which resulted in a broader August MCP for Beaufort males and affected spatial estimates of relative probability of use.

### 4.5.3 *Sexual segregation*

Distinct morphological or reproductive investment between sexes can result in divergence in the spatial and temporal energetic demands of male and female marine predators (e.g. Beck et al.

2003, Breed et al. 2006). Belugas are sexually dimorphic where larger males presumably have higher energetic demands than females. However, calves wean after at least 2 yr and exert additional energetic demands to nursing females. We found sexual segregation for both beluga populations across summer-fall, although there was generally stronger sexual segregation of habitat predictors for Beaufort than Chukchi belugas. Our results add to the previous literature supporting sexual segregation of belugas due to divergent energetic and reproductive demands in the summer where males were associated with deeper water, heavier ice, and were generally farther from shore than females (e.g. Barber et al. 2001, Loseto et al. 2006). Female belugas closely associate with offspring (both calves and older juveniles) in summering areas, and males likely remain with family groups as juveniles before segregating from females in space and time as they mature (Colbeck et al. 2013). Females, especially those accompanied by calves, may choose ice edge or shallow and coastal habitat that reduces predation or risk of ice entrapment. Males likely segregate from females as they mature to exploit alternative prey resources and reduce competition with females, similar to other socially-structured cetaceans (e.g. Whitehead and Weilgart 2000). We found that males selected steeper slopes than females, and proximity to the continental slope was a particularly strong predictor for Chukchi males where oceanographic processes in the Beaufort Sea likely facilitate foraging. Barrow Canyon was also an important predictor for both Chukchi sexes, although it was selected more strongly by females. There are few differences in regional dive behavior of Chukchi sexes (Citta et al. 2013, Hauser et al. 2015), but fatty acid and mercury analyses of Beaufort belugas indicate that larger, adult males target offshore concentrations of Arctic cod compared to smaller belugas selecting more nearshore aggregations (Loseto et al. 2009, Loseto et al. 2015). Thus, our results add further evidence that males may be targeting different prey resources or spatiotemporal concentrations of prey than females.

Age composition of our tagged whale sample complicates interpretation of sexual segregation. Juvenile whales of both sexes associate with females (Colbeck et al. 2013) and select more coastal habitat with lower ice concentrations (Loseto et al. 2006). Our monthly sample sizes precluded an analysis of age effects, but our sample of Beaufort males was slightly biased towards juvenile whales (65%), and 46% of our tagged Beaufort females were associated with a nursing calf. In contrast, the majority of our Chukchi tagged whales were adults (63% and 68% of females and males, respectively), and our results most likely reflect adult habitat selection of the two sexes.

### 4.5.4 *Sea ice selection in a changing Arctic*

Sea ice characteristics, in addition to bathymetric features that affect regional productivity, were important but rarely the strongest predictors of monthly beluga habitat. Sea ice conditions typically vary throughout the broad geographic range of these populations, and Pacific Arctic belugas can navigate heavy ice (we observed 0.3% and 0.8% of all locations from Chukchi and Beaufort belugas, respectively, in >95% ice concentration). Our analyses contribute to others suggesting that these populations use a range of light to heavy ice conditions during summer and fall (Moore et al. 2000, Richard et al. 2001, Suydam et al. 2001, Loseto et al. 2006).

Rather than directly impacting habitat choice, sea ice likely functions to structure foraging opportunities and affects access to preferred habitat for belugas and other Arctic cetaceans (Moore and Huntington 2008). Proximity to the sea ice edge was a particularly important predictor of habitat selection in several months for both Chukchi and Beaufort belugas, other than Beaufort females. Ice edge habitat has been identified as important beluga habitat for several populations, including Beaufort belugas entering the Mackenzie River Estuary in spring

(Asselin et al. 2011, Hornby et al. 2016). The ice edge is a dynamic and productive region that could fuel foraging opportunities for predators like belugas, especially when the location of the ice edge might interact with the effects of localized oceanographic features such as the Beaufort shelfbreak jet (Bluhm and Gradinger 2008). The ice edge could also confer refuge from predation, particularly pelagic predators like killer whales in summer (Shelden et al. 2003, Higdon et al. 2012). During Beaufort migration west in September, close proximity to the sea ice edge was the strongest predictor for males. However, there has been strong interannual variation in the location of the ice edge in September over the two decades of our study. The predicted habitat map for Beaufort belugas in September (i.e. Figure 4-3) averaged across four different years and presented a muted association with the ice edge in September due to the dynamic nature of ice edge habitat. Closer comparison among years revealed the strong selection for the ice edge by Beaufort males in September (Figure 4-4). Interaction effects of the ice edge and ice concentration with slope values were also strong predictors of Beaufort male habitat selection in September, which resulted in the persistent predictions of high use along the Beaufort Sea slope. Habitat selection by Beaufort females in September, although assessed as not highly predictive, was strongly associated with the coastline instead of the ice edge. Nearshore habitat also likely reduces predation risk, particularly for females that could be accompanied by calves during this migration period (Shelden et al. 2003, Laidre et al. 2006). Alternatively, coastline or ice edge habitat may serve navigational purposes (e.g. like Arctic terns, *Sterna paradisaea*, Fijn et al. 2013) or contribute to a suite of navigational cues that help them follow a specific westward course, similar to humpback whales (*Megaptera novaeangliae*) migrating between foraging and breeding grounds (Horton et al. 2011).

Given contemporary reductions in sea ice as well as projections for continued loss (Frey et al. 2015, Wang and Overland 2015), there is a renewed interests in economic development throughout the Arctic (Huntington 2009). Proposed shipping, tourism, and oil and gas development directly overlap the range of several beluga populations, with potential implications for individual and population-level effects (Reeves et al. 2014). Our analyses provide quantitative predictions of habitat selection for two beluga populations over the entire open water season when a suite of anthropogenic activities are expected to increase. In addition to conservation concern for these top predators, belugas are integral cultural and subsistence resources for Inupiat and Inuvialuit hunters along the northwest Alaskan and Canadian coasts (Harwood and Smith 2002, Frost and Suydam 2010). Although mitigation of sea ice loss primarily requires global reduction of greenhouse gas emissions, habitat models can help inform management of anthropogenic activities and conservation planning efforts that will increasingly need to identify seasonally important areas of these critical species. Yet it remains unclear what changing sea ice conditions mean for Pacific Arctic belugas. There is recent evidence of declining body condition and growth rates for Beaufort belugas as well as other Beaufort Sea predators that consume Arctic cod, possibly as a result of ecosystem changes related to sea ice loss (Harwood et al. 2014, Harwood et al. 2015). Further research is needed to clarify whether population or individual-level changes are directly linked to sea ice as well as what broader impacts of changing sea ice conditions may be on Pacific Arctic belugas. Ultimately, our results provide a benchmark on which to assess future changes in beluga habitat and help guide regional development of offshore areas.

## 4.6 ACKNOWLEDGEMENTS

We are grateful to the long-term collaborative efforts of the communities of Point Lay, AK and the Inuvialuit Settlement Region, NWT who have facilitated our tagging efforts. For Chukchi belugas, L. Lowry, K. Frost, G. O’Corry-Crowe, D. Pikok, R. Small, T. Romano, J. Tazruk, B. and M. Tracey, J. Rexford, J. Orr, A. Ashby, V. Dollarhide, L. Ferreira, L. Pierce, L. Stalker, H. Smith, R. Hobbs, R. Hoover, T. Nukapigak, M. Sparck, S. Speckman, D. Susook, C. Aniskette, J. Tuckfield, C. Rea, G. Marshall, N. Hank, L. Hansen, L. Hoberecht, L. Quakenbush, T. Robeck, A. Simon, G. and K. VanBlaricom, J. Taylor, J. Edwards, D. Ramey, B. Achootchook, and J. Citta have supported various aspects of tagging and data processing. We appreciate funding from the Alaska Beluga Whale Committee, North Slope Borough of Alaska, National Marine Fisheries Service (NMFS), Alaska Department of Fish and Game, National Fish and Wildlife Foundation, Minerals Management Service, and Village of Point Lay. Thanks also to the Inuvialuit Hunter and Trapper Corporations of Inuvik, Aklavik, and Tuktoyaktuk and the Polar Continental Shelf Project for the support and assistance tagging Beaufort belugas. J. Orr, A. Martin, and B. Leblanc offered field assistance and data processing, and tagging of Beaufort belugas was funded by the Fisheries and Oceans Canada (DFO), Fisheries Joint Management Committee, Environmental Studies Revolving Fund, Minerals Management Service, and NMFS. We thank R. Wilson for useful discussion of RSF modeling approaches and example R code for model validation. R. McGovern helped develop R code and processed sea ice data for predictive mapping of habitat selection models. Analyses were funded by a NASA Climate Indicators Program Grant (NNX13AN28G) and fellowships to D. Hauser from the University of Washington’s (UW) Integrative Graduate Education and Research Traineeship Program on Ocean Change (National Science Foundation) and UW School of Aquatic & Fishery Sciences. Helpful feedback, guidance, and review of the manuscript was provided by R. Hobbs and D. Schindler. Capture and tagging of belugas was approved by NMFS (Permit nos. 14610, 782-1438, and 782-1719) and DFO for Chukchi and Beaufort belugas, respectively.

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Table 4-1. Number of female and male beluga whales tagged, providing locations, from the Beaufort and Chukchi populations in July-November.

| | | | | | No. locations | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Population** | **Year** | **Sex** | **No. tagged whales** | **Mean no. days transmitting (range)** | **Jul** | **Aug** | **Sep** | **Oct** | **Nov** |
| Beaufort | 1993 | F | 1 | 27 | 18 | 9 | | | |
| | | M | 3 | 45 (11-91) | 46 | 49 | 18 | 3 | |
| | 1995 | F | 4 | 34 (7-68) | 53 | 30 | 6 | | |
| | | M | 11 | 37 (23-85) | 229 | 91 | 6 | | |
| | 1997 | F | 3 | 83 (55-128) | 5 | 84 | 58 | 32 | |
| | | M | 6 | 86 (67-120) | 11 | 177 | 149 | 82 | 11 |
| | 2004 | F | 3 | 96 (15-172 | 51 | 36 | 33 | 8 | 5 |
| | | M | 5 | 182 (17-301) | 72 | 67 | 65 | 15 | 14 |
| | 2005 | F | 2 | 221 (159-283) | 45 | 60 | 60 | 62 | 16 |
| | *Total* | | *38* | *82 (7-301)* | *530* | *603* | *395* | *202* | *46* |
| Chukchi | 1998 | M | 5 | 54 (11-99) | 74 | 88 | 31 | 7 | |
| | 1999 | F | 1 | 73 | 14 | 28 | 10 | | |
| | | M | 3 | 75 (56-86) | 80 | 62 | 42 | | |
| | 2001 | F | 3 | 91 (18-146) | 57 | 56 | 59 | 53 | 25 |
| | | M | 5 | 75 (16-153) | 91 | 79 | 60 | 62 | 47 |
| | 2002 | F | 1 | 68 | 12 | 16 | 7 | | |
| | | M | 3 | 64 (46-82) | 27 | 39 | 17 | | |
| | 2007 | F | 2 | 130 (126-134) | 57 | 62 | 58 | 38 | 13 |
| | | M | 1 | 521 | 28 | 31 | 30 | 31 | 30 |
| | 2008 | M[a] | 1 | | 31 | 31 | 30 | 31 | 30 |
| | 2010 | M | 2 | 133 (101-164) | 59 | 61 | 60 | 31 | 17 |
| | 2012 | F | 1 | 313 | 22 | 31 | 30 | 31 | 31 |
| | *Total* | | *27* | *105 (27-521)* | *552* | *584* | *434* | *284* | *193* |

[a] The Chukchi male tagged in 2007 continued to provide locations during July-November 2008.

Table 4-2. Daily 95th percentile displacement rates (km/day) used as buffer distances to generate random ‘control’ locations for Chukchi and Beaufort beluga monthly habitat selection models.

| **Month** | **Chukchi** | **Beaufort** |
|---|---|---|
| July | 116.3 | 118.6 |
| August | 119.4 | 116.9 |
| September | 119.0 | 127.8 |
| October | 119.0 | 108.2 |
| November | 127.3 | 42.1 |

Table 4-3. List of candidate models, including covariates for sea ice concentration (Conc), squared terms of concentration ($\mathrm{Conc}^2$), proximity to the 15% sea ice edge (Dist_15) and 90% dense pack ice (Dist_90), underwater percent slope (Slope), water depth (Depth), and proximity to the shore (Dist_shore), 400-1000 m continental slope region (Dist_slope), and Barrow Canyon (Dist_canyon).

| **Model number** | **Model structure** |
|---|---|
| 1 | Conc + $\mathrm{Conc}^2$ + Dist_15 +Dist_90 + Slope + Depth |
| 2 | Conc + Slope + (Conc * Slope) |
| 3 | Conc + Dist_15 + Dist_90 + Slope + Depth + (Conc*Slope) + (Dist_15 *Slope) |
| 4 | Dist_slope + Dist_15 + (Dist_slope*Dist_15) |
| 5 | Dist_slope + Dist_canyon + Conc + $\mathrm{Conc}^2$ + Dist_15 + Dist_90 + Slope + Depth |
| 6 | Dist_slope + Dist_canyon + Conc + Dist_15 + Dist_90 + Slope + Depth + (Conc*Slope) + (Dist_15*Slope) |
| 7 | Dist_slope + Dist_canyon + Conc + Dist_15 + Dist_90 + Slope |
| 8 | Dist_slope + Conc + $\mathrm{Conc}^2$ + Dist_15 + Slope + Depth |
| 9 | Dist_slope + Conc + Dist_15 + Dist_90 + Slope + Depth + (Conc*Slope) + (Dist_15*Slope) |
| 10 | Dist_shore + Conc |
| 11 | Dist_shore + Conc + $\mathrm{Conc}^2$ |
| 12 | Dist_shore + Dist_15 + Dist_slope |
| 13 | Dist_shore + Conc + $\mathrm{Conc}^2$ + (Dist_shore*Conc) |
| 14 | Dist_shore + Dist_canyon + Conc + $\mathrm{Conc}^2$ + Slope |
| 15 | Dist_canyon + Conc + Slope + Depth + Dist_90 + (Conc*Slope) |
| 16 | Dist_shore + Conc + Slope + Depth + (Conc*Depth) |

Table 4-4. Parameters from top resource selection models for female and male Chukchi and Beaufort beluga whales each month (July-November).

| | | **Chukchi female** | | | **Chukchi male** | | | **Beaufort female** | | | **Beaufort male** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Month** | **Predictor** | **Estimate** | **SE** | ***p*** | **Estimate** | **SE** | ***p*** | **Estimate** | **SE** | ***p*** | **Estimate** | **SE** | ***p*** |
| *Jul.* | Conc | 0.0040 | 0.0168 | 0.803 | -0.0220 | 0.0048 | **<0.001** | 0.0507 | 0.0165 | **0.002** | -0.0100 | 0.0060 | 0.096 |
| | Conc$^2$ | -0.0006 | 0.0003 | **0.028** | | | | -0.0010 | 0.0003 | **0.002** | | | |
| | Dist_15 | | | | 0.0051 | 0.0014 | **<0.001** | | | | | | |
| | Dist_90 | | | | -0.0006 | 0.0012 | 0.637 | | | | | | |
| | Slope | | | | 0.0609 | 0.0403 | 0.131 | | | | -0.0113 | 0.0667 | 0.090 |
| | Depth | | | | -0.0001 | 0.0001 | 0.207 | | | | 0.0005 | 0.0002 | **0.043** |
| | Dist_slope | | | | 0.0030 | 0.0016 | 0.057 | | | | | | |
| | Dist_canyon | | | | -0.0099 | 0.0015 | **<0.001** | | | | | | |
| | Dist_shore | -0.0249 | -0.0033 | **<0.001** | | | | -0.0030 | 0.0022 | 0.170 | -0.0070 | 0.0019 | **<0.001** |
| | Conc*Dist_shore | 0.0003 | 0.0001 | **<0.001** | | | | | | | | | |
| | Conc*Depth | | | | | | | | | | 0.0000 | 0.0000 | 0.207 |
| *Aug.* | Conc | -0.0283 | 0.0145 | 0.051 | -0.0007 | 0.0080 | 0.932 | -0.0257 | 0.0108 | **0.017** | 0.0260 | 0.0110 | **0.022** |
| | Conc$^2$ | | | | | | | | | | -0.0004 | 0.0001 | **0.004** |
| | Dist_15 | -0.0024 | 0.0022 | 0.213 | 0.0001 | 0.0012 | 0.963 | | | | 0.0045 | 0.0013 | **<0.001** |
| | Dist_90 | 0.0001 | 0.0029 | 0.749 | -0.0014 | 0.0012 | 0.241 | | | | | | |
| | Slope | 0.1747 | 0.0348 | **<0.001** | 0.1450 | 0.0242 | **<0.001** | 0.0669 | 0.0912 | 0.463 | -0.1885 | 0.0675 | **0.005** |
| | Depth | -0.0004 | 0.0002 | **0.009** | -0.0003 | 0.0001 | **<0.001** | 0.0004 | 0.0004 | 0.283 | 0.0007 | 0.0001 | **<0.001** |
| | Dist_slope | -0.0100 | 0.0035 | **0.003** | -0.0010 | 0.0015 | 0.495 | | | | -0.0124 | 0.0019 | **<0.001** |
| | Dist_canyon | -0.0149 | 0.0023 | **<0.001** | -0.0082 | 0.0012 | **<0.001** | | | | | | |
| | Dist_shore | | | | | | | -0.0118 | 0.0027 | **<0.001** | | | |
| | Conc*Depth | | | | | | | 0.0000 | 0.0000 | 0.073 | | | |
| *Sep.* | Conc | 0.0067 | 0.0106 | 0.530 | -0.0009 | 0.0066 | 0.891 | 0.0049 | 0.0165 | 0.765 | 0.0001 | 0.0042 | 0.973 |
| | Conc$^2$ | | | | | | | -0.0006 | 0.0003 | 0.064 | | | |
| | Dist_15 | | | | -0.0035 | 0.0016 | **0.027** | | | | -0.0050 | 0.0015 | **0.001** |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dist_90 | -0.0059 | 0.0022 | **0.008** | -0.0024 | 0.0016 | 0.131 | | | | | | |
| | Slope | 0.1831 | 0.0348 | **<0.001** | 0.0823 | 0.0651 | 0.206 | | | | 0.0326 | 0.0613 | 0.595 |
| | Depth | -0.0004 | 0.0001 | **0.004** | -0.0002 | 0.0001 | 0.077 | | | | -0.0002 | 0.0001 | 0.124 |
| | Dist_slope | | | | -0.0039 | 0.0019 | **0.043** | | | | | | |
| | Dist_canyon | -0.0087 | 0.0020 | **<0.001** | -0.0059 | 0.0016 | **<0.001** | | | | | | |
| | Dist_shore | | | | | | | -0.0059 | 0.002 | **0.003** | | | |
| | Conc*Slope | -0.0144 | 0.0060 | **0.017** | 0.0034 | 0.0012 | **0.003** | | | | -0.0027 | 0.0012 | **0.023** |
| | Dist_15*Slope | | | | 0.0002 | 0.0002 | 0.281 | | | | 0.0011 | 0.0003 | **0.002** |
| | Conc*Dist_shore | | | | | | | 0.0001 | 0.0001 | **0.014** | | | |
| | | | | | | | | | | | | | |
| *Oct.* | Conc | 0.0686 | 0.0187 | **<0.001** | 0.0045 | 0.0136 | 0.739 | 0.1169 | 0.0893 | 0.191 | -0.0119 | 0.0127 | 0.347 |
| | Conc$^2$ | -0.0012 | 0.0000 | **<0.001** | -0.0003 | 0.0002 | 0.120 | -0.0042 | 0.0035 | 0.231 | | | |
| | Dist_15 | | | | -0.0057 | 0.0029 | 0.051 | | | | | | |
| | Dist_90 | | | | -0.0041 | 0.0023 | 0.075 | | | | | | |
| | Slope | 0.1444 | 0.0480 | **0.003** | 0.1770 | 0.0398 | **<0.001** | | | | | | |
| | Depth | | | | -0.0001 | 0.0001 | 0.478 | | | | | | |
| | Dist_slope | | | | -0.0003 | 0.0013 | 0.800 | | | | | | |
| | Dist_canyon | -0.0041 | 0.0019 | **0.035** | -0.0005 | 0.0011 | 0.676 | | | | | | |
| | Dist_shore | 0.0009 | 0.0020 | 0.664 | | | | 0.0002 | 0.0022 | 0.941 | -0.0032 | 0.0022 | 0.143 |
| | | | | | | | | | | | | | |
| *Nov.* | Conc | 0.0988 | 0.0274 | **<0.001** | 0.0547 | 0.0164 | **<0.001** | -0.0072 | 0.0560 | 0.897 | 0.0040 | 0.0345 | 0.908 |
| | Conc$^2$ | -0.0017 | 0.0005 | **<0.001** | -0.0009 | 0.0002 | **<0.001** | | | | | | |
| | Dist_15 | -0.0121 | 0.0050 | **0.016** | 0.0006 | 0.0026 | 0.804 | | | | | | |
| | Dist_90 | 0.0086 | 0.0041 | **0.038** | 0.0001 | 0.0023 | 0.951 | | | | | | |
| | Slope | | | | 0.3273 | 0.0819 | **<0.001** | | | | -6.0055 | 8.7343 | 0.492 |
| | Depth | | | | -0.0013 | 0.0005 | **0.014** | | | | | | |
| | Dist_slope | 0.0038 | 0.0028 | 0.175 | 0.0046 | 0.0020 | **0.024** | 7.308 | 4.091 | 0.074 | | | |
| | Dist_canyon | -0.0088 | 0.0034 | **0.009** | -0.008 | 0.0022 | **<0.001** | | | | | | |
| | Dist_shore | | | | | | | | | | 0.0009 | 0.0067 | 0.96 |
| | Conc*Slope | | | | | | | -0.3655 | 0.3381 | 0.28 | -0.0728 | 0.3414 | 0.831 |

Table 4-5. K-fold cross validation results of top monthly (July-November) habitat selection models for Chukchi and Beaufort male and female belugas.

| | **Chukchi female** | | **Chukchi male** | | **Beaufort female** | | **Beaufort male** | |
|---|---|---|---|---|---|---|---|---|
| **Month** | $\bar{r}_s$ | ***p*** | $\bar{r}_s$ | ***p*** | $\bar{r}_s$ | ***p*** | $\bar{r}_s$ | ***p*** |
| July | 0.74 | <0.001 | 0.79 | <0.001 | 0.44 | 0.035 | 0.60 | 0.010 |
| August | 0.86 | <0.001 | 0.74 | <0.001 | 0.54 | 0.013 | 0.67 | <0.001 |
| September | 0.62 | 0.001 | 0.63 | <0.001 | 0.42 | 0.091 | 0.61 | 0.001 |
| October | 0.57 | 0.004 | 0.60 | 0.005 | 0.21 | 0.383 | 0.40 | 0.059 |
| November | 0.68 | <0.001 | 0.70 | <0.001 | 0.23 | 0.288 | 0.26 | 0.21 |

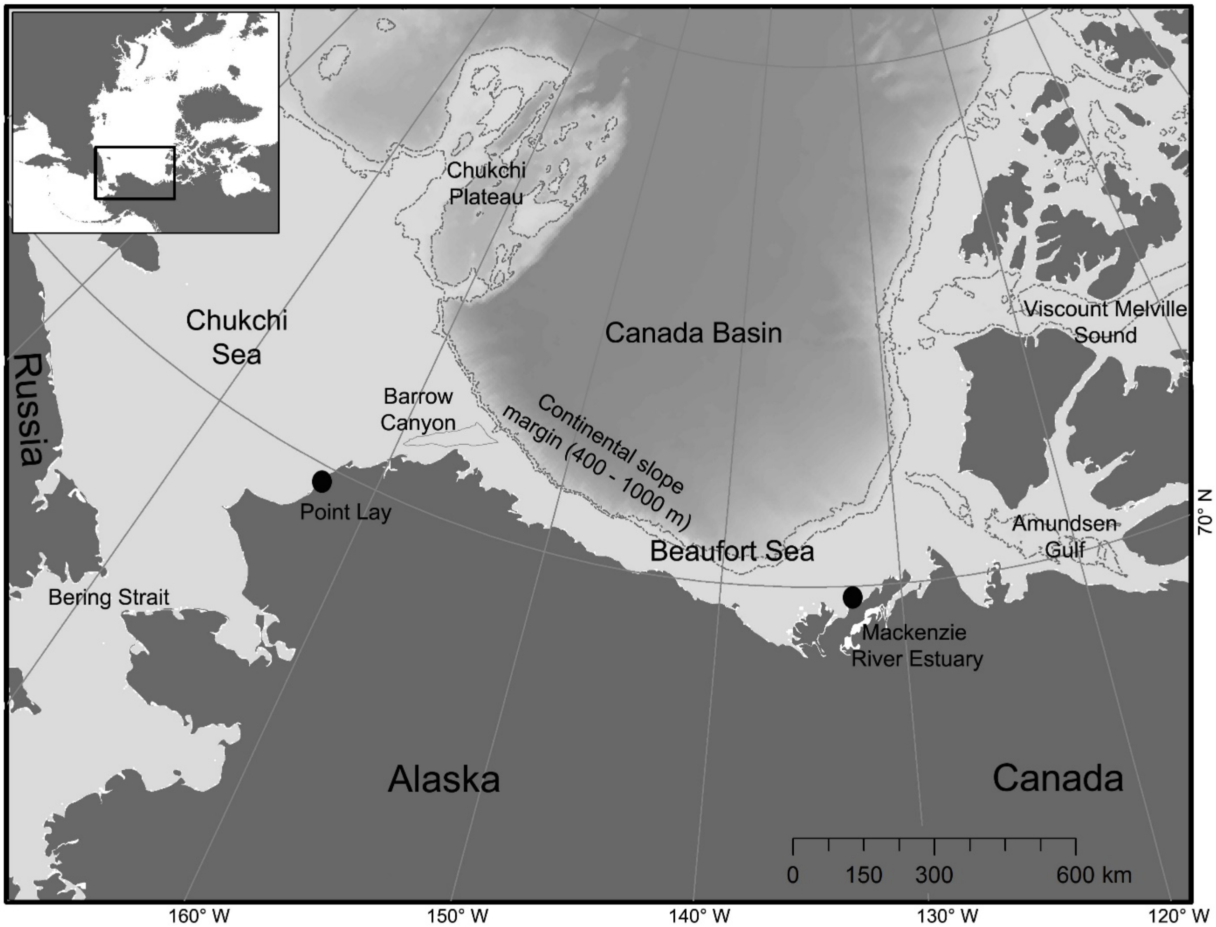

Figure 4-1. Pacific Arctic study area where Chukchi and Beaufort belugas were tagged, near Point Lay, Alaska and the Mackenzie River Estuary, Canada (black circles). The location of Barrow Canyon and the 400-1000 m isobaths that outline the continental slope margin were used to calculate proximity predictors.

