Behavioral divergence in a changing Arctic: Novel insights into the movement ecology of Eastern Beaufort Sea belugas from historical tracking data

by

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A Thesis submitted to the Faculty of Graduate and Postdoctoral Studies of

The University of Manitoba

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Environment and Geography

University of Manitoba

Winnipeg

Abstract

The Eastern Beaufort Sea (EBS) population undertakes an annual migration from their summering grounds in the western Canadian Arctic to their winter range in the Chukchi and Bering Seas. EBS belugas were instrumented with satellite-linked transmitters in the shallow waters of the Mackenzie Delta over the course of the 1990s, 2000s and 2010s in collaboration with Inuvialuit communities. This thesis aggregated these datasets to examine the range and diversity of EBS beluga movements at two different scales. First, dynamic Brownian Bridge Movement Models (dBBMMs) were used to re-establish seasonal ranges and high-use areas across the annual migration cycle. Evidence of individual stopovers on bathymetric features, together with a potential fall staging area in the Chukchi Sea, suggests that EBS belugas depend on a network of sites across their annual range to support long-distance movements. Second, variation in summer space use was quantified, individuals with similar summer movements were clustered, and the link between space use and migration timing was examined. Three main summering groups were identified, and targeted distinct high-use areas and were generally associated with different individual traits: A group of mature males departed from the Mackenzie Estuary by mid-July and travelled to Viscount Melville Sound, a mixed group remained in the Amundsen Gulf and travelled between nearshore and offshore sites throughout the season, while a smaller, mixed group targeted the Beaufort Sea slope and similarly returned to the Estuary before migrating. Fall migration timing varied between and within groups, suggesting that summer space use, individual variation and external drivers influence the date of departure. These findings highlight avenues for future research on EBS beluga space use, migration timing, population structure and abundance that may better account for the presence of spatially and temporally segregated groups.

Acknowledgements

I would like to thank my supervisor, Lisa Loseto, for agreeing to take me on as a student during a pandemic, for working tirelessly to guide this thesis to its conclusion and for offering me opportunities to learn from several other teams and collaborators. Thank you to my committee members: Nigel Hussey, for sharing your wealth of movement ecology knowledge, for providing insightful ideas and positive energy during every meeting, and for your willingness to engage deeply with this work from the very beginning of this project. To Cortney Watt, for believing in me enough to include me in your field program at Creswell Bay, and for being a supportive presence on my committee and at DFO throughout this degree. Thank you to CJ Mundy for diligently keeping an eye on deadlines and program requirements when the rest of us were too busy nerding out about whales.

I was fortunate to be guided by several mentors over these past few years. Thank you to Luke Storrie for the consistent, thoughtful feedback, to Harri Pettitt-Wade for being a great role model in the field, and to Courtney Shuert for being a calm and friendly presence in the DFO office with a keen eye for methodological issues. Thank you to the community of Tuktoyaktuk for a deeply memorable summer and especially to Jim Elis for keeping us safe and providing endless knowledge and conversation during trips on the land; I feel truly privileged to have learned about your corner of the world from you. Thank you to the members of the Creswell Bay field camp for the opportunity to learn about beluga, narwhal and a few wayward bowheads in their natural environment.

Thank you to the Department of Fisheries and Oceans, the University of Manitoba, ArcticNet and the Weston Foundation for funding this research. The data used in this project is the result of decades of collaboration, partnerships and funding from several institutions, notably:

DFO, ArcticNet, the Fisheries Joint Management Committee, the Inuvialuit Game Council, the Joint Secretariat, and the Inuvik and Tuktoyaktuk Hunters and Trappers Committees. I am grateful for the valuable feedback on preliminary findings offered by community partners during FJMC, IGC and ArcticNet meetings, and during the 2025 Beluga Summit in Inuvik.

Thank you to Winnipeg for being such an unforgettable character of a city filled with contradictions, to my dear friends near and far who have provided emotional support and laughs across great distances and many chapters of our respective lives; and to my family for supporting my highly impractical dreams despite the ups and downs and cross-country moves.

Land Acknowledgement

This thesis was carried out over several regions and geographies, but was primarily based in Winnipeg, on Treaty 1 territory, on the traditional lands of the Anishinabe (Ojibway), Ininew (Cree), Oji-Cree, Dene, and Dakota as well as the heart of the Métis Nation. I was fortunate to spend time on the lands and waters of Inuit Nunangat over the last three years, notably in Tuktoyaktuk and Inuvik in the Inuvialuit Settlement Region, and on Somerset Island in Nunavut. I am grateful to the communities that have cared for and stewarded these lands and waters for many generations, and deeply thankful to those who chose to share their knowledge and teachings with me. With humble gratitude to those Indigenous knowledge holders that graciously choose to engage in the often-imperfect processes set forth by southern research institutions, I dedicate myself to move forward in partnership with Indigenous communities in a spirit of reconciliation and collaboration, in both my professional and my personal life. I support the ongoing struggle for Indigenous self-determination in Canada, Palestine and beyond.

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Contributions of authors

The research reported in Chapter 2 was conducted by Emma Sutherland (conceptualization, methodology, visualization, writing). The methodology and early drafts of this chapter have been reviewed by Lisa Loseto (Fisheries and Oceans Canada, University of Manitoba), Luke Storrie (University of Manitoba) and Nigel Hussey (University of Windsor). Shannon MacPhee contributed to the overall research program, leading community consultations and coordinating data collection. The manuscript is in preparation for submission.

The research reported in Chapter 3 was conducted by Emma Sutherland (conceptualization, methodology, visualization, writing). The methodology and early drafts of this chapter have been reviewed by Lisa Loseto (Fisheries and Oceans Canada, University of Manitoba), Luke Storrie (University of Manitoba), Courtney Shuert (Assiniboine Park Conservancy) and Nigel Hussey (University of Windsor). Shannon MacPhee contributed to the overall research program, leading community consultations and coordinating data collection. The manuscript is in preparation for submission.

Chapter 1: Introduction

1.1 Background

1.1.1 Migration and movement

Migration is a phenomenon by which organisms exploit multiple sites to form a single ecological niche (Alerstam & Högstedt, 1982). Across a broad range of taxa, migration is employed as an adaptation to spatiotemporal variation in resource availability, allowing populations to synchronize their movements with optimal conditions for survival and reproduction (Dingle, 1996; Dingle & Drake, 2007). In the classical definition of migration, predictable fluctuations in resources drive seasonal movements, and animals pre-emptively depart from residency areas before the habitat has fully degraded (Dingle & Drake, 2007). In the Arctic, hundreds of species undertake annual migrations to high latitudes, benefitting from productive summer months and departing when decreasing temperatures, increased snow and ice cover and declining resource availability render the environment inhospitable (Davidson et al., 2020). However, Arctic marine migrants inhabit an increasingly unpredictable environment, subject to reduced sea ice cover and rising sea surface temperatures (Meier & Stroeve, 2022; Yang et al., 2023), which could, in turn, shift the distributions of important prey species (Geoffroy et al., 2023). These rapidly changing and heterogeneous conditions can lead animals to modulate their movements in response to shifting habitat features (Cohen et al., 2018; Tombre et al., 2019).

Animal telemetry, the study of gathering information about the movement and behavior of an organism using animal-borne sensors, continues to steadily gain popularity, with the number of telemetry studies published annually increasing rapidly since the 1990s (Chung et al., 2021; Robichaud et al., 2025). One of the main advantages of telemetry lies it the ability to study animals in contexts when observation would be otherwise challenging, such as for species that spend much if their time underwater or far from shore (Hussey et al., 2015; Lennox et al., 2017). In recent years, rapid technological advances have reduced the constraints limited to cost, battery duration, weight and size of tracking devices (Chung et al., 2021; Lennox et al., 2017), allowing researchers to better understand the complexity of animal movements (Hussey et al., 2015; Lennox et al., 2017). Thus, alongside advances in animal tracking technology, the conceptual understanding of animal migration and movement has also evolved (Austin et al., 2004; Poole et al., 2024; Seigle-Ferrand et al., 2021; van de Kerk et al., 2021). While migration is often understood as a repeated, direct journey between summer and winter residency areas, in reality, animals can also migrate across multiple ranges or undertake multiple round trips within a year (van de Kerk et al., 2021). Animals can also exhibit nomadic movements, consisting of irregular long-distance trips between distant sites (Teitelbaum & Mueller, 2019), or partial migration, in which only a portion of the population is migratory (Singh & Leonardsson, 2014). In the classic definition of migration, animals suppress maintenance activities such as feeding during the migration phase (Dingle, 1996; 2007), however, the delineation between foraging and transiting is more nebulous for many swimming and walking organisms, which can sometimes migrate and feed concurrently rather than relying on pre-existing energy stores to sustain their journey (Evans & Bearhop, 2022). Animals can additionally employ stopovers during migration which can be opportunistic or based on memory of resource availability (Evans & Bearhop, 2022). Migratory mammals are often highly mobile outside the migration season (Avgar et al., 2013) further complicating the definition of migration for species that transit extensively within seasonal residency areas. For mobile species navigating heterogenous environments, multiple movement patterns can occur within a single population, underscoring the need for studies that examine year-round distribution and account for individual variation (Austin et al., 2004; Poole et al., 2024; Shaw, 2020; van de Kerk et al., 2021).

Tracking the movements of individual animals has provided the means to examine how individual traits shape how animals respond to external conditions. Studies can observe and quantify the extent of variation within populations in terms of the timing, frequency, and occurrence of long-distance movements (Carneiro et al., 2017; García-Vernet et al., 2024). Movement behaviour is influenced by stable traits such as sex (Debeffe et al., 2019) and early life conditions (Shaw, 2020), as well as labile traits which shift throughout the animal's life, including age (Newton, 2011; Wobker et al., 2021), reproductive status (Craig et al., 2003; Singh & Ericsson, 2014), size (Hein et al., 2012; Webber & McGuire, 2022), body condition (Duijns et al., 2017; Russell et al., 2022) and experience (Abrahms et al., 2019; Shaw, 2020; Tombre et al., 2019). Learned information, often transmitted culturally, is a key mechanism for disseminating migratory behavior, further allowing long-lived individuals and successive generations to navigate and exploit reliable resources (Abrahms et al., 2019; Jesmer et al., 2018). An increasing number of studies leverage the growing availability of telemetry data to integrate multiple taxa (Citta et al., 2018) or years (Buechley et al., 2018; Haest et al., 2019; Monteith et al., 2011; Shuert et al., 2023), thereby enabling the examination of broader patterns in space use (Hamilton et al., 2022) and migration timing (Davidson et al., 2020), as well as the identification of conservation priorities (Sequeira et al., 2025).

1.1.2 Study species

Beluga whales (*Delphinapterus leucas*), referred to as *qilalugaq* in Inuvialuktun (Byers & Roberts, 1995), are medium-sized odontocetes comprising 22 genetically and geographically distinct stocks globally, of which seven occur in Canadian waters (Hobbs et al., 2019; Montana et al., 2024). Beluga populations can be migratory (Belanger et al., 2025; Sergeant, 1973;

Suydam et al., 2001) or resident (Shelden et al., 2022; Simard et al., 2023; St-Pierre et al., 2024). They occupy a broad ecological range, from the seasonally ice-laden expanses of the high Arctic to the temperate estuarine environments of the St. Lawrence, regularly traversing saline and freshwater systems (Simard et al., 2023; Watt et al., 2023). Their diet varies by location and season, encompassing a variety of benthic and pelagic fish species such as Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*), as well as invertebrates including cephalopods, crustaceans, and polychaetes (Choy et al., 2019; Lesage et al., 2020; Marcoux et al., 2012; Quakenbush et al., 2015). Arctic belugas are thought to be moderately sensitive to the impacts of climate change due to their high abundance, extensive distribution and varied diet (Laidre et al., 2008). While they are flexible to a range of sea ice conditions, sometimes occurring in areas of very high (>99%) sea ice concentration (Barber et al., 2001; Loseto et al., 2006; Richard et al., 2001), belugas can exhibit abnormal migration and residency events during anomalous ice years (O'Corry-Crowe et al., 2016). Beluga distribution are influenced by a combination of individual, social and environmental drivers: In the Pacific Arctic, the Eastern Beaufort Sea and Eastern Chukchi Sea populations demonstrate differences in habitat selection despite having access to the similar environmental conditions (Hauser et al., 2017) which in turn results in different seasonal home ranges (Hauser et al., 2014) and migratory timing (Hauser et al., 2014). In other beluga populations, groups within a single population exhibit distinct movements and migration chronologies (Bailleul et al., 2014; Colbeck et al., 2013).

1.1.3 Study population

The Eastern Beaufort Sea (EBS) beluga population is one of the seven beluga populations which spend at least a portion of the year in Canadian waters (Richard et al., 2001). EBS belugas undertake predictable long-distance movements each year from the eastern Beaufort Sea in the summer, travelling across the Arctic Ocean during the fall and spending the winter months in the

Bering Sea (Hill, 1999; Stafford et al., 2018a). Thousands of EBS belugas aggregate each summer in the Mackenzie Estuary in the Inuvialuit Settlement Region, NT. Overall, EBS beluga growth rates appear to be in decline (Harwood et al., 2014), and blubber thickness varies across sites and years, but shows a negative correlation with sea ice cover (MacMillan, 2018). Animal and human health are tightly linked in Inuvialuit communities where the harvest of wildlife plays a key cultural and nutritional role (Byers & Roberts, 1995; Ostertag et al., 2018; Ovitz et al., 2024; Sudlovenick et al., 2024; Waugh et al., 2018); for example, changes in beluga body condition (Choy et al., 2017; MacMillan et al., 2019) or contaminant in tissues (Loseto et al., 2015; Sudlovenick et al., 2024) can signal shifts in prey (i.e. fish) abundance or pollution levels, which impact humans and non-human species in the region (Doubleday, 2007; Morris et al., 2022; Muir et al., 1999). Shifts in the timing and distribution of beluga movements can signal important changes in beluga habitat (Hauser et al., 2018; Loseto et al., 2018; Scharffenberg et al., 2025), while resulting in less predictable beluga presence and impacting harvesting practices (Harwood et al., 2015; Ovitz et al., 2024; Scharffenberg et al., 2019; Waugh et al., 2018).

1.2 Rationale

Belugas, like many marine mammals (Bartholomew & Collias, 1962; Christal et al., 1998; Fox et al., 2017; Mann et al., 2012), are highly social animals (Colbeck et al., 2013; Mayette et al., 2022). They form complex, multi-level fission-fusion societies, consisting of groups that converge and diverge throughout the year (Colbeck et al., 2013; Mayette et al., 2022; O’Corry-Crowe et al., 2018). Evidence of social and cooperative behaviours have been recorded in captivity and in the wild, including acoustic communication (Garland et al., 2015; Scharffenberg et al., 2019; Vergara & Mikus, 2019), sociosexual behaviours (Hill et al., 2015;

Lilley et al., 2020; Lomac-Macnair et al., 2015; Lydersen et al., 2023), and care of offspring by both parents and non-parents (Aubin et al., 2023; Krasnova et al., 2009; Leung et al., 2010).

For Eastern Beaufort Sea belugas, variability in long-distance movements has been documented across multiple spatial and temporal scales. Passive acoustic monitoring has identified spatially and temporally distinct peaks in beluga vocalizations in the Mackenzie Delta suggesting the presence of separate groups (Scharffenberg et al., 2019, 2025; Simard et al., 2014), and aerial surveys have detected smaller clusters travelling in proximity to one another (Harwood & Norton, 1996; Mayette et al., 2022), providing snapshots of group structure. While such observations represent short-term patterns, additional evidence indicates recurring, persistent and diverging long-distance movement patterns. Inuvialuit harvesters have reported distinct groups of belugas targeting different areas during summer (Harwood et al., 2020; KAVIK-AXYS, Inc., 2012; Richard et al., 1997) and diverging along different directions at the onset of fall migration (MacPhee et al., 2025; Murray et al., 2023; Ovitz et al., 2024). Previous analyses of satellite telemetry data have noted diverging movement patterns (Hauser et al., 2014; Richard et al., 2001; Storrie et al., 2022, 2023), while genetic analyses of samples from whaling camps in the Inuvialuit Settlement Region noted the presence of different lineages (Postma, 2017). These repeated patterns of divergence suggest the existence of distinct movement strategies, which may allow belugas to partition habitat and resources across the seasonal range.

Despite these multiple lines of evidence, these recurring movement patterns have not been explicitly described. Abundance estimates (Marcoux et al., 2025), analyses of seasonal distribution (Hauser et al., 2014; Storrie et al., 2022), and migration timing (Hauser et al., 2017) typically consider the population as a single unit, rarely accounting for variation beyond sex or calf presence, likely owing to the population’s vast seasonal distribution and the limited sample sizes of existing satellite telemetry studies. To establish metrics of beluga occurrence timing and distribution at the population level, or compare beluga movement ecology across multiple years, variation in long-distance movements within the population must first be established and characterized. To address this gap, this thesis investigates variation in beluga movements across scales, from population-level seasonal movements to group-level space use, providing a more complete understanding of how behavioral diversity shapes movement behaviour and influences interpretations of population-level change.

1.3 Thesis objectives

The overarching goal of this thesis is to gain a better understanding of the diversity of long-distance movements of Eastern Beaufort Sea belugas. Belugas were instrumented with satellite-linked transmitters in the shallow waters of the Mackenzie Delta over the course of the 1990s (1993, 1995, 1997), 2000s (2004 and 2005) and 2010s (2018 and 2019) to gather information on migration patterns, habitat preferences and seasonal use areas (Citta et al., 2017; Hauser et al., 2014; Richard et al., 2001; Storrie et al., 2022). These datasets were combined to address several thesis sub-objectives:

1) Identify high-use areas (i.e. residency areas, migration corridors, stopover sites) across the annual migration cycle,
2) Examine the influence of internal drivers including individual traits (sex, age, calf presence) and social group on beluga movement timing and distribution,
3) Quantify inter-individual variation in beluga space use,
4) Examine timing of beluga occurrence in key areas,

1.4 Thesis structure

This thesis is composed of four chapters. Chapter 1 outlines the background, rationale, objectives and structure of this thesis.

Chapters 2, and 3 are written in manuscript style. Chapter 2 addresses sub-objective 1, combining satellite telemetry data across all available years to provide a thorough exploration of year-round distribution. I provide a comparison of the satellite telemetry data derived from the various tagging campaigns conducted on this population. I then combine data from all available individuals to establish high-use areas throughout the migratory cycle. These analyses provide context for the subsequent chapter and showcases population-level stopovers which have which have not been previously highlighted in the literature. This chapter is in preparation for submission.

Chapter 3 addresses sub-objectives 2-4. This chapter links summer space use to fall migration timing. I quantify inter-individual variation in summer space use to identify distinct summering groups, then describe individual traits (sex, calf presence, body length) and summer high-use areas for each group. I then examine the influence of summer space use on the timing of departure from the population-level aggregation area in the Mackenzie Estuary and the beginning of the fall migration. This chapter is in preparation for submission.

Chapter 4 includes a summary of findings, limitations and future directions.

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Chapter 2: Defining the annual range and seasonal high-use areas of Eastern Beaufort Sea belugas through three decades of collaborative satellite tagging

Abstract

The Eastern Beaufort Sea beluga (*Delphinapterus leucas*) population migrates through Canadian, Alaskan, and Russian waters, relying on a broad network of habitats to meet their life-history needs. Examining where belugas concentrate their movements is critical for identifying key habitats and evaluating the ecological function of different areas within their annual range. Here we aggregated satellite telemetry data from 45 belugas instrumented in the Mackenzie Delta between 1993 and 2019 aimed to 1) quantify year-round relative space use and 2) define seasonal high-use areas. We used dynamic Brownian Bridge Movement Models (dBBMMs) to quantify relative space use for each beluga and produce an aggregated occurrence distribution. Areas of high beluga occurrence were scattered in the summer and early fall. In the late fall, belugas converged in the Chukchi Sea in two staging sites east of Wrangel Island and north of the Bering Strait. Belugas remained in the Bering Sea during the winter and early spring, then migrated along the continental slope before scattering in the early summer, targeting sites west of Banks Island, within the Amundsen Gulf and along the continental slope. The number and variety of sites targeted between summer and winter residency areas highlighted the importance of considering stopovers and staging sites when defining key habitats, given their importance in supporting energetic requirements and life-history events throughout the year. These findings highlight the spatial and temporal variability of EBS beluga movements, which extended beyond those reported by previously published satellite telemetry datasets and delineate a network of ecologically important sites spanning the full migration cycle.

2.1 Introduction

Many long-distance migrants depend on a network of sites to complete their migratory cycle and fulfill their life-history and maintenance needs (Bolger et al., 2008; Middleton et al., 2020). Conditions at one stage of a migration may influence subsequent periods (Harrison et al., 2011; Norris & Taylor, 2005), and the disruption of one or more sites can have cascading effects on individual or population health (Bolger et al., 2008; Runge et al., 2014). The study of movement ecology plays a key role in the conservation and management of wildlife populations (Allen & Singh, 2016), offering the means to examine distribution and behaviour, and identify the key habitats and their ecological functions (Reisinger et al., 2022). Seasonal ranges, used intensively during specific times of year, represent key habitats that structure the annual cycle (Avgar et al., 2014; Nielsen & Seitz, 2017) and can serve functions including foraging, breeding, and raising offspring (Powell & Mitchell, 2012). Stopover sites along connecting migration routes allow individuals to rest and replenish energy stores (Linscott & Senner, 2021; Sheehy et al., 2011) and in some cases act as staging areas where large aggregations gather at predictable locations for extended periods (Ma et al., 2013; Warnock, 2010). Many migratory species undertake long-distance movements across multiple geopolitical boundaries, and require cross-jurisdictional collaborations to understand and mitigate stressors across their annual range (Harrison et al., 2018; Middleton et al., 2020). Effective management of wide-ranging species requires knowledge not only of movement patterns, but also of the ecological functions served by sites used across their range (Bolger et al., 2008; Runge et al., 2014; Schuster et al., 2019).

Belugas from the Eastern Beaufort Sea (EBS) population travel annually from their expansive summering grounds, which encompass the Beaufort Sea from the Beaufort continental shelf to the Nunavut border, navigating across the Arctic Ocean, through the Chukchi Sea and into their winter range in the Bering Sea (Richard et al., 2001; Storrie et al., 2022). As a result of their extensive distribution, which crosses through the western Canadian Arctic, Alaska, and Russia (Hauser et al., 2014; Storrie et al., 2022), the management and monitoring of EBS belugas is a highly collaborative endeavour involving multiple levels of government, co-management organizations, resource users and members of the scientific community (Harwood et al., 2020; Harwood & Smith, 2022). EBS belugas are harvested by Alaskan hunters during their spring migration (Frost & Sydham, 2010), as well as by hunters in the Inuvialuit Settlement Region during the summer months (Harwood et al., 2020). They inhabit a dynamic region experiencing unprecedented environmental change and emerging anthropogenic stressors, including declining sea ice (Galley et al., 2008; Howell et al., 2023), shifting prey assemblages (Logerwell et al., 2015), as well as increasing noise and pollution from marine vessel traffic linked to growing tourism and oil and gas exploration (Dawson et al., 2018). Although the general seasonal distribution of EBS belugas is well documented (Citta et al., 2017; Hauser et al., 2014; Richard et al., 1998), less is known about finer-scale spatial patterns across the full migratory cycle. Identifying the network of sites used throughout the annual migration, including seasonal residency areas and stopover sites, can identify regions where environmental change or anthropogenic stressors may affect EBS beluga health.

Satellite telemetry, which involves attaching electronic transmitters to individual animals to record their movements (Hussey et al., 2015), has played an essential role in tracking EBS belugas in remote offshore habitats. Studies using satellite telemetry were conducted on EBS belugas in the 1990s (Richard et al., 2001), 2000s (Hauser et al., 2014), and late 2010s (Storrie et al., 2022). While specific study objectives and sampling designs varied across decades (e.g., age, sex, or location of tracked individuals) (Hauser et al., 2014; Richard et al., 1998; Storrie et al., 2022), synthesizing these datasets using updated analytical methods (Kranstauber et al., 2012) allows for a broader understanding of EBS beluga distribution across the annual range.

Here, we use data from 45 EBS belugas tracked during seven years of satellite telemetry studies between 1993 and 2019. The aims of this study were to 1) quantify year-round relative space use and 2) define seasonal high-use areas. We fitted dynamic Brownian Bridge Movement Models (dBBMMs) to quantify space use along individual beluga tracks, then rescaled and merged individual occurrence distributions to quantify year-round space use for all belugas in the study. We defined high-use areas, including residency areas and stopover sites, by delineating the 50% and 25% occurrence contours for each season. These findings contribute to better delineating key habitats for the EBS beluga populations, enabling more effective conservation planning in the face of environmental or anthropogenic stressors.

2.2 Methods

2.2.1 Study area

The annual range of Eastern Beaufort Sea belugas encompasses the Inuvialuit Settlement Region (ISR) in the Western Canadian Arctic (Harwood & Norton, 1996; Hauser et al., 2014), the coastal waters of Alaska and the Chukotka peninsula in Russia, as well as offshore areas in the Central Arctic Ocean, the Chukchi Sea and the Bering Sea (Citta et al., 2017; Luque & Ferguson, 2010) (Figure 2.2.1). In summer, belugas aggregate in the Mackenzie Delta, typically entering once sea ice break-up permits access (Hornby et al., 2016). Two marine protected areas, the Tarium Niryutait MPA and the Anguniaqvia niqiqyuam MPA, were signed into effect in 2010 and 2016 to protect nearshore habitats in the Beaufort Sea, including beluga calving areas (Government of Canada, 2019a, 2019b). In late July and August, belugas are dispersed across the summer range, travelling east toward the Nunavut border, north of Banks Island into Viscount Melville Sound, and west along the continental slope (Hauser et al., 2014; Richard et al., 2001;

Storrie et al., 2022). The Beaufort Sea continental shelf gradually slopes into the deep Canada Basin, which exceeds depths of 4000 m (Carmack & Macdonald, 2002; Weber, 1989). Belugas initiate their fall migration west across the Arctic basin or along the coast of Alaska (Hauser et al., 2017; Richard et al., 1998; Storrie et al., 2022). Late fall, winter, and early spring are spent in the relatively shallow Chukchi and Bering Seas (Citta et al., 2017; Luque & Ferguson, 2010). EBS belugas begin their spring migration in March and April, often using leads in the sea ice (Asselin et al., 2012; Hornby et al., 2016). These seasonal patterns occur across a region undergoing rapid environmental change (Ershova et al., 2021; Howell et al., 2023), declining sea ice, and increasing industrial interest (Dawson et al., 2018; Van Pelt et al., 2017).