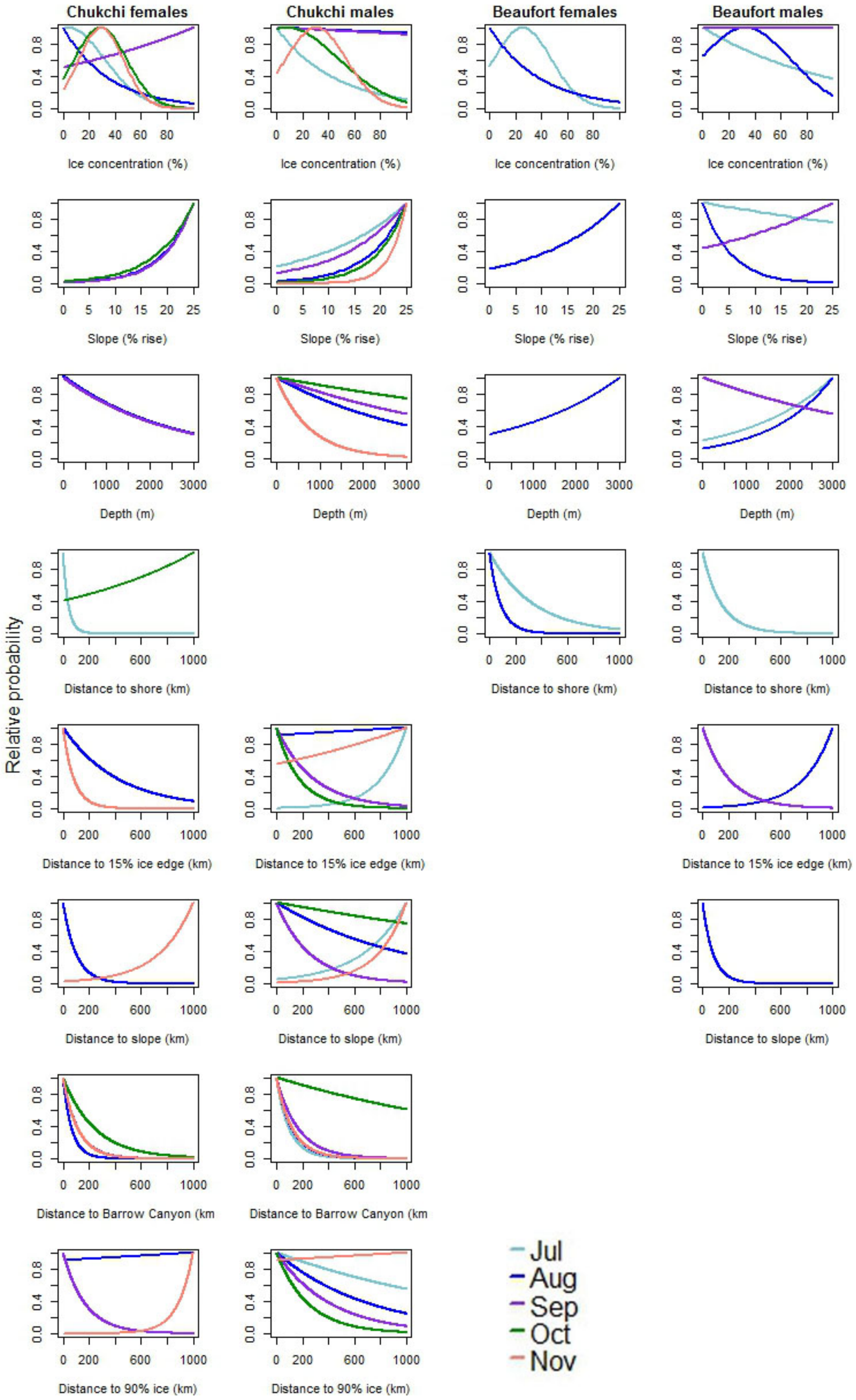

Figure 4-2. Monthly (July-November) habitat selection predictions, scaled to 1.0, for male and female Chukchi and Beaufort belugas based on best monthly models. Missing plots indicate a predictor was not included in the top model, and months with poor predictive capacity for Beaufort belugas are not included (see Table 4-5).

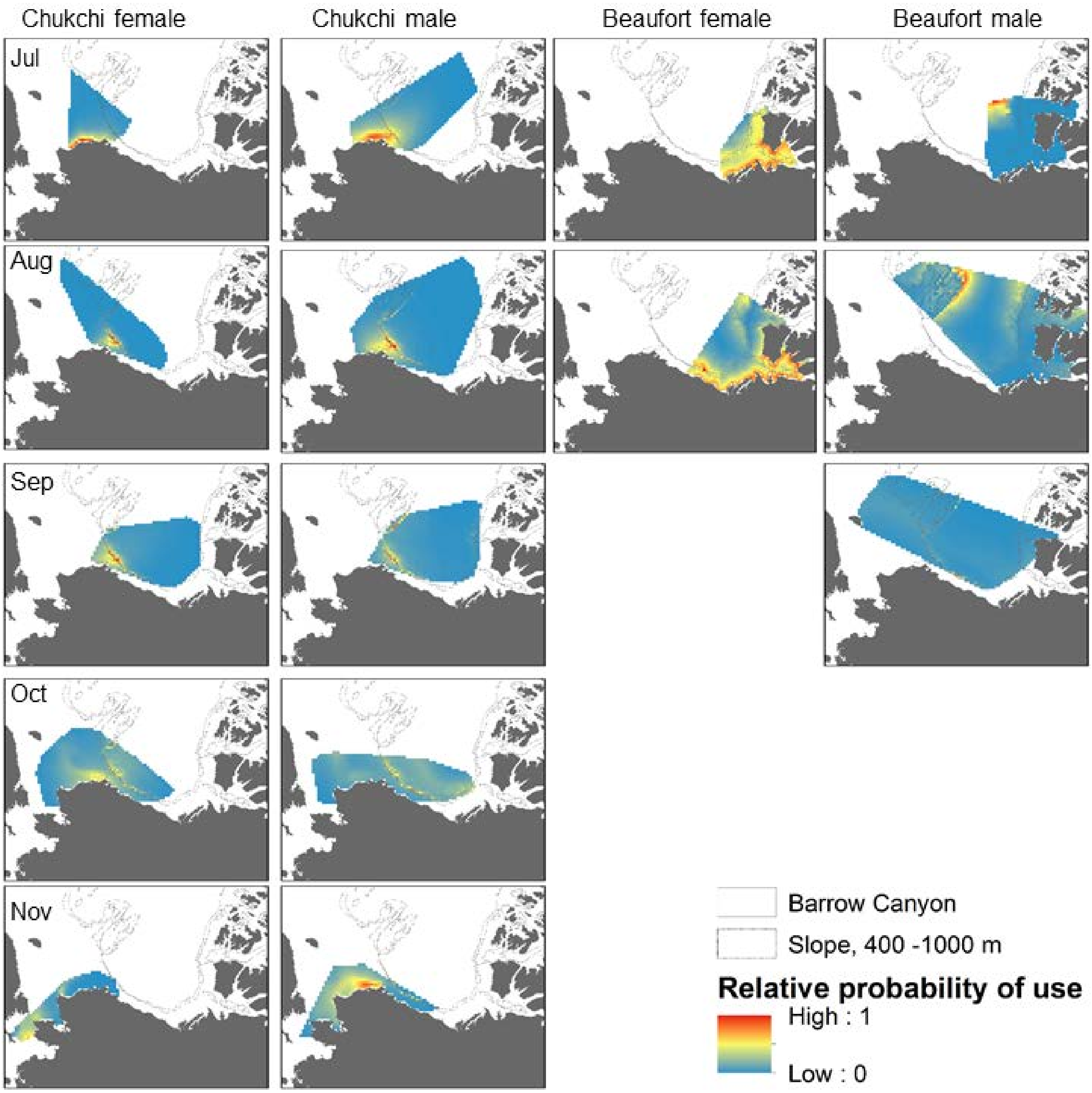

Figure 4-3. Monthly (July-November, top-bottom) maps of predicted beluga whale use for females and males of Chukchi and Beaufort populations based on the results of habitat selection models. For each monthly model, predicted habitat use is limited to the scope of inference by averaging across the years when whales were tagged (see Table 4-1) and restricting spatial extent to the minimum convex polygon of tagged whales in the month. Months with poor predictive capacity for Beaufort belugas are not included.

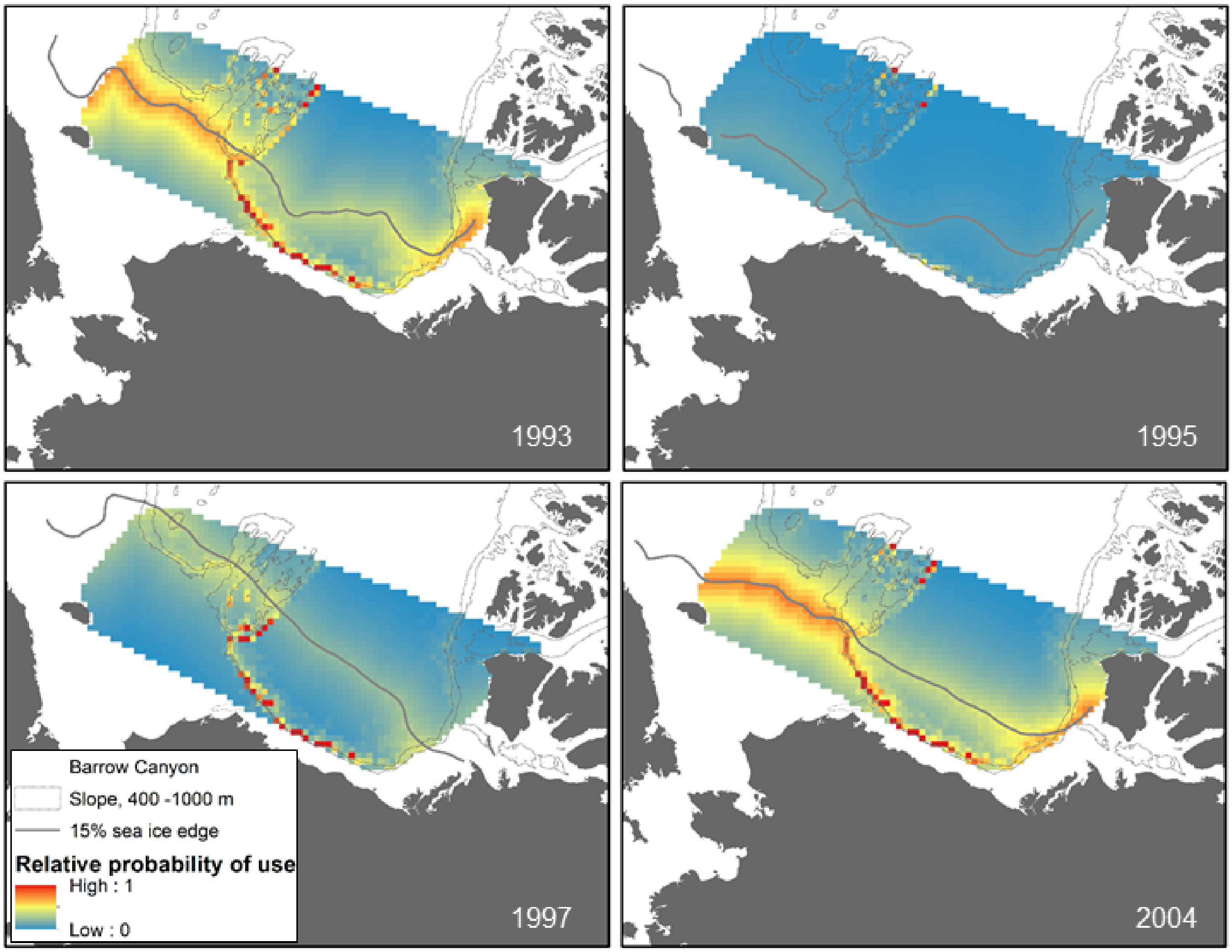

Figure 4-4. Maps of predicted Beaufort male beluga whale use in September, for years when Beaufort males were tagged (see Table 4-1). These four years were averaged to produce the map of September Beaufort male relative probability of use in Figure 3.

# Chapter 5. DECADAL SHIFTS IN MIGRATION TIMING BY PACIFIC ARCTIC BELUGA WHALES ARE RELATED TO DELAYED ANNUAL SEA ICE FORMATION

## 5.1 ABSTRACT

Migrations are often triggered by seasonal environmental gradients that are increasingly being altered by climate change. Migrations may be timed to coordinate access to ephemeral resources, which may also be responding to changing conditions, or may be innate behaviors. The consequences of rapid changes in sea ice in the Pacific Arctic have not been investigated for beluga whales (*Delphinapterus leucas*) that follow matrilineally-maintained seasonal migration routes. For the Eastern Chukchi Sea (‘Chukchi’) and Eastern Beaufort Sea (‘Beaufort’) beluga populations, we investigated population-specific responses in migration timing to increasingly delayed regional sea ice freeze-up since the 1990s, using two independent data sources: satellite telemetry data and passive acoustics. Comparing dates of migration between ‘early’ (1993-2002) and ‘late’ (2004-2012) tagging periods, Chukchi belugas migrated significantly later (more than 2 weeks, depending on location) from the Beaufort and Chukchi seas in the late period. Home range analyses also revealed a delayed departure by Chukchi whales from Beaufort Sea foraging regions in the late period, and migration timing was positively related to regional freeze-up timing. In contrast, Beaufort belugas did not shift migration timing between periods, nor was migration timing related to freeze-up timing, other than for Bering Strait. Acoustic data from 2008-2014 provided supplementary support for delayed migration from the Beaufort Sea (4 d/y) by Chukchi belugas. Here we report the first phenological responses by beluga whales in the Pacific Arctic to their rapidly transforming ecosystem, illustrating how flexible population-specific responses will

complicate predictions of how species may fare in a changing Arctic but which may enable their persistence in a rapidly changing world.

## 5.2 INTRODUCTION

The evolution and maintenance of migratory behavior represents a response to seasonal environmental gradients, and thus climate change is expected to affect the frequency and magnitude of migratory behaviors (Cresswell et al. 2011). However, migratory species are somewhat of a paradox when assessing potential vulnerability to climate change (Robinson et al. 2009). On one hand, migratory species are mobile, often characterized by populations exhibiting multiple migration strategies, and could be expected to trail changes in environmental suitability. Alternatively migrations are innate behaviors that could be socially maintained (Colbeck et al. 2013), and migratory species may be adapted to and dependent on predictable habitat in important areas (e.g., breeding or foraging grounds) during the migration cycle, which may be differentially affected by climate change. Several life history characteristics of migratory individuals could be affected by climate-related physical changes such as timing, distance, and direction of migration as well as the propensity to migrate (Shuter et al. 2011).

Arctic marine ecosystems are experiencing some of the most prominent physical signals of global climate change, demonstrated as unprecedented rates of seasonal ice loss occurring over broad spatial scales. Sea ice extent, volume, and duration of cover have declined on a pan-Arctic scale, regional variability not withstanding (Stroeve et al. 2012, Barnhart et al. 2016). There have been shifts in lower-level productivity, associated with changing physical conditions in Arctic marine ecosystems (e.g., Grebmeier 2012). However limited research has been conducted to consider the implications of physical changes at the highest trophic levels (Wassmann et al. 2011). In particular, the duration of the open water season has significantly increased in all Arctic regions besides the

Bering Sea, and the timing of annual ice retreat and advance more likely affect the life history of Arctic marine mammals than the area or volume of ice (Laidre et al. 2015b). Arctic marine mammals are long-lived with low reproductive rates and have life histories, reproduction, and foraging strategies matched temporally to sea ice conditions, which can make them particularly susceptible to broad-scale, sudden, and unidirectional changes (Laidre et al. 2008, Kovacs et al. 2011). Impacts of sea ice loss are unmistakable for species directly dependent on ice as a platform for specialized feeding, reproduction, or resting (e.g., polar bears *Ursus maritimus*, Cherry et al. 2013, Rode et al. 2015). However it is less clear what changing environments mean for Arctic cetaceans that indirectly use sea ice habitat and will likely be most impacted by shifts in prey productivity and community structure that result from changes in sea ice conditions (Moore and Huntington 2008). Responses in distribution and phenology are most expected for these ice-associated cetaceans (Gilg et al. 2012).

The rate and intensity of sea ice changes have been particularly pronounced since the 1990s in the Pacific Arctic (Maslanik et al. 2011, Frey et al. 2015, Wood et al. 2015), which could affect two migratory populations of beluga whales (*Delphinapterus leucas*), the Eastern Chukchi Sea (‘Chukchi’) and Eastern Beaufort Sea (‘Beaufort’) populations (Figure 5-1). Chukchi and Beaufort belugas migrate thousands of kilometers during the open water season from the sub-Arctic northern Bering Sea to the seasonally productive Chukchi and Beaufort seas (Richard et al. 2001, Suydam et al. 2001), which have each experienced significant increases in the average open water season over the last three decades (~13 and 15 d/decade, respectively, Laidre et al. 2015b). Each genetically-distinct population is philopatric to discrete summering areas (O'Corry-Crowe et al. 1997, Hauser et al. 2014), and the annual retreat and advance of dense pack ice presumably affects the ability of Chukchi and Beaufort belugas to access foraging habitat in the Chukchi and Beaufort seas (Moore 2000, Garland et al. 2015, Hauser et al. 2015).

Beluga whales exhibit predictable migration behaviors that have been passed down matrilineally (Colbeck et al. 2013), and it is unknown if Pacific Arctic belugas will adjust migrations as sea ice shifts, or to what extent, since beluga migrations respond to both environmental gradients and matrilineal learning. In this paper, we use two independent types of data (telemetry and passive acoustics) to examine potential changes in Chukchi and Beaufort beluga fall migration timing associated with changes in the timing of seasonal ice cover. Assuming that timing of sea ice advance affects access to Chukchi and Beaufort sea foraging regions, we predict that west and southward fall migration is related to the timing of sea ice freeze-up, which has occurred an average of at least 1 wk later per decade over 1979 to 2013 (Laidre et al. 2015b). If regional sea ice timing is an important factor determining beluga migration timing, we would additionally expect that migration timing would shift later as freeze-up occurs later.

## 5.3 METHODS

### 5.3.1 *Study area and migratory 'passage points'*

Chukchi and Beaufort beluga whales make extensive migrations between winter areas in the northern Bering Sea and summer foraging regions in the Pacific Arctic (Hauser et al. 2015), requiring fall passage of several key latitudes and longitudes referred to here as 'passage points' on return trips to the Bering Sea (Figure 5-1). Beaufort belugas commence westward fall migration in September by crossing 141° W, the northward extension of the United States-Canada border, and traversing the Beaufort Sea approximately 1 month earlier than Chukchi whales (Richard et al. 2001, Hauser et al. 2014). Beaufort whales remain in the Chukchi Sea before both populations typically commence southward migration around November (Hauser et al. 2014). To consider fall migration timing, we considered 3 Chukchi and 4 Beaufort beluga passage points that correspond to exits from the Beaufort and Chukchi seas and southbound migration (Figure 5-1, Table 5-1).

### 5.3.2 *Telemetry data*

We used previously-described location data from satellite-linked data recorders attached to Chukchi and Beaufort beluga whales near Point Lay, Alaska and the Mackenzie River Estuary, Canada, respectively (Table 5-2; Orr et al. 2001, Richard et al. 2001, Suydam et al. 2001). We used data from Chukchi belugas from 1998-2012, including one male (‘B07-1’) in 2007 that provided locations through the 2008 fall migration. We used data from Beaufort whales tagged between 1993-2005. Chukchi tags transmitted continuously, but some Beaufort tags were programmed to transmit either continuously or according to 1-6 d duty cycles (Richard et al. 2001). We used a filtering algorithm to eliminate poor quality locations (Freitas et al. 2008) and used the Hauser et al. (2014) standardized approach to identify a single, best-quality daily location along the track of each whale. We estimated monthly (July-November) home ranges of both populations using quartic kernel density estimation of the utilization distribution. We used the Geospatial Modeling Environment ‘kde’ tool (spatialecology.com/gme) following parameters set in Hauser et al. (2014) to estimate utilization distributions. Home ranges were defined as the 95% probability contour of the estimated utilization distribution. We compared the spatial distribution of monthly home ranges for each population among clustered years when tagging occurred to consider changes in distribution and migration timing over time. These generally correspond to sea ice conditions experienced in the 1990s (‘early tagging period’: 1993-2002) and 2000s (‘late tagging period’: 2004-2012; Table 5-2).

We identified the day of the year when tagged whales transited each passage point without return. The sample size of whales crossing each passage point decreased the further west and south each point occurred in the fall migration path because tag longevity decreased along the fall migration path (i.e. because batteries failed, tags detached, antennae broke; Table 5-1). We excluded a few cases when passage dates were also the date of last transmission, so we could not definitively determine passage of the whale. We considered trends in migration timing between tagging periods at each passage point using Kruskal-Wallis rank sum tests.

### 5.3.3 *Passive acoustic data*

Hydrophone packages (Multi-électronique Aural M2) were deployed on moorings in the eastern Beaufort Sea (71.4° N, 152° W) and just north of Bering Strait (66.3° N, 168.95° W) to monitor ambient noise (Figure 5-1). The Beaufort Sea instrument recorded year-round from September 2008 through July 2013 on a 30% duty cycle. The Bering Strait instrument recorded fall data (September through December) from 2009 through 2014 on a 25% duty cycle. Acoustic data were sampled at 8192 Hz for an effective monitored bandwidth of 10-4096 Hz, which is sufficient to record the whistles and pulsed signals of beluga whales, but not higher frequency echolocation signals. Spectrograms of each data file were visually examined for the presence beluga whale calls and the number of hours per day with calls was determined to examine seasonal occurrence.

For the Beaufort Sea mooring, we identified the last day each year when belugas were detected as the date of fall migration away from the Beaufort Sea. We assumed that the last beluga whale calls detected at the Beaufort Sea mooring were Chukchi belugas, based on distribution and migration timing previously described in telemetry studies (Richard et al. 2001, Suydam et al. 2001, Hauser et al. 2014). However, both populations overlap spatially in the Bering Strait region in November, so we could not deduce which population was acoustically detected during fall migration at the Bering Strait hydrophone. At the Bering Strait hydrophone, we determined the first day each year when beluga vocalizations were observed to examine migration past Bering Strait.

### 5.3.4 *Comparisons with regional sea ice phenology*

We examined the relationship between fall migration timing (from both telemetry and acoustic data) and regional sea ice timing using the day of sea ice advance (‘freeze-up’), determined in Laidre et al. (2015b) for each year in the Bering, Chukchi, and Beaufort seas (Figure 1). Briefly, the daily sea ice area for each year (1979-2014) and region was estimated from SSM/I satellite-derived sea ice products (Cavalieri et al. 1996, updated yearly). We defined the day of sea ice advance in each region as the day each fall when the area of sea ice first exceeded half the area of the region. We used least-squares regression to compare the day of migration each year to the day of sea ice freeze-up in the Bering, Chukchi, and Beaufort seas.

## 5.4 RESULTS

### 5.4.1 *Migration phenology of tagged belugas*

A total of 65 Chukchi and Beaufort belugas were tagged between 1993-2012, but the number of tagged belugas whose tags transmitted through November or that crossed each passage point varied due to variable deployment durations (Tables 5-1, 5-2). Home ranges of Chukchi whales were distributed similarly between tagging periods in July-September when Chukchi belugas forage in the Beaufort and northeast Chukchi seas (Hauser et al. 2015), although home range size increased during the late period in September (Figure 5-2). The home range size of late period tagged whales contracted in October, and Chukchi belugas remained in the continental slope regions of the Beaufort Sea compared to the October home range of whales tagged in the early period extended west- and southward. In November, the home range of Chukchi belugas tagged in the late period spanned from the Bering Strait to Beaufort Sea compared to the more compacted home range focused in Bering Strait for whales tagged in the early period. July-November home ranges of

Beaufort belugas were generally similarly distributed between tagging periods, other than in September when two distinct paths were detectable in the late period compared to the early period. Beaufort beluga home ranges were smaller in the late period than the early period in all months but November, when sample size was small.

Chukchi beluga fall migration timing was later in the late period (i.e. 2007-2012) than early period (i.e. 1998-2002) for all passage points and was also correlated with the timing of sea ice advance (Table 5-1, Figure 5-3). Specifically, the date of exit from the Beaufort Sea (152° W), commencement of southward migration (70° N), and passage south of Bering Strait (65.9° N) were consistently significantly delayed in the late tagging period by at least 2-5 weeks. In each case, passage date was positively related to the date of sea ice freeze-up in the Beaufort, Chukchi, and Bering seas. Correlations with regional freeze-up timing were best explained by freeze-up timing in the region whales were departing.

In contrast, there were no changes in migration timing or correlations with regional freeze-up timing for Beaufort belugas between early (i.e. 1993-1997) and late (i.e. 2004-2005) tagging periods, other than entrance into the Bering Sea (Table 5-1). Although sample sizes precluded statistical comparison, Bering Strait was the only passage point where Beaufort belugas tagged in the late period delayed migration when compared to early period whales and where there was a significant correlation with regional freeze-up timing (only for the Bering Sea). Beaufort belugas also passed each location ahead of Chukchi belugas as expected from previous analyses (Hauser et al. 2014), other than at Bering Strait. At Bering Strait, Beaufort belugas' median migration dates were ~2 wk later than those of Chukchi belugas for both the early and late period.

### 5.4.2 *Migration phenology of acoustically-detected belugas*

Available evidence from tag data suggests that the last belugas to pass the Beaufort Sea hydrophone are Chukchi belugas (Hauser et al. 2014). The last date of beluga vocalizations occurred 3.9 d later each year (2008-2013) at the Beaufort Sea hydrophone, although the relationship was not statistically significant ($r^2 = 0.43$, $p = 0.16$; Figure 5-4). While there was no relationship between the date of the last beluga calls at the Beaufort Sea hydrophone and the date of freeze-up in the Chukchi or Bering seas ($p = 0.99$ and $p = 0.86$, respectively), the date of last beluga calls was positively related to the date of Beaufort Sea freeze-up ($r^2 = 0.57$, $p = 0.08$; Figure 5-4).

It was not possible to determine which population was acoustically detected at the Bering Strait hydrophone, though the date of first beluga vocalizations occurred 1.3 d later each year, from 2009-2014 ($r^2 = 0.16$, $p = 0.44$; Figure 5-4). There were no strong relationships with freeze-up date in the Chukchi or Beaufort seas ($p = 0.78$ and $p = 0.95$, respectively) although the strongest positive correlation occurred with Bering Sea freeze-up timing ($p = 0.463$; Figure 5-4).

## 5.5 DISCUSSION

Arctic ecosystems as a whole are experiencing some of the most profound and rapid changes on Earth, yet limited baselines among multiple regions have hindered assessments of impacts to regional marine mammal populations (Laidre et al. 2015b). Few studies examine ice-related responses of Arctic cetaceans, and primarily focus on regional shifts in distribution or changes in body condition of well-sampled populations (e.g., Heide-Jørgensen et al. 2010, Heide-Jørgensen et al. 2011, George et al. 2015). In contrast, establishing an understanding of the impacts of sea ice loss has been more forthcoming for ice-obligate Arctic pinnipeds and polar bears that require predictable ice phenology to match the timing of reproduction, foraging, and other critical behaviors (e.g., Cherry et al. 2013, Hamilton et al. 2015, Laidre et al. 2015a).

We used two independent data sources to show consistent trends toward delayed autumn departure from the Beaufort (Chukchi belugas) and Chukchi seas (both Beaufort and Chukchi belugas). Our acoustic data provided an Eulerian perspective over a shorter time frame that overlapped and extended the ‘late’ period telemetry data. Our telemetry data offered higher resolution Lagrangian tracks of individuals as they moved across different passage points. There were assumptions associated with each dataset. Passive acoustics relies on belugas vocalizing in close proximity to hydrophones (~5-10 km), and we could not ascertain population identity. The Beaufort Sea hydrophone was placed near a Chukchi beluga core area, and population-specific migration timing supports our assumption that the last day of beluga vocalizations would likely specifically detect Chukchi belugas (Hauser et al. 2014). However both populations transit near the Bering Strait hydrophone in November, so we expect both populations were acoustically detected. There were also relatively few years of data to detect changes in migration timing from acoustic data, and all of these fell within the late period for tagged whales. For telemetry data, we assumed our limited sample size of tagged whales were representative of the entire population. Recent evidence shows that Chukchi males migrate from the Beaufort Sea later (~1 wk) than females (Hauser et al. 2014), but we did not examine sex-based differences in migration timing due to small sample size. No differences in migration timing have been detected between Beaufort sexes, and we do not expect sex-based migration timing would have changed our conclusions. Nearly equal proportions of Chukchi males and females made up our late period sample, and more males were tagged than females in the early period (Table 5-2). Thus, if anything, we would expect fall migration timing of the Chukchi population to have been biased later in the early period due to the greater proportion of males in the early period sample. Similarly, duty-cycling of our Beaufort tags occurred in both tagging periods and likely did not affect conclusions about changes in migration timing. However, the actual dates of migration could have been biased later if there was a 1-6 d lag between successive locations due to duty-cycling, which could potentially affect our ability to detect a relationship with regional sea ice phenology. Still, westward migration by Beaufort belugas occurred well in advance of Chukchi or Beaufort sea freeze-up. Despite the limitations of each dataset, our inferential power comes from the combination of these independent data sources, both of which indicate similar trends in beluga migration phenology as it relates to regional sea ice.

Our home range, passage point, and acoustics results all suggest that Chukchi belugas are extending their occupancy of Pacific Arctic regions during the open-water season. Some have predicted that sea ice decline may actually be positive for seasonal migrants as well as some upper trophic level marine predators due to ice-related changes in biophysical forcing (Bhatt et al. 2014, Moore and Stabeno 2015). Longer ice-free seasons in combination with increased wind-driven mixing has increased the heat content in upper layers of the Pacific Arctic, likely contributing to enhanced primary and secondary production as well as zooplankton advection (Pickart et al. 2009, Arrigo and van Dijken 2015, Wood et al. 2015). Accordingly, body condition of bowhead whales (*Balaena mysticetus*) harvested in the Beaufort Sea improved during 1989-2011 and correlated with sea ice declines, fitting predictions for more productive foraging during the recent reduced ice regime (George et al. 2015). Limited time series are available to demonstrate that an increased and extended duration of lower-level productivity is also generating improved foraging opportunities for belugas. One primary prey item, Arctic cod (*Boreogadus saida*), is the dominant and most widespread fish species in recent benthic and pelagic surveys across the Pacific Arctic, in addition to other prey species that appear to be expanding their range into the region (Logerwell et al. 2015). Barrow Canyon and the Beaufort Sea slope are considered summer to fall ‘hotpots’ for Chukchi belugas where oceanographic conditions promote pelagic aggregations of fish, thereby improving foraging opportunities for belugas (e.g. Moore et al. 2000, Stafford et al. 2013, Hauser et al. 2015). Given regional trends towards improved lower-level productivity and warmer falls, we expect that foraging opportunities for Chukchi belugas were more extensive and productive in the late than early tagging period.

Our telemetry and acoustic data consistently revealed that fall migration timing for Chukchi belugas was associated with the onset of freeze-up, particularly in the regions that whales were departing. These results suggest that access to Beaufort and Chukchi summer foraging areas is limited by the annual advance of fast ice, as suggested for beluga distribution elsewhere (e.g. Heide-Jørgensen et al. 2010). The formation of fall fast ice is dynamic and rapid, and has been particularly delayed since 2000 in the Chukchi and Beaufort seas due to intensified thermal and wind-driven processes (Frey et al. 2015). Therefore, our results indicate that Chukchi beluga presence north of Bering Strait is temporally-constrained by the advance of fast ice and that belugas can respond to variations in the timing of freeze-up.

We found limited evidence that Beaufort beluga westward migration was similarly influenced by sea ice phenology, so other factors likely cue migration for Beaufort belugas. We presume migration into the western Chukchi Sea is motivated by predictable foraging opportunities. Maximum and modal depths of diving Beaufort belugas typically target the seafloor in the Chukchi Sea (Hauser et al. 2015), which is characterized by productive benthic invertebrates and Arctic cod prey (Norcross et al. 2013, Grebmeier et al. 2015), except near Herald Canyon where diving targeted mid-water depths and oceanographic properties may establish conditions favorable for pelagic foraging (Pickart et al. 2010, Spall et al. 2014). Beaufort belugas remain north of 70°N in the Herald Canyon region during October before shifting south to the southwestern and central Chukchi Sea in November where the two populations converge (Hauser et al. 2014). Furthermore, Beaufort belugas may not detect as strong of a sea ice signal in the western portion of the Chukchi Sea relative to the eastern portion used by Chukchi belugas, which is more strongly influenced by Bering Strait advection. While foraging is likely related to Beaufort beluga westward migration from the Beaufort into the Chukchi Sea, additional research is needed to identify other potential factors that may drive migration such as sea-surface temperature or other climate indicators of ecosystem productivity related to foraging (e.g. Bailleul et al. 2012, Loseto et al. 2015) or simply a more static predictor of heritable migration timing such as day length.

The only passage point where both populations delayed migration was Bering Strait, evidenced by our telemetry data and weakly supported by acoustics. We had a limited sample of tagged Beaufort belugas, but migration south of Bering Strait was later for Beaufort than Chukchi belugas (~2 wk) and was the only passage point where migration timing was significantly correlated with regional sea ice freeze-up (i.e. the Bering Sea). Thus, our telemetry results suggested that the fall advance of sea ice eventually excludes both populations from preferred foraging habitat in the southern Chukchi Sea. Passive acoustics further supported a delay in migration over time, related to Bering Sea ice advancement timing, albeit weakly and with unknown population identification. It is unclear whether the first date of detection is the best metric of migration at this location. Belugas are recorded at the Bering Strait hydrophone in November and early December, and often in pulses separated by multiple days (K. Stafford unpublished data), so perhaps individuals move around the hydrophone location before ultimately departing the Chukchi Sea or different pulses represent distinct movement timing by the populations. Unlike in the Chukchi Sea, freeze-up timing in the northern Bering Sea has not changed (Laidre et al. 2015b). As a result whales would need to transit the Bering Strait chokepoint before they may necessarily need to exit the Chukchi Sea, explaining the stronger association with Bering Sea freeze-up timing over the Chukchi Sea. Overall, we have the greatest uncertainty in whether there have been phenological changes by belugas at Bering Strait, due largely to small sample sizes from both datasets.

Another uncertainty regarding Beaufort belugas rests in the years in which Beaufort belugas were tagged. Although sea ice freeze-up has been progressively delayed over the satellite record (i.e. since 1979), the trends have been particularly accelerated over the past decade (Frey et al. 2015). Our 'late' period tagging of Beaufort belugas occurred in 2004-2005 before the most dramatic sea ice changes occurred (e.g. 2007). This may explain why Beaufort beluga migration timing was not related to regional sea ice freeze-up trends, other than their final departure from the Chukchi Sea through Bering Strait. Our ability to detect climate-related responses is generally limited by our relatively short time series for either population. Long-term studies have greater capacity to detect and attribute biological responses to changing conditions, although our datasets were typical of marine biological response studies in many disciplines (Hauser et al. 2016). In any case, continued monitoring of both populations will help elucidate phenological responses by Pacific Arctic belugas.

Understanding variability among populations is particularly relevant to management and planning for the effects of climate change at regional scales (Laidre et al. 2015b), and an important result of our study was that there were non-uniform phenological responses between sympatric beluga whale populations to shifts in regional sea ice phenology. Variable responses to climate signals among populations may result from multiple factors such as distinct patterns of utilization, population productivity, life history strategies, or trophic interactions (Gilg et al. 2012), which complicate predictions of species success or failure in the context of transforming ecosystems

(Moritz and Agudo 2013, Post et al. 2013). Detecting variable responses by beluga populations to shifting sea ice may reflect plasticity in the face of dynamic Arctic conditions over the last several million years. Belugas are long-lived (e.g., oldest Beaufort whales observed >60 y; Harwood et al. 2014) with predictable matrilinealy-derived migrations, so individuals of each population have experienced dramatic physical changes even within their lifespans and the phenological changes we detected for Chukchi belugas indicate strong adaptive capacity by individuals. In contrast, Beaufort belugas did not strongly respond to the changing environmental stimulus, and migration timing may be more innate. Behavioral flexibility among individuals and populations may facilitate adaptive responses by belugas as a species, although it is still hard to anticipate what changing phenologies, or non-response, will mean for long-term population persistence.

Shifts in migration timing are not only ecologically meaningful, but also affect many indigenous communities who have relied on belugas for subsistence, cultural, and spiritual resources over millennia. Shifting migration phenology could impact the accessibility and availability of belugas to hunters, though most harvests of Chukchi and Beaufort belugas in Alaska and western Canada occur in the spring and early summer when we have limited data. Additional studies that can further illuminate changes in spring migration will enhance our ability to understand future beluga responses as well as resource security for people who depend on them.

## 5.6 ACKNOWLEDGEMENTS

We are grateful to the long-term collaborative efforts of hunters and others in the communities of Point Lay, AK and the Inuvialuit Settlement Region, NWT who have facilitated access to belugas since the 1990s. For Chukchi belugas, L. Lowry, K. Frost, G. O’Corry-Crowe, D. Pikok, R. Small, T. Romano, J. Tazruk, B. and M. Tracey, J. Rexford, J. Orr, A. Ashby, V. Dollarhide, L. Ferreira, L. Pierce, L. Stalker, H. Smith, R. Hobbs, R. Hoover, T. Nukapigak, M. Sparck, S. Speckman, D.

Susook, C. Aniskette, J. Tuckfield, C. Rea, G. Marshall, N. Hank, L. Hansen, L. Hoberecht, L. Quakenbush, T. Robeck, A. Simon, G. and K. VanBlaricom, J. Taylor, J. Edwards, D. Ramey, B. Achootchook, and J. Citta have facilitated various aspects of tagging and data processing. Funding was provided by the Alaska Beluga Whale Committee, North Slope Borough of Alaska, National Marine Fisheries Service (NMFS), Alaska Department of Fish and Game, National Fish and Wildlife Foundation, Minerals Management Service, and Village of Point Lay. We also thank the Inuvialuit Hunter and Trapper Corporations of Inuvik, Aklavik, and Tuktoyaktuk and the Polar Continental Shelf Project for the support and assistance tagging Beaufort belugas. In addition, J. Orr, A. Martin, and B. Leblanc provided invaluable field assistance and data processing. Beaufort beluga tagging was funded by the Fisheries and Oceans Canada (DFO), Fisheries Joint Management Committee, Environmental Studies Revolving Fund, Minerals Management Service, and NMFS. Acoustic data collection was supported by grants N00014-08-1-0311 from the National Ocean Partnership Program, ARC-0855282 and ARC-1107106 from the National Science Foundation and Dr. K. Crane of the Russian-US Long-term Census of the Arctic (RUSALCA).  Analyses were supported by a NASA Climate Indicators Program Grant (NNX13AN28G) and fellowships to D. Hauser from the University of Washington's (UW) Integrative Graduate Education and Research Traineeship Program on Ocean Change (National Science Foundation) and UW School of Aquatic & Fishery Sciences. D. Schindler, R. Hobbs, and S. Moore provided useful feedback, guidance, and review of the manuscript. Additional feedback on beluga range maps was provided by L. Quakenbush and L. Lowry. Permits necessary for capture and tagging of belugas were approved by NMFS (nos. 14610, 782-1438, and 782-1719) and DFO for Chukchi and Beaufort belugas, respectively.

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Table 5-1. Passage points transited by tagged belugas without return in a given year, and comparisons between early and late period sample sizes, median (and range) migration day of year, and overall number of days between median dates (and results of Kruskal-Wallis rank sum test). The results of linear regressions comparing beluga fall migration day and regional freeze-up day (Laidre et al. 2015) are shown in the last column. Significant statistical relationships ($p < 0.05$) are bolded.

| **Passage point** | **No. tagged whales in early, late periods** | **Median migration day of year (range) in early, late periods** | **Days between median dates (late – early)** | **Trend, fit ($r^2$), and F-statistics of migration date and regional sea ice timing** |
|---|---|---|---|---|
| **Eastern Chukchi Sea belugas** | | | | |
| Exit Beaufort Sea (first day west of 152°W) [a] | 8, 7 | 259.5 (244-283),<br>306 (294-311) | **+46.5** ($\chi^2$ = 10.6, df = 1, p = 0.001) | Bering: +0.3, $r^2$ = 0.01 (F = $0.15_{1,13}$, p = 0.705)<br>Chukchi: +0.68, $r^2$ = 0.26 (F = $4.5_{1,13}$, p = 0.055)<br>Beaufort: **+1.39**, $r^2$ = 0.41 (F = $8.9_{1,13}$, p = 0.011) |
| Commence southward migration (last day north of 70°N) | 4, 6 | 294.5 (286-299),<br>316.5 (310-327) | **+22** ($\chi^2$ = 6.54, df = 1, p = 0.011) | Bering: **+1.1**, $r^2$ = 0.55 (F = $9.7_{1,8}$, p = 0.014)<br>Chukchi: **+0.44**, $r^2$ = 0.54 (F = $9.5_{1,8}$, p = 0.015)<br>Beaufort: **+0.87**, $r^2$ = 0.66 (F = $15.2_{1,8}$, p = 0.005) |
| Enter Bering Sea (first day south of Bering Strait, 65.9°N) | 3, 4 | 312 (311-317),<br>329.5 (320-351) | **+17.5** ($\chi^2$ = 4.5, df = 1, p = 0.034) | Bering: +1.16, $r^2$ = 0.51 (F = $5.2_{1,5}$, p = 0.073)<br>Chukchi: **+0.59**, $r^2$ = 0.71 (F = $12.4_{1,5}$, p = 0.017)<br>Beaufort: +0.53, $r^2$ = 0.28 (F = $1.9_{1,5}$, p = 0.226) |
| **Eastern Beaufort Sea belugas** | | | | |
| Exit Canada (first day west of 141°W) | 11, 10 | 251 (213-263),<br>245 (240-262) | -6 ($\chi^2$ = 0.58, df = 1, p = 0.446) | Bering: -0.02, $r^2$ < 0.001 (F = $0.01_{1,17}$, p = 0.935)<br>Chukchi: -0.72, $r^2$ = 0.08 (F = $1.5_{1,17}$, p = 0.243)<br>Beaufort: -0.90, $r^2$ = 0.13 (F = $2.4_{1,17}$, p = 0.141) |
| Exit Beaufort Sea (first day west of 152°W)[a] | 11, 7 | 258 (249-274),<br>250 (247-266) | -8 ($\chi^2$ = 1.39, df = 1, p = 0.238) | Bering: -0.19, $r^2$ = 0.12 (F = $2.1_{1,16}$, p = 0.163)<br>Chukchi: -0.64, $r^2$ = 0.10 (F = $1.8_{1,16}$, p = 0.201)<br>Beaufort: +0.746, $r^2$ = 0.11 (F = $2.0_{1,16}$, p = 0.174) |
| Commence southward migration (last day north of 70°N) | 8, 7 | 289.5 (278-302),<br>288 (276-295) | -1.5 ($\chi^2$ = 0.21, df = 1, p = 0.643) | Bering: -0.13, $r^2$ = 0.08 (F = $0.1_{1,13}$, p = 0.343)<br>Chukchi: -0.37, $r^2$ = 0.04 (F = $0.4_{1,13}$, p = 0.525)<br>Beaufort: +0.24, $r^2$ = 0.004 (F = $0.1_{1,13}$, p = 0.814) |
| Enter Bering Sea (first day south of Bering Strait, 65.9°N) | 1, 5 | 331,<br>344.5 (325-353) | +13.5[b] | Bering: +**0.48**, $r^2$ = 0.82 (F = $22.2_{1,5}$, p = 0.005)<br>Chukchi: +1.40, $r^2$ = 0.47 (F = $4.5_{1,5}$, p = 0.087)<br>Beaufort: -2.01, $r^2$ = 0.21 (F = $1.4_{1,5}$, p = 0.300) |