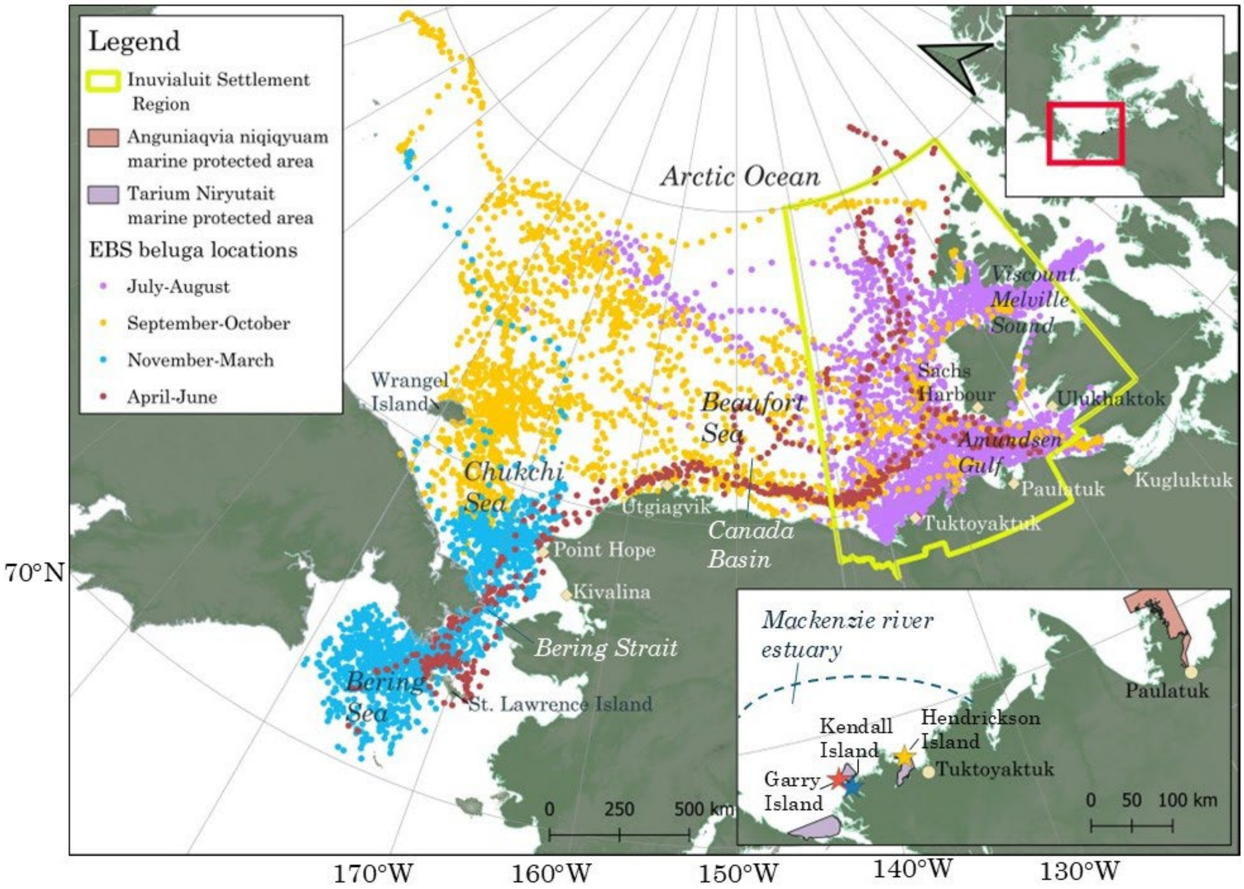

Figure 2.1 Annual range of the Eastern Beaufort Sea beluga population, shown with filtered locations from 45 belugas tagged between 1993 and 2019.

2.2.2 Collaborative research process and study co-design

The Eastern Beaufort Sea beluga population is co-managed by Fisheries and Oceans Canada (DFO) and Inuvialuit under the provisions of the Inuvialuit Final Agreement (IFA), which was signed in 1984 and formally recognizes Inuvialuit rights and responsibilities concerning fisheries and aquatic resources within the ISR (Doubleday, 2007; Keeping, 1989). Research and monitoring efforts in the ISR are shaped by a collaborative governance model that includes community-based Hunters and Trappers Committees (HTCs), the Inuvialuit Game Council, and regional co-management bodies such as the Fisheries Joint Management Committee and the Wildlife Management Advisory Council (Keeping, 1989). Cross-border coordination is facilitated through the Inuvialuit-Inupiat Beluga Whale Commission (IIBWC), established in 2000 as a means to share scientific research, observations and recommendations for EBS beluga management between resource users and co-management groups in the ISR and Alaska (Adams et al., 1993; Breton-Honeyman et al., 2021). Three satellite telemetry programs have been conducted on Eastern Beaufort Sea (EBS) belugas.

The initial telemetry program (1993-1997) was developed through collaborative discussions between researchers, co-management partners, and harvesters from the ISR and Alaska (Richard et al., 1997; Richard et al., 2001). Key objectives included quantifying movements between inshore and offshore habitats, assessing transboundary migrations across Canadian, Alaskan, and Russian waters, identifying potential overlap with neighboring beluga stocks, and developing surfacing correction factors to refine aerial abundance estimates (Duval, 1993; Richard et al., 1997, 1998). Tagging efforts in 1993 and 1995 were carried out at several different field sites before eventually selecting Hendrickson Island, NT, for future tagging operations (Richard et al., 1997). Additional tagging in 1997 targeted the fall period to better capture late-season movements given the short duration of transmitted location data (Richard et al., 1998).

A key priority of the second EBS beluga tagging program (2004-2005) was to determine the timing of spring arrival to the Mackenzie Estuary and the potential for overlap with industrial activities (Loseto, pers. comm). Tags were programmed to maximize longevity, enabling data collection across winter, spring, and early summer. In the early 2000s, the announcement of a new proposal for the Mackenzie Valley Pipeline triggered a series of assessments of the Beaufort Sea ecosystem (Cobb et al., 2008; Osadetz et al., 2005). Renewed interest in resource development in the Mackenzie Delta resulted in new funding streams to support telemetry research aimed at informing industrial and regulatory decision-making (Loseto, pers.comm).

The most recent EBS beluga tagging program (2018-2019) took place after the 2016 Beluga Summit in Inuvik, NT, where community members, researchers, managers, and co-management organizations collaboratively defined updated research priorities (Murray et al., 2023). Objectives of the 2018-2019 program included comparisons with previous tagging studies, and understanding the potential impacts of changes in prey distribution and increasing anthropogenic noise from vessel traffic on beluga behavior and movement patterns (MacPhee et al., 2025). The study design was refined through consultations with all six Inuvialuit communities, with particular attention to animal welfare and the potential impacts of tagging (MacPhee et al., 2024); this included initiatives to implement Inuvialuit Knowledge into the Animal Use Protocol (Storrie et al., 2025) and the development of new tools and deployment techniques to reduce handling effects during the tagging process (Scott, 2018).

2.2.3 Beluga instrumentation and data collection

Belugas were primarily tagged using live-capture methods, whereby animals were herded to shallow water, then captured using a hoop net around the head or by encircling the animal in a wide-mesh seine net (Orr et al., 2001; Richard et al., 2001; Storrie et al., 2022). Satellite transmitters were attached to the dorsal ridge using belts (Orr et al. 2001) or stainless-steel cables (Storrie et al. 2022), secured with nylon pins. In 2019, a remote deployment method was tested, whereby Inuvialuit research partners used a custom anchor and pole to attach telemetry devices to free-swimming whales (MacPhee et al., 2024, in prep.). Full details on tagging methods can be found in Richard et al. (2001) and Orr et al. (2001) for tags deployed between 1993 and 2005, and in Storrie et al. (2022) for tags deployed in 2018 and 2019.

Length, sex and calf presence (for females) were recorded during tagging operations on live-captured belugas, and sex was later verified using genetic analyses (Richard et al., 2001). Based on prior consultation with Inuvialuit research partners, each study strove to include both sexes and a range of body sizes and aimed to avoid females with calves to minimize disturbance (Loseto. pers. comm). Despite these efforts, the studies in the 1990s and 2000s resulted in the capture of several females with calves (Richard et al., 1998), while only males were instrumented in 2018 and 2019 (Table 2.1).

Table 2.1 Resolution and duration of available satellite telemetry data for belugas instrumented between 1993 and 2019. Telemetry devices that transmitted <=28 days were omitted.

Year	Location of tagging operations	# of belugas tagged			Resolution (x̄ points/ day)	Duration (x̄ days)
		Male	Female, w/ calf	Female, no calf		
1993	Garry & Hendrickson Island	2	0	0	8	62
1995	Hendrickson Island	10	0	3	10	39
1997	Hendrickson Island	6	1	2	8	83
2004	Hendrickson Island	4	0	1	3	270
2005	Kendall Island	0	1	1	5	221
2018	Hendrickson Island	8	0	0	46	210
2019	Hendrickson Island	6	0	0	45	64

Satellite tags deployed on belugas between 1993 and 2004 transmitted locations to polar-orbiting Argos satellites, after which locations were retrieved from the Argos platform (Hauser et al., 2014). Tags included a combination of SMRU 1, 2 and 3 types manufactured by the Sea Mammal Research Unit (SMRU; University of St. Andrews) or WC SPOT and WC SPLASH tags manufactured by the Wildlife Computers Ltd. (WC; Redmond, WA) (Richard et al., 2001; Hauser et al., 2014). From 1993-1997, tags were programmed to estimate up to four Argos locations per day, which resulted in most tags elapsing during the summer and fall, while tags from 2004-2005 were programmed to favour longer duration and improve understanding of winter movement and habitat use (Richard et al., 2001). For belugas instrumented in 2018 and 2019, SPLASH10-F238 and SPLASH10-F-321 tags estimated Argos locations during each transmission and were programmed to collect Fastloc-GPS locations every 7-30 minutes, each day from July until September or October; before switching to a lower resolution setting (collect Fastloc GPS locations every 7th day, and lower daily transmission limits) (see Storrie et al., 2022 for full details); several of these tags continued to record locations into the subsequent year. Location of tagging operations, telemetry devices used and tag deployment method for each whale are listed in the Supplemental material. Due to variations in available technology, study design, tag programming, and sex and age composition of instrumented belugas, available data varied among years and decades, including disparities in data resolution and duration (Table 2.1; Figure 2.2).

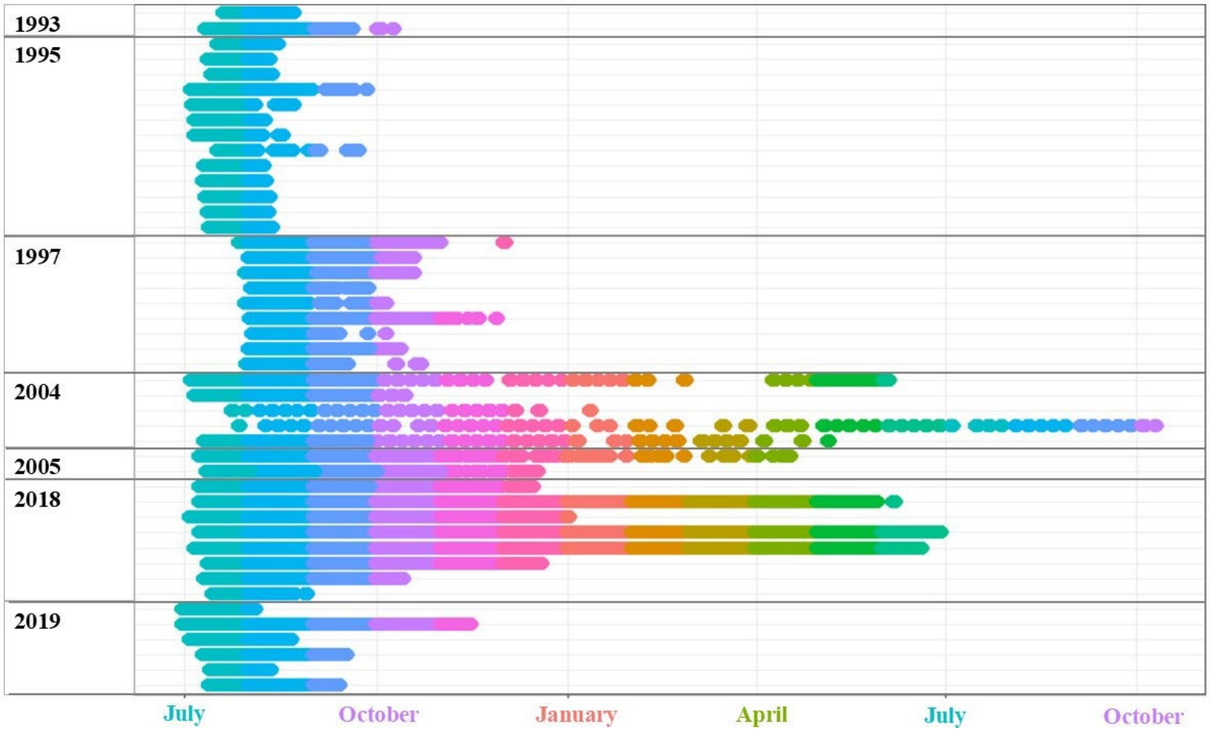

Figure 2.2 Resolution and duration of available satellite telemetry data for belugas instrumented between 1993 and 2019. Telemetry devices that transmitted <=28 days were omitted.

2.2.4 Pre-processing locations

Locations were first filtered to omit extreme outliers prior to fitting a state-space model (Freitas et al. 2008). For all years, we omitted locations with an Argos location class of "Z" which have undefined accuracy (Douglas et al., 2012). We also filtered unrealistic locations that occurred over land, while considering that EBS belugas can occupy shallow nearshore areas (Hauser et al., 2017; Mayette et al., 2022). To avoid omitting valid nearshore locations, we first applied a 1km buffer outside the Global Oceans and Seas boundary (Flanders Marine Institute, 2021), then used the *st_intersection* function from the *sf* package to omit locations that occurred outside the resulting polygon, i.e. > 1km inland from the coast.

To filter and regularise data while accounting for variable location quality, we fit a continuous time correlated random walk model using the *fit_ssm function* from the *aniMotum* R package (Jonsen et al., 2023). This model accounts for the accuracy of Argos location classes, Kalman smoothing and Fastloc-GPS error estimation when interpolating locations (Jonsen et al., 2005). Argos error locations can be influenced by the latitude at which a study is conducted (Christin et al., 2015) and by the dive behaviour of the study population (Irvine et al., 2020). Thus, we replaced the default Argos class error ratios with values derived from wild ringed seals and bearded seals in Svalbard (LC 3 = 920m, LC 2 = 1470m, LC 1 = 2670m, LC 0 = 4670m, LC A = 5070m, LC B = 5290m) (Lowther et al., 2015), which more closely approximated our study population than the default values included in the *aniMotum* package. We used a conservative Fastloc-GPS error estimate of 724m (Dujon et al., 2014) since most remaining GPS locations were estimated using 4 or more satellites.

The *fit_ssm()* function first applies a speed-distance-angle filter to remove unrealistic locations, i.e. impossible swimming speeds (> 5km) between locations and spikes deviating from the main track (Freitas et al., 2008). To remove only extreme outliers, we set the angle filter to NA and set the maximum speed filter to 15 m/s, exceeding the upper range of published values for swimming speeds of wild belugas in the Arctic (Richard et al., 1998, 2001). The state-space model was then used to interpolate remaining locations at a time step of 12 hours to match the resolution of the most sparsely sampled beluga.

Lastly, we calculated an error radius around each location using the horizontal and vertical standard error values ("x.se" and "y.se") estimated by the *fit_ssm* function. We used the formula $r = \sqrt{x.se \times y.se}$ yielding an area equivalent to the estimated error ellipse (Cusson et al., 2025). To omit highly unreliable locations resulting from fitting the state-space model across large data gaps, such as those associated with belugas instrumented in 2004-2005 (see Figure 2.2), we removed points with error radii >=100km. We retained all belugas with at least 28 days of locations (n=45).

2.2.5 Quantifying year-round space use

2.2.5.1 Quantifying relative space use

To quantify year-round space use for 45 belugas, we fit individual dynamic Brownian Bridge Movement Models (dBBMMs) which calculate the distribution of beluga occurrences in each cell on a raster grid, while accounting for the accuracy of individual tracks (Kranstauber et al., 2012). Compared to kernel density estimates (KDEs) and traditional Brownian Bridge Movement Models (BBMMs), dBBMMs provide more accurate space use estimates across varying sampling intervals and tracking regimes (Cohen et al., 2018; Joly et al., 2022; Peris et al., 2020). While KDEs calculate the occurrence distribution based on individual locations (Steury et al., 2010; Worton, 1987), BBMMs improve on this by modeling the movement path between locations, incorporating temporal structure and location error (Walter et al., 2011).

The dBBMM refines the BBMM approach by allowing the Brownian motion variance δ_m^2, which quantifies path diffusiveness, to vary along the movement path to account for behavioral changes (Kranstauber et al., 2012). This is especially appropriate for EBS belugas, which exhibit a range of resident, exploratory, and transiting behaviours throughout the year (Hauser et al., 2017; Storrie et al., 2023). The δ_m^2 is calculated using a leave-one-out method, connecting each first and third location and treating the middle location as an independent observation, then calculating the distance between the resulting path and the actual middle location (Horne et al., 2007). While BBMMs utilize a single δ_m^2 value over the entire trajectory based on the average of all available values (Horne et al., 2007), the dBBMM detects shifts in δ_m^2 over time, avoiding overly precise corridors along straight paths between distant locations, or excessively high δ_m^2 estimates when movements are localized (Kranstauber et al., 2012).

To fit the dBBMMs, we needed to select appropriate window and margin parameters. Changes in δ_m^2 are identified using a behavioral change point analysis inside a sliding window of width *w*, with margins of size *m* at each end of the window where no breakpoint is estimated (Kranstauber et al., 2012; Lai et al., 2015). Window size *w* should be biologically relevant and correspond to the temporal scale at which behavioral changes are likely to occur, although larger margins provide more power to identify breakpoints (Kranstauber et al., 2012). However, breakpoints are only estimated between the *m* and the *w-m* locations within the window (Kranstauber et al., 2012), incurring significant data loss at the start and end of each beluga's track if *w* and *m* are very large. To retain as much data as possible while ensuring that our analysis effectively captured year-round space use, we first ran our analyses using a *w* and *m* of 45 and 21 locations, respectively, then repeated this process while gradually decreasing *m* and *w*, selecting the smallest values that still reflected the same high-use areas as those obtained using the larger margin and window sizes. For our final analysis, we used a window size of 11 locations, corresponding to 5.5 days, which is biologically relevant to the study population given that individual EBS belugas typically remain in the Mackenzie Delta for less than a week at a time (Richard et al., 2001; Scharffenberg et al., 2025) and thus likely transition from relatively stationary to transient behaviour during that period. Since the model requires *w* to be at least twice the value of the margin *m*, we selected a margin size of 5 locations (2.5 days).

To fit a dBBMM for each individual beluga, we used the *move* package in R, specifying a raster resolution of 5 km^2 to account for the error associated with the least accurate (LC = 0, A or B) Argos locations, for which directional error can reach several kilometers (Lowther et al., 2015). To avoid excessively large error radii from fitting Brownian bridges across gaps, we only fit the dBBMM to continuous locations, using the *brownian.motion.variance.dyn()* function to first calculate the δ_m^2 for all locations before omitting instances where gaps between locations were > 48 hours, excluding these gaps from the final distribution (Kranstauber et al., 2024).

For 40 of the 45 belugas, tags elapsed prior to the spring migration. For these individuals, we fit a single dBBMM spanning the full duration of each track to capture behavioural variation across seasons (Kranstauber et al., 2012). For the remaining five individuals, which transmitted locations during the spring, we generated two models to separate fall and spring migration patterns, which can overlap spatially (Hauser et al., 2014; Storrie et al., 2022; Figure 2.1): The first dBBMM included locations from summer through winter, while the second included winter through spring (beginning in January, excluding July-December). Winter locations were included in both sets of dBBMMs to minimize data loss during the under-sampled spring season, as locations corresponding to *w-m* are omitted at the beginning and end of each track (Kranstauber et al., 2012). However, only the outputs from the first set of models (summer, fall, and winter) were combined with those of the other individuals to estimate winter space use in the Bering Sea.

2.2.5.2 Calculating combined occurrence distributions

To obtain an estimate of year-round space use for EBS belugas, we rescaled individual dBBMMs to a consistent temporal and spatial scale, then combined individual cell values from all belugas into a single raster, following the methodology outlined by Palm et al. (2015) to generalize individual-level dBBMMs to population-level estimates.

To ensure that the values in each raster represented time spent in each 5 x 5 km^2 cell on a consistent temporal scale, we rescaled the individual dBBMMs calculated by the *move* package, which are by default normalized so cell values sum to 1 for each beluga, and each cell value reflects the relative proportion of the beluga's time spent within the pixel after accounting for all locations, error radii and paths between locations. We obtained the duration (in days) of each beluga's track, then multiplied all cell values within each individual raster by the corresponding duration (Palm et al., 2015). This step was especially important given that track length varied considerably among belugas (from 28-365 days).

To ensure a consistent resolution and projection across all individual beluga occurrence distributions, we first used QGIS to create a reference raster encompassing the full spatial range of all pre-processed locations, including error radii. This raster was reprojected to an Albers Equal Area projection centered on the longest beluga track and set to a resolution of 5 km^2. We then resampled each individual beluga's rescaled occurrence distribution raster to match the extent, projection, and resolution of the reference raster using bilinear interpolation via the *terra* package in R, allowing for direct comparison and integration of spatial data across individuals.

Finally, we summed the rescaled individual occurrence distributions to generate a single raster representing cumulative space use. For the five individuals that transmitted location data during the spring, we repeated the same processing steps on a second set of occurrence distributions corresponding to the winter and spring migration period.

2.2.6 Examining seasonal high-use areas

2.2.6.1 Rescaling seasonal ranges

Because many tags stopped transmitting at different points in the year, more belugas contributed location data during the summer and fall than in winter or spring, resulting in higher occurrence values during earlier seasons. To reduce this bias, we divided the combined dBBMM into four seasonal segments, approximately corresponding to summer, fall, winter, and spring, and rescaled each segment separately. This approach has been used to examine high-use areas for other species with similar distribution (Citta et al., 2015) and ensured equal weighting across seasons despite variation in tracking duration among individuals.

To define appropriate boundaries for selecting these segments, we relied on current knowledge of EBS beluga seasonal distribution (Richard et al., 1997; Hauser et al., 2014; Storrie et al., 2022), selecting boundaries that typically correspond to migratory movements to avoid splitting inferred residency areas. The first boundary between regions was located at 150°W, corresponding to the deepest region of the Canada Basin (Mahoney et al., 2014), one of the main ecological barriers that EBS belugas cross during the fall and spring migrations (Hauser et al., 2014; Storrie et al., 2022). The second boundary was placed at 66°N, corresponding to the Bering Strait, which belugas cross in the late fall en-route to the Bering Sea, and again as they initiate their spring migration (Citta et al., 2017; Storrie et al., 2022). Using these boundaries, we clipped the combined summer-fall-winter raster into three regions: (A) east of 150°W (summer), (B) between 150°W and 66°N (fall), and (C) south of 66°N (winter). We then clipped the winter-spring raster along 66°N to obtain a fourth region (D), corresponding to spring migration north of the Bering Strait. The four regional raster images were normalized so that cell values summed to 1.

2.2.6.2 Calculating seasonal high-use areas

To obtain seasonal high-use areas for each region (A-D), we used the *raster.vol* function from the *SpatialEco* package in R to obtain the contours of the 25% and 50% occurrence distributions, selecting these values since these effectively delineated high-use areas for species with similar distribution to our study population (Citta et al., 2015).

To describe the sample size of belugas and timing of locations associated with regions A-D, we used the *dplyr()* package in R to subset pre-processed locations according to the established passage boundaries (see Supplemental material).

2.3 Results

2.3.1 Year-round space use

EBS belugas occupied regions between 59 and 79°N, and 103°W and 178°E, and one whale was tracked as far west as 154°E (Figure 2.3). Tagged belugas were dispersed over distances of 1170km while over the Arctic Basin. Relative beluga space use was highest in Viscount Melville Sound, followed by the Amundsen Gulf.

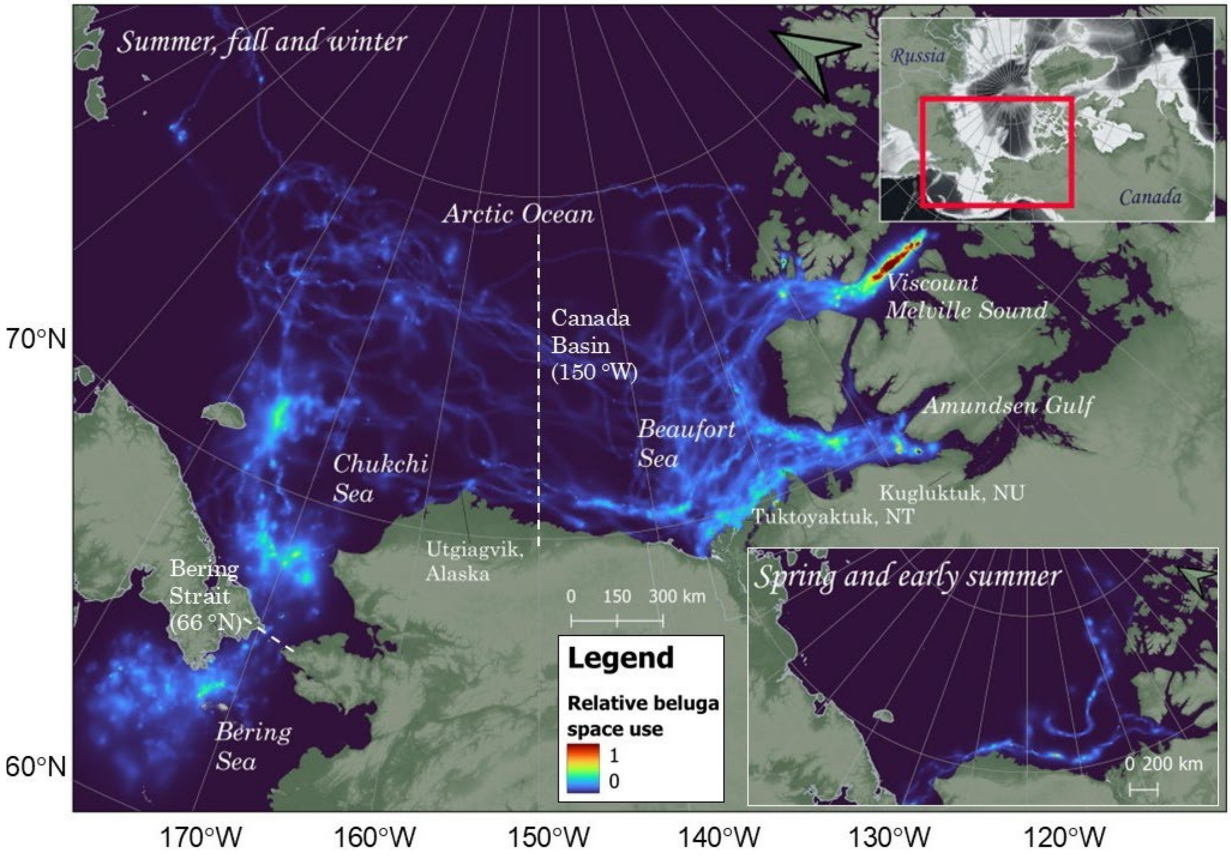

Figure 2.3 Space use estimates obtained by combining dBBMMs based on individual beluga locations, transmitted during summer, fall and winter (n = 45), and spring and early summer (n=5).