[a] same longitude as acoustic mooring in Beaufort Sea

[b] No statistical testing based on small sample size of whales tagged in the early period

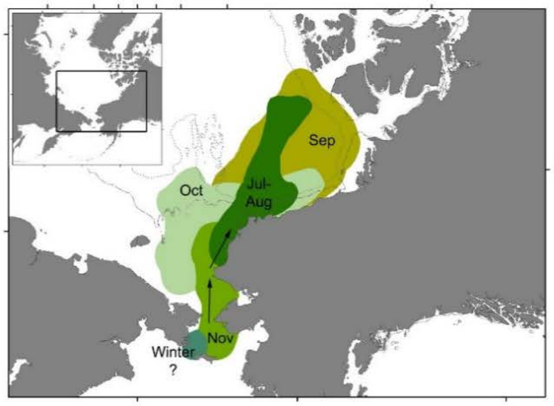
Table 5-2. Details on 65 Beaufort and Chukchi beluga whales (n = 38 and n=27, respectively) satellite-tagged during the early (1993-2002) and late (2004-2012) periods. Longevity refers to the number of days from capture until the last location ($\bar{x}_{Beaufort}$ = 81.9 d, $\bar{x}_{Chukchi}$ = 105.0 d).

| Population | Period | Year | Tag ID | Sex | Capture date | Date of last transmission | Longevity (d) |
|---|---|---|---|---|---|---|---|
| *Beaufort* | *Early* | 1993 | 1993-17002 | M | 7/19/1993 | 8/22/1993 | 34 |
| | | | 1993-17005 | M | 7/10/1993 | 10/9/1993 | 91 |
| | | | 1993-17006 | M | 7/10/1993 | 7/21/1993 | 11 |
| | | | 1993-17009 | F | 7/11/1993 | 8/7/1993 | 27 |
| | | 1995 | 1995-17001 | M | 7/3/1995 | 9/26/1995 | 85 |
| | | | 1995-17002 | M | 7/6/1995 | 8/22/1995 | 47 |
| | | | 1995-17003 | M | 7/5/1995 | 7/28/1995 | 23 |
| | | | 1995-17004 | M | 7/5/1995 | 8/7/1995 | 33 |
| | | | 1995-17005 | M | 7/4/1995 | 8/16/1995 | 43 |
| | | | 1995-17007 | F | 7/16/1995 | 9/22/1995 | 68 |
| | | | 1995-17008 | F | 7/18/1995 | 7/25/1995 | 7 |
| | | | 1995-17010 | M | 7/8/1995 | 8/7/1995 | 30 |
| | | | 1995-17011 | M | 7/9/1995 | 8/8/1995 | 30 |
| | | | 1995-17012 | M | 7/9/1995 | 8/8/1995 | 30 |
| | | | 1995-17013 | M | 7/11/1995 | 8/10/1995 | 30 |
| | | | 1995-17014 | F | 7/12/1995 | 8/11/1995 | 30 |
| | | | 1995-5800 | M | 7/15/1995 | 8/14/1995 | 30 |
| | | | 1995-5801 | M | 7/11/1995 | 8/10/1995 | 30 |
| | | | 1995-8754 | F | 7/12/1995 | 8/10/1995 | 29 |
| | | 1997 | 1997-10692 | F | 8/1/1997 | 10/5/1997 | 65 |
| | | | 1997-10693 | M | 7/31/1997 | 10/12/1997 | 73 |
| | | | 1997-2118 | F | 7/27/1997 | 12/2/1997 | 128 |
| | | | 1997-25846 | M | 7/30/1997 | 10/22/1997 | 84 |
| | | | 1997-8754 | M | 7/30/1997 | 10/28/1997 | 90 |
| | | | 1997-8755 | M | 7/29/1997 | 10/18/1997 | 81 |
| | | | 1997-8756 | F | 8/2/1997 | 9/26/1997 | 55 |
| | | | 1997-8757 | M | 7/30/1997 | 10/5/1997 | 67 |
| | | | 1997-8758 | M | 7/31/1997 | 11/28/1997 | 120 |
| | *Late* | 2004 | 2004-10899 | M | 7/5/2004 | 5/2/2005 | 301 |
| | | | 2004-10927 | M | 7/8/2004 | 7/25/2004 | 17 |
| | | | 2004-10971 | F | 7/9/2004 | 7/24/2004 | 15 |
| | | | 2004-10972 | F | 7/6/2004 | 10/14/2004 | 100 |
| | | | 2004-36641 | F | 7/24/2004 | 1/12/2005 | 172 |
| | | | 2004-37023 | M | 7/27/2004 | 4/22/2005 | 269 |
| | | | 2004-37024 | M | 7/10/2004 | 4/23/2005 | 287 |
| | | | 2004-40152 | M | 7/6/2004 | 8/12/2004 | 37 |
| | | 2005 | 2005-57591 | F | 7/8/2005 | 4/17/2006 | 283 |
| | | | 2005-57593 | F | 7/11/2005 | 12/17/2005 | 159 |

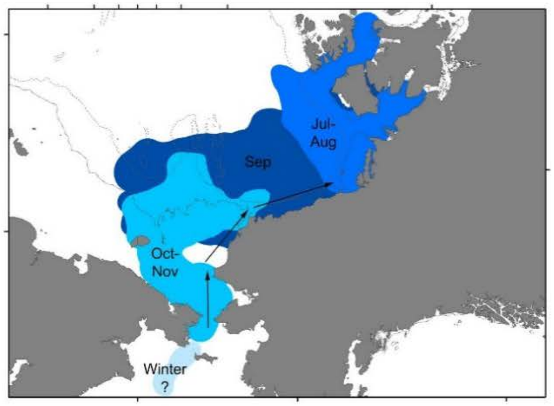
| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Chukchi* | *Early* | 1998 | B98-1 | M | 6/27/1998 | 7/8/1998 | 11 |
| | | | B98-2 | M | 6/29/1998 | 7/12/1998 | 13 |
| | | | B98-3 | M | 6/30/1998 | 10/7/1998 | 99 |
| | | | B98-4 | M | 7/1/1998 | 9/29/1998 | 90 |
| | | | B98-5 | M | 7/2/1998 | 8/30/1998 | 59 |
| | | 1999 | B99-1 | M | 7/1/1999 | 9/25/1999 | 86 |
| | | | B99-2 | F | 7/1/1999 | 9/12/1999 | 73 |
| | | | B99-3 | M | 7/1/1999 | 8/26/1999 | 56 |
| | | | B99-4 | M | 7/1/1999 | 9/23/1999 | 84 |
| | | 2001 | B01-1 | M | 7/5/2001 | 8/10/2001 | 36 |
| | | | B01-2 | F | 7/4/2001 | 7/22/2001 | 18 |
| | | | B01-3 | F | 7/6/2001 | 11/29/2001 | 146 |
| | | | B01-4 | M | 7/6/2001 | 12/6/2001 | 153 |
| | | | B01-5 | F | 7/7/2001 | 10/23/2001 | 108 |
| | | | B01-6 | M | 7/8/2001 | 11/17/2001 | 132 |
| | | | B01-7 | M | 7/8/2001 | 7/24/2001 | 16 |
| | | | B01-8 | M | 7/8/2001 | 8/13/2001 | 36 |
| | | 2002 | B02-1 | F | 7/8/2002 | 9/14/2002 | 68 |
| | | | B02-2 | M | 7/8/2002 | 9/28/2002 | 82 |
| | | | B02-3 | M | 7/10/2002 | 8/25/2002 | 46 |
| | | | B02-4 | M | 7/9/2002 | 9/11/2002 | 64 |
| | *Late* | 2007 | B07-1 | M | 7/2/2007 | 12/4/2008 | 521[a] |
| | | | B07-2 | F | 7/2/2007 | 11/13/2007 | 134 |
| | | | B07-3 | F | 7/3/2007 | 11/6/2007 | 126 |
| | | 2010 | B10-1 | M | 6/25/2010 | 12/6/2010 | 164 |
| | | | B10-2 | M | 6/30/2010 | 10/9/2010 | 101 |
| | | 2012 | B12-1 | F | 7/2/2012 | 5/11/2013 | 313 |

[a] Tag provided fall migration timing in 2007 and 2008

A. Chukchi belugas



B. Beaufort belugas



C. phenology analyses

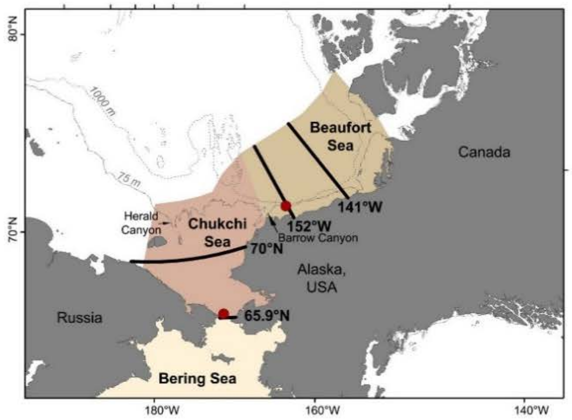


Figure 5-1. Schematic of seasonal ranges of (A) Chukchi and (B) Beaufort beluga whales, based on telemetry locations and home ranges (Richard et al. 2001, Suydam et al. 2001, Hauser et al. 2014). Winter locations are uncertain, based on the small number of tags transmitting past November (Hauser et al. 2015). Black arrows indicate potential spring migration routes for Chukchi (May-June) and Beaufort belugas (April-June), based on historic sightings (Lowry et al. 1987, Frost and Lowry 1990, Frost et al. 1993), acoustic detections (Garland et al. 2015) and few tagged whales (P. Richard, R. Suydam, unpubl. data). Passage points and sea ice regions (Laidre et al. 2015) used in phenological analyses are shown in (C), in addition to place names mentioned in the text and red dots identifying hydrophone locations.

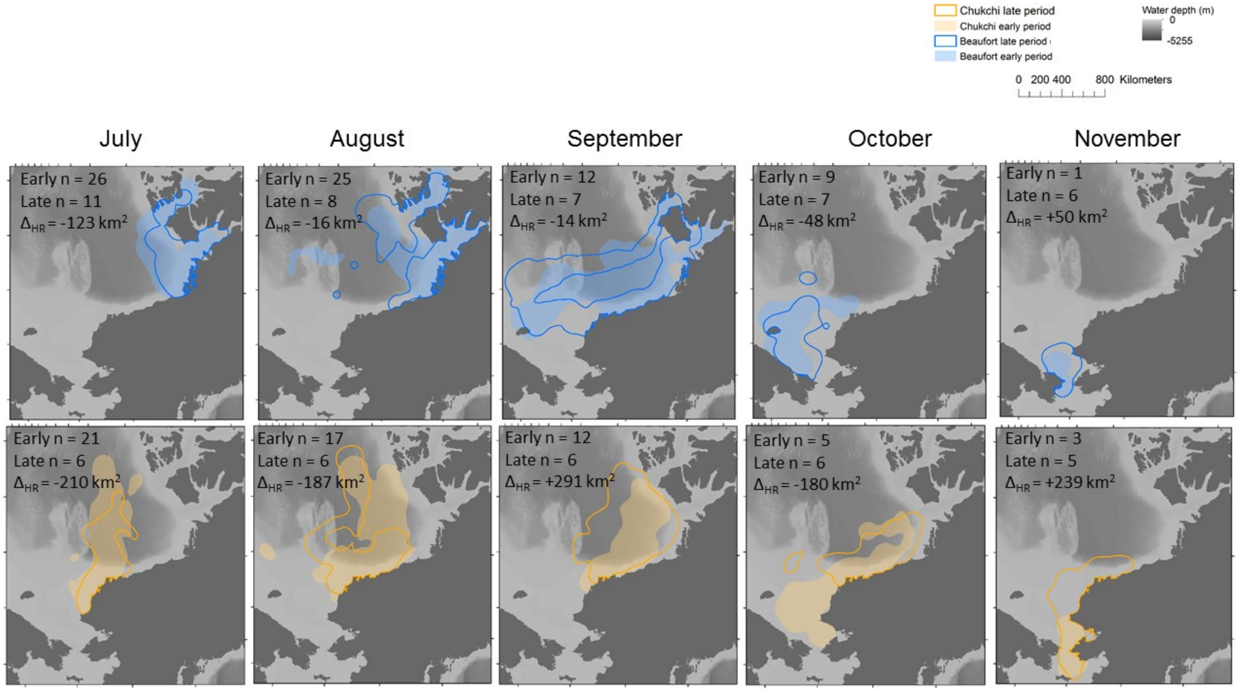


Figure 5-2**.** Spatial distribution, sample size, and differences between periods (in thousands of km$^2$) of monthly home range (HR) size, July-November, for tagged Chukchi and Beaufort beluga whales.

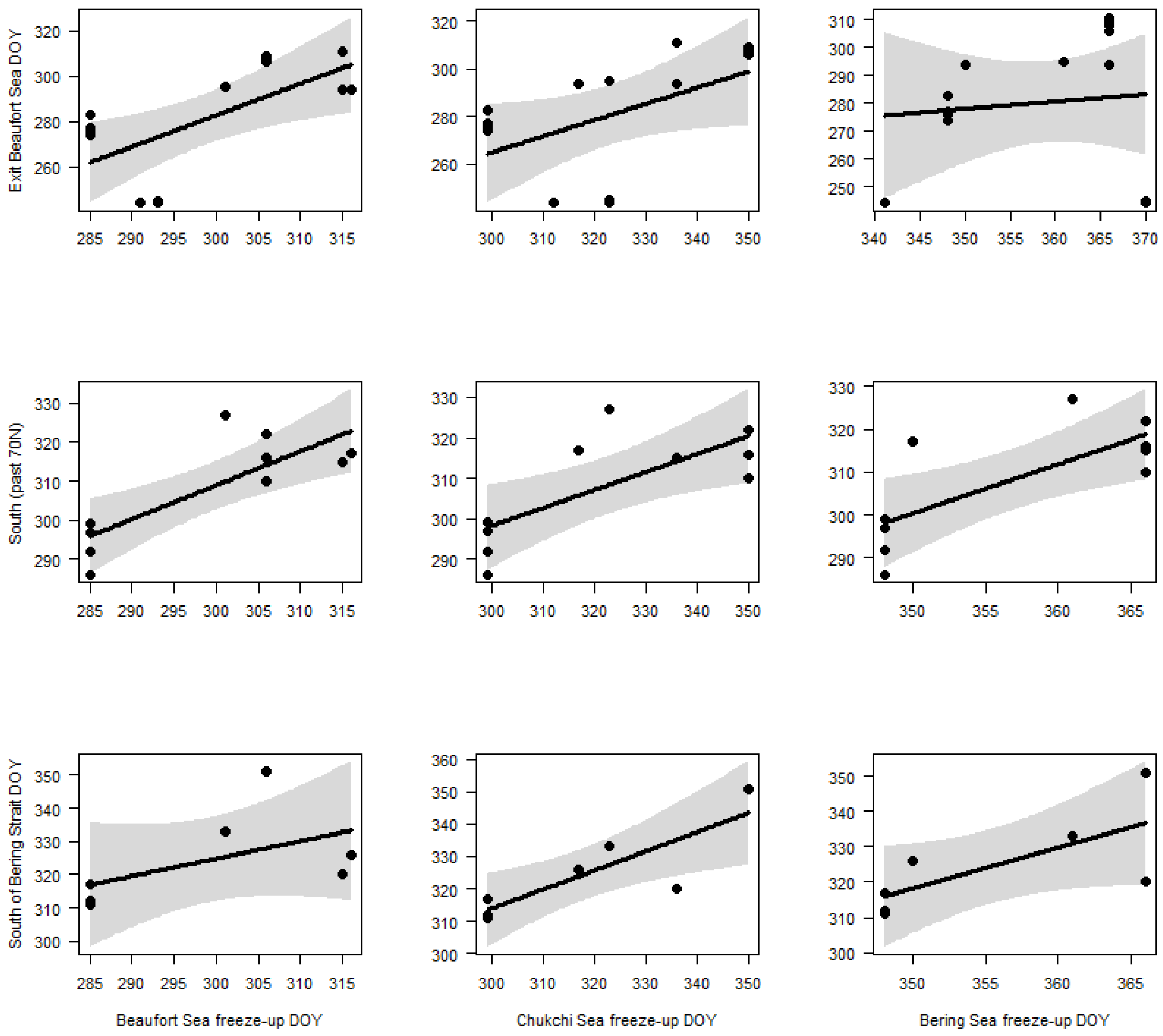


Figure 5-3. Linear relationships between Chukchi beluga migration day of year (DOY) compared to freeze-up DOY in the Beaufort Sea (left column), Chukchi Sea (middle column), and Bering Sea (right column; Laidre et al. 2015b). Significant relationships are identified in Table 5-1. Beaufort beluga relationships are not shown, because only Bering Sea freeze-up timing was strongly positively correlated with migration timing south of Bering Strait (Table 5-1).

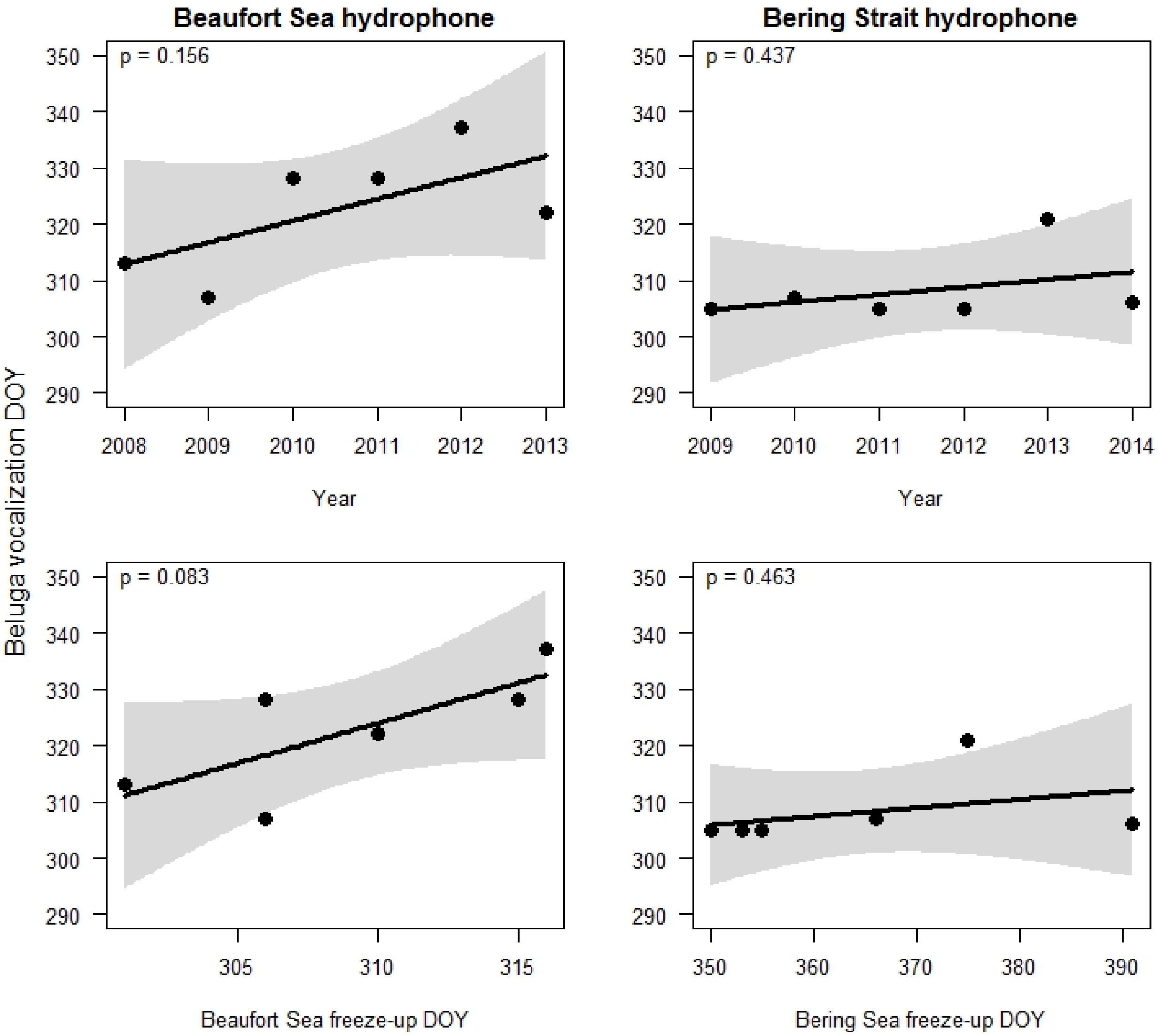


Figure 5-4. Linear regressions (and 95% confidence intervals) of the day of year (DOY) when belugas were last detected at the Beaufort Sea hydrophone 2008-2013 (top left) or first detected at the Bering Sea hydrophone 2009-2014 (top right), and compared to freeze-up timing in the Beaufort Sea (Beaufort Sea hydrophone; bottom left) or Bering Sea (Bering Sea hydrophone; bottom right). Previous work suggests the last fall beluga observations were of Chukchi whales, but it is unknown which population was detected at the Bering Strait hydrophone. Note that freeze-up in the Bering Sea sometimes did not occur until early the next year, so DOY can be >365.

# Chapter 6. SEA ICE LOSS INDIRECTLY AFFECTS THE POPULATION-SPECIFIC HABITAT USE AND BEHAVIOR OF BELUGA WHALES

## 6.1 ABSTRACT

Sea ice cover has declined in the Pacific Arctic with implications for ice-associated marine predators. We used satellite telemetry data collected from tagged beluga whales (*Delphinapterus leucas*) to investigate changes in summer and fall sea ice habitat associations and diving behavior for two distinct but sympatric populations. We examined use of sea ice (SSM/I passive microwave data) in the Eastern Chukchi Sea (‘Chukchi’) and Eastern Beaufort Sea (‘Beaufort’) beluga populations, comparing two periods: early (1993-2002) and late (2004-2012). We used generalized estimating equations to assess changes in ice habitat used by beluga whales as well as shifts in diving behavior between periods. We also used resource selection functions to predict trends in habitat selection and amount of optimal habitat during 1990-2014. Our results revealed that Chukchi belugas used significantly lighter sea ice concentrations (early=29.9±0.9%; late=12.2±0.7%), were farther from the sea ice edge (early = 154.6±4.4 km; late=190.1±6.2 km) and more likely to be located in open water during the late tagging period. We found no significant differences between periods for Beaufort whales. Overall there were few significant changes in sea ice selection between periods for either population, suggesting that sea ice has retreated away from preferred Chukchi beluga summer habitat in recent years. Predictions of preferred habitat were also consistent among decades, other than in October when Chukchi belugas were predicted to prolong occupancy in the Beaufort Sea during the 2000s compared to the 1990s. Chukchi belugas tagged during 2007-2012 made significantly more long-duration (early=0.9 ± 0.03 dives/d >20 min; late=2.8±0.07 dives/d >20 min) and deeper dives (early=49.3±1.7 m; late=64.0±1.9 m)

than those tagged during 1998-2002. Predictions for delayed October departure combined with deeper longer diving suggest fall foraging opportunities may have shifted for Chukchi belugas in the Beaufort Sea as ice retreated since the 1990s. Our results demonstrate that Chukchi belugas are more tightly linked to sea ice than Beaufort belugas during summer-fall, and distinct population-specific responses indicate non-uniform responses to a changing Arctic.

## 6.2 INTRODUCTION

Arctic marine ecosystems provide some of the most prominent physical signals of global climate change, particularly in the case of unprecedented rates of seasonal ice loss occurring over broad spatial scales. Sea ice extent and thickness has decreased (Kwok and Rothrock 2009, Stroeve et al. 2012) and largely shifted from multi-year pack to seasonal ice with an extended duration of ‘open’ water during summer (Comiso 2012, Barnhart et al. 2016). It is expected that the Arctic Ocean will be ice-free in summer within only a few decades and likely continue for several decades even if greenhouse gas emissions, the primary driver of climate change, are immediately reduced (Overland and Wang 2013).

There are already several biological signals of Arctic marine ecosystems responding to sea ice loss (Wassmann et al. 2011), but the eleven species of ice-associated Arctic marine mammals are considered particularly vulnerable (Laidre et al. 2008). Ice-obligate pinnipeds and polar bears (*Ursus maritimus*) rely on sea ice as a platform for critical life history events (e.g. reproduction, molting, resting) and foraging, and population status is uncertain or declining for many (Laidre et al. 2015b). For some populations of polar bears, declining sea ice has been attributed to reduced population productivity (Regehr et al. 2007, Rode et al. 2010) as well as changes in habitat use, movements, and migration phenology (Cherry et al. 2013, Laidre et al. 2015a, Rode et al. 2015) and future population persistence is questionable (Stirling and Derocher 2012).

While changing sea ice conditions have more directly attributable implications for ice-obligate species, ice loss is hypothesized to indirectly impact Arctic cetaceans that depend on sea ice conditions to structure short Arctic marine food webs (Moore and Huntington 2008, Kovacs et al. 2011). Behavior and movements of ice-associated species are tightly coupled to the annual sea ice cycle (Laidre et al. 2008, Laidre et al. 2015b), and ice presumably serves two functions for Arctic cetaceans. First, sea ice affects oceanographic processes and productivity that in turn influences regional foraging opportunities for belugas. The annual retreat and advance of sea ice also affects access to seasonal habitat. In both cases, changes in the timing, location, and concentrations of sea ice cover would be expected to affect the behavior and movements of cetaceans.

In this study we address the potential indirect effects of changing sea ice regimes for two populations of beluga whales (*Delphinapterus leucas*) that migrate from the Bering Sea into the Chukchi and Beaufort seas of the Pacific Arctic during the summer-fall period of sea ice retreat (Figure 6-1). The Eastern Chukchi Sea (hereafter referred to as 'Chukchi') and Eastern Beaufort Sea (hereafter referred to as 'Beaufort') beluga whale populations[1] are genetically distinct and philopatric to separate summer core areas in the western and eastern Beaufort Sea, respectively (O'Corry-Crowe et al. 1997). In September Beaufort belugas shift west and their home range overlaps that of Chukchi belugas, resulting in both populations using the Chukchi Sea in fall (Hauser et al. 2014). A combination of benthic and pelagic foraging occurs in the Beaufort and Chukchi seas (Hauser et al. 2015), which have experienced profound loss of summer sea ice cover and significantly delayed autumn freeze-up since 1979 (at least 7 d later in each region, Frey et al. 2015, Laidre et al. 2015b). Chukchi and Beaufort belugas use a range of sea ice conditions (Richard

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[1] In the United States, the Eastern Beaufort Sea population is referred to by the acronym 'BS' to distinguish it from the Eastern Bering Sea population denoted as 'EBS'. However, in Canada, the Eastern Beaufort Sea population is referred to as 'EBS'. To avoid confusion, we avoid using acronyms and instead use the place names throughout for the 'Chukchi' and 'Beaufort' belugas.

et al. 2001, Suydam et al. 2001), and sea ice is one predictor of seasonal habitat selection (Moore 2000, Moore et al. 2000, Chapter 4). Pacific Arctic belugas also sexually segregate; males use deeper, steeper habitats with heavier ice concentrations farther from shore than females (Loseto et al. 2006). Sea ice loss affects the complex regional hydrography and circulation of the Beaufort and Chukchi sea, impacting wind-forcing, upwelling, and localized productivity (Schulze and Pickart 2012, Pickart et al. 2013, Wood et al. 2015), which in turn affects beluga foraging opportunities for pelagic prey like Arctic cod *(Boreogadus saida*; Stafford et al. 2013, Hauser et al. 2015).

We examined beluga responses to sea ice changes using satellite telemetry data collected from tagged belugas and passive microwave sea ice concentration data. Our telemetry data spanned two decades and could be used to assess changes in population-specific habitat use and diving behavior in the Pacific Arctic. Our objectives focused on contrasting July-October sea ice associations for Chukchi and Beaufort beluga populations between 'early' and 'late' periods when belugas were tagged (1993-2002 and 2004-2012, respectively) and during which regional sea ice declined: 1) to identify sea ice habitat (concentration and proximity to ice edge and dense ice habitat) used by both sexes and populations; 2) to quantify changes in habitat selection, predict preferred habitat from 1990-2014, and identify trends in optimal habitat; and 3) to examine potential shifts in diving behavior. We expected a difference in ice habitat selection between tagging periods would indicate whether belugas are shifting habitat preferences or whether sea ice is retreating away from preferred habitat. We expected a change in diving behavior to signal a change in foraging effort, indicating that regional ice loss may impact prey distribution and beluga foraging opportunities.

## 6.3 METHODS

### 6.3.1 *Study area*

The Pacific Arctic, north of Alaska and western Canada, is comprised of the wide and shallow (<75 m) Chukchi Sea that connects via Barrow Canyon to the narrow continental shelf of the Beaufort Sea, which slopes steeply into the Canada Basin (Figure 6-1). Circulation and hydrography is complex and seasonally dynamic. Barrow Canyon is the main conduit carrying warm and fresh Alaskan Coastal Water in the Alaska Coastal Current (ACC) northward where it overlies a pool of cooler Chukchi Summer Water and denser, cold Pacific Winter Water (Pickart 2004, Gong and Pickart 2015). A shelfbreak jet extends these Pacific waters above a dense layer of Atlantic Water (AW), and the water column stratifies along the Alaskan Beaufort Sea continental slope. Wind-forcing affects water column stratification; persistent upwelling-favorable easterly winds have enforced stratification and a deep hydrographic front (Pickart et al. 2013). Sea ice cover is typically at its minimum in September, but more recently wind anomalies are associated with increased regional sea ice loss, changes in circulation, and increased freshwater (e.g. Morison et al. 2012, Overland et al. 2012, Woodgate et al. 2012, Frey et al. 2015). Ultimately, the Pacific Arctic marginal sea ice zone is warmer, fresher, and windier since the 1990s and characterized by reduced sea ice extent, thickness, and shorter duration of cover, all of which impact primary and secondary production (see Wood et al. 2015).

### 6.3.2 *Beluga satellite telemetry data*

In the Mackenzie River Estuary, we captured and tagged Beaufort beluga whales in July 1993-2005 (Figure 6-1, Table 6-1) following previously described methodology (Orr et al. 2001, Richard et al. 2001). We also tagged beluga whales from the Chukchi population near the village of Point

Lay, Alaska in late June-early July from 1998-2012 (Suydam et al. 2001). We tracked whales for an average of 91.5 d (range: 7-521 d), and most tags transmitted continuously although some Beaufort tags were programmed according to 1-6 d duty cycles (Richard et al. 2001). Tag longevity decreased with time and varied among sex and populations, so we focused analyses on July-October when the most data were available. We eliminated poor quality locations using a speed and angle filter (Freitas et al. 2008) and found a single, best-quality daily location along the track of each whale as in Hauser et al. (2014). We compared clustered years when tagging occurred to consider changes in behavior and habitat, selecting specific periods that generally corresponded to contrasting sea ice conditions : an 'early' period (1993-2002) and 'late' period (2004-2012; Table 6-1).

All but one tag used for the Chukchi population were Wildlife Computers (Redmond, WA) SPLASH tags that also provided diving information (Table 6-1), summarized over four 6-h periods each day. Dive data comparable between periods were not collected for the Beaufort population, so we only examined changes in diving behavior between tagging periods for Chukchi belugas. The tags collected three types of dive data summarized as histograms for each 6-h period: the number of dives to pre-defined depths, proportional time within each depth, and number of dives to pre-defined duration bins (described in Hauser et al. 2015). We scaled up these data to estimate several daily diving metrics, including dive rates (total dives/d, dives/d to <10 m, dives/d <1 min, dives/d >20 min), proportion of time <10 m, mean dive depth, and whether the maximum depth reached the seafloor (binary) as an indicator of proximity to benthic habitat. Diving data can be used to infer behavior at depth, and we assumed that daily dive depth, rates (daily and >20 min), and benthic-oriented diving were related to foraging (Hauser et al. 2015). In contrast, we assumed short duration (<1 min) dives as well as dive rates and proportional time near the surface (<10 m) were representative of surface-based recovery, travel, or resting. We assigned daily locations to each daily dive period and extracted the depth associated with each location from the 500 m resolution International Bathymetric Chart for the Arctic Ocean (Jakobsson et al. 2012).

### 6.3.3 *Sea ice data*

We matched a suite of sea ice characteristics to each beluga daily location based on daily sea ice concentration values estimated from satellite passive microwave data (SSM/I), available at a nominal grid resolution of 25 km (Cavalieri et al. 1996) and relevant to beluga summer to fall habitat selection (Chapter 4). We identified the daily sea ice concentration at each whale location as well as the distance to the daily 15% sea ice edge and to dense pack ice (i.e. 90% concentration). Each day, we also found whether whales were located within open water or among pack ice (>15% concentration). We used least-squares regression to estimate linear trends in sea ice concentration within areas specifically relevant to Chukchi and Beaufort belugas by calculating monthly (July-October) home ranges of each populations (see methodology in Hauser et al. 2014) and estimating the daily mean ice concentration for each month over the sea ice satellite record (1979-2014).

### 6.3.4 *Changes in ice associations*

We assessed changes in ice habitat used by whales using nested generalized estimating equations (GEEs), which are extensions of generalized linear models that facilitate regressions of longitudinal data (Zuur et al. 2009). The assumption of independent model errors is replaced with a correlation structure that accounts for spatial and temporal autocorrelation, and GEEs have been successfully applied to telemetry and distribution data including habitat analyses for cetaceans (e.g. Bailey et al. 2013, Russell et al. 2015). GEEs use sandwich-based estimates of variance so the uncertainty around parameter estimates are robust to the presence of serial autocorrelation within individuals while not explicitly modeling the correlation, so are commonly used when the population-averaged response (marginal mean) is of primary interest (Hardin and Hilbe 2013). Thus, the mean response reflects only the covariates and not the random effects (Zuur et al. 2009). We built Gaussian nested GEEs using package ‘geepack’ (Højsgaard et al. 2006) in R (R Development Core Team) to model population-specific beluga ice associations (i.e. mean concentration used, distance to 15% edge, and distance to 90% edge). We modeled one response, the probability of being located in >15% ice, as a Binomial function. Acknowledging monthly variations in movement and sexual segregation (e.g. Loseto et al. 2006, Hauser et al. 2014), we built models that included factors for month, sex, and tagging period as predictors and used Wald tests for model selection (Zuur et al. 2009).

### 6.3.5 *Changes in preferred habitat*

We used two approaches to examine possible changes in preferred habitat over time. First, we compared habitat selection between periods as the sea ice habitat used by whales (concentration, distances to 15% and 90% ice) relative to availability using a case-control univariate conditional logistic regression approach. We applied the ‘clogit’ function in the ‘survival’ package in R that includes a robust variance estimator to control for repeated measures of tagged whales (Therneau 2015). We established habitat availability for each observed beluga location based on a set of 25 random locations within a circular buffer representing plausible daily movement trajectories, as done in Chapter 4. These univariate between-period comparisons tested whether the sea ice parameter used by males or females of each population in the early period was different than that used in the late period.

We also used habitat selection models developed by Hauser et al. (Chapter 4) to assess spatial changes in preferred habitat over time. We produced monthly maps of relative probability of use, scaled from 0-1 for comparison (DeCesare et al. 2012), for each year 1990-2014. Predictor variables included some combination of sea ice (concentration, distance to the 15% and 90% ice edge) and topographic (depth, slope, proximity to shore, the continental slope, and subsea canyons) variables that explained monthly preferred habitat of each population and sex. The models were found to be highly predictive using cross-validation, other than for Beaufort females in September-October and Beaufort males in October (Chapter 4), so we excluded these fall months for Beaufort belugas. We restricted mapping to the minimum convex polygon for each month (Chapter 4) and estimated spatial probability of use for July-October each year, 1990-2014. We mapped the mean probability of use for each decade (1990-1999, 2000-2009, 2010-2014) in ArcGIS 10.2 (ESRI, Redlands, CA) to visually assess whether the spatial distribution of preferred habitat may have shifted across decades. Last, we identified 'optimal habitat' as grids with ≥75% predicted probability of use, similar to analyses for polar bear optimal habitat (e.g. Durner et al. 2009), and estimated 1990-2014 trends in monthly optimal habitat for males and females of each population using least-squares regression.

### 6.3.6 *Changes in Chukchi beluga diving behavior*

We evaluated shifts in daily diving behavior of the Chukchi population between tagging periods using GEEs. Similar to our approach to assess changes in habitat associations, we included sex, month, and tagging period as potential predictors of each daily diving metric as well as an interaction factor for month x tagging period. We used Wald tests for model selection. We modeled each dive rate response variable with Poisson errors while proportional time at depth and mean dive depth were log-transformed and modeled using the Gaussian distribution. We estimated the probability that maximum dive depth coincided with the seafloor using the Binomial distribution.

## 6.4 RESULTS

Our data set consisted of 65 belugas tagged in the Chukchi and Beaufort populations from 1993-2012 (Table 6-1). Sea ice significantly declined ($p<0.02$) within population-specific home ranges in July-October from 1979-2014 and particularly between the early period and late period in Chukchi beluga home ranges (Figure 6-2).

### 6.4.1 *Changes in sea ice habitat associations*

Month was the only predictor included in all GEEs estimating sea ice use by Chukchi belugas, although sex and tagging period were also included in most models (Table 6-2). Fitting previous assessments of sexual segregation (Loseto et al. 2006, Chapter 4), Chukchi males were significantly more likely to be located in heavier ice than Chukchi females (Table 6-2; Figure 6-3). Significantly heavier ice that was closer to ice edges (15% and 90% concentration) ice was used by Chukchi whales tagged in 1998-2002 (early period) than in 2007-2012 (late period), and whales tagged during the early period were significantly more likely to be located in the ice pack than those tagged in the late period. Differences between tagging periods were greatest in July and August. We found similar sea ice associations for Beaufort belugas, except the habitat used in the late period was not significantly different from that in the early period despite trends for less dense and farther ice edges between periods overall (Table 6-2, Figure 6-3). Sex was a significant predictor for all sea ice habitat response variables for Beaufort belugas, with males more likely to be found in heavier ice than females as expected (Loseto et al. 2006). Month was almost always a significant predictor of the ice habitat used by Beaufort belugas.

### 6.4.2 *Changes in preferred habitat*

Despite changes in the ice habitat used by Chukchi belugas between tagging periods, there were few significant changes in the sea ice habitat (concentration, proximity to 15% or 90% ice edge) selected (relative to available habitat) by whales in the early versus late tagging period (Table 6-3). In August and October, there were only significant differences in the proximity to the ice edge used relative to available by Chukchi females in the early period compared to that in the late period. In both months, the habitat used by Chukchi females was farther from the ice edge (265 km in August and 253 km in October) than the habitat that was available (247 km and 234 km, respectively). There were also no significant differences in selection of ice habitat by Beaufort belugas between the early tagging period and late tagging period (Table 6-3).

There were also few cases where the spatial distribution of preferred habitat changed during 1990-2014 (Figure 6-4). The most striking changes in preferred habitat maps occurred in October for Chukchi males and females suggesting a prolonged persistence along the continental slope or near Barrow Canyon in the Beaufort Sea in the 2000s compared to selection of the Chukchi Sea in the 1990s. For Beaufort males, the probability of use increased in more recent years during September and especially across Canada Basin near the approximate 15% sea ice edge. Preferred habitat predictions for Beaufort females indicated a shift to the east in the Amundsen Gulf and northwest along Banks Island in July as sea ice declined during 1990-2014. Similar to other indicators of changing sea ice habitat selection, there was only a single significant change in the amount of optimal habitat for belugas 1990-2014 (Table 6-4, Figure 6-5). The amount of optimal habitat for Chukchi females in August significantly declined ~103 $km^2$/year ($F=15.07_{1,23}$, $p<0.001$). The majority (69%) of the 13 monthly trends were negative, although not significant.

### 6.4.3 *Changes in behavior*

In general, a suite of diving metrics consistently indicated that Chukchi belugas tagged during 2007-2012 (late period) spent more time at deeper depths than those tagged during 1998-2002 (early period). Less time was spent near the surface in the late period, evidenced by fewer short duration and shallow dives (i.e. dives/day <10 m or <1 min, percent of time <10 m) and a lower overall daily dive rate (Table 6-5). Meanwhile, there were more long duration (>20 min) dives that corresponded with deeper mean dive depths, and maximum dive depths were more likely to reach the seafloor in the late period (Table 6-5, Figure 6-6). Month was also a significant factor for nearly all diving metrics, as would be expected due to diving differences among regions used each month (Hauser et al. 2015). Thus, tagging period or an interaction between month and tagging period was a significant predictor of all but one diving metric (i.e. number of dives/d < 10 m). Patterns for deeper, longer dives in the late tagging period were consistent each month, July-October, but the strongest contrasts were in July and October (Figure 6-6). In October, Chukchi belugas tagged in the late period remained in deeper continental slope portions of Alaskan Beaufort Sea while those tagged in the early period had already migrated to the shallower (<75 m) Chukchi Sea (Chapter 5). Chukchi belugas most frequently target pelagic depths in the Alaskan Beaufort Sea compared with benthic diving in the Chukchi Sea (Hauser et al. 2015), which explains why there would be more benthic-oriented and fewer shallow dives in October between tagging periods. Similar to previous analyses (Citta et al. 2013, Hauser et al. 2015), there was limited evidence of sex-based diving differences since sex was only included as a significant predictor of the percent of time <10 m and the probability maximum dive depths reached the seafloor.

## 6.5 DISCUSSION

We present one of the first comprehensive analyses of the indirect effects of changing sea ice regimes on population-specific habitat use and behavior of an Arctic cetacean. Our results supplement a growing assemblage of indicators suggesting the Pacific Arctic ecosystem is in flux with several emergent properties since 2004 (Moore and Stabeno 2015). Coincident with declining ice, conditions may be more advantageous for baleen whales that forage in either benthic or pelagic realms (Moore et al. 2011, George et al. 2015, Grebmeier et al. 2015) as well as sub-Arctic cetaceans (Clarke et al. 2013). However, sea ice platforms have retreated from optimal polar bear foraging habitat (e.g. Rode et al. 2015), but with divergent impacts on feeding and reproductive success in Southern Beaufort and Chukchi Sea populations (Rode et al. 2014). There have also been mixed results of ice loss for ice-obligate seal populations in addition to some seabird and fish species (Crawford et al. 2015, Harwood et al. 2015, Lovvorn et al. 2015).

One of our most striking results was that two Pacific Arctic beluga populations have generally not changed their habitat selection despite long-term and persistent reductions in sea ice cover. Sea ice cover is not the primary determinant of summer-fall beluga habitat selection (Moore 2000, Moore et al. 2000, Chapter 4), and our results confirm that sea ice concentrations do not particularly matter to beluga summer distribution. Instead summer distribution is more likely governed by philopatry and site fidelity. Beaufort belugas, especially females, generally used lighter sea ice than Chukchi belugas, which is why declines in sea ice cover (i.e. between tagging periods) was a significant predictor of habitat used by Chukchi belugas but not for Beaufort belugas. Especially for Chukchi whales, changes in habitat associations between tagging periods are likely a consequence of sea ice retreat from preferred summer habitat rather than a change in distribution. This retreat was most dramatic in July and August for Chukchi belugas when they are particularly philopatric

(O'Corry-Crowe et al. 1997) and home ranges were relatively similar between tagging periods (Chapter 5). While neither population changed ice habitat selection between tagging periods, Chukchi belugas have shifted fall migration later as freeze-up timing has become delayed compared to Beaufort belugas that have not changed fall migration timing (Chapter 5). Our results suggest this is likely related to the weaker association with sea ice for Beaufort belugas, particularly in the fall when they move into the Chukchi Sea (where freeze-up occurs later) ahead of Chukchi belugas.

We also found limited evidence of shifts in optimal habitat or probability of use for either population during 1990-2014, further suggesting that sea ice cover has limited effect on beluga preferred habitat. For Chukchi belugas, we predicted the highest probability of use shifted eastward in October during the 2000s indicating that both males and females would depart the Beaufort Sea later and supporting recent analyses that fall migration out of the Beaufort Sea is positively correlated with Beaufort Sea freeze-up timing (Chapter 5). Migration occurred >1 month later in the 2000s as freeze-up also became delayed. Combining results from both studies implies that the role of advancing sea ice in the fall is to limit access to preferred habitat where Chukchi belugas may be experiencing improved or extended foraging in the 2000s.

The results of our diving behavior analyses additionally indicate that sea ice may indirectly impact foraging opportunities during summer-fall for Chukchi belugas. We did not have adequate data to test changes in diving behavior for Beaufort belugas, but Chukchi belugas spent more time at deeper depths during 2007-2012 (late tagging period) than 1998-2002 (early tagging period). We used a suite of metrics to collectively illustrate this consistent shift across all months (July-October) indicative of either deeper or more extensive and productive foraging opportunities in the late tagging period. As the summer melt season has lengthened (e.g. >15 d in the Beaufort Sea;

Laidre et al. 2015b), increased solar radiation in the upper ocean layers combined with more storms has enhanced upwelling of nutrient-rich AW onto the continental slope and shelves to fuel primary as well as secondary production, including novel fall phytoplankton blooms (Carmack and Chapman 2003, Pickart et al. 2009, Pickart et al. 2013, Ardyna et al. 2014). Wind-forcing also promotes advection of zooplankton that become ‘trapped’ near Barrow Canyon (Ashjian et al. 2010), and both processes enhance water-column secondary production that concentrate pelagic prey such as Arctic cod (Logerwell et al. 2011) targeted by Chukchi belugas in the Alaska Beaufort Sea (Hauser et al. 2015). As a result, diminished ice cover may be improving the extent and concentration of foraging opportunities for belugas, possibly explaining why Chukchi belugas spent more time at depth in the later period. However, wind stress also affects stratification and the creation of hydrographic fronts in the Alaska Beaufort Sea that function to concentrate zooplankton, thereby aggregating pelagic prey, and positively impacting beluga presence; strong northeasterly winds can reverse ACC transport in Barrow Canyon and set up a deeper front to which Chukchi belugas dive (Okkonen et al. 2009, Stafford et al. 2013, Stafford et al. In Review). Summer easterly winds increased from 2002-2011 and decreased ACC transport into the Beaufort Sea (Brugler et al. 2014), presumably deepening fronts and favoring deeper dives for Chukchi belugas. Thus we hypothesize that changing oceanographic properties, related to reduced ice cover, either create more foraging opportunities, a deeper prey base, or a combination of the two that have contributed to deeper and longer summer-fall dives in recent years for Chukchi belugas. The implications of deeper, prolonged diving in recent years for the Chukchi population are unclear. On one hand, changes in diving behavior could result from improved foraging opportunities that can translate to healthier body condition. Our results and others suggest Chukchi belugas are staying in the Beaufort Sea longer into the fall where foraging is presumably enhanced by increased productivity (Chapter 5). Improvements in feeding efficiency are implicated in the population recovery of Pacific Arctic bowhead whales (*Balaena mysticetus*) (Givens et al. 2013). Significant increases in bowhead body condition during 1989-2011 are correlated with reduced summer sea ice, apparently as greater primary productivity and wind stress favored water-column zooplankton prey (George et al. 2015). Belugas feed at higher trophic levels than bowheads, yet may be experiencing similarly improved feeding. Alternatively, increased diving effort is energetically costly for individuals and may negatively impact vital rates. Several intrinsic (e.g. age, sex, reproductive status) and environmental factors affect energy expenditure, in addition to diving depth and duration or prey availability (e.g. Costa 2002, Noren 2011, Goundie et al. 2015), so understanding the impacts of deeper, longer dives is complicated and warrants additional research.