2.3.2 Seasonal high-use areas

The first region (Figure 2.4A), encompassing the time from tagging in July through the peak of the fall migration, included location data from 45 individuals which were transmitted between June and mid-October (Figure 2.5). The easternmost extent of the summer range was at

103°W in Viscount Melville Sound, while individuals in the southern part of the range in the Amundsen Gulf travelled as far west as 115°W, crossing into Nunavut waters. The northernmost summer location occurred at 78°N, corresponding to one individual that followed the continental slope before turning west. During this period, belugas were widely dispersed (Figure 2.4A), with 50% of the occurrence distribution spanning the Amundsen Gulf, Viscount Melville Sound, the Mackenzie Shelf, and the continental slope of the Beaufort Sea. High-use areas (25% of the occurrence distribution) included nearshore regions such as the Mackenzie Delta, Tuktoyaktuk Peninsula, Baillie Island, and southern Melville Island, as well as offshore areas along the continental slope and within the Amundsen Gulf. Viscount Melville Sound was identified as the most prominent high-use area, used by 21/45 tracked belugas.

The second region (Figure 2.4B) included data from 28 individuals (Figure 2.5). Belugas first began crossing the Arctic basin in August and the last belugas exited this region through the Bering Strait in mid-December (Figure 2.5). One individual travelled as far as 78.5°N and 139°E. The 50% occurrence distribution during this period included several small areas along deep-sea ridges and seamounts such as the Chukchi Plateau, Northwind Ridge, and the continental slope south of the Canada Basin. These offshore sites were typically used by single belugas, but two belugas tagged in different years targeted the same site in Barrow Canyon, adjacent to Utgiagvik, Alaska. Belugas were scattered across a large latitudinal gradient as they transited towards the Chukchi Sea from their summer range, but by late October and November, they converged in two regions east of Wrangel Island and north of the Bering Strait (Figure 2.4B), corresponding to Herald Canyon and the southern edge of the Chukchi Basin (Grebmeier et al., 2006). 25% of the occurrence distribution was concentrated in these two large areas, which were targeted sequentially by all individuals across all years of the study before continuing towards the Bering Sea, contrasting with the more dispersed summer and early fall distribution.

Throughout winter and early spring, belugas primarily occupied the Bering Sea (Figure 2.4C). Belugas began crossing South through the Bering Strait in mid-November and the last individual departed from this region in mid-May (Figure 2.5). High-use areas were located north and west of St. Lawrence Island, though some individuals ranged as far south as St. Matthew Island and along the Russian coast into the Gulf of Anadyr (Figure 2.4C). This region was calculated using data from 11 individuals, and the 95% occurrence distribution extended from 179°E to the West to 167°E to the East, and 60°N to the South. 50% and 25% of the occurrence distribution were concentrated at the center of this range (Figure 2.4C).

During their spring migration, belugas travelled back north through the Bering Strait into the Chukchi Sea, returning toward their summer range (Figure 2.4D). Belugas cross the 66°N boundary as they travelled South into the Chukchi Sea between mid-April and mid-May (Figure 2.5). Of the six individuals that transmitted locations during this period, four individuals were tracked in June as they followed the Alaskan coastline and dispersed shortly after reaching waters east of Utqiagvik. Of these, one travelled to offshore regions of the Amundsen Gulf, while three moved north, transmitting locations above 77°N (Figure 2.4D).

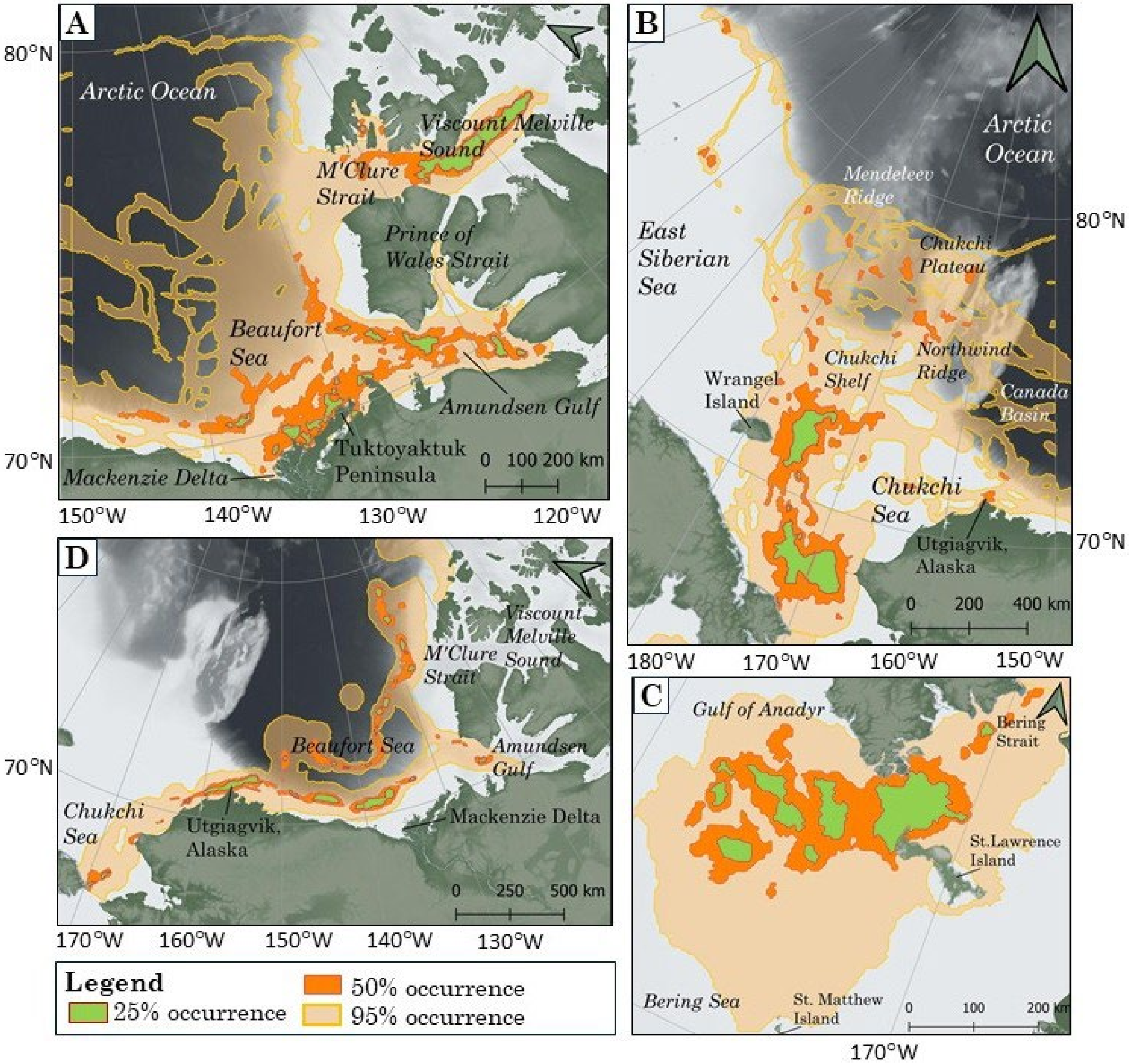

Figure 2.4 High use areas corresponding to 95%, 50% and 25% of occurrences during A) Summer and early fall, B) Fall and early winter, C) Winter and early spring, and D) Spring and early summer.

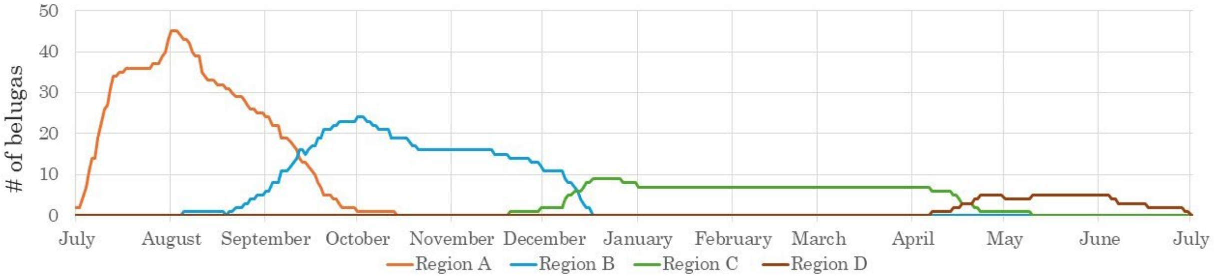

Figure 2.5 Number of belugas that transmitted locations in each region (A-D) over the course of the calendar year. The total number of belugas increased in July and August, since individuals were tagged on different days, and decreased as tags elapsed over time.

2.4 Discussion

This study describes year-round space use and seasonal high-use areas for Eastern Beaufort Sea (EBS) belugas, based on satellite telemetry data collected from 45 individuals tagged between 1993 and 2019. We used dynamic Brownian Bridge Movement Models (dBBMMs) to quantify individual space use, then rescaled and aggregated individual estimates to produce a representation of relative space use across the annual range. Belugas undertook large-scale movements which encompassed over 20 degrees of latitude and 100 degrees of longitude. High-use areas varied among individuals during summer, early fall, and late spring, whereas belugas aggregated more densely during late fall and winter. These findings reflect known fission-fusion social dynamics across several circumpolar beluga populations, whereby groups of belugas converge and diverge throughout the year (O'Corry-Crowe et al., 2020). Areas of relatively high beluga occurrence were evident during fall and spring migrations, suggesting stopover behaviour and supporting the notion that belugas rely on regions beyond established summer and winter residency areas to meet their resting and foraging needs (Storrie et al., 2023). Notably, belugas converged in two areas of the Chukchi Sea at the end of the fall migration, suggesting these regions serve key ecological roles in the annual cycle. Together, these findings describe a range of seasonal movements which extended spatially and temporally beyond those reported by individually published decadal datasets (Hauser et al., 2014; Hauser et al., 2017; Luque & Ferguson, 2010; Storrie et al., 2022) and delineate a network of ecologically important sites spanning the full migration of EBS belugas.

2.4.1 Ecological functions of seasonal high-use areas

2.4.1.1 Summer and early fall

During the summer, high-use areas in Viscount Melville Sound and the Amundsen Gulf contained bathymetric features and water temperatures aligned with the habitat requirements of adult Arctic cod *Boreogadus saida* (Geoffroy et al., 2023), the preferred prey of EBS belugas (Choy et al., 2020; Loseto et al., 2009). In particular, Arctic cod associate most strongly with depths of 350-500 m and temperatures of > 0° C along the Beaufort Sea slope (Majewski et al., 2016), and gadids dominated benthic trawls at similar depth ranges in Viscount Melville Sound (Bouchard et al., 2018). In previous studies, summer habitat selection (Hornby et al., 2017), dive behaviour (Storrie et al., 2022, 2025) and seasonal increases in blubber thickness (MacMillan et al., 2019; Ostertag et al., 2018) provide evidence for active foraging. Thus, the offshore summer habitats highlighted in our findings may play a key role in allowing belugas to access energy-rich prey (Choy et al., 2020) and rebuild energy reserves following the spring migration.

In contrast, nearshore habitats along the Tuktoyaktuk Peninsula and within the Mackenzie Delta likely support non-foraging activities such as calf-rearing, socializing, and moulting. Calves born in the spring and summer (Brown Gladden et al., 1999) benefit from the shallow, sheltered waters along the Tuktoyaktuk Peninsula where mother-calf pairs are known to occur in late summer (Waugh et al., 2018). Annual aggregations in the Delta (Harwood et al., 1996, 2015) appear to be driven more by social and physiological needs than prey availability, as harvested belugas often have empty stomachs (Harwood et al., 2002), despite occasional foraging observations (Ostertag et al., 2019). Acoustic recordings indicate high vocal activity in Kugmallit Bay, suggesting its importance for social interactions (Scharffenberg et al., 2025), while warm, turbid waters (Noel et al., 2022) and abrasive sediments (Whalen et al., 2020) provide conditions favorable for moulting. Together, these findings highlight a functional division between offshore foraging habitats and nearshore environments that support reproduction, social behaviour, and moulting.

2.4.1.2 Late fall

In the late fall, the 50% occurrence distribution included a series of regions used by single or multiple animals, which may represent stopover events or staging behaviour. Stopovers consist of interruptions of directional transit, often in response to resource availability (Alerstam et al., 2003; Dingle & Drake, 2007), and have been described across marine mammal species based on relatively localized movements during the migration period (Durban et al., 2023; Mayaud et al., 2025; Shuert et al., 2023).

Smaller high-use areas, typically targeted by single animals, were associated with deep benthic dives (Hauser et al., 2015; Storrie et al., 2022), where belugas could be targeting productive upwellings associated with prey availability (Gusev et al., 2017; Ren et al., 2020). In the Central Arctic Ocean, which includes a portion of the late fall range, sea ice cover has declined dramatically in the past decade (Ershova et al., 2021; Vylegzhanin et al., 2020), driving poleward shifts in the distribution of ice-dependent copepods, as well as Arctic cod (David et al., 2016; Ershova et al., 2021). Surveys in the CAO have revealed the presence of various fish species, although the density and diversity of potential beluga prey items varied among years and locations, and existing coverage of the region is relatively limited (David et al., 2016; Snoeijs-Leijonmalm et al., 2020; Turanov et al., 2025; Zhang et al., 2023). Some surveys detected Arctic cod (David et al., 2016; Turanov et al., 2025), suggesting that this region could contain energetically dense prey for EBS belugas to target during individual stopovers in the late fall.

The two regions delineated by the 25% occurrence distribution corresponded to Herald Canyon and the southern edge of the Chukchi Basin (Grebmeier et al., 2006), and were targeted sequentially by all individuals across all years of the study before continuing towards the Bering Sea. Fish assemblages in Herald Canyon prominently feature Arctic cod (Norcross et al., 2010), and both regions were associated with benthic dives to the relatively shallow (~50m) seafloor of the Chukchi shelf (Hauser et al., 2015; Storrie et al., 2022). These areas meet the definition of staging sites: stopovers where animals can reliably expect to encounter abundant resources, in which individuals frequent the area for several weeks in anticipation of an upcoming ecological barrier (Ma et al., 2013; Warnock, 2010). Since the central high-use area of the winter range is ~300 km further south, these sites may be critical for replenishing energy reserves after the Arctic Basin crossing and sustaining the journey to the Bering Sea.

While refueling is the most well-understood and thoroughly-studied driver of stopover behaviour (Alerstam & Lindström, 1990), stopover sites can serve a variety of other functions including recovering, waiting, information gathering and social interactions (Linscott & Senner, 2021). Group dynamics are especially likely in the two regions delineated by the 25% occurrence distribution, given that multiple belugas were present within a similar period. Belugas exhibited shallow dives that could indicate social behaviours (Storrie et al., 2022), and aerial surveys in the Chukchi Sea between the 1970s and 1990s reported groups of over 100 belugas around Wrangel Island beginning in October, which they ascribed to the EBS or Eastern Chukchi Sea population (Kochnev, 2003; Shpak et al., 2020). Together with the results of this study, these observations highlight the potential role of these late fall staging sites as aggregation areas to maintain communication and group cohesion. Further research on prey availability and beluga behaviour is needed to better understand the drivers of individual and collective stopover behaviour in the late fall.

2.4.1.3 Winter and early spring

During winter period spent in the Bering Sea, belugas exhibited characteristics of range residency, including relatively concentrated movements with greater overlap between individuals (Mueller et al., 2011). While belugas can navigate a broad range of sea ice conditions (Barber et al., 2001; Loseto et al., 2006), pack ice constrains winter movements (Citta et al., 2017; Luque & Ferguson, 2010). This could explain why the 50% occurrence distribution during the winter was less than half the size of the summer and fall, a pattern also observed in other circumpolar beluga populations (Luque & Ferguson, 2010). The more contracted southern distribution in recent years (2018-2019) may be influenced by lighter sea ice conditions (Thorson, 2019), which could enable greater use of the northern region of the Bering Sea (Suydam et al., 2001) compared to previous years (see Supplemental material for individual tracks). However, differences in sex or social group could also explain this interannual variation given the limited sample size of this study.

The winter is a highly social period, including the inferred mating season, which is believed to typically occur in winter and spring (Brown Gladden et al., 1999; Manitzas Hill et al., 2024). For many wild beluga populations, the estimated gestational period and breeding season are based on field observations of neonates, and vary among regions (Robeck et al., 2015). For example, belugas in western Greenland calve from April-May (Heide-Jørgensen & Teilmann, 1994) while those in Hudson Bay calve in July-August (Sergeant, 1973), similar to EBS belugas (Harwood et al., 2020). Although sociosexual behaviours have only been described in detail for captive animals (Hill et al., 2015), a peak in social communication signals occurred in December-January at a mooring placed near the southwest edge of the 50% contour detected in this study (Garland et al., 2015), supporting our findings that belugas congregate in this region. Belugas also forage throughout the winter, targeting a range of benthic and pelagic prey. In the 1990s and 2000s (Hauser et al., 2017) and 2018-2019 (Storrie et al., 2022) tagged belugas exhibited frequent benthic dives into the water column and close to the seafloor. While the compact size of the winter range may reflect socializing, mating, and foraging, the size of seasonal high-use areas is also likely influenced by the number of belugas transmitting locations, which was greater in the summer and early fall. Additionally, the exact duration and location of breeding activities could extend beyond this region, given the lack of direct observations of breeding behaviour.

2.4.1.4 Spring and early summer

Early spring movements appear linked to sea ice conditions (Harwood et al., 2020): In years with heavy ice cover, belugas often navigate toward their summer range through a system of leads stretching from Utqiagvik, Alaska, to Banks Island (Asselin et al., 2011; Fraker et al., 1978; Hornby et al., 2016), as displayed by two males in our study that followed this route in the spring of 2005. Under lighter ice conditions, belugas can follow the edge of the Mackenzie Shelf into Franklin Bay (Hornby et al., 2016; Asselin et al., 2012b), possibly selecting these habitats due to their higher productivity compared to adjacent open water. Three belugas in our study followed this route in spring 2019, when sea ice extent was especially low, with early and rapid breakup in the Beaufort Sea (Mokhov & Parfenova, 2021; Huang et al., 2022).

Our findings suggest that belugas target productive foraging areas during the latter portion of their spring migration. EBS beluga stomach contents from Diomede and Point Lay, Alaska, after beluga had departed from the Bering Sea, were dominated by benthic prey including shrimp and cephalopods, while Arctic cod was the most commonly ingested fish (Quakenbush et al., 2015), suggesting that belugas forage at various depths during the early spring migration. However, high-use areas identified in our analysis were concentrated in the late spring and summer, and included the deepest region of the Amundsen Trough, which reaches depths of 750 m (Jakobsson et al., 2020) and was heavily used by belugas during spring in the 1975-1979 surveys (Asselin et al., 2011). One individual exhibited highly localized movements along the continental slope after sea ice break-up had occurred (Trishchenko et al., 2022), suggesting prolonged use of a stopover site even when sea ice conditions permitted travel into the Delta. 3/4 belugas that transmitted locations until June travelled north of Banks Island, consistent with surveys carried out in the Beaufort Sea in the 1970s (Asselin et al., 2011; Fraker, 1979; Fraker et al., 1978). Behaviour along the continental slope and the region West of Banks Island (Storrie et al., 2022) suggests foraging activity during this period.

2.4.2 Function of key sites within the migration cycle

While EBS belugas have historically been described as migrants, they undertake a complex annual journey, exhibiting behaviours that transcend the classic definition of directed movements between discrete seasonal residency areas (Poole et al., 2024; Storrie et al., 2023; van de Kerk et al., 2021). Beyond the winter range, belugas exhibit foraging during directed transiting (Storrie et al., 2023), ranging and opportunistic stopover behaviour suggestive of nomadism (Storrie et al., 2023; Teitelbaum & Mueller, 2019), stopover and staging behaviour at predictable sites (Warnock, 2010), and a vast summer range structured around multiple sites fulfilling various ecological functions (Hauser et al., 2014; Storrie et al., 2022). Additionally, movement patterns varied between individuals. Atypical movement behaviour was apparent in the summer, where several individuals spent the majority of the season beyond the 25% and 50% high-use areas but within the 95% occurrence distribution, which extended east of the Beaufort Sea slope and included Prince of Wales Strait (Richard et al., 1997; Richard et al., 1998).

The annual migration of EBS belugas can be partially understood by multiple hypotheses that have been presented to explain the drivers of cetacean migration (Abrahms et al., 2019; Horton et al., 2011; O'Corry-Crowe et al., 2016; Pitman et al., 2020). The feeding-breeding hypothesis, which has been discussed primarily in the context of mysticetes, posits that whales migrate between productive foraging sites and warmer breeding habitats (Geijer et al., 2016). The skin molt hypothesis suggests that several cetacean species modulate their long-distance movements to seek optimal conditions for molting (St. Aubin et al., 1990; Fortune et al., 2017; Pitman et al., 2020). Seasonal variation in resource availability is perhaps the most widely-understood explanation, is a key driver of migration across taxa (Alerstam, 2011; Alerstam et al., 2003; Monteith et al., 2018). These three hypotheses are applicable to EBS belugas, given the annual journey to the winter breeding grounds (Citta et al., 2017), as well as the summer preference for prey-rich offshore habitats (Hauser et al., 2015; Storrie et al., 2025) and warm, shallow nearshore sites conducive to molting (Mayette et al., 2023; Noel et al., 2022; Whalen et al., 2020), where warm, sheltered bays offer benefits for calves during the summer (Mayette et al., 2023; Waugh et al., 2018) but become inhospitable in the winter due to encroaching sea ice (Citta et al., 2017; S. R. Noren & Suydam, 2016). However, these hypotheses frame EBS beluga migration solely in terms of summer feeding and winter breeding, and overlook key habitats between these residency areas. In our study, belugas demonstrated behaviour reminiscent of nomadic movement patterns, in which animals respond to heterogenous resource availability (Storrie et al., 2023; Teitelbaum & Mueller, 2019). Belugas revisited sites with predictable foraging opportunities across seasons, including repeated use of a continental slope stopover in fall and spring, and recurrent visits to the Amundsen trough during summer and spring migration. Several other cetacean populations balance real-time responses to ephemeral resources with fidelity to reliable sites. Humpback whales make repeated use of stopovers during their migration in the southern hemisphere (Castrillon et al., 2023), utilizing specific sites for socializing among juveniles while others primarily feature resting mother-calf pairs (Mayaud et al., 2025). Killer whales gather to feed on gray whale calves during the spring, departing from the area earlier in years with fewer calves (Durban et al., 2023). In our data, EBS belugas used multiple types of stopovers, highlighting their integral role in maintaining both energetic and social needs throughout the journey.

Understanding the EBS beluga annual migration also requires considering carry-over effects, whereby conditions experienced at one site influence behavior, physiology, and survival at subsequent sites (Harrison et al., 2011; Norris & Taylor, 2005). Cetaceans exhibit carry-over effects from various energetically costly events; entanglement in fishing gear impacts the 4-year reproductive energy budget of North Atlantic right whales (van der Hoop et al., 2017), the fecundity of female northern resident killer whales *(Orcinus orca)* is impacted by prior availability of chinook salmon (Ward et al., 2009), and poor summer foraging conditions impacted calving success during the subsequent winter for gray whales (*Eschrichtius robustus*) (Perryman et al., 2002). For belugas, blubber plays a key role in buoyancy and thermoregulation (Ball et al., 2017), and a decline in individual blubber stores could later impact fitness and foraging success (Choy et al., 2019). Indeed, belugas require substantial energetic intake to meet their daily needs (John et al., 2024), and forage year-round (Belanger et al., 2025; Storrie et al., 2023). The use of multiple stopovers, including both opportunistic and reliable sites, demonstrates that each habitat contributes not only to immediate energy needs but also to maintaining social cohesion and reproductive success throughout the year. Foraging success during spring and early summer at sites such as the Mackenzie Trough or areas west of Banks Island likely affects blubber thickness and body condition during the summer, when belugas are harvested in the Inuvialuit Settlement Region (Harwood et al., 2002; Ostertag et al., 2018), while conditions at fall stopover sites could impact beluga's ability to socialize at aggregation areas in the Chukchi Sea (Kochnev, 2003) or reproduce during the winter breeding season (Citta et al., 2017). Because EBS belugas exhibit complex social organizations, including multiple levels of group structures that converge and diverge throughout the year (Mayette et al., 2022; O'Corry-Crowe et al., 2020), individual variation in body condition can also have cascading effects on group dynamics and potentially on population-level outcomes (Choy et al., 2019). Consequently, effective interpretation of beluga movement ecology, and the potential impacts of environmental change or anthropogenic stressors, necessitates accounting for the full network of habitats across the migratory cycle, rather than focusing solely on summer or winter residency areas.

2.4.3 Limitations

The analysis in this study is based on a small sample of belugas (n = 45; <1% of the estimated 38,500 in 2019; Marcoux et al., 2025), biased toward adult males tagged near Hendrickson Island, NT, in early July. While small samples are common in marine mammal telemetry studies (median = 15; McIntyre, 2014), robust inference ideally requires ≥20 individuals per population stratum such as age, sex, or social group (Roberts et al., 2018). The high cost of satellite telemetry tags (Hebblewhite & Haydon, 2010), the labour-intensive live-capture methods (Orr et al., 2001), the potential effect of capture and handling on belugas (MacPhee et al., 2025; Walker et al., 2011), and the remoteness of the EBS summer range

(Hauser et al., 2014) limit deployments using current methods. Consequently, this dataset precludes some well-established summer movement patterns, such as belugas that frequent Darnley Bay each summer, documented via aerial surveys (Ovitz et al., 2025), drone-based behavioral studies (Fisheries and Oceans Canada, 2025) and decades of harvest monitoring near Paulatuk, NT. Two whales in this study were tagged remotely using a harpoon deployment method developed with the Inuvialuit (Scott, 2018), showing promise as a minimally invasive sampling approach. Future work could use these tools to include individuals that summer outside the Delta, belugas that aggregate earlier and later in the season, and, perhaps most notably, females, to better capture heterogeneity within the EBS beluga population.

Our analyses were further complicated by variations in location accuracy, data resolution and track length between individuals and seasons. Dynamic Brownian Bridge Movement Models (dBBMM) are sensitive to location accuracy, and Argos data produce larger home range estimates using dBBMMs than Fastloc-GPS (Kale et al., 2025). While we mitigated this by using a raster resolution which exceeded the estimated error for most Argos locations (Kranstauber et al., 2024), and omitting the Brownian motion variance for gaps >48 h to avoid inflated error radii (Kranstauber et al., 2024), the winter and spring featured larger individual dBBMMs as a result of smaller samples sizes and relatively more Argos data and location gaps than earlier seasons. Despite these caveats, dBBMMs present several advantages over kernel density estimates (Hauser et al., 2014), including autocorrelation-adjusted versions (Alston et al., 2022), which assume range residency and were thus unsuitable for the migratory movements examined in this study (Horne et al., 2007; Kale et al., 2025; Silva et al., 2022). To account for variable track lengths, we rescaled individual dBBMMs to standardize the units of beluga-time spent within each grid cell while integrating location accuracy and paths between locations (Palm et al., 2015) and calculated relative space use separately for four biologically relevant areas broadly corresponding to seasonal ranges (Citta et al., 2015). These adjustments allowed us to overcome common limitations of long-term datasets with evolving telemetry technologies to reveal key sites not apparent in single-year or single-individual analyses. This approach could be applied to other study populations to synthesize long-term telemetry datasets and facilitate the identification of critical habitats.

2.4.4 Future directions

The high-use areas described in this study provide a basis to examine potential overlap with anthropogenic stressors. The summer and fall ranges of EBS belugas overlap with key shipping corridors along the Alaska coast, where maritime activity, driven in part by the expanding Arctic tourism industry, is expected to grow (Dawson et al., 2018). Summer shipping activity has increased substantially in recent years given the potential of the Northwest Passage as a key route for cargo, tourism, and fisheries (Dawson et al., 2018). Interest in fossil fuel development persists in the Mackenzie Delta, where oil and gas reserves have been assessed and various projects have been proposed since the 1970s (Dewing et al., 2025a). Commercially viable species are present in the CAO (David et al., 2016; Zhang et al., 2023), prompting international collaboration to manage potential industrial fishing in the region (Molenaar, 2024).

While existing studies focus the overlap between beluga habitat, environmental change, and anthropogenic stressors in the summer range (Loseto et al., 2018; Martin et al., 2021; Storrie et al., 2025), we recommend that future efforts examine these factors across the migration cycle, especially with respect to key habitats between the summer and winter ranges. The existence of inferred staging areas in the Chukchi Sea, as well as repeated use of stopovers along the continental slope of the Beaufort Sea in the spring and fall, highlight the relevance of delineating key habitats that influence individual and population health beyond known breeding and feeding areas (Castrillon et al., 2023; Sheehy et al., 2011).

2.4.5 Conclusion

This study integrates satellite telemetry from 1993-2019 to present an overview of year-round EBS beluga distribution, establishing a baseline for assessing future changes. The dataset used in this study represents an achievement in collaborative research, as the study design and tagging program were executed by a broad team including Inuvialuit harvesters, co-management partners and knowledge holders (Murray et al., 2023; MacPhee et al., 2024). Our findings support the development of long-term monitoring strategies and contribute to ongoing efforts to assess the effects of climate change and industrial activity on Arctic marine ecosystems (Dawson et al., 2018; Dewing et al., 2025a; Molenaar, 2024). This study underscores the value of analyzing the full multi-year satellite tracking dataset for EBS belugas as an integrated whole, and highlights the potential of this method for uncover collective space-use patterns and identify key habitats for mobile populations, contributing to more effective wildlife management under a changing climate (Calvert et al., 2009; Klaassen et al., 2008; Norris, 2005).

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2.6 Supplemental material

Table S2.1 List of belugas included in the study (all individuals with >28 days of available locations).

ID	Sex, Calf	Length (m)	Tagging date	Duration (days)	Tagging location	Tag type
002118-01	F	3.74	1997-07-26	128	Hendrickson Island	WC ST-10
005800-01	M	4.67	1995-07-15	29	Hendrickson Island	SMRU2
005801-01	M	4.06	1995-07-12	30	Hendrickson Island	SMRU2
008754-01	F	3.63	1995-07-13	29	Hendrickson Island	SMRU 2
008754-02	M	4.05	1997-07-31	80	Hendrickson Island	SMRU 3
008755-01	M	4.00	1997-07-29	81	Hendrickson Island	SMRU3
008756-01	F	3.62	1997-08-01	56	Hendrickson Island	SMRU3
008757-01	M	3.79	1997-07-30	68	Hendrickson Island	SMRU 3
008758-01	M	4.21	1997-07-31	119	Hendrickson Island	SMRU 3
010692-01	F,Y	3.38	1997-08-01	64	Hendrickson Island	SMRU 2
010693-01	M	3.95	1997-07-31	73	Hendrickson Island	SMRU 2
017001-01	M	4.27	1995-07-04	78	Hendrickson Island	SMRU1
017002-01	M	4.57	1993-07-17	33	Garry Island	SMRU 1
017002-02	M	4.04	1995-07-05	45	Hendrickson Island	SMRU1
017004-01	M	3.73	1995-07-05	34	Hendrickson Island	SMRU1
017005-01	M	4.42	1993-07-10	90	Garry Island	SMRU 1
017005-02	M	4.04	1995-07-05	42	Hendrickson Island	SMRU1
017007-01	F	3.73	1995-07-08	68	Hendrickson Island	SMRU1
017010-01	M	3.99	1995-07-09	29	Hendrickson Island	SMRU2
017011-01	M	4.02	1995-07-10	30	Hendrickson Island	SMRU2
017012-01	M	4.04	1995-07-10	29	Hendrickson Island	SMRU2
017013-01	M	4.02	1995-07-12	30	Hendrickson Island	SMRU2
017014-01	F	3.40	1995-07-13	30	Hendrickson Island	SMRU2
025846-01	M	3.74	1997-07-29	84	Hendrickson Island	WC ST-10
04-10899	M	3.70	2004-07-04	336	Hendrickson Island	WC SPOT
04-10972	F	3.00	2004-07-05	101	Hendrickson Island	WC SPOT
04-36641	M	4.00	2004-07-08	172	Hendrickson Island	WC SPOT
04-37023	M	3.9	2004-07-08	440	Hendrickson Island	WC SPOT
04-37024	M	4.40	2004-07-06	300	Hendrickson Island	WC SPOT
05-57591	F,Y	2.75	2005-07-06	284	Kendall Island	WC SPLASH
05-57593	F	3.50	2005-07-11	159	Kendall Island	WC SPLASH
174962	M	4.06	2018-07-06	160	Hendrickson Island	SPLASH10-F-238
174963	M	4.44	2018-07-08	334	Hendrickson Island	SPLASH10-F-238
174964	M	4.25	2019-06-30	35	Hendrickson Island	SPLASH10-F-238
174965	M	4.20	2018-07-03	182	Hendrickson Island	SPLASH10-F-238
174966	M	4.40	2018-07-08	356	Hendrickson Island	SPLASH10-F-238
174967	M	4.70	2018-07-04	348	Hendrickson Island	SPLASH10-F-238
174969	M	4.25	2018-07-09	156	Hendrickson Island	SPLASH10-F-238
174972	M	4.20	2019-06-29	139	Hendrickson Island	SPLASH10-F-238
174976	M	4.06	2019-07-03	49	Hendrickson Island	SPLASH10-F-238
174978	M	3.70	2018-07-09	95	Hendrickson Island	SPLASH10-F-238
174282	M	4.34	2018-07-12	45	Hendrickson Island	SMRU CTD-SRDL
179901	M	4.20	2019-07-10	69	Hendrickson Island	SPLASH10-F-321
179902	M	NA	2019-07-13	29	Hendrickson Island	SPLASH10-F-321 (Remote deployment)

179915	UNK	NA	2019-07-12	63	Hendrickson Island	SPOT torpedo (Remote deployment)

Table S2.2 Date of each beluga's first location after crossing the 150□W and 66□N boundaries during their fall migration and again in the spring. Empty cells indicate that the beluga's tag elapsed before they could cross the boundary.

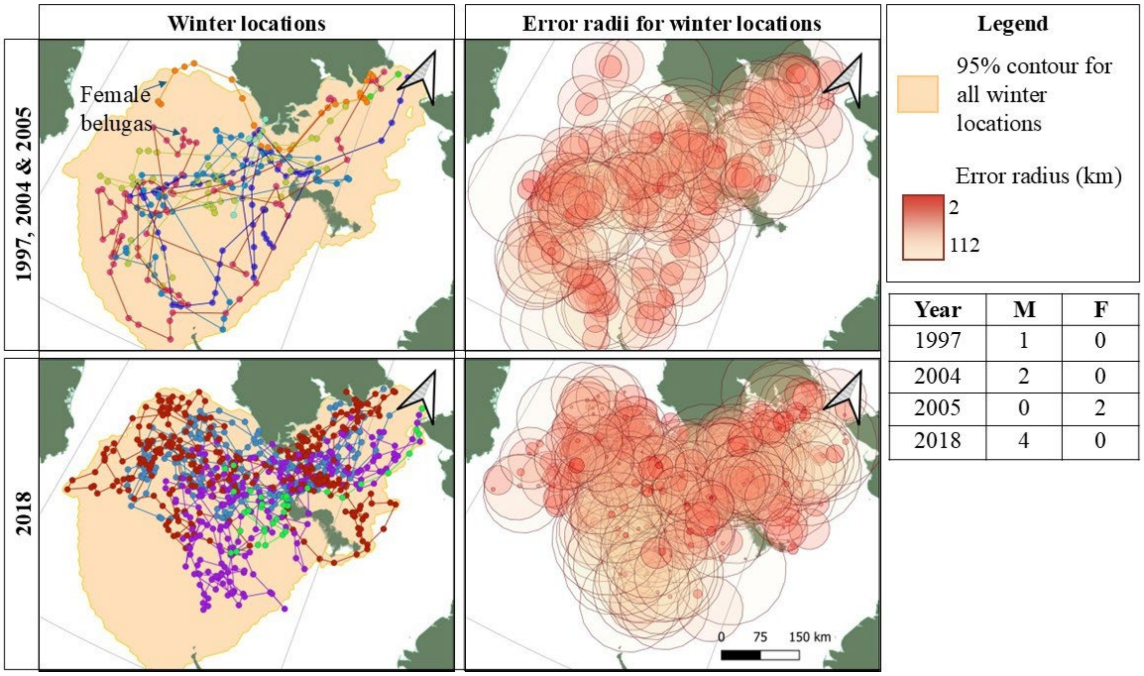
ID	First location after passing boundary			
	150°W (Fall)	66°N (Fall)	66°N (Spring)	150°W (Spring)
002118_01	1997-09-11			
008754_02	1997-09-18			
008755_01	1997-09-25			
008757_01	1997-09-19			
008758_01	1997-09-15	1997-11-27		
010692_01	1997-09-12			
010693_01	1997-09-10			
017001_01	1995-09-06			
017002_01	1993-08-05			
017005_01	1993-10-01			
017007_01	1995-09-20			
025846_01	1997-09-12			
04_10899	2004-09-03	2004-12-09	2005-04-21	2005-05-06
04_10972	2004-09-18			
04_36641	2004-08-29	2004-12-17		
04_37023	2004-08-27	2004-12-08	2005-04-14	2005-05-24
04_37024	2004-09-16	2004-12-11	2005-04-23	
05_57591	2005-09-06	2005-11-30		
05_57593	2005-09-23	2005-11-20		
174962	2018-09-01			
174963	2018-09-17	2018-12-15	2019-04-07	2019-04-30
174965	2018-09-09	2018-12-14		
174966	2018-09-06	2018-12-17	2019-04-17	2019-04-30
174967	2018-10-14	2018-12-08	2019-05-10	2019-05-22
174969	2018-08-25			
174972	2019-09-03			
175278	2018-08-20			
179901	2019-08-22			

Table S2.3 Sample size, and earliest, mean and latest dates of locations transmitted inside each region as defined in Figure 2.3.

Region	Sample size (# of belugas)	Date of transmitted locations		
		Minimum	Mean	Maximum
A	45	June 30th	July 19th	October 14th
B	28	August 5th	October 13th	December 16th
C	11	November 27th	February 7th	May 9th
D	6	April 7th	May 19th	June 29th

Table S2.4 Number of belugas, range of dates, and area of the 25% and 50% volume contours for each region as defined in Figure 2.3. Note that these values are likely skewed by differences in sample sizes and larger error radii which yield larger regions winter and spring regions.

Region	Sample size (# of belugas)	Area of 25% occurrence (km^2)	Area of 50% occurrence (km^2)
A	45	30 909	114 393
B	28	38 767	137 021
C	11	18 196	52 473
D	6	27 105	92 164



Year	M	F
1997	1	0
2004	2	0
2005	0	2
2018	4	0

Figure S2.1 Winter locations and error radii for the early period of the study (1997, 2004 and 2005) and the later period (2018). Differences between years do not appear to be due to variations in movement patterns between males and females.

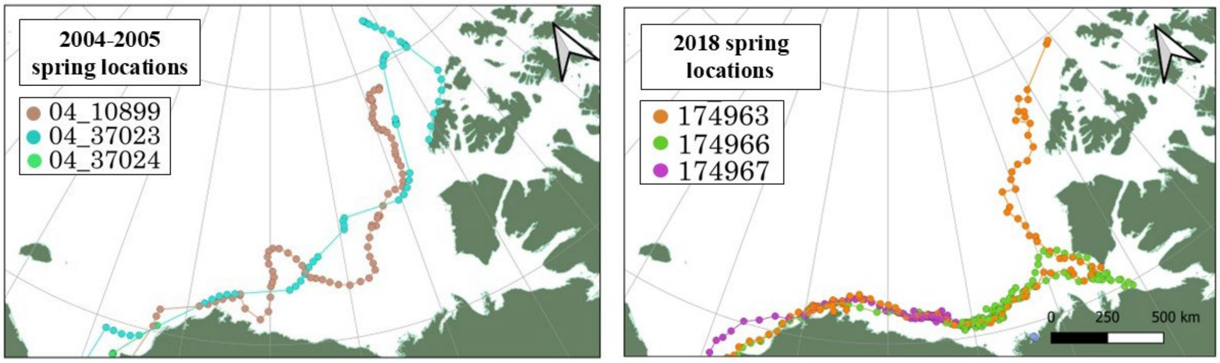


Figure S2.2 Spring locations for the early period (spring 2005) and the later period (spring 2019).

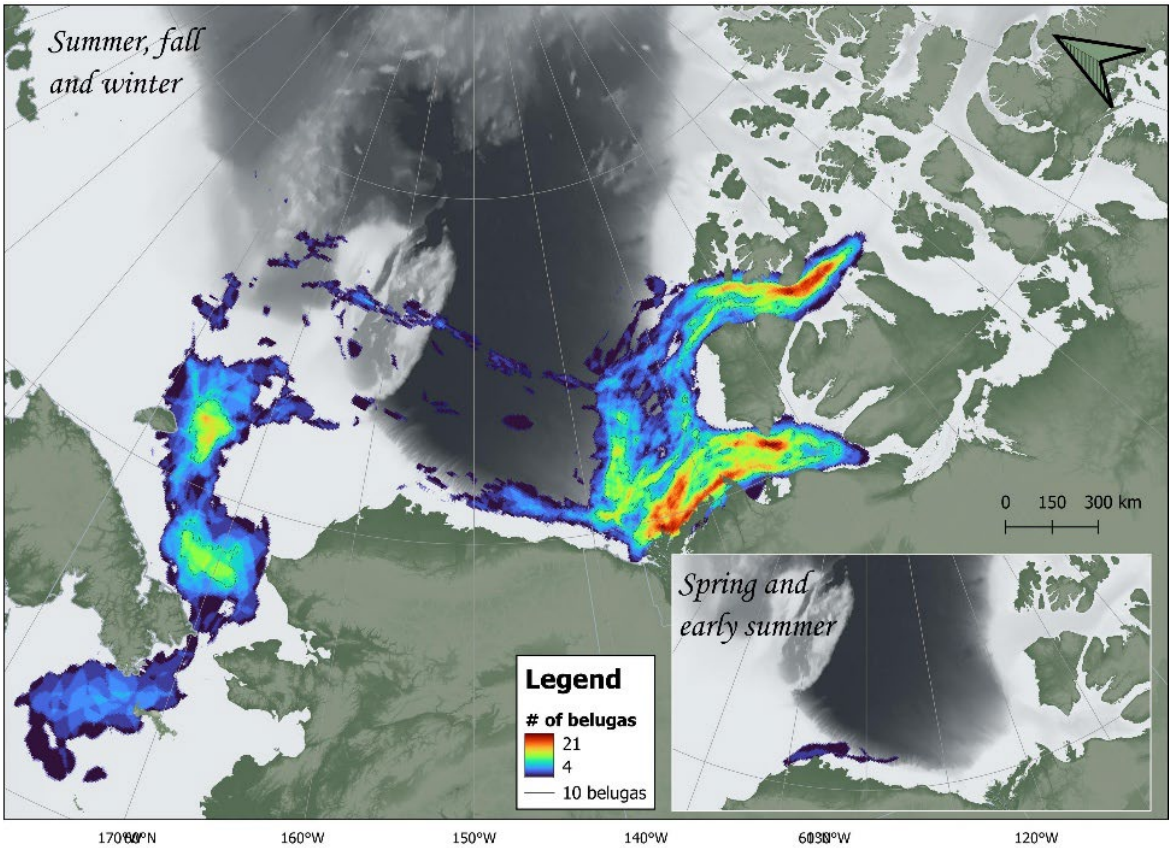


Figure S2.3 Overlap approach to examining key areas, presented for comparison.

An alternate approach used in several recent publications (Buechley et al., 2018; Cusson et al., 2025; Masilkova et al., 2025) to examining population-level space use using dBBMMs consists of aggregating seasonal ranges by overlapping the polygons representing the 95% contours for each animal to determine the number of individuals that intersected each pixel in the overall area. However, this approach does not consider relative space use within the 95% contours.

Chapter 3: Sub-population structure influences summer space use and fall migration timing in a highly gregarious Arctic cetacean

Abstract

Intra-population differences in movement behaviour are common in wildlife yet often overlooked in ecological analyses. Beluga whales *(Delphinapterus leucas)* from the Eastern Beaufort Sea (EBS) population are highly mobile outside the migration season, congregating in the warm, shallow waters of the Mackenzie Estuary, NT each summer before dispersing across a vast summer range. Here, we combine satellite telemetry data from 26 EBS belugas instrumented in the Mackenzie Estuary between 1993 and 2019 to examine inter-individual variation in summer space use and link it to fall migration timing. We clustered individuals with similar horizontal summer movements, then employed dynamic Brownian Bridge Movement Models (dBBMMs) to quantify summer space use and define key summering areas. The Viscount Melville Sound (VMS) group was composed exclusively of large males and left the Mackenzie Estuary by mid-July, before traveling directly to a single core area along the central trough of Viscount Melville Sound and remaining there for 2-6 weeks. In contrast, the Amundsen Gulf (AG) group included 5/6 females and all three females with calves in the study, while the Beaufort Basin (BB) group included both males and females. Belugas in both the AG and BB groups travelled extensively between multiple near-shore and offshore areas, and belugas in the AG group departed from the Mackenzie Estuary and initiated their fall migration latest. These findings suggest that ecologically diverse summer habitats support the life-history requirements of multiple groups, each with distinct physiological constraints and social dynamics. This study underscores the broader importance of considering sub-population structure when making inferences about space use or migration timing in highly mobile and social wildlife populations.

3.1 Introduction

Many Arctic marine species spend most of their lives in remote or offshore habitats (Citta et al., 2018; Hussey et al., 2015; Sequeira et al., 2025) experiencing climate change at roughly four times the global average rate (Rantanen et al., 2022). In such contexts, where direct observation is challenging or impossible, animal tracking has become an essential tool for understanding wildlife behaviour (Hart & Hyrenbach, 2010; Hussey et al., 2015). Advances in satellite telemetry tools have amplified our understanding of animal movement at ever-increasing spatial and temporal scales (Wilmers et al., 2015), providing valuable insights into how movement is shaped by intrinsic factors and external drivers (Barnowe-Meyer et al., 2013; Davidson et al., 2020). However, some species, including many marine mammals, remain challenging to track in large numbers due to logistical constraints or ethical considerations (Papastavrou & Ryan, 2023; Shuert et al., 2021; Walker et al., 2011). In these cases, small sample sizes may limit population-level inference (Hebblewhite & Haydon, 2010; Sequeira et al., 2019) and obscure important inter-individual variation by assuming that movement is homogeneous across individuals (Hart & Hyrenbach, 2010; Seigle-Ferrand et al., 2021). Emerging analytical methods (Barbour et al., 2023; Kranstauber et al., 2012; Pasquaretta et al., 2021) and increasingly detailed tracking datasets (Czapanskiy et al., 2021; Seidel et al., 2018) are enhancing our ability to quantify and interpret variation in movement behaviour (Carneiro et al., 2017; Hertel et al., 2020).

Within wildlife populations, individuals or social groups exhibit diversity in space use and movement behaviour (Shaw, 2020). This variation can arise from differences in physiology (Webber & McGuire, 2022), reproductive status (Craig et al., 2003), social structure (Aikens et al., 2022; Guttal & Couzin, 2010), and learned behaviours (Jesmer et al., 2018; McComb et al., 2001; Slotte et al., 2025), as well as from external pressures such as prey availability (Abrahms et al., 2019; Owen et al., 2015; Strandberg & Alerstam, 2007), competition (Drent et al., 2003), and predation risk (Breed et al., 2017). Inter-individual variation can occur at different stages of the year or migration cycle (Shaw, 2020), and movements within seasonal residency areas, or conditions encountered prior to departure, can influence subsequent migration timing (Bailleul et al., 2012; Monteith et al., 2011). Sub-population groups originating from distinct summering areas may be exposed to different environmental cues, such as snowfall or sea ice formation, that influence the onset of migration (Cherry et al., 2013; Schwemmer et al., 2021), contributing to variation in migratory phenology (Lameris et al., 2021). Many mammals are highly mobile outside the migration period (Avgar et al., 2014), and sub-population structuring during the seasonal residency period has been observed in several Arctic cetaceans, with groupings that persist across subsequent migrations (Bailleul et al., 2012; Harwood et al., 2017; Heide-Jørgensen et al., 2002; Mate et al., 2000). Within these populations, diverse behavioural strategies may allow individuals to better align with local conditions (Masilkova et al., 2025), enhancing fitness and fostering resilience at the population level (Hertel et al., 2021; Shaw, 2020).

The Eastern Beaufort Sea (EBS) beluga (*Delphinapterus leucas*) population forms large summer aggregations in the Mackenzie Estuary, NT (Harwood & Smith, 2002; Stafford et al., 2018b). During the summer, EBS belugas disperse vast distances across a seasonal range that spans over 750,000 km^2 across a broad bathymetric and latitudinal gradient (Hauser et al., 2017; Storrie et al., 2022, 2025). This region supports key life-history functions including calf rearing and moulting (Noel et al., 2022; Scharffenberg et al., 2025; Waugh et al., 2018), as well as foraging to replenish energy reserves following spring migration (Ostertag et al., 2018) and in preparation for the fall migration to the Chukchi and Bering seas (Hauser et al., 2014; Richard et al., 2001; Storrie et al., 2022). Arrival to the summer range occurs in pulses, suggesting the presence of distinct sub-groups within the population (Scharffenberg et al., 2019; Stafford et al., 2018). Individual belugas also differ in summer habitat use depending on sex, age, and calf presence (Hauser et al., 2017; Loseto et al., 2006; Richard, Heidi-Jørgensen, et al., 2001). Given this variability and the heterogeneity of the summer environment (Hauser et al., 2017; Storrie et al., 2025), EBS belugas likely employ diverse strategies to optimize resource use and prepare for migration, shaped by both individual traits and social dynamics (Choy et al., 2019; O'Corry-Crowe et al., 2020).

Differences in the summer distribution of EBS belugas may influence the timing of fall migration. Variation in the timing of summer movements is apparent: while most belugas typically exit the Mackenzie Estuary by August, others remain into late September (Harwood & Kingsley, 2013; Scharffenberg et al., 2025). Some belugas later travel to high-latitude offshore regions during summer, presumably to access highly productive foraging habitats (Hauser et al., 2017; Richard et al., 2001; Storrie et al., 2025). These northern areas of the Northwest Passage are characterized by a shorter open-water season and more persistent sea ice compared to the Beaufort Shelf and surrounding offshore waters (Bliss et al., 2019; Johnson & Eicken, 2016; Shen et al., 2021), suggesting that belugas occupying different summering areas are exposed to distinct migration cues. Together, these patterns highlight knowledge gaps in the relationship between summer space use and fall migration timing in EBS belugas. To address this gap, the objectives of this study were to 1) assess variation in summer space use and 2) examine how this variation influences fall migration timing.

In this study, we analyzed satellite telemetry data from 26 Eastern Beaufort Sea (EBS) belugas instrumented between 1993 and 2019 in the Mackenzie Estuary, NT. We hypothesize that EBS belugas segregate into distinct summering groups, shaped by individual traits such as body size, sex, and calf presence. We further predict that these summer groups occupy different areas of the summer range, potentially experiencing different environmental or social cues which influence fall migration timing. Finally, we expect that the timing of summer and early fall movements, including departure from the Mackenzie Estuary and the beginning of the fall migration, will differ among summering groups. By accounting for sub-population structure, this study offers new insights into EBS beluga movement behaviour in the pre-migration season.