Our results also underscore the importance of examining population-specific responses to climate change by highlighting differences in the sea ice habitat used by Chukchi and Beaufort belugas. Many of the same regions are used by the two populations during summer-fall but at different times (Hauser et al. 2014), which impacted the ice habitat they encountered (present study) and their access to foraging habitat (Chapter 5). Understanding variability among populations of Arctic marine mammals is particularly relevant to managing populations experiencing variable effects of climate change at regional scales (Laidre et al. 2015b), especially since predictive sea ice models function at coarse spatial and temporal scales (Overland and Wang 2013). There is an emerging pattern of distinct responses to climate forcing among subpopulations (Moritz and Agudo 2013, Post et al. 2013), which complicates predictions of how belugas may fare in a changing Arctic. Although recent evidence suggests decreasing growth rates and body condition (Harwood et al. 2015), Beaufort belugas seem to be maintaining a stable or growing population (Harwood and

Kingsley 2013). Similar analyses are not available for Chukchi belugas, but additional effort for long-term monitoring of belugas in concert with biophysical indicators of Pacific Arctic ecosystem trends will continue to elucidate population-scale implications of observed and projected sea ice declines.

## 6.6 ACKNOWLEDGEMENTS

We are grateful for the long-term collaboration many in the communities of Point Lay, AK and the Inuvialuit Settlement Region, NWT who have supported our field efforts since the 1990s. L. Lowry, K. Frost, G. O’Corry-Crowe, D. Pikok, R. Small, T. Romano, J. Tazruk, B. and M. Tracey, J. Rexford, J. Orr, A. Ashby, V. Dollarhide, L. Ferreira, L. Pierce, L. Stalker, H. Smith, R. Hobbs, R. Hoover, T. Nukapigak, M. Sparck, S. Speckman, D. Susook, C. Aniskette, J. Tuckfield, C. Rea, G. Marshall, N. Hank, L. Hansen, L. Hoberecht, L. Quakenbush, T. Robeck, A. Simon, G. and K. VanBlaricom, J. Taylor, J. Edwards, D. Ramey, B. Achootchook, and J. Citta facilitated tagging and data access for Chukchi belugas. Tagging was supported by the Alaska Beluga Whale Committee, North Slope Borough of Alaska, National Marine Fisheries Service (NMFS), Alaska Department of Fish and Game, National Fish and Wildlife Foundation, Minerals Management Service, and Village of Point Lay. The Inuvialuit Hunter and Trapper Corporations of Inuvik, Aklavik, and Tuktoyaktuk and the Polar Continental Shelf Project supported Beaufort beluga tagging, and we thank J. Orr, A. Martin, and B. Leblanc for field assistance and data processing. Funding was provided by the Fisheries and Oceans Canada (DFO), Fisheries Joint Management Committee, Environmental Studies Revolving Fund, Minerals Management Service, and NMFS. Analyses were supported by a NASA Climate Indicators Program Grant (NNX13AN28G) and fellowships (to DH) from the University of Washington’s (UW) Integrative Graduate Education and Research Traineeship Program on Ocean Change (National Science Foundation) and UW

School of Aquatic & Fishery Sciences. We thank D. Schindler, R. Hobbs, and S. Moore for helpful review and discussion and R. McGovern for assistance compiling spatial layers of sea ice data. Permits necessary for capture and tagging of belugas were approved by NMFS (nos. 14610, 782-1438, and 782-1719) and DFO.

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Table 6-1. Chukchi and Beaufort beluga whales (n = 38 and n=27, respectively) satellite-tagged from 1993-2002 (‘early period’) and 2004-2012 (‘late period’) in the Pacific Arctic. Longevity is to the number of days from capture until the last location ($\bar{x}_{\text{Beaufort}}$ = 81.9 d, $\bar{x}_{\text{Chukchi}}$ = 105.0 d).

| **Population** | **Tagging period** | **Year** | **Tag ID** | **Sex** | **Capture date** | **Date of last transmission** | **Longevity (d)** |
|---|---|---|---|---|---|---|---|
| *Beaufort* | *Early* | 1993 | 1993-17002 | M | 7/19/1993 | 8/22/1993 | 34 |
| | | | 1993-17005 | M | 7/10/1993 | 10/9/1993 | 91 |
| | | | 1993-17006 | M | 7/10/1993 | 7/21/1993 | 11 |
| | | | 1993-17009 | F | 7/11/1993 | 8/7/1993 | 27 |
| | | 1995 | 1995-17001 | M | 7/3/1995 | 9/26/1995 | 85 |
| | | | 1995-17002 | M | 7/6/1995 | 8/22/1995 | 47 |
| | | | 1995-17003 | M | 7/5/1995 | 7/28/1995 | 23 |
| | | | 1995-17004 | M | 7/5/1995 | 8/7/1995 | 33 |
| | | | 1995-17005 | M | 7/4/1995 | 8/16/1995 | 43 |
| | | | 1995-17007 | F | 7/16/1995 | 9/22/1995 | 68 |
| | | | 1995-17008 | F | 7/18/1995 | 7/25/1995 | 7 |
| | | | 1995-17010 | M | 7/8/1995 | 8/7/1995 | 30 |
| | | | 1995-17011 | M | 7/9/1995 | 8/8/1995 | 30 |
| | | | 1995-17012 | M | 7/9/1995 | 8/8/1995 | 30 |
| | | | 1995-17013 | M | 7/11/1995 | 8/10/1995 | 30 |
| | | | 1995-17014 | F | 7/12/1995 | 8/11/1995 | 30 |
| | | | 1995-5800 | M | 7/15/1995 | 8/14/1995 | 30 |
| | | | 1995-5801 | M | 7/11/1995 | 8/10/1995 | 30 |
| | | | 1995-8754 | F | 7/12/1995 | 8/10/1995 | 29 |
| | | 1997 | 1997-10692 | F | 8/1/1997 | 10/5/1997 | 65 |
| | | | 1997-10693 | M | 7/31/1997 | 10/12/1997 | 73 |
| | | | 1997-2118 | F | 7/27/1997 | 12/2/1997 | 128 |
| | | | 1997-25846 | M | 7/30/1997 | 10/22/1997 | 84 |
| | | | 1997-8754 | M | 7/30/1997 | 10/28/1997 | 90 |
| | | | 1997-8755 | M | 7/29/1997 | 10/18/1997 | 81 |
| | | | 1997-8756 | F | 8/2/1997 | 9/26/1997 | 55 |
| | | | 1997-8757 | M | 7/30/1997 | 10/5/1997 | 67 |
| | | | 1997-8758 | M | 7/31/1997 | 11/28/1997 | 120 |
| | *Late* | 2004 | 2004-10899 | M | 7/5/2004 | 5/2/2005 | 301 |
| | | | 2004-10927 | M | 7/8/2004 | 7/25/2004 | 17 |
| | | | 2004-10971 | F | 7/9/2004 | 7/24/2004 | 15 |
| | | | 2004-10972 | F | 7/6/2004 | 10/14/2004 | 100 |
| | | | 2004-36641 | F | 7/24/2004 | 1/12/2005 | 172 |
| | | | 2004-37023 | M | 7/27/2004 | 4/22/2005 | 269 |
| | | | 2004-37024 | M | 7/10/2004 | 4/23/2005 | 287 |
| | | | 2004-40152 | M | 7/6/2004 | 8/12/2004 | 37 |
| | | 2005 | 2005-57591 | F | 7/8/2005 | 4/17/2006 | 283 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  |  | 2005-57593 | F | 7/11/2005 | 12/17/2005 | 159 |
| *Chukchi* | *Early* | 1998 | B98-1 | M | 6/27/1998 | 7/8/1998 | 11 |
|  |  |  | B98-2 | M | 6/29/1998 | 7/12/1998 | 13 |
|  |  |  | B98-3 | M | 6/30/1998 | 10/7/1998 | 99 |
|  |  |  | B98-4 | M | 7/1/1998 | 9/29/1998 | 90 |
|  |  |  | B98-5 | M | 7/2/1998 | 8/30/1998 | 59 |
|  |  | 1999 | B99-1 | M | 7/1/1999 | 9/25/1999 | 86 |
|  |  |  | B99-2 | F | 7/1/1999 | 9/12/1999 | 73 |
|  |  |  | B99-3 | M | 7/1/1999 | 8/26/1999 | 56 |
|  |  |  | B99-4 | M | 7/1/1999 | 9/23/1999 | 84 |
|  |  | 2001 | B01-1 | M | 7/5/2001 | 8/10/2001 | 36 |
|  |  |  | B01-2 | F | 7/4/2001 | 7/22/2001 | 18 |
|  |  |  | B01-3 | F | 7/6/2001 | 11/29/2001 | 146 |
|  |  |  | B01-4 | M | 7/6/2001 | 12/6/2001 | 153 |
|  |  |  | B01-5 | F | 7/7/2001 | 10/23/2001 | 108 |
|  |  |  | B01-6 | M | 7/8/2001 | 11/17/2001 | 132 |
|  |  |  | B01-7 | M | 7/8/2001 | 7/24/2001 | 16 |
|  |  |  | B01-8 | M | 7/8/2001 | 8/13/2001 | 36 |
|  |  | 2002 | B02-1 | F | 7/8/2002 | 9/14/2002 | 68 |
|  |  |  | B02-2 | M | 7/8/2002 | 9/28/2002 | 82 |
|  |  |  | B02-3 | M | 7/10/2002 | 8/25/2002 | 46[a] |
|  |  |  | B02-4 | M | 7/9/2002 | 9/11/2002 | 64 |
|  | *Late* | 2007 | B07-1 | M | 7/2/2007 | 12/4/2008 | 521 |
|  |  |  | B07-2 | F | 7/2/2007 | 11/13/2007 | 134 |
|  |  |  | B07-3 | F | 7/3/2007 | 11/6/2007 | 126 |
|  |  | 2010 | B10-1 | M | 6/25/2010 | 12/6/2010 | 164 |
|  |  |  | B10-2 | M | 6/30/2010 | 10/9/2010 | 101 |
|  |  | 2012 | B12-1 | F | 7/2/2012 | 5/11/2013 | 313 |

[a] All Chukchi whales, other than B02-3, were used in the analysis of changes in Chukchi beluga diving behavior between the early and late tagging periods.

Table 6-2. Summary statistics and factors affecting sea ice habitat used by Chukchi and Beaufort populations of beluga whales, revealed using generalized estimating equations. Bolded p-values indicate factors are significant at p<0.05. Blank factors were not included in final model selection. Mean (±SE) habitat used by belugas tagged in the early (1993-2002) and late (2004-2012) tagging periods are indicated in italics for each variable.

| | **Chukchi belugas**<br>***Mean ± SE habitat***<br>***early, late*** | | | **Beaufort belugas**<br>***Mean ± SE habitat***<br>***early, late*** | | |
|---|---|---|---|---|---|---|
| | **df** | $\chi^2$ | ***p*** | **df** | $\chi^2$ | ***p*** |
| ***Probability of being located in sea ice (>15%)*** | | ***0.58, 0.27***[a] | | | ***0.58, 0.28***[a] | |
| Month | 3 | 7.62 | 0.054 | | | |
| Sex | 1 | 6.59 | **0.014** | 1 | 6.68 | **0.010** |
| Tagging period | 1 | 17.36 | **<0.001** | | | |
| | | | | | | |
| ***Sea ice concentration (%)*** | | ***29.9±0.9, 12.2±0.7*** | | | ***23.4±0.9, 20.7± 1.3*** | |
| Month | 3 | 9.39 | **0.025** | 4 | 9.84 | **0.043** |
| Sex | 1 | 14.66 | **<0.001** | 1 | 5.55 | **0.019** |
| Tagging period | 1 | 27.87 | **<0.001** | | | |
| | | | | | | |
| ***Proximity to 15% ice edge (km)*** | | ***154.6±4.4, 190.1±6.2*** | | | ***174.9±3.6, 253.3±7.7*** | |
| Month | 3 | 59.3 | **<0.001** | 3 | 40.2 | **<0.001** |
| Sex | | | | 1 | 12.6 | **<0.001** |
| | | | | | | |
| ***Proximity to 90% ice edge (km)*** | | ***528.3±8.8, 836.8±18.8*** | | | ***490.3±7.9, 484.7±11.1*** | |
| Month | 3 | 12.8 | **0.005** | 3 | 11.22 | **0.011** |
| Sex | 1 | 2.6 | 0.108 | 1 | 6.04 | **0.014** |
| Tagging period | 1 | 57.6 | **<0.001** | | | |

[a] Measure of the proportion of locations in ice during the early, late tagging periods

Table 6-3. P-values associated with changes in monthly selection of sea ice habitat variables (sea ice concentration, distance to the 15% ice edge, and distance to the 90% ice edge) in the early tagging period compared to the late tagging period for female and male Chukchi and Beaufort beluga whales. Significant changes ($p<0.05$) in habitat selection are bolded.

| | | **Conc** | **Dist 15%** | **Dist 90%** |
|---|---|---|---|---|
| **Chukchi** | | | | |
| Female | | | | |
| | July | 0.96 | 0.05 | 0.38 |
| | Aug | 0.15 | **0.01** | 0.83 |
| | Sep | 0.54 | 0.56 | 0.37 |
| | Oct | 0.23 | **0.005** | 0.96 |
| Male | | | | |
| | July | 0.13 | 0.79 | 0.54 |
| | Aug | 0.81 | 0.18 | 0.94 |
| | Sep | 0.16 | 0.21 | 0.29 |
| | Oct | 0.31 | 0.72 | 0.53 |
| **Beaufort** | | | | |
| Female | | | | |
| | July | 0.36 | 0.26 | 0.47 |
| | Aug | 0.51 | 0.48 | 0.60 |
| | Sep | 0.05 | 0.93 | 0.42 |
| | Oct | 0.05 | 0.78 | 0.93 |
| Male | | | | |
| | July | 0.49 | 0.19 | 0.34 |
| | Aug | 0.39 | 0.23 | 0.64 |
| | Sep | 0.52 | 0.09 | 0.86 |
| | Oct | 0.93 | 0.69 | 0.93 |

Table 6-4. Trends in the amount of predicted optimal habitat for Chukchi and Beaufort beluga whales in July to October, 1990-2014. One outlier for Beaufort males in September 2014 (59,375 km$^2$) was excluded from the analysis, and months with poor predictive capacity for Beaufort belugas are excluded (Chapter 4).

| **Month** | **Chukchi male (km$^2$/y)** | **Chukchi female (km$^2$/y)** | **Beaufort male (km$^2$/y)** | **Beaufort female (km$^2$/y)** |
|---|---|---|---|---|
| July | -102.9[a] | +17.8[a] | -19.7[a] | -197.1[a] |
| August | +16.3[a] | -103.4[c] | -25.5[a] | -305.8[a] |
| September | +34.1[a] | -240.9[a] | +10.9[a] | |
| October | -242.3[b] | -138.9[a] | | |

[a] $p > 0.05$ in a 2-sided F test

[b] $p = 0.05$ in a 2-sided F test

[c] $p < 0.001$ in a 2-sided F test

Table 6-5. Summary statistics and factors affecting a suite of daily diving metrics for Chukchi beluga whales based on generalized estimating equations (GEEs). Bolded p-values indicate factors are significant at p<0.05. Blank factors were not included in final model selection.

| | **Mean (SE)** | **GEE inference** | | |
|---|---|---|---|---|
| | **Early, Late** | **df** | **$\chi^2$** | ***p*** |
| ***Daily dive rate (dives/d)*** | 12.8 (0.2), 10.6 (0.2) | | | |
| Month | | 3 | 1.0 | 0.802 |
| Tagging period | | 1 | 3.8 | 0.050 |
| Tagging period:Month | | 3 | 15.0 | **0.002** |
| | | | | |
| ***Dives/d <10 m*** | 8.3 (0.2), 6.5 (0.2) | | | |
| Month | | 3 | 26.2 | **<0.001** |
| | | | | |
| ***Dives/d <1 min*** | 6.3 (0.2), 3.9 (0.2) | | | |
| Month | | 3 | 15.8 | **0.001** |
| Tagging period | | 1 | 5.6 | **0.018** |
| | | | | |
| ***Dives/d >20 min*** | 0.9 (0.03), 2.8 (0.07) | | | |
| Tagging period | | 1 | 75.9 | **<0.001** |
| | | | | |
| ***Percent of time <10 m*** | 56.6 (1.0), 49.1 (1.1) | | | |
| Month | | 3 | 10.3 | **0.016** |
| Sex | | 1 | 7.9 | **0.005** |
| Tagging period | | 1 | 9.7 | **0.002** |
| Tagging period:Month | | 3 | 10.0 | **0.018** |
| | | | | |
| ***Daily dive depth (m)*** | 49.3 (1.7), 64.0 (1.9) | | | |
| Month | | 3 | 153.0 | **<0.001** |
| Tagging period | | 1 | 30.1 | **<0.001** |
| Tagging period:Month | | 3 | 80.4 | **<0.001** |
| | | | | |
| ***Probability maximum dive depth reaches the seafloor*** | 0.455, 0.495[a] | | | |
| Month | | 3 | 27.3 | **<0.001** |
| Sex | | 1 | 10.3 | **0.001** |
| Tagging period | | 1 | 0.4 | 0.532 |
| Tagging period:Month | | 3 | 16.9 | **<0.001** |

[a] Measure of the proportion reaching the seafloor in the early, late tagging periods

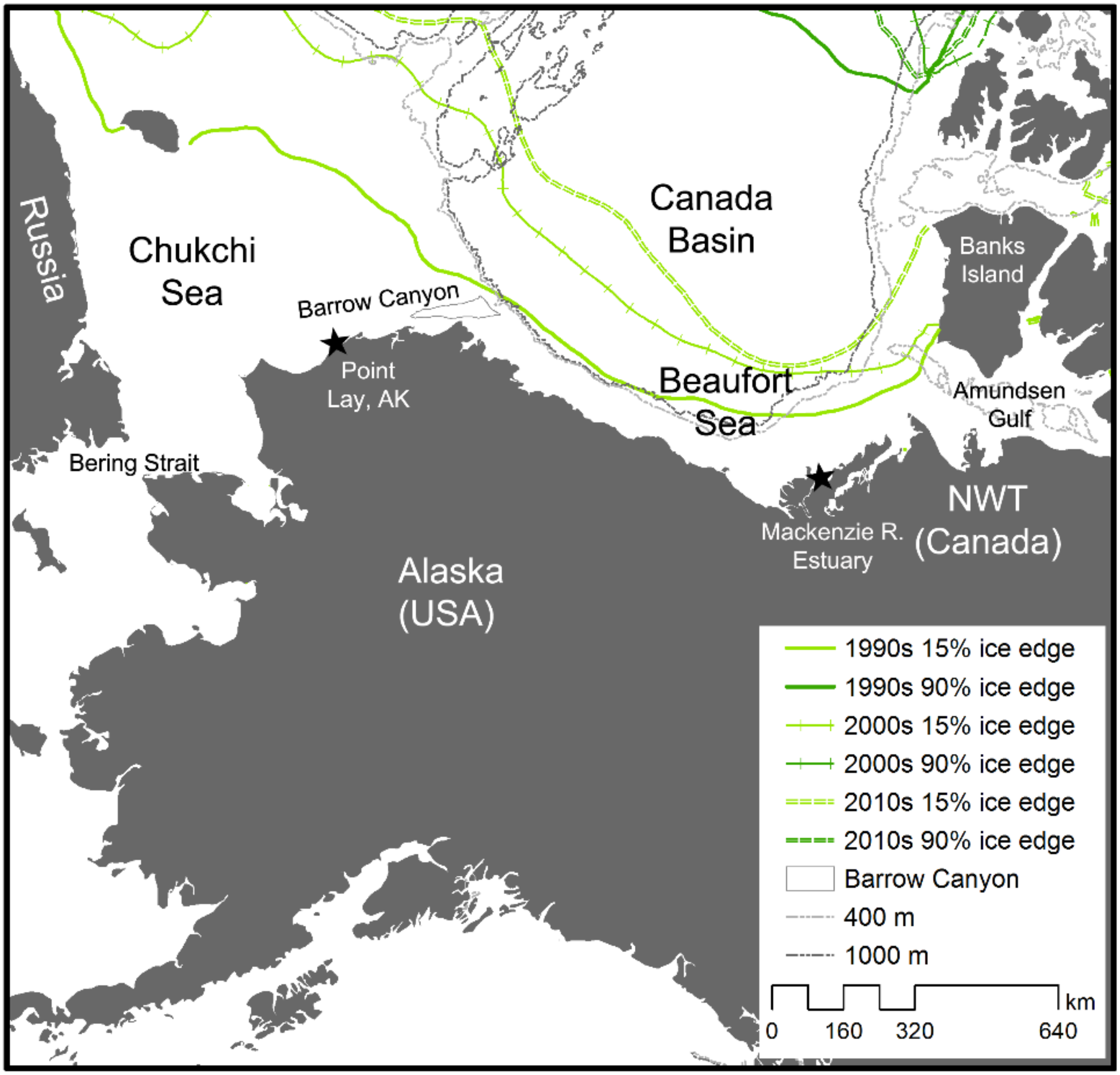

Figure 6-1. The Pacific Arctic study area, including approximate tagging locations for Chukchi beluga whales (Point Lay, Alaska) and Beaufort belugas (Mackenzie River Estuary, Northwest Territories, Canada), bathymetry, and mean 15% and 90% ice edge locations during September 1990-1999, 2000-2009, and 2010-2014. Sea ice edges were extracted from mean ice concentration grids calculated from the September sea ice concentration in each year (Cavalieri et al. 1996).