3.2 Methods

3.2.1 Study area

This study examines the summer movement patterns of EBS belugas across a broad range (Figure 3.1) that spans from the Beaufort Sea continental shelf to inshore bays of the Amundsen Gulf and extends northward to Prince Patrick Island and Viscount Melville Sound (69.4°N-74.4°N, 114.8°W-141°W) (Hauser et al., 2014; Storrie et al., 2025). The Mackenzie River discharges warm, fresh water into the Mackenzie Estuary (Carmack & Macdonald, 2002; Lee et al., 2025), creating a gradient of temperature, turbidity, and chlorophyll-a that extends into the eastern Beaufort Sea (Hilborn & Devred, 2022). Across the summer range, depths span from 1-2 m in the nearshore to over 3500 m in the Beaufort Basin, with intermediate-depth troughs (300-600 m) and steep bathymetric slopes (>10°) found in areas like the Amundsen Gulf, M'Clure Strait, and Viscount Melville Sound (Carmack & Macdonald, 2002; Jakobsson et al., 2020; Storrie et al., 2025). Sea ice cover follows a latitudinal gradient, with ice-free periods lasting several weeks longer in the southern parts of the range near the Mackenzie Estuary compared to northern regions like Viscount Melville Sound (Galley et al., 2008; Howell et al., 2023; Shen et al., 2021). The summer diversity of summer habitat features plays a key role in the annual life history of EBS belugas (Mayette et al., 2023; Waugh et al., 2018) due to these gradients in depth, bathymetry, sea ice, and oceanographic conditions.

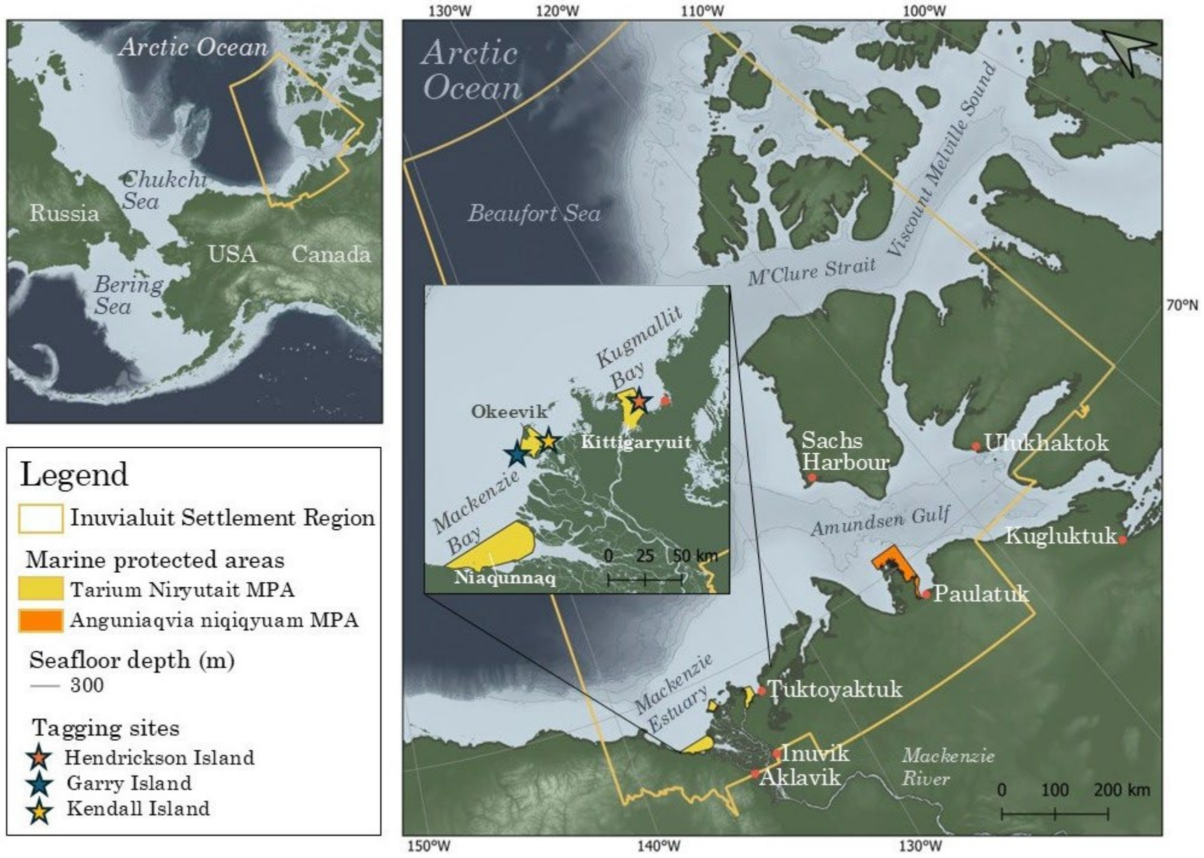


Figure 3.1 Summer range of the Eastern Beaufort Sea beluga population. Bathymetry data was obtained from the International Bathymetric Chart of the Arctic Ocean (IBCAO, 2022).

The EBS beluga summer range overlaps with the Inuvialuit Settlement Region (ISR), where belugas are culturally significant and provide an essential source of country food (Usher, 2002; Waugh et al., 2018). Inuvialuit communities harvest belugas each summer in the shallow (<5 m) nearshore waters of the estuary (Frost & Suydam, 2010; Harwood et al., 2015), sometimes based at traditional whaling camps (Ovitz et al., 2024). Inuvialuit harvesters hold extensive knowledge of beluga ecology, behaviour and habitat use (Byers & Roberts, 1995) and have contributed significantly to collaborative monitoring and research initiatives (Harwood et al., 2020), including satellite telemetry programs (MacPhee et al., 2025; Richard et al., 1997). Two marine protected areas, the Tarium Niryutait MPA and the Anguniaqvia niqiqyuam MPA, have been established within this region under Canada's Oceans Act, both with mandates to help conserve the EBS beluga population (Fisheries and Oceans Canada, 2025; Fisheries and Oceans Canada & Fisheries Joint Management Committee, 2013) given the importance of these areas for key ecological functions including replenishing energy stores (Ostertag et al., 2018; Storrie et al., 2025), moulting (Noel et al., 2022; Whalen et al., 2020) and calf-rearing (Harwood, Iacozza, et al., 2014; Mayette et al., 2023).

3.2.2 Beluga instrumentation and data collection

This study uses satellite telemetry data from EBS belugas instrumented in the ISR over the course of three tagging studies, which took place in the 1990s (Richard et al., 1997, 1998), the 2000s (Citta et al., 2017; Hauser et al., 2014) and the late 2010s (Storrie et al., 2022), with tagging operations based on Garry Island, Kendall Island and Hendrickson Island in the Mackenzie Estuary, NT.

Belugas were equipped with satellite transmitters between late June and late July using live-capture techniques described by Orr et al. (2001) and Storrie et al. (2022). Between 1993 and 2004, belugas were equipped with devices that transmitted location data to polar-orbiting Argos satellites, which estimate position based on Doppler shift (Hauser et al., 2014). These included several models: SMRU types 1, 2, and 3 from the Sea Mammal Research Unit (University of St. Andrews), as well as SPOT and SPLASH tags manufactured by Wildlife Computers (Redmond, WA) (Richard et al., 2001; Hauser et al., 2014). In 2018 and 2019, devices included SPLASH10-F238 and SPLASH10-F-321 tags, which provided both Argos-derived location estimates and high-resolution Fastloc-GPS positions to provide more precise and frequent data (Storrie et al., 2022).

Length, sex and calf presence were recorded during all tagging operations. Genetic analyses were later used to verify sex (Brown et al., 1991; Richard et al., 2001). Based on prior consultation with Inuvialuit research partners, each study strove to include both sexes and a range of body sizes and aimed to avoid females with calves to minimize disturbance (Loseto. pers. comm). Despite these efforts, only males were instrumented in 2018 and 2019 (Storrie et al., 2022). Further details on the objectives and methods for each tagging campaign can be found in chapter 2.2. Location of tagging operations, telemetry devices used and tag deployment method for each whale are listed in the Supplemental material.

3.2.3 Data pre-processing

We obtained location data from satellite telemetry devices deployed over three decades, during which tracking technologies and programming strategies evolved (Hebblewhite & Haydon, 2010; Hussey et al., 2015). As a result, sampling frequencies varied among individuals depending on device type and configuration (Hauser et al., 2014; Storrie et al., 2022). To allow comparison across all individuals, we standardized the data by filtering and resampling locations to a common temporal resolution using a state-space modeling approach (Jonsen et al., 2023). This process is described in detail in chapter 2.2.

We first removed location estimates with an Argos location class of “Z,” which are considered unreliable due to unknown error estimates (Douglas et al., 2012). Because belugas can occur in shallow nearshore environments (Mayette et al., 2023; Noel et al., 2022), we retained coastal positions but excluded any location falling more than 5 km inland. Inland positions were identified using a 5 km buffer around the Global Oceans and Seas boundaries dataset (Flanders Marine Institute, 2021) and filtered using the *st_intersection* function from the *sf* package.

To account for varying location accuracy and irregular sampling intervals, we applied a continuous time correlated random walk model using the *fit_ssm*() function from the *aniMotum* R package (Jonsen et al., 2023). Location error was modeled according to tag type: Argos positions were assigned error structures based on class-specific error ratios from Lowther et al. (2015), as these were more consistent with the movement behaviour of our study population than the default error settings in the *aniMotum* package. Fastloc-GPS positions were assigned a conservative fixed error of 724 m, based on median 95% quantiles reported by Dujon et al. (2014). We applied a maximum speed filter of 10 m/s, a threshold which exceeds the upper limit of documented swimming speeds for wild Arctic belugas (Richard et al., 1998, 2001), ensuring only extreme outliers were excluded. After filtering, locations were interpolated at regular 8-hour intervals, matching the coarsest resolution observed among individuals in the summer dataset. The correlated random walk model also estimated location uncertainty, expressed as standard error values for the longitude and latitude coordinates. We used these values to compute an error radius around each interpolated location, based on the length of the resultant vector formed by the horizontal and vertical standard errors. To omit highly unreliable locations resulting from fitting the state-space model across data gaps, we removed points with error radii >=120km. Maintaining the same sampling timing and error estimates, we rerouted paths so that nearshore locations would not cross land using the *pathroutr* package (London, 2025).

3.2.4 Identifying summering groups

3.2.4.1 Defining the pre-migration period

To examine pre-migration space use, we first needed to remove long-distance movements that occurred after belugas departed from their summer range. EBS belugas are highly mobile and travel extensively among discrete areas in the Beaufort Sea and Amundsen Gulf prior to migration (Richard et al., 2001; Storrie et al., 2023) and utilize stopovers and migratory corridors outside the summer range (see Chapter 2). Since this variable movement behaviour precludes the use of a single boundary or behavioral index to define the start of the fall migration, we developed a method based on a combination of direction and displacement rate.

To isolate the migratory phase, we first excluded all locations west of Utqiagvik, Alaska (longitude < -157°), which corresponds to the final stages of fall migration beyond the summer range (see Chapter 2). This region lies past the Arctic Basin, a major ecological barrier in beluga migrations (Citta et al., 2018; Stafford et al., 2018), suggesting that the migration period is well underway when belugas cross this longitudinal boundary. For the remaining locations, we quantified displacement using Net Squared Displacement (NSD), which calculates the squared distance between each location and the individual's starting point (Bastille-Rousseau et al., 2015) and is thus robust to gaps between locations, which were present for two individuals in the study. NSD has been widely used to distinguish large-scale movement patterns, including migrations, which appear as sharp increases in displacement over time, in contrast to the more stable patterns of residency or local exploration (Bunnefeld et al., 2010; van de Kerk et al., 2021). We calculated NSD values using the *nsd()* function in the *amt* package and then used *diff()* to derive the rate of change in NSD (ΔNSD) between successive locations.

To identify transitions to migratory movement, we selected the most likely breakpoint in the resulting time series of ΔNSD values. We first used the *cpt.mean()* function from the *changepoint* package (Killick et al., 2014) to apply a binary segmentation algorithm and detect shifts in mean displacement rate. For each individual, we calculated five breakpoints which we visually assessed in relation to the movement trajectory and NSD profile to determine which point marked the onset of sustained, unidirectional westward movement toward the Chukchi Sea. This directional criterion was necessary to distinguish true migratory departures from large-scale exploratory movements within the summer range.

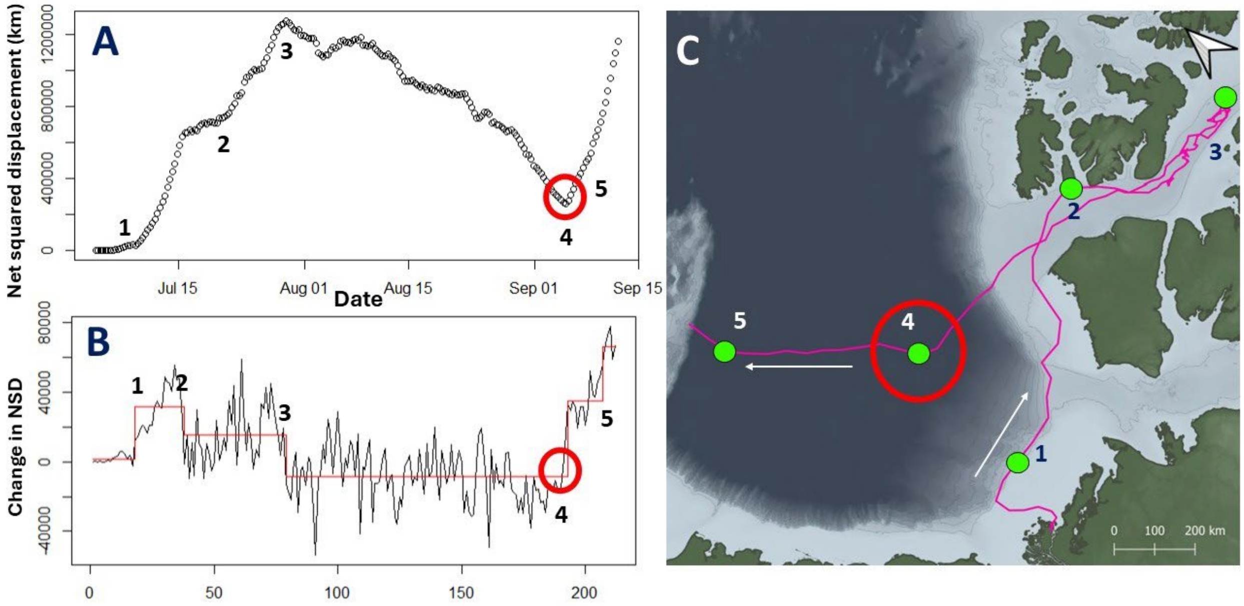


Figure 3.2 Example of the methods used to define migration timing: A) Time series of NSD values, B) ΔNSD for each location and the five potential breakpoints estimated by the *changepoint* function, and C) The summer and fall track (magenta) with the five potential breakpoints (green). The relevant breakpoint (red) corresponds to the date at which the beluga initiated rapid, directional movements towards the Chukchi Sea.

3.2.4.2 Comparing and clustering summer movements

To examine variation in summer space use, we first quantified the similarity between each pair of belugas based on their summer movement trajectories. We used a Dynamic Time Warping (DTW) algorithm, which calculates the minimum number of steps needed to align two time series (Cleasby et al., 2019). The DTW allows for shifts in time or length, making them particularly relevant as a means to evaluate similarity between horizontal or vertical animal movement tracks (Barbour et al., 2023; Cleasby et al., 2019) or to compare individuals based on time series of ecological data (García-Vernet et al., 2024). To compare every individual's summer track to that of each other beluga, we used a modified version of the code produced by Janoksa (2013) to align tracks, calculate pairwise distances using the *dtwDistance* R package (Giorgino, 2009) and organize these distances into a dissimilarity matrix.

To group individuals with similar summer movements, we used an agglomerative clustering approach. We used the *hclust* function from the *stats* package to create a dendrogram, iteratively merging the two closest groups of individuals based on the DTW values until all individuals were clustered into a single group. We used Ward's criterion as the clustering algorithm, in which the clusters are merged to minimize the total within-cluster variance, defined as the squared distance between each object and the centroid of the cluster (Legendre & Legendre, 1998). To define overall similarity, we calculated the mean DTW distance across all pairs of individuals. We used this mean as a threshold in the *cutree* function from the *stats* R package to truncate the dendrogram, assigning belugas similar-than-average movements to the same cluster. To validate cluster assignments, we applied two additional hierarchical clustering algorithms: unweighted pair-group method using arithmetic averages (UPGMA; Conner & Miller, 2004; Taylor et al., 2001) and complete linkage (Legendre & Legendre, 1998). Group membership was consistent across all methods (see Supplemental material). Following clustering, we identified three multi-individual clusters and one ungrouped individual.

3.2.4.3 Associating individual traits with groups

We examined individual traits associated with each summering group, including sex, calf presence (for females), and body length. We then calculated mean body length separately for males and females within each group.

3.2.5 Describing summer space use

3.2.5.1 Estimating individual summer space use

To estimate space use during the summer period, we fit dynamic Brownian Bridge Movement Models (dBBMMs) for each individual, which estimate an occurrence distribution based on available locations and error radii, modeling the likely path of an animal between successive locations as a Brownian bridge (Horne et al., 2007). The Brownian motion variance δ_m^2 , which reflects how diffuse or tortuous the movement is, is allowed to vary along the animal's path (Kranstauber et al., 2012). This accommodates changes in movement behaviour across the track and improves estimates of space use (Byrne et al., 2014; Peris et al., 2020), especially when animals may be transitioning between localized and directed movements, as is the case for EBS belugas during the summer (Richard et al., 2001; Storrie et al., 2023).

We used the approach described in chapter 2.2, adjusting the raster resolution and the window and margin parameters to reflect the finer sampling resolution and smaller location error during the summer period compared to the year-round analysis. Changes in the Brownian motion variance δ_m^2, are calculated using a modified behavioural changepoint analysis within a window of size w with margins of size m at each end of the window (Kranstauber et al., 2012). To obtain w and m parameters, we considered the values used in chapter 2.2 for the year-round analysis and selected values which capture behavioural transitions at timescales relevant to summer transitions between offshore and nearshore areas. We selected a window size $w = 7$ locations and a margin size $m = 3$ locations, corresponding roughly to a 2-day window and 1-day margin based on locations interpolated to 8-hour intervals. For each beluga, we retained filtered and regularized locations corresponding to the pre-migration period, then implemented the dBBMM using the *move* package in R (Kranstauber et al., 2012). We included the error radius associated with each location and used a raster resolution of 2.5 km² (see chapter 2.2). To avoid excessively large error radii from fitting Brownian bridges across gaps, we used the *brownian.motion.variance.dyn()* function to first calculate the δ_m^2 for all locations, then omit gaps of > 48 hours from the final distribution (Kranstauber et al., 2024). This produced a raster surface representing each beluga's summer occurrence distribution.

3.2.5.2 Defining group-level high-use areas

To ensure that occurrence distributions were comparable across individuals, we standardized the raster projection and temporal effort before combining the dBBMM estimates from individual belugas. We first created a reference raster encompassing the full spatial extent of all summer tracks and their associated error radii in QGIS, then resampled this reference raster to Equal Area projection with a resolution of 2.5 km². We then resampled each individual summer occurrence distribution to this reference raster using the *terra* package in R. To standardize temporal effort across individuals and ensure that cell values reflected the proportion of time a beluga was likely to occur in a given area, we multiplied each raster by the number of days with continuous location data for that individual, following the approach of Palm et al. (2015). Because dBBMMs output probability distributions where the sum of all cell values within the occurrence distribution equals 1, this approach adjusted each individual raster to account for differences in tracking duration.

To produce an overall map of summer occurrence for EBS belugas, we first summed all the rescaled raster files. To generate an estimate of summer space use for each of the three summering groups, we grouped individuals according to the three established clusters and summed the dBBMM raster images within each group. To obtain high-use areas, we used the *raster.vol()* function from the *spatialEco* package to extract the 25%, 50%, and 95% volume contours from each of the group-level occurrence distributions.

3.2.5.3 Examining movements among key summering areas

To further describe summer space use, we examined movement behaviour by determining when each beluga intersected with key summer areas. To identify key summer areas associated with group-specific high-use areas, we used the 50% volume contours from the dBBMMs of each summering group. For belugas occupying the Amundsen Gulf, where individuals were dispersed across multiple areas including sections of the continental slope, we created several polygons representing the largest regions within the 50% volume contours. We then applied a 15 km buffer along the 1 km isobath to capture additional slope-associated habitats. To capture the shallow, nearshore habitats influenced by the Mackenzie River plume and the series of bays and inlets along the Tuktoyaktuk Peninsula, where belugas aggregate in high numbers each summer (Harwood & Smith, 2002), we created polygons based on the 5 m isobath (Noel et al., 2022). To delineate the summer range, we created a convex hull around the 95% contour of the dynamic Brownian Bridge Movement Model (dBBMM) constructed from all individuals. To determine when belugas occupied each area, we used the *st_intersection()* function from the *sf* package in R to identify locations that intersected with each of the defined spatial polygons.

3.2.6 Timing of summer and early fall movements

3.2.6.1 Comparing departure timing among summering groups

To compare fall migration timing among summer groups, we examined 1) the last day spent in the Mackenzie Estuary, and 2) the beginning of directional movement towards the winter range. The Mackenzie Estuary is ecologically important as a consistent summer aggregation site for EBS belugas (Harwood et al., 2014). Given the presence of several whaling camps along its shores (Ovitz et al., 2024; Worden et al., 2020), understanding the timing of beluga occurrence in this area is also of socio-cultural relevance. To determine the day each beluga initiated directional movement towards the winter range, we used the dates previously determined based on Net Squared Displacement and direction (Figure 3.2). For each set of dates, we used analysis of variance (ANOVA) to compare dates for the three summer groups, excluding the individual identified as an outlier.

3.3 Results

3.3.1 Summering groups

3.3.1.1 Clusters based on summer movements

Clustering the summer movement paths of 26 individuals revealed three groups of belugas that were more similar than the overall sample, and one individual that did not fit any of the three groups.

The clusters were associated with spatially distinct areas in the summer range (Figure 3.3). The first cluster included individuals that travelled North and visited Viscount Melville Sound before moving West into the Arctic basin (“Viscount Melville Sound” group), and individuals in the second cluster headed East into Amundsen Gulf soon after instrumentation (“Amundsen Gulf” group). The third cluster of whales travelled North directly towards the continental slope of the Beaufort Sea basin without visiting Viscount Melville Sound or the Amundsen Gulf (“Beaufort basin” group). A single individual travelled North then veered West to initiate its migration only a few days after instrumentation (“ungrouped individual”).

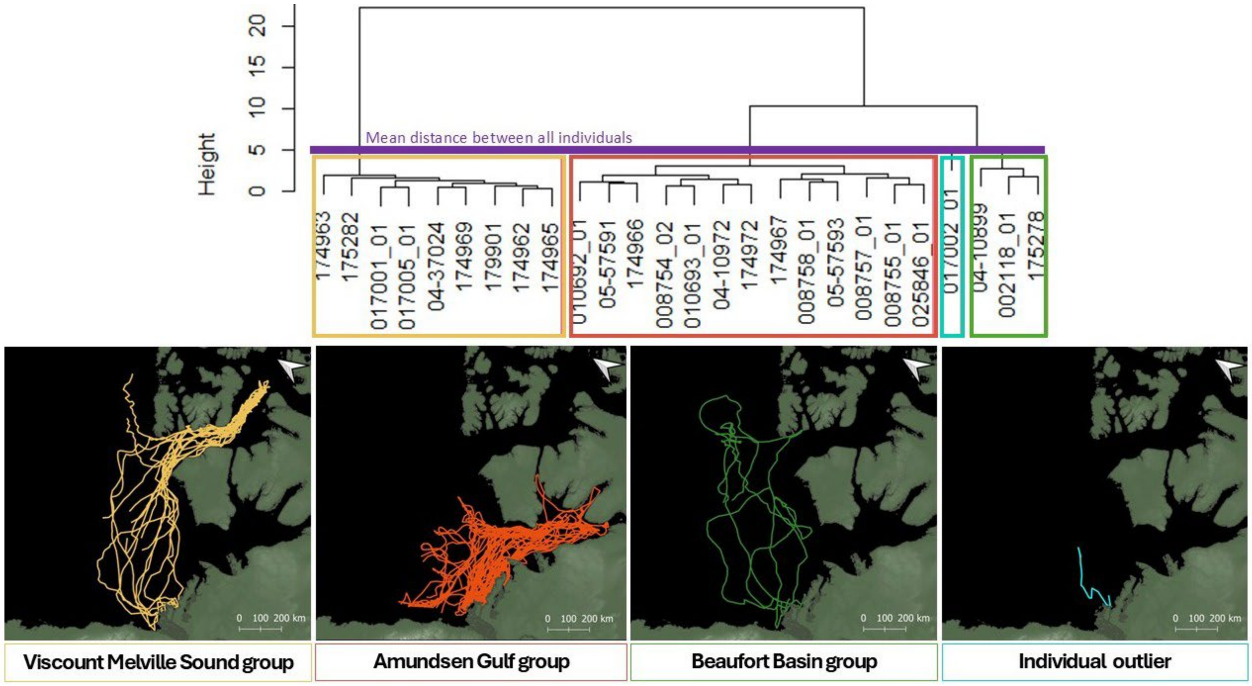


Figure 3.3 Dendrogram and clusters obtained using Ward's criterion, and summer tracks for belugas in each cluster.

3.3.1.2 Individual traits associated with clusters

Sex, calf presence and body length varied between groups. The ungrouped individual and the Viscount Melville Sound (VMS) group were larger (>4m long) males (Table 3.1). The Amundsen Gulf (AG) and Beaufort Basin (BB) groups both included a mix of males and females; however, the BB group was composed entirely of smaller (<3.8 m) individuals, with no calves present. The Amundsen Gulf, meanwhile, included females with and without calves, as well as small and large males. All but one female and all calves in the study belonged to the Amundsen Gulf group.

Table 3.1 Individual traits associated with summer groups.

Summer group	**Sex**		**Mean body length (cm)**	
	M	**F (w/ calf)**	**M**	**F**
Beaufort Basin	2	1 (0)	327	374
Amundsen Gulf	9	4 (2)	412	316
Viscount Melville Sound	8	0	429	n/a
Ungrouped individual	1	0	457	n/a

3.3.2 Summer space use

3.3.2.1 Group-specific high-use areas

Belugas in each of the three summer groups occupied distinct high-use areas, as reflected by their occurrence distributions. All individuals occurred within the Mackenzie Estuary and along the continental slope, consequently, the 95% volume contours for all three groups overlapped in these areas, reflecting common travel routes used to access their core summering habitats. In contrast, the 50% and 25% volume contours did not overlap between groups, indicating distinct high-use areas specific to each group (Figure 3.4).

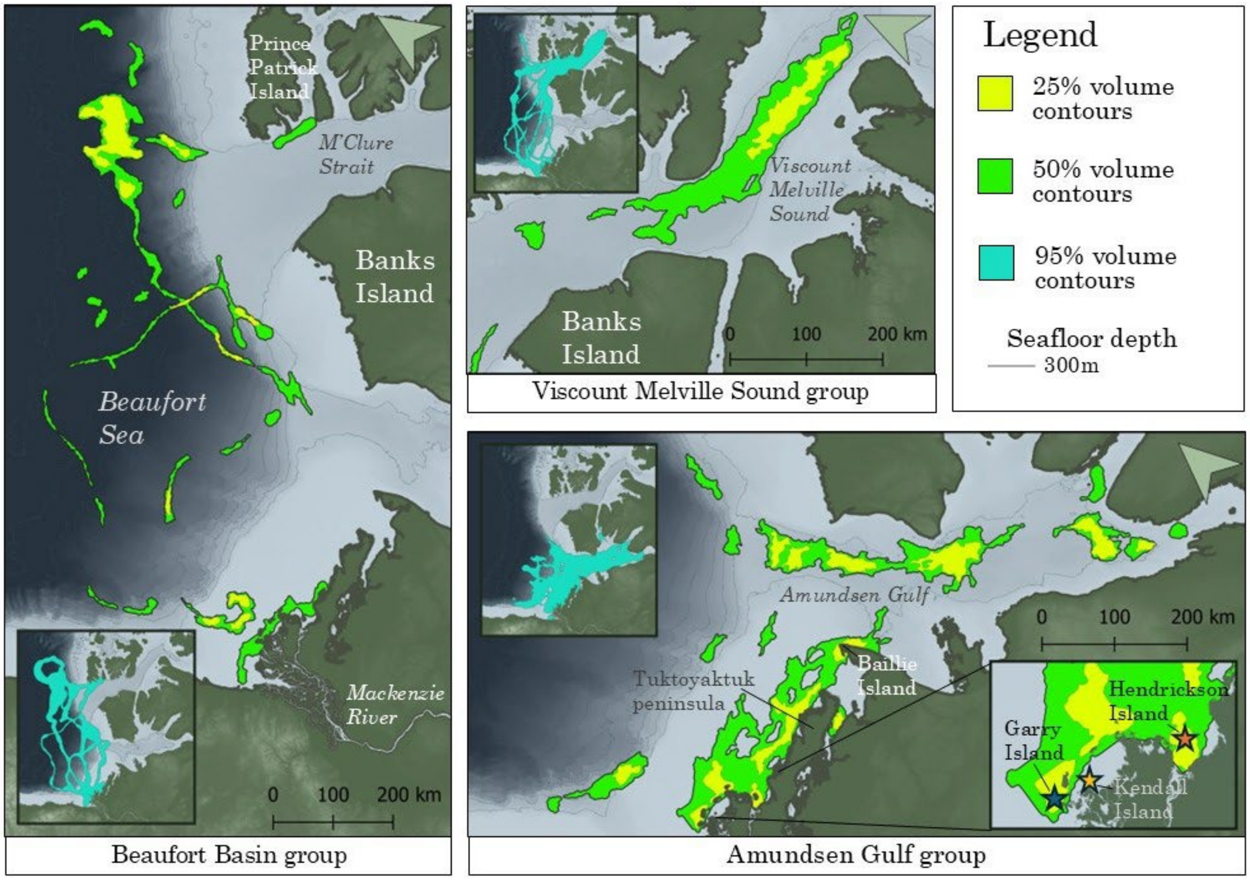


Figure 3.4 High-use areas associated with each summer group, based on the 25%, 50% and 95% volume contours obtained from group-specific dBBMMs.

For belugas in the Viscount Melville Sound group, the 25% volume contour encompassed a single concentrated area along the southern edge of the central trough in Viscount Melville Sound. The 50% volume contours expanded to include most of the trough as well as a narrow corridor along the northwestern corner of Banks Island, representing the travel route toward the core summering area.

In contrast, belugas in the Amundsen Gulf group did not concentrate their activity within a single core area but instead occupied multiple high-use regions. The primary areas encompassed by the 50% volume contours included a large region spanning the Mackenzie Estuary, nearshore Beaufort Sea shelf along the Tuktoyaktuk Peninsula, and offshore area covering the deepest parts of the Amundsen Gulf, a region along the easternmost edge of the 300 m isobath, and several smaller regions along the continental slope. The 25% contours delineated more restricted, smaller high-use areas within these broader regions. Within the Mackenzie Estuary, high-use areas were concentrated around Hendrickson Island and Garry Island, where belugas were tagged, as well as immediately offshore of Richards Island, situated between the two. An additional concentrated area of use was identified around Baillie Island.

For belugas in the Beaufort Basin group, sample size was limited (n = 3), and as a result, the 50% volume contours primarily reflected individual movement paths rather than areas of spatial overlap between individuals. Nevertheless, all three individuals traveled northward to a region along the continental slope west of Prince Patrick Island before returning southward.

3.3.2.2 Movements Between Key Summering Areas

Summer groups differed in the number of areas targeted during the summer, the duration of time spent within each region, and the amount of time spent travelling between regions (Figure 3.5).

Belugas in the Viscount Melville Sound group departed from the Mackenzie Estuary shortly after instrumentation (<7 days) and began traveling toward Viscount Melville Sound. Some individuals crossed the continental slope, while others traveled along the coast of Banks

Island. Upon arrival, belugas remained within Viscount Melville Sound and surrounding areas for periods ranging from 2-6 weeks before traveling westward to initiate their autumn migration.

Belugas in the Amundsen Gulf group exhibited more extensive regional movements, traveling between multiple areas throughout the summer. All 13 individuals in this group visited the Mackenzie Trough, located offshore and south of Banks Island. Six individuals traveled to the high-use area located at the eastern edge of the Amundsen Gulf, with one beluga remaining in this area for nearly two weeks. All but one individual returned to the Mackenzie Estuary at least once during the summer, following an initial departure shortly after tagging. Of these, 11 individuals also used nearshore habitats along the Tuktoyaktuk Peninsula, including four that entered Liverpool Bay. One female, tagged at Kendall Island, did not return to nearshore areas and instead moved exclusively between offshore regions, and entered Prince of Wales Strait, Minto Inlet and Prince Albert Sound before returning West. Most individuals in this group visited the continental slope during late August and early September, where they remained for periods ranging from several days to two weeks prior to initiating their migration.

Belugas in the Beaufort Basin group targeted the continental slope throughout the summer. In August, all individuals traveled far north, reaching the high-use area west of Prince Patrick Island before returning southward in early fall.

One ungrouped individual did not use any of these summer areas and instead departed from the summer range in early August, less than two weeks after tagging.

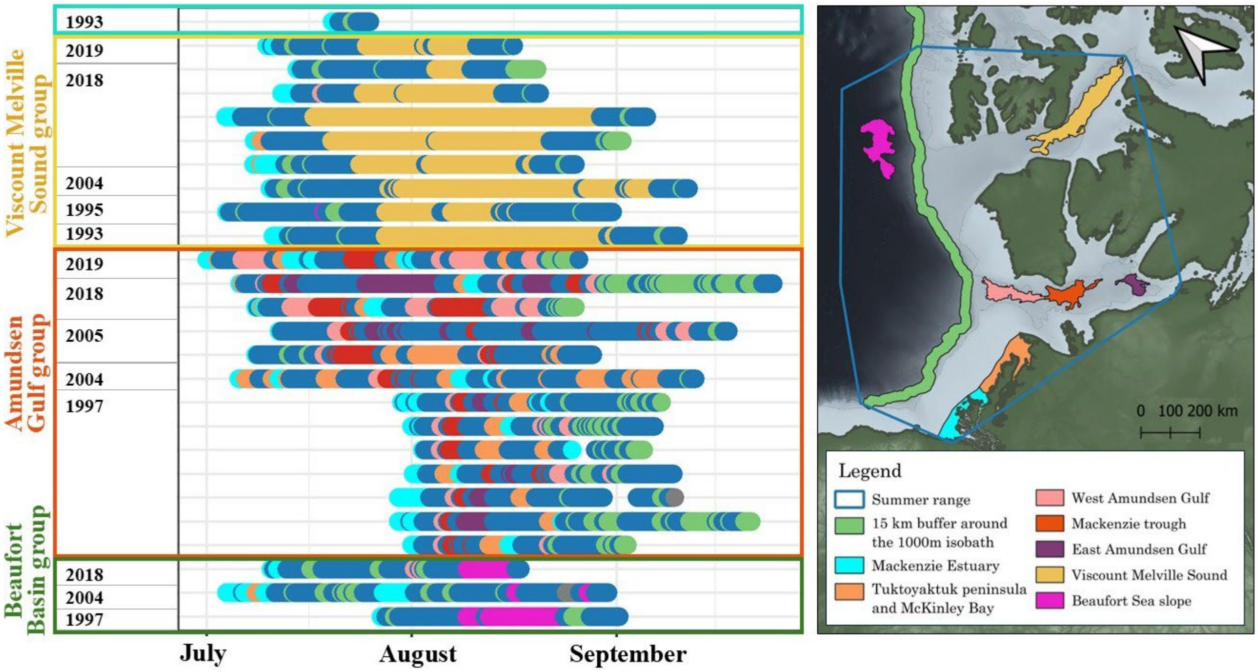


Figure 3.5 Individual timelines illustrating the spatial use patterns of belugas during the summer, showing the timing, duration, and frequency of use of different regions.

3.3.3 Migration timing

3.3.3.1 Comparison of departure dates

On average, belugas in the Viscount Melville Sound group departed first from the Mackenzie Estuary. The final day in the estuary occurred later for belugas in the Beaufort Basin and Amundsen Gulf groups due to belugas returning later in the season before initiating their fall migration. On average, belugas in the Amundsen Gulf group initiated their fall migration ~1 week later than the other two groups (Table 3.2).

Table 3.2 Mean date of departure from the Mackenzie Estuary and fall migration date for summer groups.

Summer group	**Mean calendar date**	
	Departure from Mackenzie Estuary	**Start of fall migration**
Amundsen Gulf group (n=14)	August 7th	September 8th
Viscount Melville Sound group (n=8)	July 10th	August 29th
Beaufort Basin group (n=3)	July 24th	August 26th
Ungrouped individual	July 20th	July 25th

Timing of departure from the Mackenzie Estuary varied significantly among the three summer groups (ANOVA F = 14.88, p = 8.19 e^{-05}) whereby belugas in the AG group departed significantly later than those in the VMS group (post-hoc pairwise t-test (p = $1.8e^{-05}$), but timing of departure did not differ significantly between the AG and BB groups (p = 0.068) or between the BB and VMS groups (p = 0.104) (Figure 3.6).

Individual fall migration dates, defined as the beginning of directional movement towards the winter range, varied significantly between the three summer groups (ANOVA F = 3.741, p = 0.0399). The AG group departed last, significantly later than the VMS group (post-hoc pairwise t-test p = 0.03), but not significantly later than the BB group (p = 0.054). Departure dates did not differ significantly between the BB and VMS groups (p = 0.661) (Figure 3. 7). The individual beluga, which transmitted locations well into the fall migration, initiated its fall migration in late July, significantly earlier than any of the three groups.

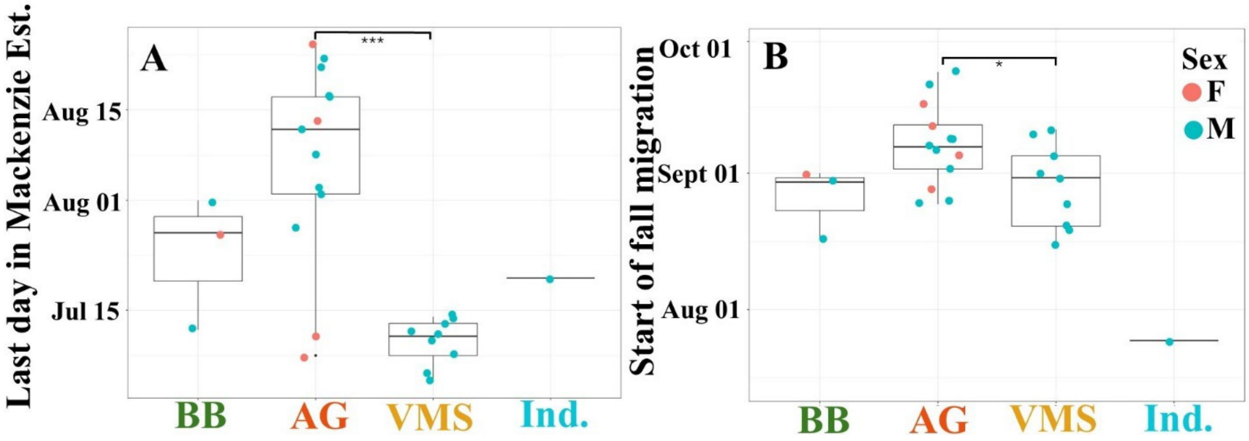


Figure 3.6 Among-group comparison of A) The last day in the Mackenzie estuary (ANOVA p = 8.19 e-05), where the AG group departed significantly earlier than the VMS group (pairwise t-test: p =1.8e-05), and B) The start of the fall migration (ANOVA p = 0.0399).

3.4 Discussion

Here we analyzed satellite telemetry data from 26 Eastern Beaufort Sea belugas instrumented between 1993 and 2019 in the Mackenzie Estuary, NT, to examine summer space use and migration timing while accounting for sub-population structure. We identified one ungrouped individual and three consistent groups including individuals tagged across multiple years, each reflecting differences in individual traits, summer space use and fall migration timing. The Viscount Melville Sound (VMS) group was comprised exclusively of large males and left the estuary by mid-July before travelling to Viscount Melville Sound and remaining there for several weeks. In contrast, the Amundsen Gulf (AG) group included males of various sizes and females with and without calves, and moved between offshore areas of the Amundsen Gulf, the Beaufort continental slope, and nearshore regions including the Mackenzie Estuary and Tuktoyaktuk Peninsula. The Beaufort Basin (BB) group contained smaller males and a lone female, and ranged primarily along the Beaufort continental slope, returning to the estuary until late July. Belugas in the BB and VMS groups left the Mackenzie Estuary and initiated their fall migration earlier than the AG group, with a significant difference between the AG and VMS groups. These divergent summer movement behaviours may reflect adaptive responses to local environmental conditions, potentially enhancing overall population resilience. However, they also point to important gaps in our understanding of EBS beluga population structure, which must be addressed to effectively use metrics like migration timing for long-term population monitoring.

3.4.1 Individual traits, social dynamics and habitat preferences

EBS belugas exhibited spatial segregation during the summer associated with age, sex and calf presence. While large (>= 4 m) males were present in all three groups, females without calves and small males (<4 m long) were only present in the AG and BB groups, and females with calves were limited to the AG group. These differences in habitat preferences can be partially attributed to physiological traits: Male belugas grow larger than females (Harwood et al., 2014; Suydam, 2009), and larger adults have greater aerobic breath-hold capacity (Choy et al., 2019; Noren & Suydam, 2016) which facilitates deeper and longer foraging and navigation through heavy sea ice (Noren & Suydam, 2016; Storrie et al., 2022). Meanwhile, calves' oxygen stores do not fully develop until ~14 months of age (Noren & Suydam, 2016), further constraining mothers to habitats that can be navigated by their offspring, which nurse for 6-32 months (Matthews & Ferguson, 2015). These physiological differences may confer broader ecological flexibility to mature males compared to other sex and age classes (Choy et al., 2019; Noren & Suydam, 2016), enabling those in the VMS group to spend several weeks Arctic archipelago while other groups spent a greater proportion of the summer at lower latitudes. These findings echo existing studies, where adult male EBS belugas occupy deep, icy, offshore areas and performed longer, deeper dives during the summer and fall more often than females or younger individuals (Hauser et al., 2017; Loseto et al., 2006; Storrie et al., 2025).

While physiological traits likely confer broader ecological flexibility to mature males compared to other sex and age classes, social affiliations also influence beluga movement. Belugas have been observed travelling as individuals, adult-calf or adult-adult pairs, and in mixed units containing multiple adults and offspring (O'Corry-Crowe et al., 2020). While older, larger males are physiologically capable of traveling to offshore areas, they may nonetheless target shallow or nearshore areas because of social affiliations with females, juveniles and calves, as observed in aerial surveys of the Amundsen Gulf, where groups of single adults occur in deeper and colder areas than groups of adults and mixed-age groups in the Amundsen Gulf

(Mayette et al., 2023). These mixed groups can confer benefits to reproducing adults, since belugas exhibit allocare, in which adults participate in caring for non-offspring calves (J. A. Aubin et al., 2023). However, in several populations, large males are more likely to disperse from matrilineal groups to form associations with other older males (Colbeck et al., 2013) and adult-only groups are more likely to be composed of males (O'Corry-Crowe et al., 2020). These distinct dynamics are reflected in our results: the mixed composition of the AG and BB groups are consistent with mixed associations of males and females, while the VMS group could exemplify the dispersal of older males away from the estuary to associate with one another. Together, these physiological and social differences influence the areas targeted by each group during the summer.

3.4.2 Summer movements and ecological functions of the summer range

The groups identified in this study targeted distinct areas of the summer range. Existing research (chapter 2.4) suggests a functional partitioning between inshore and offshore areas. Offshore habitats are often associated with foraging behaviour (Hauser et al., 2015, 2018; Storrie et al., 2022) while nearshore areas are generally more likely to support social and reproductive functions (Harwood et al., 2014; Mayette et al., 2022; Scharffenberg et al., 2019). The differences in time allocated to these summer habitats sheds light on the relative importance of these areas to different subsets of the population as they prepare for their fall migration.

All belugas in the study were instrumented in the Mackenzie Estuary, NT (Hendrickson Island = 22, Kendall Island = 2, Garry Island =2), where thousands of EBS belugas aggregate each year (Harwood et al., 1996). These gatherings are potentially driven by a combination of social behaviours and moulting (Harwood et al., 2014; Scharffenberg et al., 2019). Vocalizations near East Whitefish and the center of Kugmallit Bay indicate the presence of social interactions

(Scharffenberg et al., 2025), while aerial surveys of the estuary show that belugas exhibit a preference for warm, turbid areas (Noël et al., 2022) and abrasive seabed sediment favourable for moulting (Whalen et al., 2020). Annual estuarine aggregations occur across several other beluga populations (Belanger et al., 2024; Caron & Smith, 1990; Smith et al., 1992; Watt et al., 2023), which also have been observed moulting, selecting warm, shallow water and rough substrate (Smith et al., 1992; St. Aubin et al., 1990) and exhibiting social behaviours (Anderson et al., 2017; Mayette et al., 2022) during these periods. The occurrence of belugas from all three summering groups in the estuary during early summer indicates that these functions are important across sex and age classes (Smith et al., 2017; Smith et al., 1992; St. Aubin et al., 1990), and may represent a period when potentially distinct social groups overlap before dispersing later in the season.

After the initial instrumentation period in early July, the groups in the study used the estuary differently: The VMS group departed by mid-July and did not return, while most belugas in the BB and AG groups returned in late July or August after undertaking energetically costly trips to distant, offshore areas of the summer range. In addition to the Mackenzie Estuary, other nearshore areas including the Tuktoyaktuk peninsula and McKinley Bay were utilized by the AG and BB groups later in the summer, but not by belugas in the VMS group. This suggests that the estuary, as well as nearshore bays along the Tuktoyaktuk peninsula, may become less important for groups of mature males as the summer progresses. This could be because adult males are generally less involved in functions such as calf-rearing (Aubin et al., 2023; Krasnova et al., 2012) that are supported by warm, shallow habitats. Meanwhile, the AG and BB groups' repeated movements between nearshore and offshore areas allow them to access productive offshore foraging sites while maintaining proximity to warm, shallow nearshore habitats that may be critical for calves and smaller individuals. Belugas give birth in late spring and summer (Noren & Suydam, 2016; Suydam, 2009), and several beluga populations use estuaries for calf-rearing (Krasnova et al., 2009; Smith et al., 2017; Westdal et al., 2022), where shallow water, warm temperatures, and safety from predators can be advantageous for mothers and calves (Anderson et al., 2017; Aubin et al., 2023; Krasnova et al., 2012). Mother-calf pairs are known to occur in bays along the Tuktoyaktuk peninsula (Waugh et al., 2018), where dive behaviors have mostly been associated with transiting or recovery (Storrie et al., 2022), supporting the notion that these nearshore areas support social or reproductive functions beyond foraging.

All three groups in the study targeted offshore sites, which may be especially important for foraging (Hauser et al., 2015; Storrie et al., 2025). In previous research (chapter 2), the Mackenzie Trough and the region of the Beaufort slope west of Banks Island were visited by tagged belugas in the spring, potentially to replenish energy stores before entering the Mackenzie Estuary, and these areas were utilized by belugas in the AG and BB groups, respectively. Offshore areas targeted by the AG group featured bathymetric and oceanographic conditions corresponding to the habitat requirements of adult Arctic cod *Boreogadus saida* (Geoffroy et al., 2023) which dominated demersal fish communities in these areas during the last decade (Majewski et al., 2025). While Arctic cod is the preferred prey of EBS belugas (Choy et al., 2020; Loseto et al., 2009), they can also target a variety of prey species depending on availability (Choy et al., 2020; Loseto et al., 2018). Dive behavior in Viscount Melville Sound and along the Beaufort Sea slope were consistent with foraging behaviour (Storrie et al., 2022), while habitat characteristics similarly corresponded to those of Arctic cod (Fraker et al., 1979; Storrie et al., 2025). In particular, Arctic cod associate most strongly with depths of 350-500 m and temperatures of > 0° C along the Beaufort Sea slope, primarily feeding on copepods and amphipods (Majewski et al., 2016), and gadids dominated benthic trawls in Viscount Melville Sound (Bouchard et al., 2018), where male belugas tagged in 2018 and 2019 undertook deep benthic dives to depths > 450 m (Storrie et al., 2022, 2025). EBS belugas typically exhibit thicker blubber as the summer progresses (MacMillan et al., 2019; Ostertag et al., 2018), while habitat selection (Hornby et al., 2017) and dive behaviour (Hauser et al., 2015; Storrie et al., 2022, 2025) indicate active foraging to access energy-rich prey (Choy et al., 2020) during this season in anticipation of the fall migration.

3.4.3 Fall migration timing and interannual variation

Fall migration occurred earlier on average for the BB and VMS groups than the AG group, supporting the hypothesis that summer space use influences fall migration timing. However, migration timing also varied within groups, notably, belugas in the AG group migrated between mid-August and mid-September. Only a few of these, mostly males, visited the East Amundsen Gulf high-use area, and the three belugas that migrated latest in the study had first travelled East to visit this area (Figure 3.5). In contrast, the AG belugas that did not travel to the East Amundsen Gulf high-use area did not depart significantly later than the BB or VMS group. Additionally, the ungrouped individual departed the summer range in late July and travelled directly across the Arctic basin soon after instrumentation, almost a month before the rest of the belugas in the study. Together, these findings suggest that fall migration timing is influenced by multiple individual, social and environmental factors.

Our findings suggest that environmental cues, including sea ice conditions, only partially influence fall migration timing. We initially hypothesized that migration dates would vary based on latitude, since the Arctic archipelago typically features a shorter open-water season than the Amundsen Gulf (Howell et al., 2023; Shen et al., 2021), and belugas frequenting these high-latitude areas could experience cold temperatures or encroaching sea ice that would cue migration at an earlier date. However, the relationship between latitude and migration timing was inconsistent given the variation within groups. Similarly, interannual patterns did not support sea ice as the primary driver of migration timing. In the Beaufort Sea, freeze-up in the fall has been delayed by approximately one week per decade (Johnson & Eicken, 2016), but pooled fall migration dates from all three summering groups creates the appearance of earlier migration in recent years (Figure 3.7). This apparent trend is an artifact of sampling bias: most belugas tagged in 2018-2019 were from the VMS group, which migrates earlier on average, while tagging operations in 1997 occurred in late July, presumably after VMS belugas had already departed the Mackenzie Estuary, resulting in disproportionate representation of the later-migrating AG group. Within summering groups, sample sizes do not permit robust comparisons of migration timing across years, as data are heavily skewed toward single years for the VMS and AG groups. This finding is consistent with past satellite telemetry studies, which found no clear association between sea ice conditions and EBS beluga migration timing (Hauser et al., 2017). While climate change is understood to impact the timing and distribution of marine mammal migrations (Kuletz et al., 2024; Laidre et al., 2008), with shifts documented across several species and populations (Cohen et al., 2018; Grémillet & Descamps, 2023; Shuert et al., 2022), our findings suggest that migration timing is also influenced by other factors, including summer space use and individual variation.