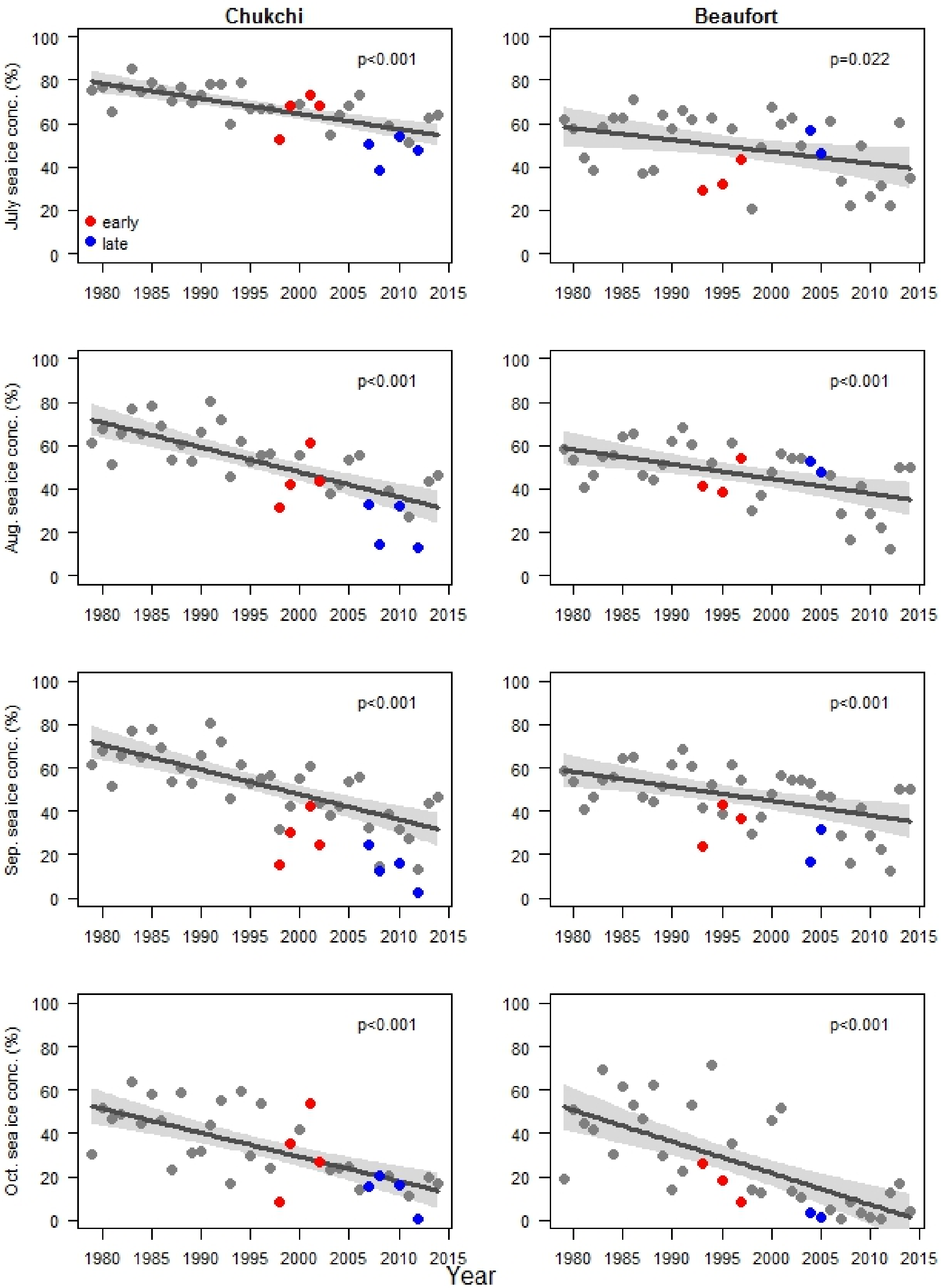

Figure 6-2. Linear trend, 95% confidence interval, and p-value in mean sea ice concentration, 1979-2014, within July-October Chukchi and Beaufort beluga home ranges and between ‘early’ (1993-2002) and ‘late’ (2004-2012) periods when belugas were tagged. Years in which belugas were tagged during the early and late periods are indicated in red and blue, respectively.

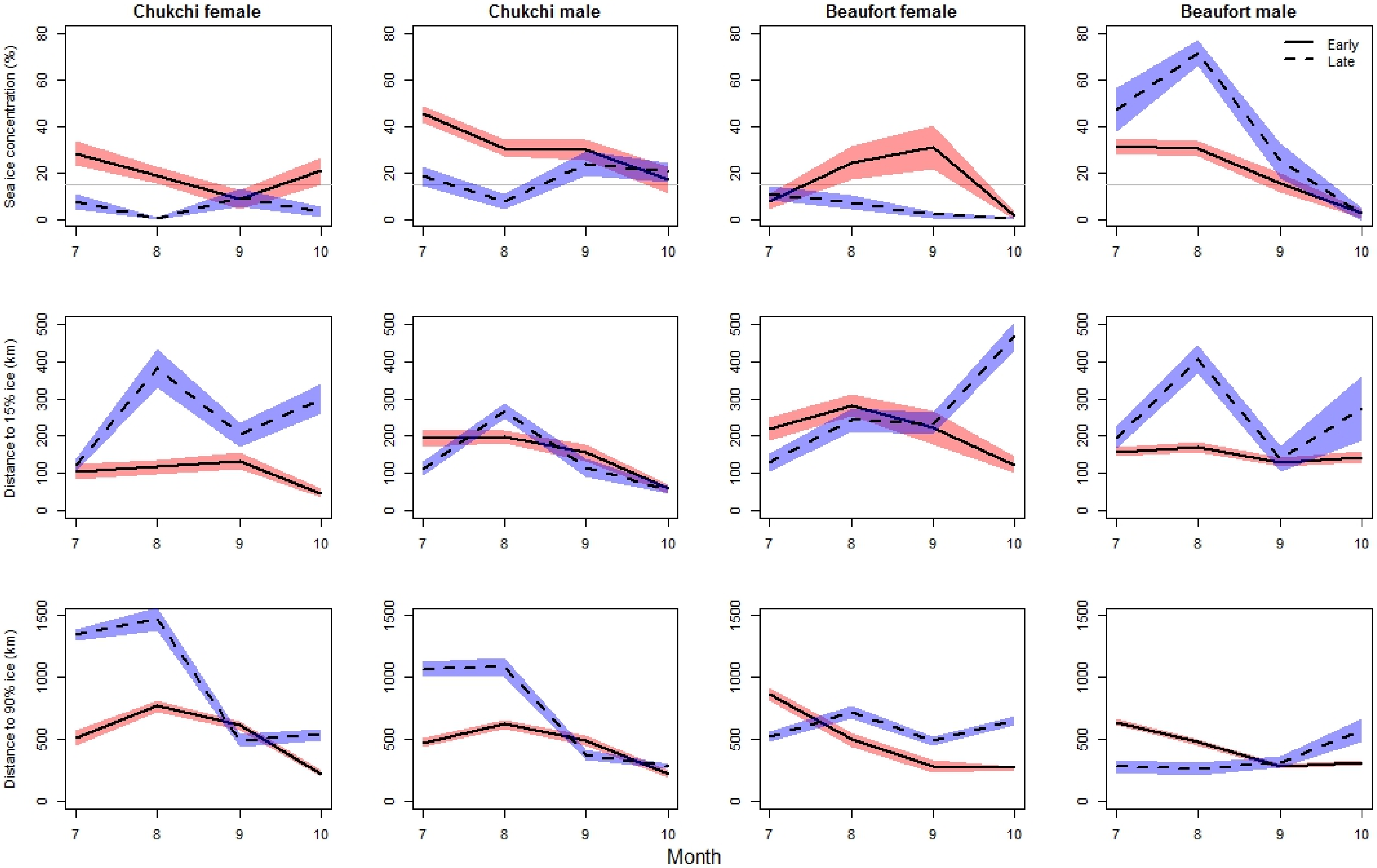

Figure 6-3. Mean (±2 SE) sea ice habitat used by Chukchi and Beaufort beluga whales tagged during 1993-2002 (early period; red, solid line) and 2004-2012 (late period; blue, dashed line). The 15% ice threshold for determining if whales were located in ice (>15%) is indicated by the solid grey line in the top row.

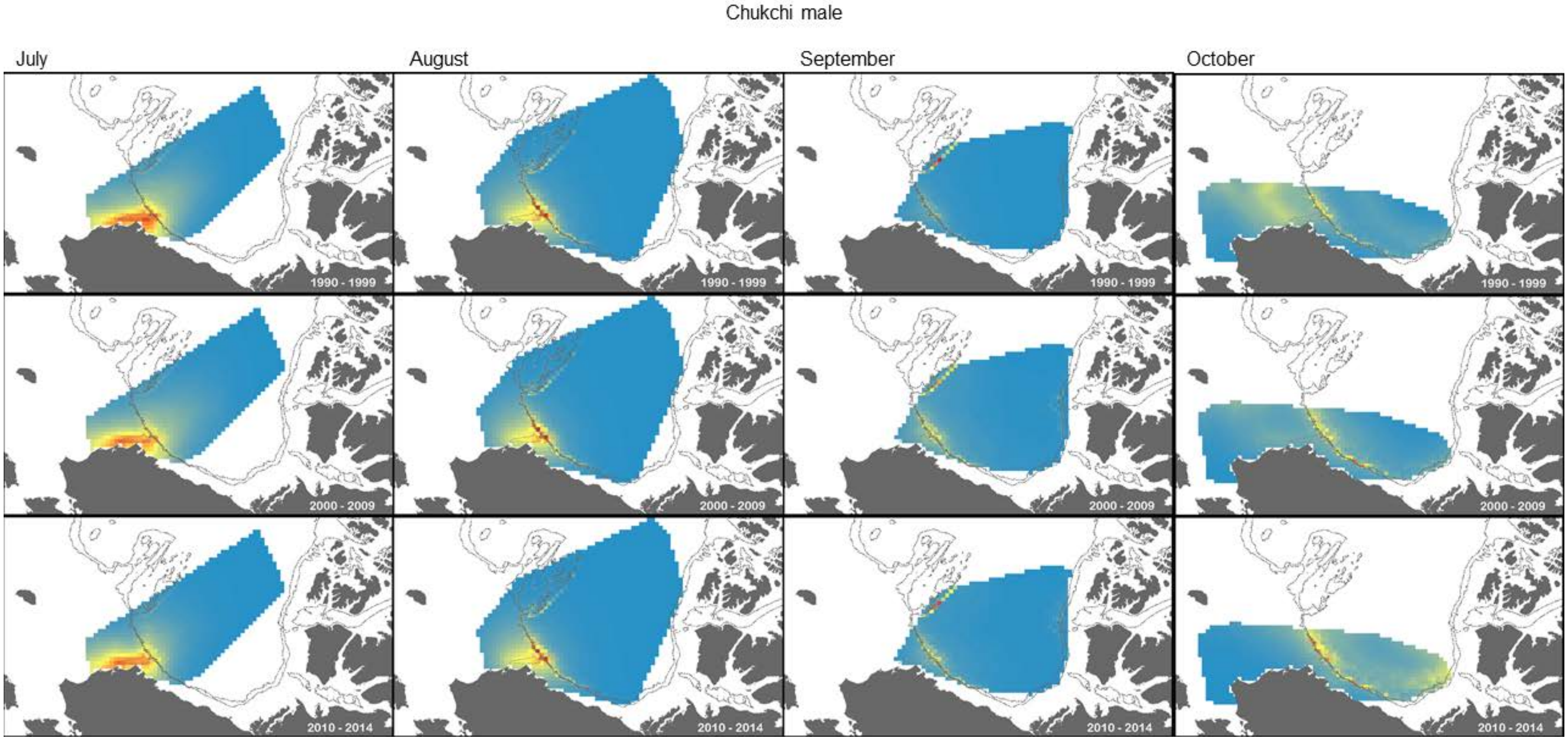

Figure 6-4. Monthly (July-October, left-right) maps of predicted beluga whale use for Chukchi and Beaufort populations, averaged across decades (1990-1999, 2000-2009, and 2010-2014) and based on habitat selection models developed in Chapter 4. For each monthly model, predicted use is restricted to the minimum convex polygon of tagged whales in the month, and months with poor predictive capacity for Beaufort belugas are not included Chapter 4.

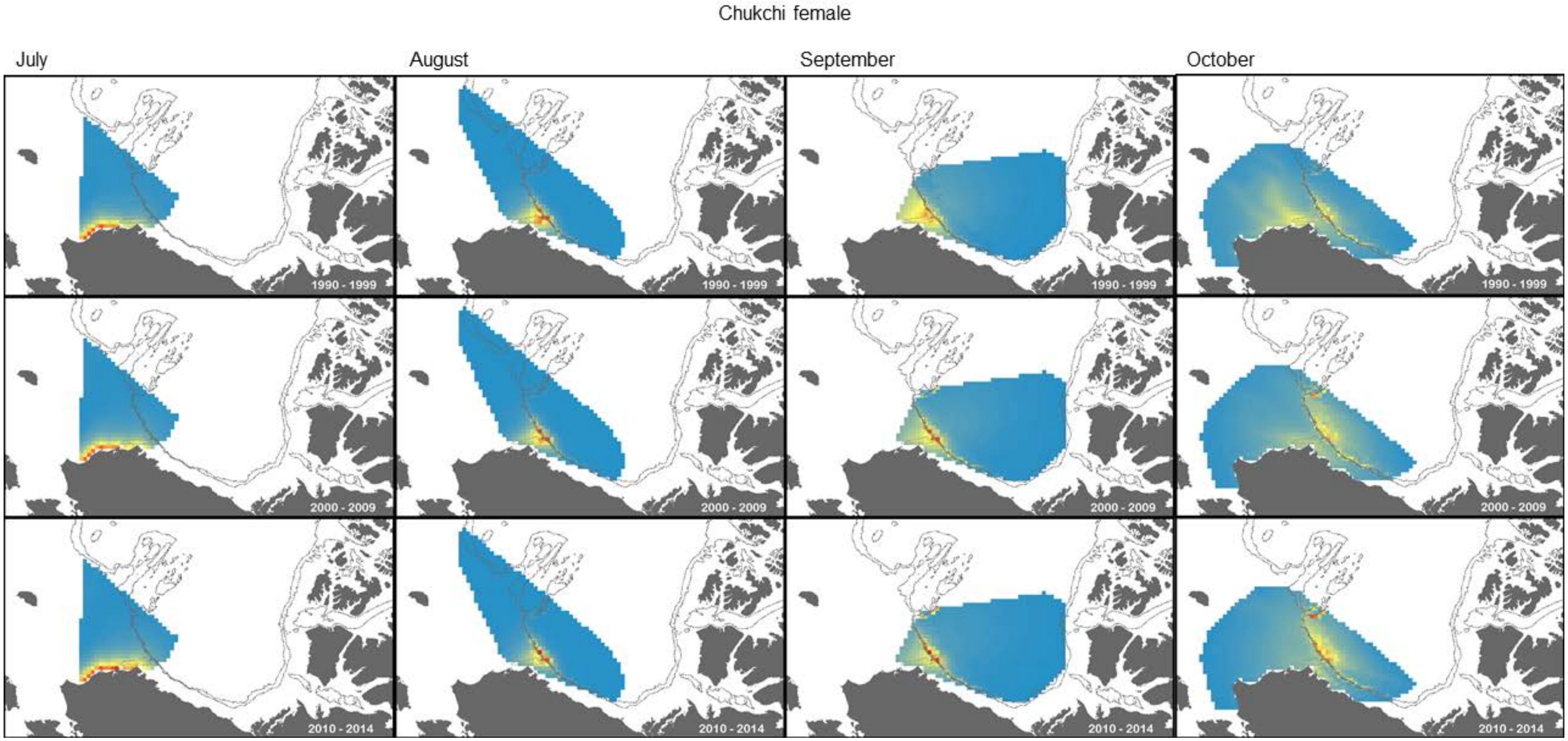

Figure 6-4 (continued). Monthly (July-October, left-right) maps of predicted beluga whale use for Chukchi and Beaufort populations, averaged across decades (1990-1999, 2000-2009, and 2010-2014) and based on habitat selection models developed in Chapter 4. For each monthly model, predicted use is restricted to the minimum convex polygon of tagged whales in the month, and months with poor predictive capacity for Beaufort belugas are not included Chapter 4.

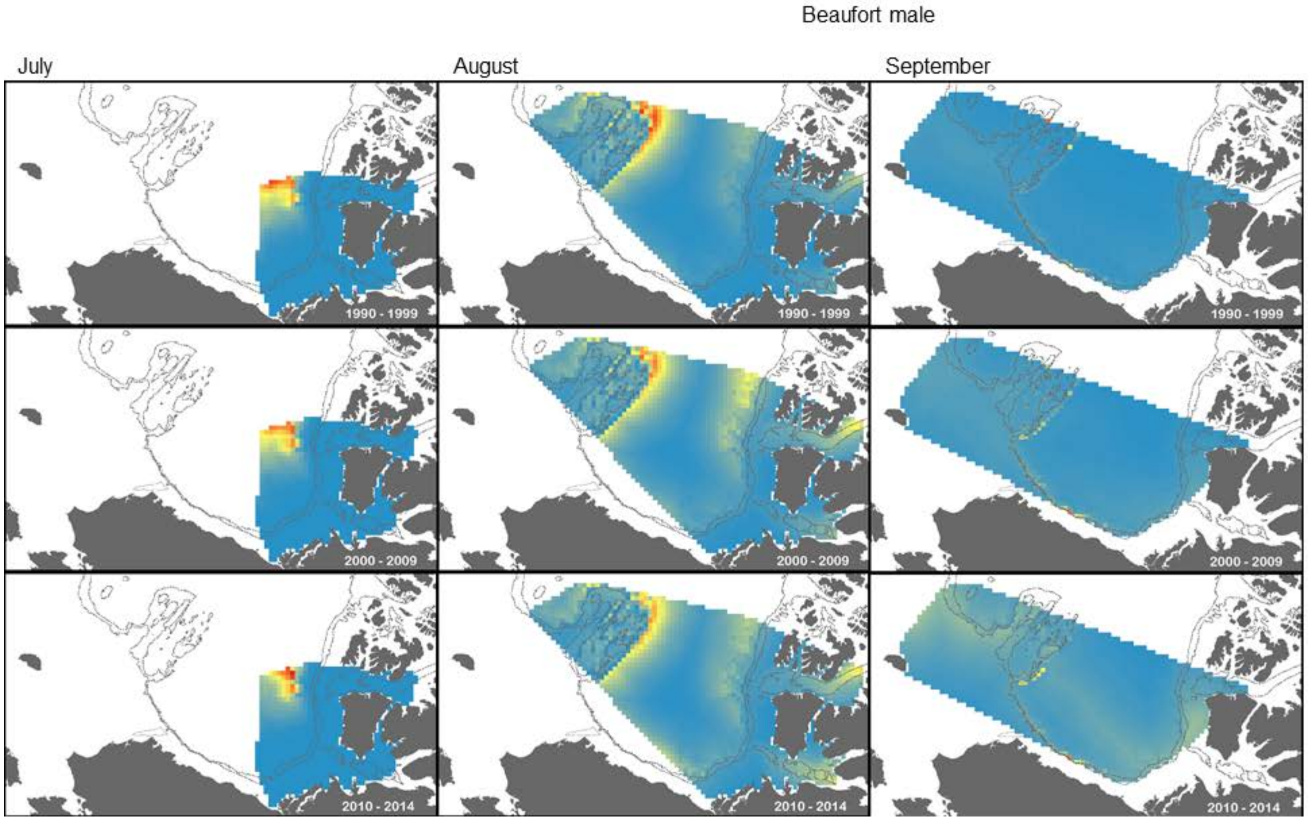

Figure 6-4 (continued). Monthly (July-October, left-right) maps of predicted beluga whale use for Chukchi and Beaufort populations, averaged across decades (1990-1999, 2000-2009, and 2010-2014) and based on habitat selection models developed in Chapter 4. For each monthly model, predicted use is restricted to the minimum convex polygon of tagged whales in the month, and months with poor predictive capacity for Beaufort belugas are not included Chapter 4.

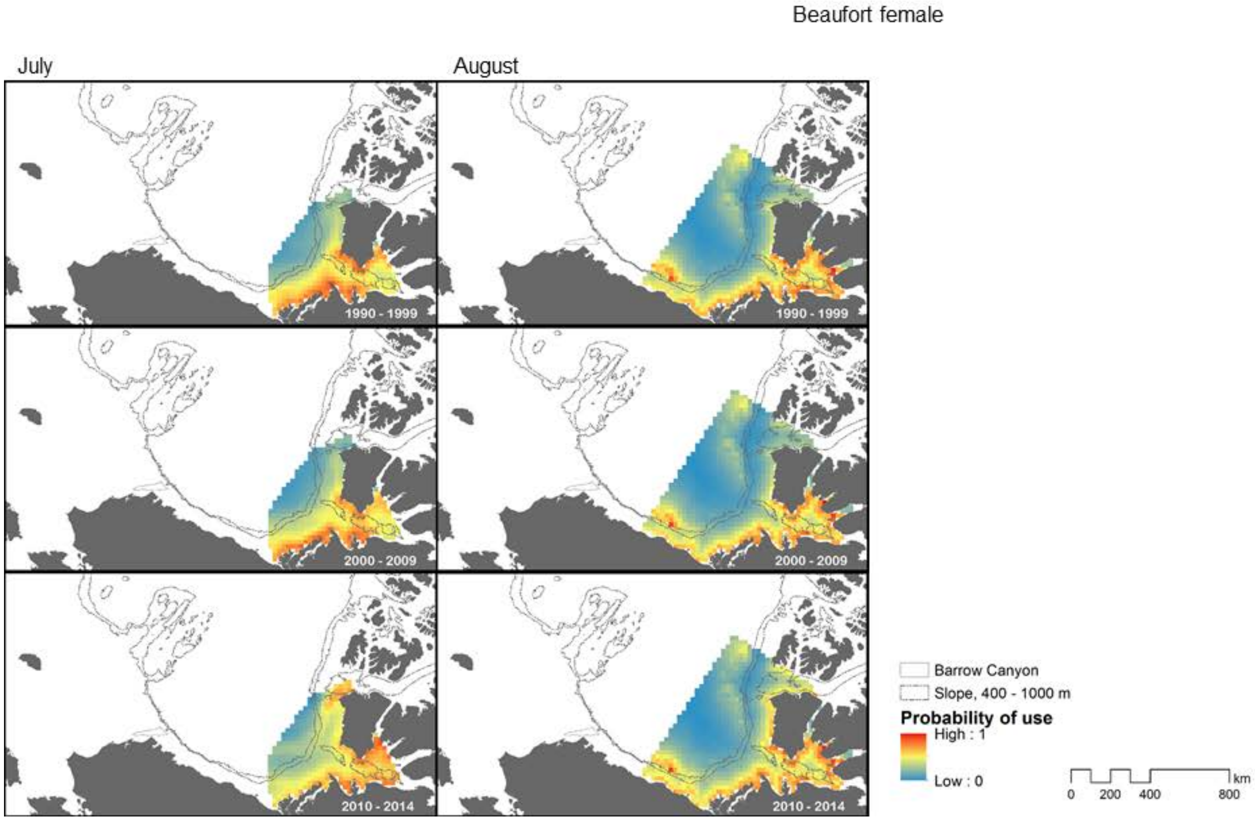

Figure 6-4 (concluded). Monthly (July-October, left-right) maps of predicted beluga whale use for Chukchi and Beaufort populations, averaged across decades (1990-1999, 2000-2009, and 2010-2014) and based on habitat selection models developed in Chapter 4. For each monthly model, predicted use is restricted to the minimum convex polygon of tagged whales in the month, and months with poor predictive capacity for Beaufort belugas are not included (Chapter 4).