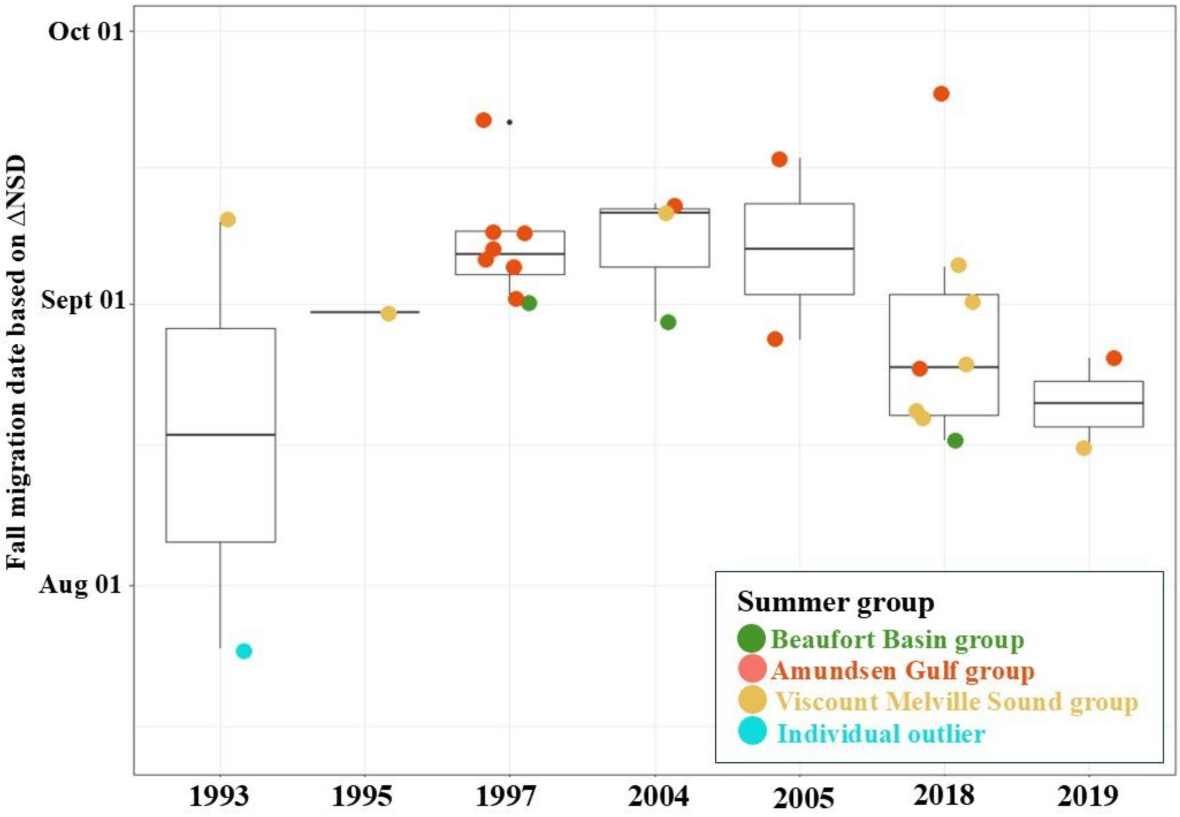


Figure 3.7 Fall migration dates shown by year and group, highlighting the bias towards AG whales in 1997 and VMS whales in 2018 due to the timing of tagging operations and the choice of animals instrumented.

Timing of beluga presence in the Mackenzie Estuary does not reflect fall migration timing. Apart from the ungrouped individual that migrated in July 1993, none of the belugas migrated soon after departing the estuary. VMS belugas spent weeks in Viscount Melville Sound, while AG and BB belugas travelled to offshore areas or frequented the continental slope before initiating directional westward movements. Given the importance of belugas for subsistence harvest by Inuvialuit (Ovitz et al., 2024; Stafford et al., 2018; Waugh et al., 2018), timing of occurrence in the estuary has been proposed as an ecological indicator to evaluate change over time (Loseto et al., 2010; Scharffenberg et al., 2025) and assess cumulative effects of stressors within the Tarium Niryutait Marine Protected Area (Loseto et al., 2018). As shown in this study, multiple subgroups occur in the estuary in the early summer, then disperse as the season progresses. Departure from the estuary represented movements towards offshore sites, while fall migration was a separate event which occurred several weeks later. Since the three summering groups exhibited contrasting use of nearshore areas, monitoring beluga presence near coastal whaling camps may lead to inconsistent observations, likely reflecting patterns within specific subgroups rather than population-wide shifts. Community-based observations varied across sites: some interviewees noted that cows spent a longer time in nearshore areas in recent years (Harwood et al., 2020) or that groups of belugas linger near whaling camps later in the season (Ovitz et al., 2024; Waugh et al., 2018), while others report earlier departures or no change in comparison to past years (Harwood et al., 2020). Similarly, acoustic monitoring found no clear relationship between the end of nearshore summer aggregations and environmental conditions (Scharffenberg et al., 2025). Spring migration timing may be better captured by Estuary-based monitoring, since the link between the date of landfast ice break-up and the arrival of belugas in the estuary is clearly established (Hornby et al., 2016) through acoustic monitoring (Scharffenberg et al., 2025) and aerial surveys (Hornby et al., 2014, 2016). On a decadal scale, knowledge holders in the ISR offered reported earlier spring arrivals in the late 2010s (Harwood et al., 2020; Ovitz et al., 2023; Waugh et al., 2018), consistent with longer ice-free periods (Johnson & Eicken, 2016; Mahoney et al., 2014).

Migration timing occurs in the context of an annual routine (McNamara et al., 1998), and is influenced by environmental, social and individual factors (Shaw, 2020). Delaying departure can be a strategy to optimize energy expenditure (Alerstam & Lindström, 1990): By remaining longer in areas with favourable foraging conditions, animals can continue replenishing energy stores before initiating migration (Newton, 2011), as exhibited by the belugas that remained by the continental slope or along the Tuktoyaktuk peninsula at the end of the summer. In contrast, the VMS belugas may replenish energy stores more efficiently by targeting prey-rich underwater slopes in Viscount Melville Sound, enabling earlier departure. At the individual level, body condition is linked to departure dates across a range of taxa (Bêty et al., 2004; Duijns et al., 2017; Monteith et al., 2011; Russell et al., 2022). Migrants must ensure sufficient energetic reserves to sustain the upcoming journey (Lennox et al., 2016), and to minimize risk in the event of unfavorable conditions encountered after departure (Anderson et al., 2020; Debeffe et al., 2019; Shuert et al., 2023). This may be particularly important for individuals that are less robust to stress due to differences in age (Newton, 2011) or reproductive status (Craig et al., 2003). A host of other individual traits can also influence migratory behaviour, including early life conditions, personality and learned information (Shaw, 2020). Group-specific migratory schedules may reflect social learning within groups (Whitehead, 2010), or knowledge transfer across generations, as belugas exhibit migratory cultures which are thought to be transmitted matrilineally (O'Corry-Crowe et al., 2020). Given the differences in summer space use and migration timing among groups, accounting for sub-population structure is necessary to accurately monitor migration timing at the population level.

3.4.4 EBS beluga sub-population structure

In this study, we define "groups" as clusters of individuals which are more similar to one another than the overall sample, based on long-distance horizontal movements over the course of a season. Prior analyses of this satellite telemetry dataset (Hauser et al., 2014; Richard et al., 1998; Storrie et al., 2022) identified diverse summer movement patterns, but this study is the first to demonstrate that these same movement groups occur across multiple decades. Many beluga population constitute fission-fusion societies, with groups that diverge and converge throughout the year (O'Corry-Crowe et al., 2020), as reflected in our study. Despite exhibiting distinct space-use strategies, the three summering groups likely overlap during at least two periods of the year: in the summer, belugas were instrumented in the Mackenzie Estuary and each group included belugas captured near Hendrickson Island, and individuals that transmitted locations during their fall migration later overlapped in space and time in the Chukchi Sea in October and November (Chapter 2.3). Although belugas breed in the winter (Suydam, 2009), these periods of spatial proximity during the summer and fall could represent opportunities for dispersal between groups. These movement patterns suggest two non-mutually exclusive explanations: the three groups represent 1) behavioral variation driven by habitat preferences and social affiliations within a single, larger group of interrelated individuals, or 2) genetically distinguishable subpopulation groups that overlap in the Mackenzie Estuary before dispersal towards offshore sites.

Within populations, groups can be defined based on spatial, genetic or demographic structure (Wells & Richmond, 1995), and many subpopulations have been established through complimentary use of spatial and genetic data (Finnegan et al., 2012; Hampton et al., 2004; Martinez-Bakker et al., 2013; Sacks et al., 2004; Scribner et al., 2005; Viengkone et al., 2016). Several studies have examined genetic structure of harvested belugas in the ISR, using mitochondrial DNA (mtDNA) to identify maternal lineages and nuclear DNA microsatellites to assess biparental relatedness. Some spatial structure was discernible using mtDNA analyses, which identified several maternal lineages (Brown Gladden et al., 1997; Postma, 2017) that occurred at different frequencies among the samples from the central Mackenzie Delta, Paulatuk, Husky Lakes and Shingle Point (Postma, 2017). However, combined analyses of field observations and genetic data from multiple beluga populations suggest that DNA microsatellites may better reflect group structure: groups typically included multiple maternal lineages, and many links within groups involved paternal, not maternal relatives (O'Corry-Crowe et al., 2020). For EBS belugas, DNA microsatellites did not distinguish between sampling sites (Brown Gladden et al., 1999), and revealed genealogical clusters dispersed across sites (Postma, 2017). Overall, genetic analyses point to the existence of multiple genetics groups which overlap spatiotemporally in nearshore areas and are represented among the samples from multiple whaling camps. Similarly, the three groups highlighted in this study based on satellite telemetry data also occur at multiple nearshore sites, and individuals from each group travel between multiple sites throughout the summer. Disentangling the relationship between EBS beluga relatedness and movement behaviour would require genetic analyses using DNA microsatellites or whole-genome sequencing approaches (Montana et al., 2024) to detect fine-scale variation. Importantly, genetic structure and movement-based groups may not correspond; across multiple beluga populations, whales form social groups with both kin and non-kin (O'Corry-Crowe et al., 2020) and closely related individuals do not necessarily associate together.

3.4.5 Limitations

This study's dataset represents a small fraction of the estimated Eastern Beaufort Sea beluga population (n = 26; estimated population size = 38,500 in 2019; Marcoux et al., 2025), and the location and timing of tagging operations differed across years (Richard et al., 2001; Storrie et al., 2022). Most individuals that transmitted high-resolution data throughout summer were instrumented at Hendrickson Island, either in the most recent decade (Storrie et al., 2022), where only large males were tagged and VMS belugas dominated the dataset, or in 1997, when the tagging campaign was carried out in late July and did not include any VMS whales, presumably because they had already begun travelling north towards Viscount Melville Sound.

Meanwhile, two belugas instrumented outside Hendrickson Island exhibited atypical movements: a female tagged at Kendall Island travelled to Prince of Wales Strait, Minto Inlet, and Prince Albert Sound before returning west, while the ungrouped individual tagged at Garry Island migrated within days of instrumentation. These strong effects of tagging date and location indicate that the proportion of belugas shown in each summering group may not reflect their true prevalence in the population, while "uncommon" behaviors observed rarely in our dataset may be more widespread in the actual population than our limited sample suggests. Additionally, variation in space use and migration timing within the AG and BB groups suggests further sub-structure beyond the three summering groups identified here, which may be resolved with larger sample sizes.

The summering groups described in this study do not fully encompass the variation in summer space use and migration timing within the population. Several additional belugas were excluded from the study because they ceased transmitting locations before the end of the summer (Figure S3.2). Of these, two belugas travelled to Viscount Melville Sound, then travelled to the Amundsen Gulf via Prince of Wales Strait. Another individual transmitted location from the Mackenzie Trough in late September before tag failure, suggesting it migrated in October or afterwards, later than any individual included in our analysis. Beyond the three groups identified through satellite telemetry, belugas have been recorded summering in Darnley Bay, NT (Harwood et al., 2015; Ovitz et al., 2024), or migrating west along the coast near Shingle Point, NT (Shannon MacPhee, pers. comm.). Further, harvest monitoring programs in the ISR have recorded occasional beluga harvests in Ulukhaktok and Sach’s Harbour, NT, beginning in the mid-2010s (Campbell et al., 2024; Harwood et al., 2020), and acoustic moorings detected belugas in Minto Inlet between June and September (Halliday et al., 2022) and in November near

Ulukhaktok, NT (Halliday et al., 2019). While these additional sources indicate that summer movements vary spatially and temporally beyond the ones presented here, our findings highlight the importance of this group structure for population management.

3.4.6 Future directions

In addition to describing several distinct movement patterns, and echoing existing observations of sub-population variability from Inuvialuit knowledge holders (Harwood et al., 2020; KAVIK-AXYS, Inc., 2012; MacPhee et al., 2025; Murray et al., 2023) and western science (Harwood & Norton, 1996; Mayette et al., 2022; Ovitz et al., 2025; Scharffenberg et al., 2025), our findings highlight important knowledge gaps in the summer movements of EBS belugas. Existing monitoring methods may only capture a subset of the EBS beluga population. For example, the most recent EBS beluga abundance estimate is based on aerial surveys conducted in the Amundsen Gulf in late July and early August 2019 (Marcoux et al., 2025), but our findings indicate that VMS belugas had likely departed from the surveyed area by this time. Similarly, monitoring of beluga occurrence at nearshore sites (Harwood et al., 2020; Scharffenberg et al., 2025) does not capture the beginning of the fall migration for belugas that depart from distant offshore locations, as was the case for most belugas in our study. Emerging tools such as very high resolution (VHR) satellite imagery could be used to monitor beluga presence in Viscount Melville Sound or Prince of Wales Strait, as this approach has been successfully applied to detect belugas in other remote High Arctic locations (Sherbo et al., 2025; Stewart et al., 2024; Watt et al., 2023). However, this method requires precise knowledge of when and where belugas occur, given the cost of purchasing VHR satellite imagery (Stewart et al., 2024). Identifying sub-population groups within the EBS beluga population would enable study design that accounts for distinct space use and migration patterns.

For EBS belugas, a combination of movement data, genetic analyses, and behavioral observations can contribute to disentangling sub-population structure. The development of a harpoon-based method (MacPhee et al., 2025; Scott, 2018) for remote tagging (Andrews et al., 2019; McIntyre, 2014) of EBS belugas presents opportunities to instrument individuals at a variety of nearshore sites, without some of the logistical challenges associated with live-capture (Orr et al., 2001, see Chapter 2). Remote biopsies (Noren & Mocklin, 2012) collected in tandem with telemetry studies could supplement the existing genetic dataset, which is predominantly obtained from camps in the Mackenzie Estuary during the peak July whaling season (July-August, similar to the tagging dataset) (Harwood et al., 2015). Most work on EBS beluga social structure has focused on short-term associations observed during aerial surveys, where individuals traveling in proximity are treated as social units (Fraker et al., 1979; Harwood & Norton, 1996; Mayette et al., 2022; Ovitz et al., 2025). To resolve social dynamics over longer timescales, photo-identification catalogues have been applied to belugas elsewhere (Ryan et al., 2022) as well as to narwhals, another small Arctic odontocete that is similarly challenging to monitor due to their remote distribution and elusive nature (Auger-Méthé et al., 2010; Charry et al., 2020; Marcoux, Auger-Méthé, et al., 2012).

In general, behavioral diversity benefits wildlife by limiting the proportion of individuals exposed to any single, area-specific threat (Costa et al., 2016), and species with greater within-population variability in migratory routes and destinations face lower risks of decline (Gilroy et al., 2016). However, these group-specific risks must be understood for effective population management. EBS beluga subgroups that occupy different parts of the summer range at different times be experience different levels of exposure to shifting sea ice conditions (Shen et al., 2021), harvest pressure (Harwood et al., 2015), changes in prey availability (Choy et al., 2020) and anthropogenic disturbance from shipping traffic (Dawson et al., 2018) and natural resource extraction (Dewing et al., 2025b). To further understand subgroup-specific pressures, future research could examine whether summering groups partition during migration and across the remainder of the annual cycle, particularly in the case of breeding females, which are less dispersed than males in this study. Overall, sociality is increasingly recognized as a critical element of cetacean management, and several populations of orcas and dolphins are managed with consideration of distinct social groups (Hauser et al., 2007; Parsons et al., 2009; Silber et al., 2017; Smith et al., 2016). Effective management of the EBS beluga population, which is closely linked to the culture and well-being of coastal communities in the ISR and Alaska (Adams et al., 1993; Byers & Roberts, 1995; Ostertag et al., 2018), relies on understanding how behavioral diversity either amplifies risk or confers resilience in a changing Arctic Ocean.

3.4.7 Conclusion

These findings provide new insight into EBS beluga pre-migration movement. Our findings confirmed the hypotheses that EBS belugas exhibit spatial segregation during the summer, with groups composed of belugas of different age and sex classes targeting distinct high-use areas. Groups also differed in the timing of departure from the Mackenzie Estuary; mature males that travelled to Viscount Melville Sound departed by mid-July, while two other groups with mixed composition returned later in the summer, in some cases visiting the estuary in late August. Although mean fall migration dates differed among groups, departure dates varied within groups and overlapped to some extent, with certain differences likely linked to within-group differences in space-use patterns. These findings highlight behavioral variation during the summer, where population structure affects both space use and migration timing. While previous satellite telemetry studies (Richard et al., 2001; Storrie et al., 2022) have hinted at the existence of distinct long-distance movements, combining data across years allowed us to apply clustering algorithms to individual trajectories with sufficient sample sizes to robustly identify divergent space-use patterns that persisted across decades. This study demonstrates the value of pooling long-term telemetry datasets to reveal hidden population structure in species with small sample sizes, a common limitation in marine mammal research (Sequeira et al., 2019). These distinct movement patterns may reflect adaptive responses to local environmental conditions, potentially enhancing overall population resilience, while warranting further attention to account for spatially and temporally segregated groups and the distinct pressures they may face.

3.5 References

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3.6 Supplemental material

Table S3.1 ID, sex, body length, tagging date, duration and location, and tag type for individual belugas.

ID	Sex, calf	Length (m)	Tagging date	Tag duration (days)	Tagging location	Tag type
017002_01	M	4.57	1993-07-17	34	Garry Island	SMRU 1
017005_01	M	4.42	1993-07-08	91	Garry Island	SMRU 1
002118_01	F	3.74	1997-07-26	129	Hendrickson Island	WC ST-10
017001_01	M	4.27	1995-07-04	85	Hendrickson Island	SMRU 1
017007_01	F	3.73	1995-07-08	81	Hendrickson Island	SMRU 1
008754_02	M	4.05	1997-07-31	90	Hendrickson Island	SMRU 3
008755_01	M	4.00	1997-07-29	81	Hendrickson Island	SMRU 3
008757_01	M	3.79	1997-07-30	68	Hendrickson Island	SMRU 3
008758_01	M	4.21	1997-07-31	120	Hendrickson Island	SMRU 3
010692_01	F,Y	3.38	1997-08-01	65	Hendrickson Island	SMRU 2
010693_01	M	3.95	1997-07-31	73	Hendrickson Island	SMRU 2
025846_01	M	3.74	1997-07-29	85	Hendrickson Island	WC ST-10
04-10972	F	3.00	2004-07-05	101	Hendrickson Island	WC SPOT
04-10899	M	3.70	2004-07-04	335	Hendrickson Island	WC SPOT
04-37024	M	4.40	2004-07-06	304	Hendrickson Island	WC SPOT
05-57591	F,Y	2.75	2005-07-06	319	Kendall Island	WC SLASH
05-57593	F	3.50	2005-07-11	163	Kendall Island	WC SLASH
174962	M	4.06	2018-07-06	161	Hendrickson Island	SPLASH10-F-238
174963	M	4.44	2018-07-08	334	Hendrickson Island	SPLASH10-F-238
174965	M	4.20	2018-07-03	183	Hendrickson Island	SPLASH10-F-238
174966	M	4.40	2018-07-08	356	Hendrickson Island	SPLASH10-F-238
174967	M	4.70	2018-07-04	350	Hendrickson Island	SPLASH10-F-238
174969	M	4.25	2018-07-09	162	Hendrickson Island	SPLASH10-F-238
174972	M	4.20	2019-06-29	138	Hendrickson Island	SPLASH10-F-238
175278	M	3.70	2018-07-09	96	Hendrickson Island	SPLASH10-F-238
175282	M	4.34	2018-07-12	47	Hendrickson Island	SMRU CTD-SRDL
179901	M	4.20	2019-07-10	68	Hendrickson Island	SPLASH10-F-321

Table S3.2 Comparison of agglomerative clustering algorithms used to validate group associations.

ID	**Sex,calf**	**Length (m)**	**Summer groups**		
			UPGMA	Complete linkage	Ward's
002118_01	F	3.74	1	1	1
04-10899	M	3.70	1	1	1
175278	M	3.70	1	1	1
008754_02	M	4.05	2	2	2
008755_01	M	4.00	2	2	2
008757_01	M	3.79	2	2	2
008758_01	M	4.21	2	2	2
010692_01	F,Y	3.38	2	2	2
010693_01	M	3.95	2	2	2
025846_01	M	3.74	2	2	2
04-10972	F	3.00	2	2	2
05-57591	F,Y	2.75	2	2	2
05-57593	F	3.50	2	2	2
174966	M	4.40	2	2	2
174967	M	4.70	2	2	2
174972	M	4.20	2	2	2
017001_01	M	4.27	3	3	3
017005_01	M	4.42	3	3	3
04-37024	M	4.40	3	3	3
174962	M	4.06	3	3	3
174963	M	4.44	3	3	3
174965	M	4.20	3	3	3
174969	M	4.25	3	3	3
175282	M	4.34	3	3	3
179901	M	4.20	3	3	3
017002_01	M	4.57	4	4	4

In addition to Ward's criterion, we clustered summer movements two other algorithms to ensure that group associations were consistent regardless of algorithm used: 1) UPGMA (unweighted pair-group method using arithmetic averages): To determine proximity between groups at each step, the proximity between every pair of objects in the first group and every pair of objects in the second groups is computed and averaged. This algorithm has been used in similar studies to cluster animal movement tracks based on shared movement patterns (Conner & Miller, 2004; Taylor et al., 2001), and 2) Complete linkage (farthest neighbour): Proximity between groups is defined using furthest members in each group (Legendre & Legendre, 1998).

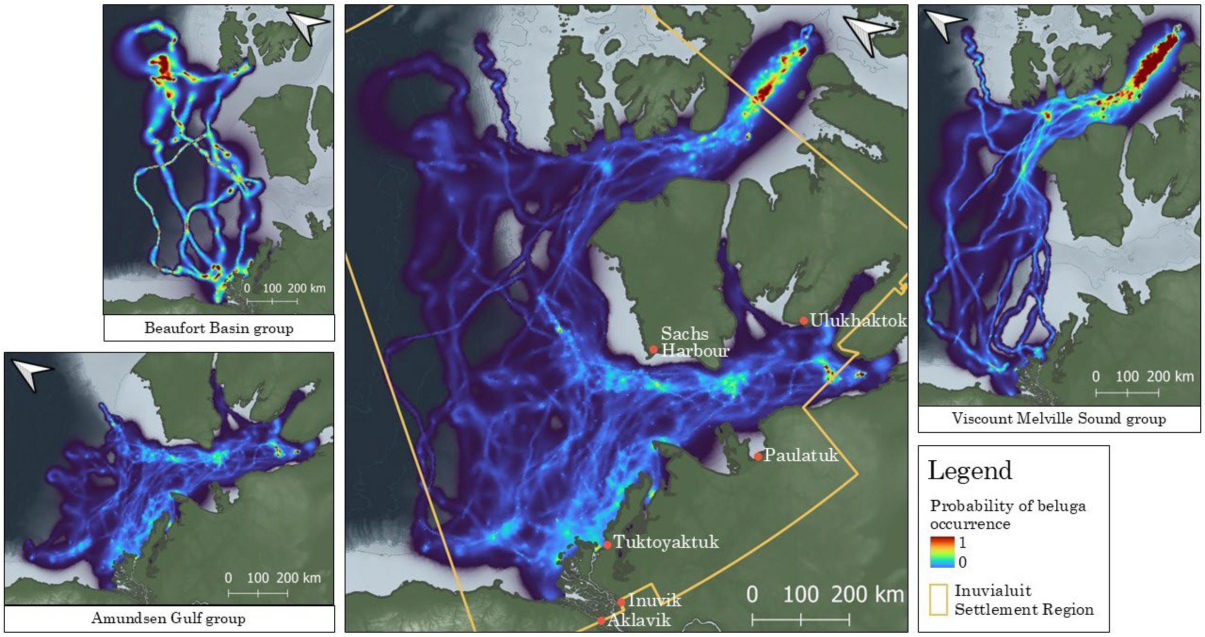

Figure S3.1 Summer occurrence distribution for all individuals (n=26) and for each summering group. Cell values for each image are rescaled (0-1) to highlight variation in space use within groups.

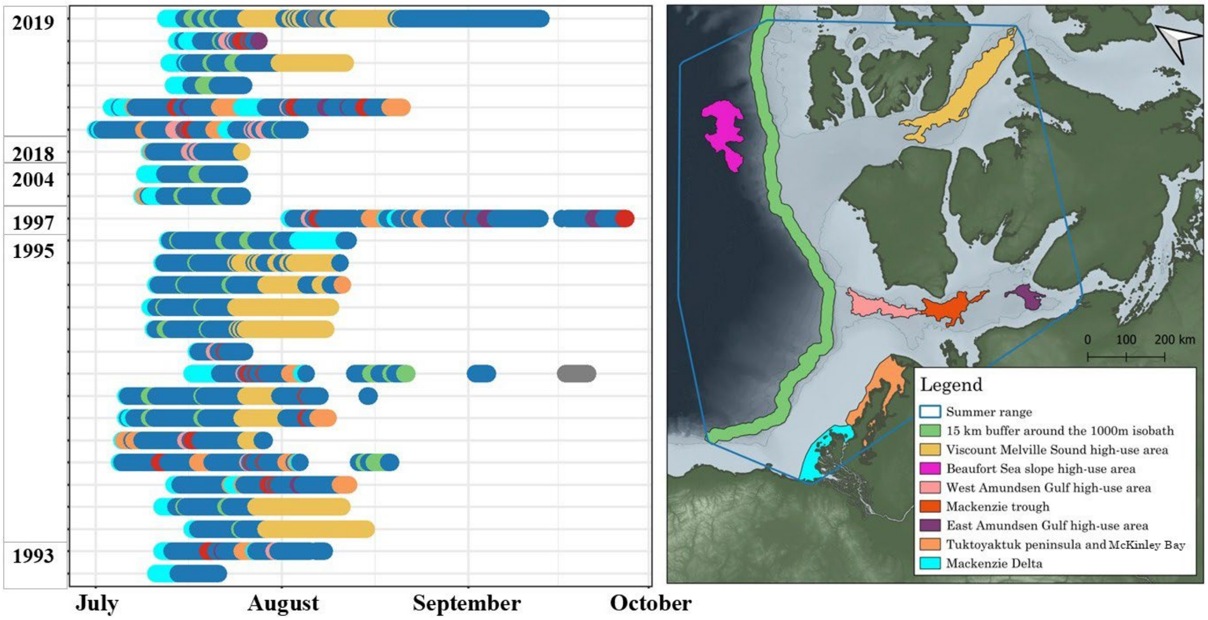

Figure S3.2 Timeline of summer movements for belugas that ceased transmitting locations before the end of the summer (n=26).

Table S3.3 Comparison of two methods to determine fall migration timing: 1) Dates based on Net Squared Displacement, and 2) Date of each beluga's last location inside the summer range.