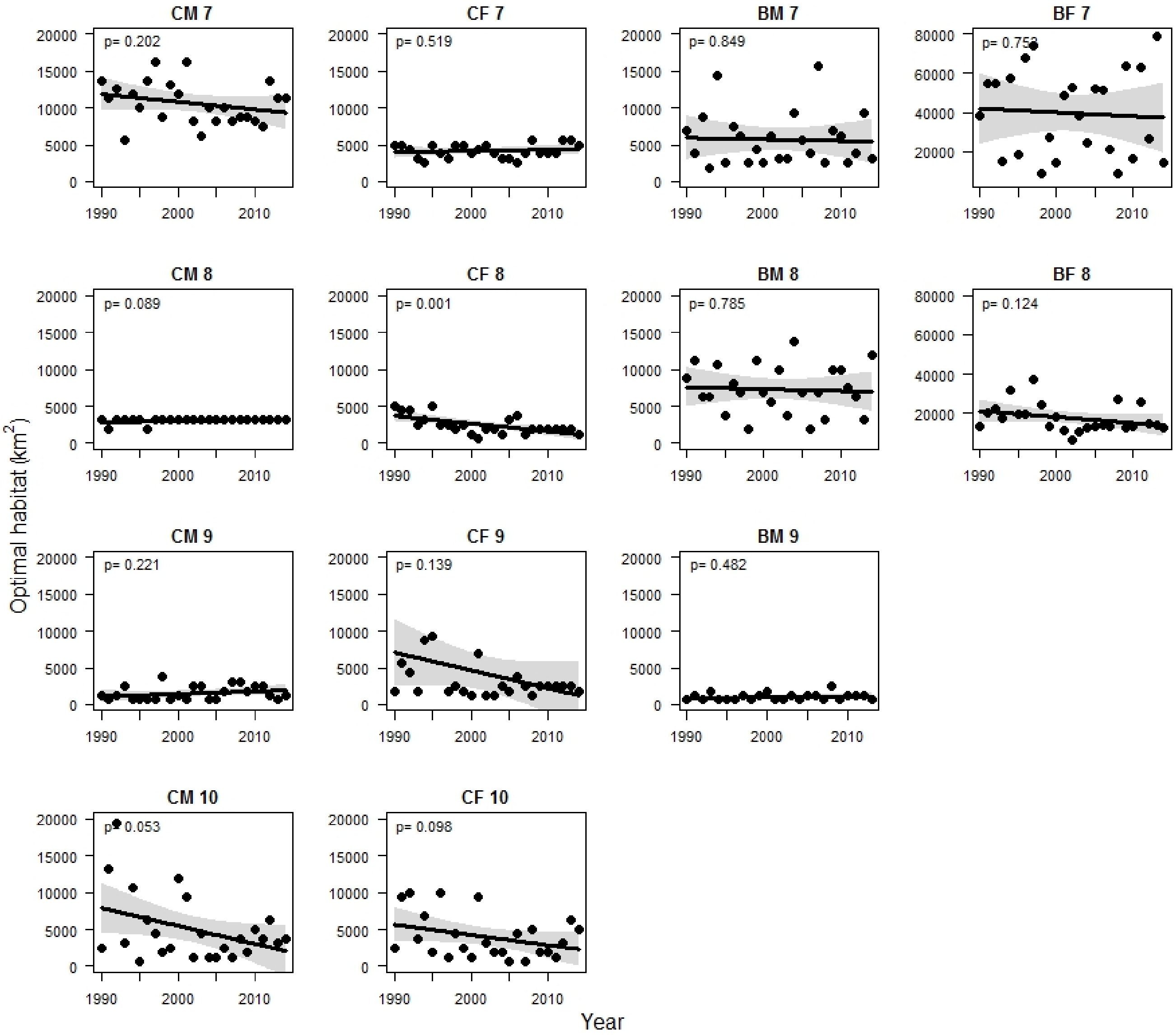

Figure 6-5. Trends (including 95% confidence interval and p-value) in optimal habitat for Chukchi and Beaufort beluga whales in July to October (7-10), 1990-2014 (CM = Chukchi male, CF = Chukchi female, BM = Beaufort male, BF = Beaufort female). Note different y-axis for Beaufort females. One outlier for Beaufort males in September 2014 (59,375 $km^2$) was excluded from the analysis. Months with poor predictive capacity for Beaufort belugas are not included (see Chapter 4).

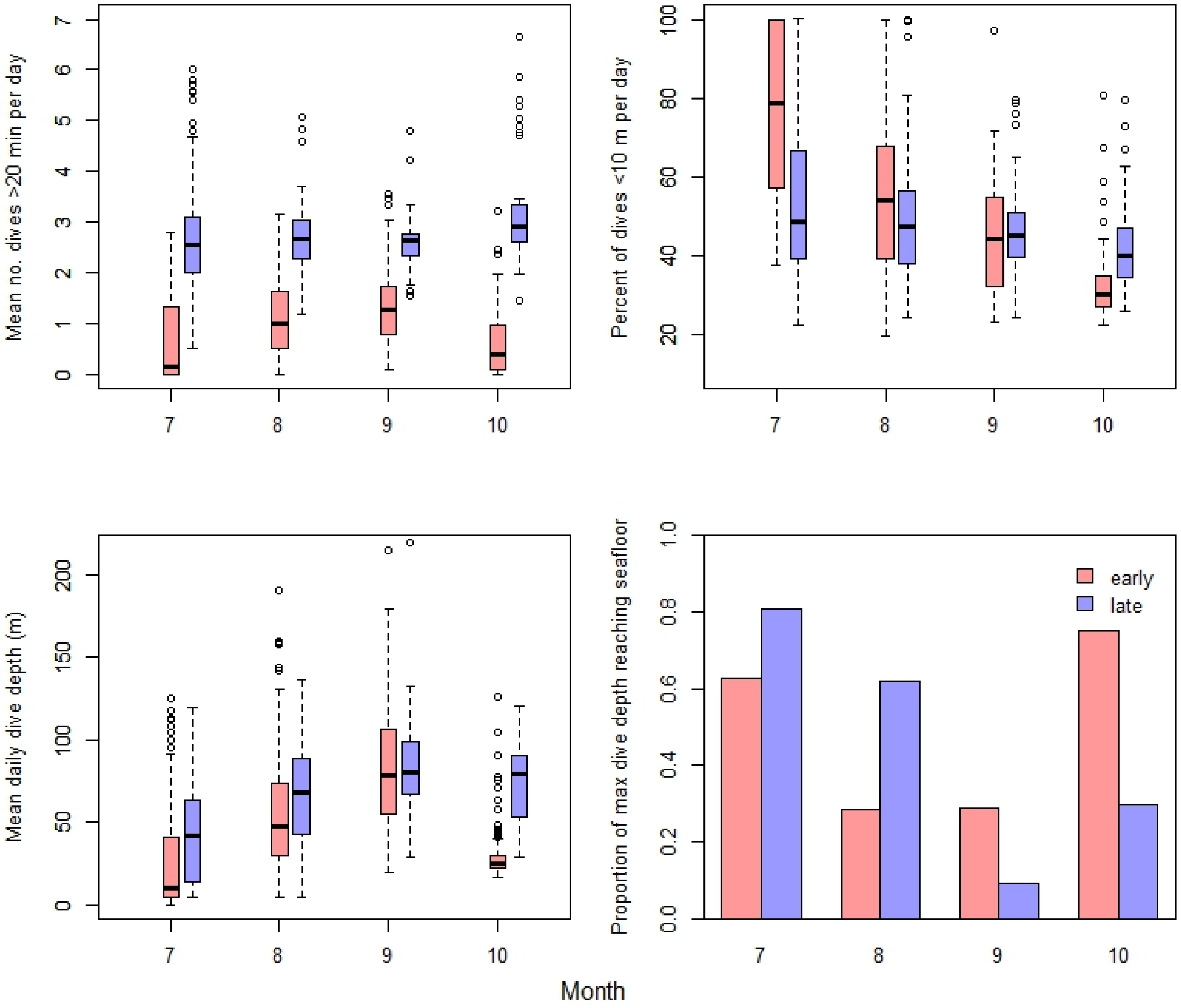

Figure 6-6. Monthly differences in mean number of long-duration dives, percent of time in shallow depths, daily dive depth, and proportion of maximum daily dive depth measures that reached the seafloor between the early tagging period (1998-2002) and late tagging period (2007-2012) for Chukchi beluga whales.

# Chapter 7. SYNTHESIS AND CONCLUSIONS

Sea ice loss is pervasive and occurring at unprecedented rates in the Pacific Arctic, with several direct impacts to ice-dependent pinnipeds and polar bears (e.g. Regehr et al. 2010, Rode et al. 2010, Udevitz et al. 2013). Less clear, however, has been the indirect impacts to cetaceans that depend on sea ice to structure seasonal access and foraging opportunities (Moore and Huntington 2008, Kovacs et al. 2011). In this dissertation, I have taken a population-level approach to explore how and to what extent Pacific Arctic beluga whale distribution, movements, and behavior are influenced by environmental factors, including changing sea ice conditions.

## 7.1 BENCHMARKS IN DISTRIBUTION, MIGRATION, AND BEHAVIOR

Belugas have encountered a highly seasonal and ephemeral sea ice environment since at least the Late Miocene (Harington 2008, Murray 2008), and the fidelity to distinct summer areas, sexual segregation, and migration timing quantified in Chapter 2 appear to be shaped by seasonal fluctuations in summer to fall conditions. Belugas also mediate their behavior to respond to patchy prey, as illustrated by the variations in diving behavior among Pacific Arctic regions reported in Chapter 3. Both the Chukchi and Beaufort populations dive to depths and portions of the water column that would presumably optimize foraging opportunities, based on the available information of prey distributions as well as oceanographic properties that concentrate prey. Additional research that collates information on beluga foraging ecology simultaneous to prey distributions and oceanographic processes, especially at finer scales, would further enhance the results presented here. This feat is increasingly possible with technological advances in telemetry devices that can record aspects such as ocean temperature and salinity, animal acceleration, and acoustics (e.g. Cagnacci et al. 2010, Costa et al. 2012, Hays et al. 2016).

The population-scale patterns quantified in the first few chapters are presumably genetically-based adaptive responses (i.e., increase survival and lifetime fitness) to the historically seasonal and variable Pacific Arctic environment. However, beluga philopatry and migration patterns are also culturally transmitted, passed down through matrilineal social interactions (O'Corry-Crowe et al. 1997, Colbeck et al. 2013). Therefore, beluga distribution, movements, and behavior are presumably driven by combined effects of genetic, social, and environmental influences. Chapters 2 and 3 established benchmarks against which to assess changes in distribution, migration, and behavior, all of which are relevant to the conservation and management of populations

## 7.2 RESPONSES TO A SHIFTING SEA ICE ECOSYSTEM

My dissertation also intended to address whether belugas would adjust their distribution, migration, and behavior with shifting sea ice conditions, or to what extent, given tradeoffs in social versus environmental forcing. Although Chapter 4 established that sea ice is not the only determinant of beluga habitat preferences, additional results suggest that belugas may be able to mediate changing sea ice conditions with behaviorally plastic responses in movement and behavior (Chapters 5 and 6); responses that differ between populations. Given these population-specific responses, it is likely that the capacity for potentially adaptive behavioral change is not shared equally and that some populations will be more likely to adapt in the face of a changing climate.

Specifically, results from Chapter 5 suggest that Chukchi belugas delayed migration to allow for a prolonged presence in the Pacific Arctic, especially in the Beaufort Sea, as freeze-up occurred later in more recent years. Chapter 6 further indicated that Chukchi belugas responded to changing conditions that favored deeper, longer dives. These results correspond to a conclusion that Chukchi belugas are coping with a changing Pacific Arctic environment through behavioral plasticity in migration timing and foraging behavior. In contrast, there were few examples where migration timing of Beaufort belugas changed between the 1990s and 2000s nor was there evidence that freeze-up timing cues migration. Rather, Beaufort beluga migration timing appears to be ‘pre-programmed’, which is consistent with a canalized genetic cue to migrate west and south at a particular time each year. Additional analyses of population-specific transit time from the Beaufort Sea (152° W) to the southward (70° N) and Bering Strait passage points support these conclusions. Table 7.1 shows that relative variation in crossing dates as well as transit times were generally consistent for Beaufort belugas compared to those for Chukchi belugas. Ultimately, these sympatric populations appear to have different associations with sea ice cover (Chapter 6) as well as migratory triggers in the fall (Chapter 5). In both cases, Chukchi and Beaufort beluga populations are balancing socially-maintained, heritable movements (e.g. Colbeck et al. 2013) and phenotypic plasticity in migratory and behavioral responses to environmental forcing. Calves spend at least two fall migrations with their mothers, learning migration routes and experiencing environmental cues for migration. Southward movements in the Chukchi Sea are spatially segregated (Hauser et al. 2014) and the two populations may receive distinct environmental signals. Northward advection through Bering Strait is biased towards the eastern Chukchi Sea (Woodgate et al. 2005, Woodgate et al. 2012), so Chukchi belugas may get more information on Bering Sea conditions (e.g. ice, temperature, or related hydrography) to mediate migrations than Beaufort belugas that may depend on more seasonally-predictable cues like day length. Additional research could investigate alternative hypotheses of other potential environmental factors that may cue fall migrations of the two populations, but these genotype versus environmental influences thus affect how each population respond to sea ice changes (see Figure 7.1). My results clearly indicate that beluga responses to changing sea ice are population-specific and a single conceptual model of the impacts of sea ice loss is not suitable for belugas, at least in the Pacific Arctic.

However, my research does not have the ability to determine whether these responses positively or negatively impact the population dynamics, vital parameters, or potential for persistence of Chukchi or Beaufort belugas. Persistence of Arctic vertebrates will likely result from a combination of phenotypically plastic response to climate-related changes and adaptation in response to selection (Gilg et al. 2012). It is not known whether the plasticity observed here is adaptive, non-adaptive, or even mal-adaptive (Ghalambor et al. 2007). Shifts in beluga migration timing and behavior would be adaptive if the change moved the phenotypic mean of the population toward a new optima in the changed environment; conversely if plasticity shifted the populations further from a fitness optima it would be non-adaptive. Recent evidence indicates that Beaufort beluga body condition and intrinsic growth rates have declined, possibly as a result of ecosystem changes (Harwood et al. 2014, Harwood et al. 2015). Yet, relative abundance of Beaufort belugas increased between 1982-1985 and 2007-2009 (Harwood and Kingsley 2013). Similar analyses have not been conducted for Chukchi belugas. It is possible that delayed migration and prolonged seasonal use in the Beaufort Sea foraging areas, as well as deeper diving, in recent years reflect adaptive responses by Chukchi belugas to improved foraging conditions that will lead to better body condition and population persistence. Perhaps, similar to Pacific Arctic bowhead whales (i.e., Moore and Stabeno 2015), it is a good time (for now) to be a Chukchi beluga. Alternatively, perhaps Chukchi belugas are making the best of a bad situation.

Deeper, longer dives are energetically costly and a consistent shift to this dive type may convey negative population implications. Delayed departure from the High Arctic in the fall could also expose belugas to variable ice conditions with swift freeze-up that could result in increased entrapment risk (e.g., Laidre et al. 2012). Future research should further examine population-scale implications to life histories and demography, as well as continue to monitor movements and distribution over longer time series.

Taken as a whole, the chapters of my dissertation contribute to a stronger understanding of the interplay of environmentally-induced behavioral plasticity and regional environmental variability in determining adaptive responses, critical pieces to improving our predictive capacity for future climate alterations (Reed et al. 2010, Reed et al. 2011). Results of Chapter 6 suggest that the amount of optimal habitat has not significantly declined since 1990, although there were subtle spatial shifts in preferred habitat areas and the majority of optimal habitat trends were negative. It is expected that ice-free areas and duration of the open water periods will continue to expand if sea ice trends continue as predicted (Wang and Overland 2015). The ‘New Normal’ Pacific Arctic ecosystem (since 2003) and that anticipated for the future is characterized by a shift from a benthic- to pelagic-dominated marine ecosystem, which would promote zooplankton and forage fish production and benefit belugas (Grebmeier et al. 2006, Grebmeier 2012, Moore and Stabeno 2015). Indeed the behavioral responses I detected for Chukchi belugas correspond to potentially improved foraging opportunities, and more research is needed to establish whether these are adaptive responses that will facilitate these distinct beluga populations to persist into the future.

## 7.3 FUTURE RESEARCH NEEDS

The research presented in this dissertation also contribute to the growing body of literature illustrating that marine predator populations are responsive to climatic fluctuations (e.g. Forcada and Trathan 2009, Regehr et al. 2010, Weimerskirch et al. 2012), yet the functional relationship between climate and range-wide demography remains difficult to predict (Sydeman et al. 2015). Few papers link finer-scale shifts in distribution or behavior to demographic traits such as reproductive success (e.g. New et al. 2014, Thorne et al. 2015), but this is precisely the type of examination needed for Pacific Arctic belugas to help elucidate the consequences of changes (or not) in phenology and behavior. In the case of phenological shifts, marine predator responses are variable and it is not always clear that a phenological shift intercedes fitness loss (Sydeman et al. 2015). The development of an individual-based model for belugas could help explore climate change effects as well as the level of phenotypic plasticity expected to result from climate alteration (e.g. Anderson et al. 2013, Bailleul et al. 2013). My work illustrates that at least Chukchi belugas have the ability to adjust their movements and behavior on relatively short scales. However, the capacity for adaptation rests in the interacting effects of exposure and sensitivity that determine vulnerability across ecological scales, from individuals to populations and up to species and the broader ecosystem (Dawson et al. 2011, O'Connor et al. 2012, Sydeman et al. 2015). A diversity of responses, such as I have quantified for Pacific Arctic belugas, could actually enhance species and ecosystem resilience in new environmental regimes via portfolio effects (Schindler et al. 2015). In such cases, adaptive management and conservation should spread risk to maintain genetic diversity, ecological heterogeneity and connectivity. Continued monitoring of beluga responses to sea ice changes within and between populations, as well as over extended timeframes, will enhance predictions of future climate change impacts.

The vast physical alterations of the Pacific Arctic are also occurring in concert with expanding anthropogenic activities that may have compounding effects on marine ecosystems. Humans have been living in the Arctic for millennia, but recent loss of seasonal ice cover has spurred an advance of economic interests, chiefly commercial shipping and industrial activities. Projections of navigability suggest open-water crossings of the Arctic by mid-century (Smith and Stephenson 2013), raising questions of how to juggle economic development and environmental protection related to food security of indigenous people (Reeves et al. 2014, Laidre et al. 2015). For example in U.S. portions of the Northwest Passage (NWP), Arctic marine mammals constitute critical subsistence, cultural, and spiritual resources to Inupiat communities along the northern Alaska coast (Frost and Suydam 2010).

One way to consider future resilience of belugas and other Arctic marine mammals is to investigate intersecting issues of current and future sea ice loss, increased use of previously unaffected areas like the NWP, and shifting marine mammal habitat as it relates to the health and productivity of these ‘sentinel’ species. By extension, such research will improve forecasting of potential impacts to coastal Inupiat. One extension of my dissertation would be to use the resource selection models developed in Chapter 4 to predict availability of future preferred habitat under projected sea ice scenarios. I used these models to map predictions of preferred beluga habitat for both sexes in the 1990s, 2000s, and 2010s in Chapter 6, but it could still be applied to future sea ice states using the latest coupled climate models (e.g. CMIP5) over the next several decades (e.g. Wang and Overland 2015). Currently the only quantitative predictions of future Arctic marine mammal habitat exist for polar bears (Durner et al. 2009), but forwardlooking information is needed for conservation and management (Laidre et al. 2015). Such results would constitute novel, innovative research directly responding to practitioner needs. In addition to altered physical and biological habitats, increasing anthropogenic pressures make it particularly timely to develop detailed estimates on the spatiotemporal overlap of vulnerable species and likely future shipping routes and the related industrial development that may follow. My dissertation research coupled with future projections could inform and identify intersecting areas of critical habitat and human activities. Estimation of spatial and temporal overlap would guide managers in protecting areas most likely to be affected as well as less important regions that will minimize impacts, thus potentially contributing to conversations balancing both environmental protection and responsible development within changing sea ice regimes.

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Table 7-1. Relative variation (CV, coefficient of variation) in crossing dates and transit times for Beaufort and Chukchi beluga whale populations, based on satellite telemetry data collected in an early period (1993-2002) and a late period (2004-2012). For sample sizes and details see Chapter 5.

| | **Early period** | **Late period** |
|---|---|---|
| **Beaufort beluga CV** | | |
| Depart date from Beaufort Sea (152° W) | 3.0 | 3.1 |
| Date South of 70° N | 2.9 | 2.2 |
| Date past Bering Strait | 2.9 | 2.2 |
| Beaufort Sea-70° N transit time | 37.6 | 37.8 |
| Beaufort Sea-Bering Strait transit time | * | 17.9 |
| **Chukchi beluga CV** | | |
| Depart date from Beaufort Sea (152° W) | 6.8 | 2.6 |
| Date South of 70° N | 2.0 | 1.9 |
| Date past Bering Strait | 2.0 | 1.9 |
| Beaufort Sea-70° N transit time | 27.0 | 82.4 |
| Beaufort Sea-Bering Strait transit time | 4.3 | 48.8 |

*A single tag continued transmitting past Bering Strait for Beaufort whales in the early period

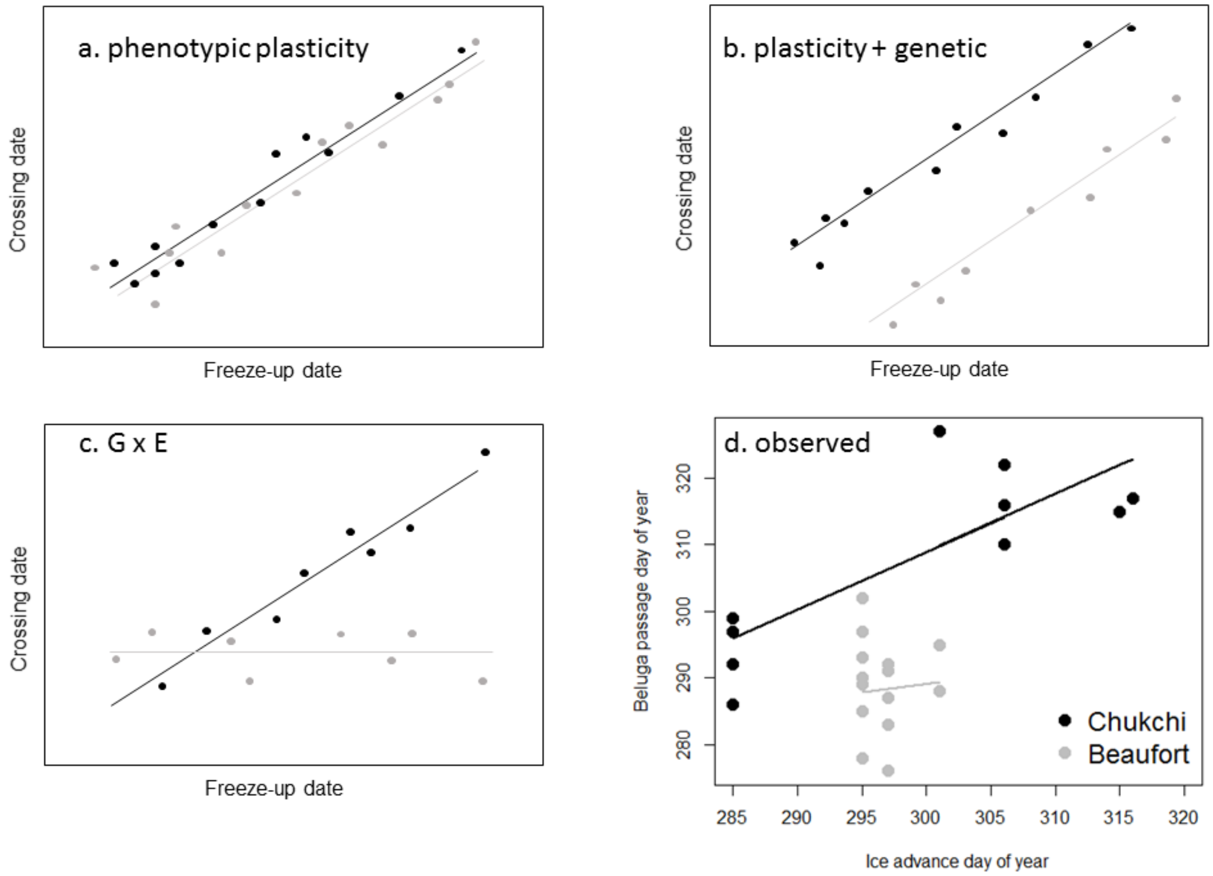

Figure 7-1. An example of reaction norms for population-specific Pacific Arctic beluga whale phenotypic versus genetic responses to changing summer sea ice conditions, using date of southward migration (south of 70° N) relative to Beaufort Sea freeze-up date. In panel a, both populations exhibit phenotypic plasticity to changing conditions compared to panel b, where both populations have common plastic responses but distinct genetic variation, and panel c where variation among population-specific genotypes mediates responses to environmental change as genotype X environment (G X E) reactions. Responses similar to panel a would be expected if both populations were responding similarly to the environmental change, but in reality I found divergent responses by populations (panel d) illustrative of G X E reactions (see Chapter 5). It is unclear whether these differences represent adaptive or non-adaptive plasticity (Ghalambor et al. 2007).