Summer group	**Mean calendar date**	
	Migration dates based on ΔNSD	**Departure from summer range**
Amundsen Gulf group (n=14)	September 8th	September 11th
Viscount Melville Sound group (n=8)	August 29th	September 1st
Beaufort Basin group (n=3)	August 26th	August 27th
Ungrouped individual	July 25th	July 31st

The summer range was defined by drawing a concave hull around the 95% dBBMM contour encompassing all individuals. On average, belugas began travelling West in a directional manner 1.8 days before crossing the boundary to leave the summer range.

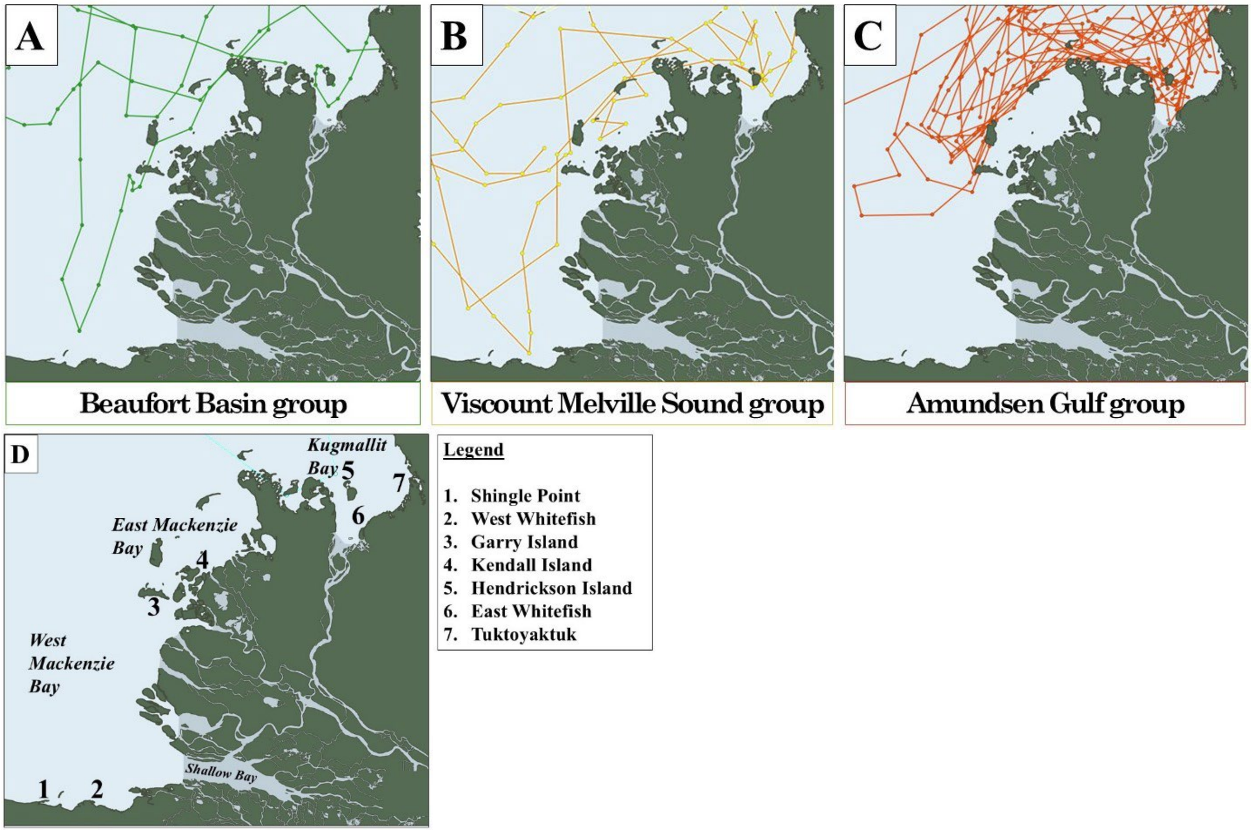

Figure S3.3 Tracks for the belugas in each summering group, shown alongside the locations of whaling camps in the Mackenzie Estuary.

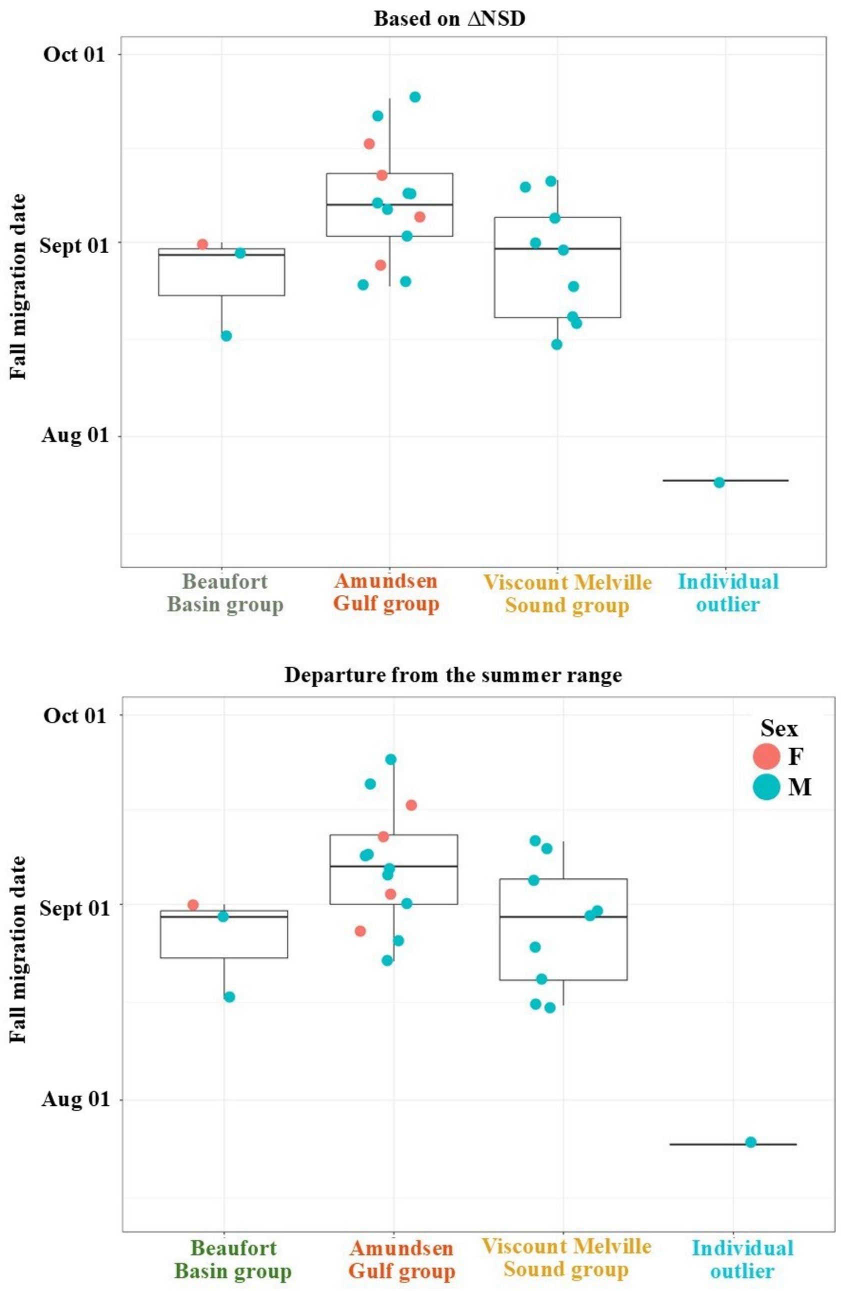

Figure S3.4 Date of the start of the fall migration, determined based on 1) changes in Net Squared Displacement and 2) departure from the summer range.

Variation between groups reflected similar patterns for both methods: for both groups, timing of departure varied significantly between groups (method 1 p = 0.399, or method 2 p = 0.0491), where the Amundsen Gulf departed latest.

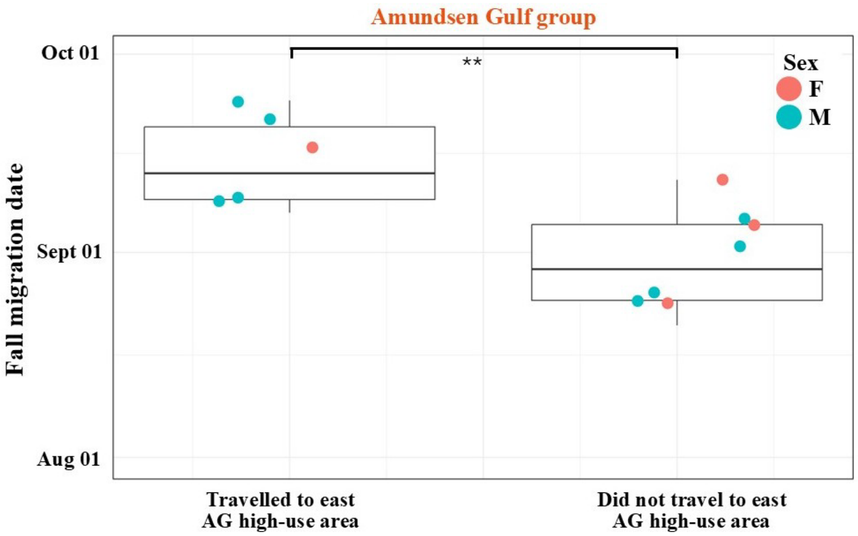

Figure S3.5 Fall migration dates of belugas in the AG group, showing the significant difference (p = 0.0034) between the belugas that travelled to the easternmost high-use area in the Amundsen Gulf, and those that remained west of the Amundsen Trough.

Chapter 4: Conclusion

4.1 Summary of findings

The overarching goal of this thesis was to gain a better understanding of the diversity of long-distance movements within the Eastern Beaufort Sea beluga population. Three satellite telemetry studies were conducted on this population in the 1990s, 2000s, and 2010s (Hauser et al., 2014; Richard et al., 2001; Storrie et al., 2022), largely facilitated by the involvement of Inuvialuit harvesters and co-management boards (MacPhee et al., 2025; Richard et al., 2001; Storrie et al., 2025). One of the research priorities outlined during consultations with Inuvialuit before and during the 2018-2019 program (MacPhee et al., 2025; Murray et al., 2023; Storrie et al., 2025), was to compare space use and migration timing across years, and assess whether beluga movement had shifted in response to climate change or anthropogenic pressures (MacPhee et al., 2025; Murray et al., 2023). While interannual comparisons were challenged by the sampling biases discussed throughout this thesis, my findings suggest that movement behaviour is influenced by the presence of distinct sub-groups, which may play a critical role in shaping migration and habitat use in addition to year-to-year environmental variability. This highlights the importance of considering social structure and group-level dynamics when assessing the responses of EBS belugas and other marine mammal populations to environmental change.

In chapter 2, I aggregated satellite telemetry data from 45 EBS belugas instrumented between 1993 and 2019 to describe year-round space use and define seasonal high-use areas, using dynamic Brownian Bridge Movement Models (dBBMMs) to account for the differences in sampling resolution and error structure within the dataset. This chapter addressed thesis sub-objective 1: Identify high-use areas (i.e. residency areas, migration corridors, stopover sites) across the annual migration cycle. Overall seasonal residency areas and migratory ranges echoed existing studies based on different subsets of the dataset (Hauser et al., 2014; Storrie et al., 2022). However, my analysis revealed several areas of overlap among individuals from different years and decades that were not highlighted in the literature; perhaps most notably, almost all the belugas in the study exhibited localized movements in the Chukchi Sea which overlapped in space and time. Additionally, the dBBMM identified sites where locations were densely concentrated outside of seasonal residency areas, highlighting potential individual stopover sites along submarine features such as the Chukchi Plateau, Northwind Ridge or the Beaufort Sea slope during fall and spring migrations. I suggest that these sites, which are less intensively monitored than the summer and winter ranges, may play a key role in sustaining year-round movements for EBS belugas and are worthy of further study.

In chapter 3, I compared the summer movements of 26 EBS belugas to quantify differences in space use patterns and examined whether these influenced fall migration timing. This chapter addressed thesis sub-objectives 2) Examine the influence of internal drivers including individual traits (sex, age, calf presence) and social group on beluga movement timing and distribution; 3) Quantify inter-individual variation in beluga space use; and 4) Examine timing of beluga occurrence in key areas. I quantified the distance between the movement paths of each pair of belugas using a Dynamic Time Warping algorithm, then established the summer high-use areas for each group of similar belugas using the dBBMM approach developed in chapter 2. I also defined the last day each beluga was in the Mackenzie Estuary, and used Net Squared Displacement to identify each individual's date of departure from the summer range, which occurred offshore in most cases. Groups exhibited significant differences in the timing of their last day in the Mackenzie Estuary, while migration timing differed among and within groups. While existing satellite telemetry studies have noted different movement patterns among belugas tagged at Hendrickson Island (Hauser et al., 2014; P. R. Richard, Heidi-Jørgensen, et al., 2001; Storrie et al., 2022), my analysis quantified the different movement patterns within the entire satellite telemetry dataset, noted that these movement patterns persist across years and decades, and demonstrated that they are linked to differences in age and sex. These findings suggest that research and monitoring approaches should aim to represent these different groups.

More broadly, this thesis contributes to the field of movement ecology by highlighting methods for aggregating long-term satellite telemetry datasets. Given the proliferation of animal tracking studies within the last few decades (Hart & Hyrenbach, 2010; Hussey et al., 2015), and the rapid technological advances in the field of satellite telemetry (Balmer et al., 2014; Béland et al., 2017; Robichaud et al., 2025), many long-term research programs now find themselves contending with decades of data, in which the quality and quantity of varies considerably between years or individuals. In chapter 1, I utilize methods developed by Kranstauber et al. (2012) to calculate occurrence distributions for each beluga while accounting for the temporal structure of the data, the quality of each location, and the sampling resolution. I then used methods outlined by Palm et al. (2015) to rescale and combine the dBBMMs across individuals to create seasonal occurrence distributions which accounted for both the intensity of use, and the overlap between belugas, associated with each 5 km x 5 km pixel. In chapter 2, I pooled all individuals that transmitted locations for the entire summer, then used a Dynamic Time Warping (Giorgino, 2009) algorithm to identify sub-population structure. Clustering algorithms like DTW provides a means of highlighting broadly similar movement patterns, and can be combined with multiple data streams including vertical data (Barbour et al., 2023) or environmental drivers (Giorgino, 2009), presenting an approach for rapidly assessing the presence of potential subgroups even with limited sample sizes. An increasing number of studies highlight the importance of sociality and group structure on marine mammal space use and migration timing (Charry et al., 2020; Christal et al., 1998; Craig et al., 2003; Genov et al., 2018; Hauser et al., 2007). Concurrently, given the interest in understanding the impacts of climate change on marine top predators, a growing body of research examines linkages between climate change and marine mammal behaviour (Cohen et al., 2018; Meynecke et al., 2021; Shuert et al., 2022; Silber et al., 2017; van Weelden et al., 2021), but some of these studies do not examine other sources of variability, such as group or individual-level variation (Grémillet & Descamps, 2023). I argue that testing for subgroup structure should be a standard assumption check when modeling population responses to environmental or other external drivers, especially in highly social species or in instances when limited sample sizes may limit population-level inference (Hebblewhite & Haydon, 2010; Lindberg & Walker, 2007; Sequeira et al., 2019).

4.2 Limitations

The summering groups described in this study do not fully encompass the variation in summer space use and migration timing within the population, nor do they likely represent the real-world relative frequency of the movement behaviour described. As discussed in each of the chapters, tagging studies were biased towards adult males, especially in 2018-2019 (Hauser et al., 2014; Storrie et al., 2022). Within the satellite telemetry dataset, most belugas ceased transmitting locations before the end of the summer and were thus not represented in this study. These included a potentially separate group that travelled through Prince of Wales Strait, and a beluga that remained in the summer range throughout all of September before tag failure. Beyond the three groups identified through satellite telemetry, additional movement patterns have been recorded via aerial surveys (Ovitz et al., 2025), drone-based behavioral studies

(Fisheries and Oceans Canada, 2025) and harvest monitoring (Harwood et al., 2015, 2020). While the data used here represents only a subset of the population's summer movement patterns, the results indicate persistent groups that endure across years despite environmental change and that differ in both the areas they target during the summer and the timing of their occurrence along nearshore sites in the Mackenzie Estuary.

Since I pooled data across years, my study does not account for interannual variation, which has been highlighted in the summer range through several studies and long-term monitoring programs, including aerial surveys (Harwood et al., 1996; Mayette et al., 2023), acoustic monitoring (Scharffenberg et al., 2025) and harvest monitoring (Campbell et al., 2024; Harwood et al., 2020). Aerial surveys carried out over the offshore Beaufort Sea shelf in the 1980s (Harwood & Norton, 1996) and late 2000s (Harwood & Kingsley, 2013) showed a greater number of belugas along the shelf in the latter study (Harwood & Kingsley, 2013), a trend which persisted in the most recent 2019 survey (Mayette et al., 2023). Harvest monitoring programs in the ISR have recorded occasional beluga harvests in Ulukhaktok and Sach's Harbour, NT, beginning in the mid-2010s (Campbell et al., 2024; Harwood et al., 2020). Inuvialuit knowledge studies have reported shifts in the timing of beluga occurrence at Kendall Island (Ovitz et al., 2024) and near Tuktoyaktuk (Waugh et al., 2018), potentially linked with earlier sea ice break-up in the spring. Finally, beluga vocalizations in the TN MPA varied between years and hydrophone deployment sites across 8 years, suggesting that belugas respond to the timing of sea-ice break-up and local environmental conditions (Scharffenberg et al., 2025), both of which have changed significantly in past decades (Lee et al., 2025). Together, these additional sources of information present long-term changes in the timing and distribution of EBS beluga summer movements, suggesting that these may have shifted significantly over the duration of this study, however, these interannual changes are challenging to assess based on the satellite telemetry data alone. By contributing a fuller understanding of the movement patterns in this dataset, specifically in terms of their variability and spatiotemporal range, this thesis provides a more reliable baseline against which to assess future change.

The two data chapters in this thesis relied on horizontal movements, interpolated to 12-hour and 8-hour intervals. Fine-scale movement patterns were likely missed as a result, as belugas can enter and leave areas in response to real-time environmental conditions, as recorded via hourly analyses of acoustic moorings (Scharffenberg et al., 2019, 2025). Vertical data, which was collected in tandem with horizontal movements for all whales instrumented in 2018-2019 and some of the belugas from 1993-2005 (Hauser et al., 2015; Storrie et al., 2022), was not included. I made this decision in order to include as many individuals as possible from 1993-2005 in the analysis, and because dive behaviour has previously been analysed and discussed in detail where feasible (Citta et al., 2020; Hauser et al., 2015; Storrie et al., 2022, 2025). However, I recognize that horizontal movements do not always reflect behaviour, especially when locations are interpolated to coarse temporal scales. While real-time observations of individual beluga surface activities can approximate individual dive profiles from concurrent telemetry data (Lemieux Lefebvre et al., 2018), animal movement models can exhibit varying levels of success when approximating foraging behaviour from horizontal telemetry data (Florko et al., 2023). In particular, EBS belugas can undertake deep, foraging-type dives during directional movements (Storrie et al., 2023), suggesting that horizontal data alone do not reflect the true distribution of subsurface activities. I described likely ecological functions associated with different sites based on horizontal movements, existing studies on EBS beluga dive behaviour (Hauser et al., 2015; Storrie et al., 2022) and environmental conditions, including their potential associations with key prey species (Choy et al., 2020; Majewski et al., 2025; Quakenbush et al., 2015). However, more recent studies integrate horizontal and vertical data, alongside environmental conditions, to identify behaviour and better infer the ecological functions associated with different areas (Hornby et al., 2025). While such an analysis would not be possible for all individuals in our study that did not transmit vertical data, examining potential behaviours based on horizontal and vertical data (for the belugas where such data is available) could be used to better understand the behaviours associated with key summer areas. Such an analysis may yield slightly different regions by better distinguishing surface activities from dive behaviour, potentially allowing a better understanding of the proportion of time dedicated to behaviours such as molting, foraging, socializing (or other localized surface activities), and transiting.

4.3 Future directions

4.3.1 Space use, migration timing, abundance and group structure

These findings highlighted several key knowledge gaps with respect to space use, migration timing, abundance and group structure of EBS belugas. Here I briefly reiterate some of the questions and future directions described in chapters 2 and 3.

Firstly, several summer movement patterns detected by harvesters, community members and acoustic monitoring were not represented in the satellite telemetry dataset. Community members in Paulatuk, NT, reported such reoccurring movements over a decade ago (KAVIK-AXYS, Inc., 2012; Beluga Summit 2025) and more recently during the 2025 Beluga Summit in Inuvik. In particular, harvesters described belugas travelling past Paulatuk from the east, sometimes later in the season (C.Ruben, pers. comm), and a belugas have been recorded in Darnley Bay via aerial surveys and drone-based behavioral studies (Ovitz et al., 2025), as well as long-term harvest monitoring programs (Harwood et al., 2015). Tagged belugas also did not travel to Husky Lakes (Trana et al., 2016) or initiate their migration near Shingle Point, NT (Worden et al., 2020). The lack of representation of these movements within the satellite telemetry dataset may point to spatial or temporal partitioning with the belugas frequenting Hendrickson Island in July.

Secondly, my findings suggest that fall migration dates extend beyond the typical range described in the literature for EBS belugas, and current monitoring approaches may not effectively capture this diversity. Chapter 2 and prior studies describe fall migration dates typically occurring in late August or September (Hauser et al., 2014, 2017), yet the ungrouped individual in chapter 3 migrated in July, one individual instrumented in 1997 transmitted its final location in the Amundsen Trough in October, and acoustic monitoring near Ulukhaktok recorded a beluga in November (Halliday et al., 2019). Additionally, occurrence in the Mackenzie Estuary did not reflect fall migration timing (except for the ungrouped individual that migrated soon after instrumentation). Fall migration timing varied among years, among groups and within groups. Monitoring future analyses should therefore avoid using estuary departure timing as a proxy for fall migration timing and apply caution when interpreting interannual or environmental effects. Future telemetry studies could capture a more representative sample of the population by instrumenting belugas across a broader range of dates and sites. Where feasible, remote tagging (Scott, 2018; Storrie et al., 2022) can reduce costs, simplify logistics, and lessen animal stress compared with live-capture (Orr et al., 2001; Storrie et al., 2022).

Third, the current abundance estimate may under-represent the population size of EBS belugas. This is a known limitation of the most recent aerial surveys, conducted in 2019, where inclement weather prevented the team from completing all of the planned survey transects (Marcoux et al., 2025). Given the resulting survey coverage, belugas in the VMS group, as described in chapter 3, were likely not included. One of the assumptions of the aerial survey was that belugas moved randomly between survey strata (Marcoux et al., 2025), however, my findings suggest that this assumption is only met for a proportion of the population: Belugas in the VMS group, and the ungrouped individual, moved in a directed manner beyond the survey area, while belugas in the AG and BB groups undertook back-and-forth movements that intersected several survey strata. To augment the existing aerial surveys, very-high-resolution (VHR) satellite imagery could estimate abundance in remote areas such as Viscount Melville Sound, as demonstrated elsewhere in the High Arctic (Belanger et al., 2024; Stewart et al., 2024; Watt et al., 2023). Chapter 3's high-use areas and timelines can guide image acquisition to coincide with peak beluga presence in these remote locations.

Fourth, EBS beluga social structure represents an important area for future study. In chapter 3, the AG group encompassed a broader range of movement patterns than the other groups, potentially highlighting further sub-structure. Existing genetic data from nearshore whaling camps in the ISR also indicate the presence of distinct genetic lineages (Brown Gladden et al., 1999; Postma, 2017), however, it is unclear whether spatially distinct groups correspond to different genetic groups. Additionally, long-term group structure has not been thoroughly investigated for EBS belugas, but methods like photo-ID catalogues have been applied elsewhere to examine long-term associations within other beluga populations (Panova et al., 2025; Ryan et al., 2022). Integrating telemetry, genetics, and field observations, as shown elsewhere (O'Corry-Crowe et al., 2020) would clarify how social and genetic structure are linked to movement strategies

4.3.2 Environmental drivers of behaviour and habitat selection

While the questions outlined above would require additional data collection, the existing satellite telemetry dataset could support many additional analyses. Given their rapidly changing environment (Lee et al., 2025; Shen et al., 2021) and high mobility, clarifying the mechanisms of habitat selection remains a central focus of EBS beluga research. Several studies have examined EBS beluga summer habitat selection using satellite telemetry data (Hauser et al., 2017, 2018; and occurrence data from aerial surveys (Harwood et al., 2014; Mayette et al., 2023; Noel et al., 2022; Whalen et al., 2020). While these approaches have successfully identified beluga habitat preferences within a broader study area, they do not necessarily reflect individual responses to dynamic resource availability. A variety of analytical tools including step selection functions (SSFs) can be used to examine resource selection as animals move through the landscape, comparing the environmental attributes of observed steps (segments between two consecutive locations) with alternative random steps taken from the same starting point (Thurfjell et al., 2014). In other words, if a beluga can be expected to travel ~80 km per day, the environmental covariates associated with a daily location would only be compared to “available” locations within an 80 km radius, reflecting real-time conditions along the animal’s individual path, rather than overall environmental variability within the seasonal range. Integrated step selection analyses (iSSFs) (Avgar et al., 2016) can be used to examine environmental drivers and the properties of the animals’ movement path (ex: speed or tortuosity) within a unified framework to better understand the effect of external conditions on behaviour. These models could be used to examine how belugas respond to dynamic environmental conditions like water temperature, currents or sea ice conditions at various spatial scales, and how these responses shape movement behaviour at different stages of the migration cycle.

In chapter 3, belugas exhibited seemingly random movements within nearshore areas before travelling offshore. Inuvialuit harvesters have expressed an interest in understanding how belugas may modulate their movements in response to short-term changes in environmental conditions (B. Alikamik pers. comm, Beluga Summmit 2025). Additionally, analyses of acoustic data (Halliday et al., 2019; Scharffenberg et al., 2019; Scharffenberg et al., 2025; Simard et al., 2014) suggest that belugas enter or leave nearshore areas in response to short-term changes in meteorological or oceanographic conditions. By combining all available years of data and interpolating locations to a moderately fine resolution (ex: 4 hours) a SSF or iSSF approach could be used to examine how belugas respond in real time to dynamic environmental conditions such as temperature or wind as they travel through the Mackenzie Estuary. This analysis could include belugas with relatively short tag duration that were not examined in this thesis, utilizing EBS beluga telemetry data that has not been analyzed elsewhere.

Animals can exhibit different responses to environmental conditions depending on their migratory stage; in many cases, migration is a demanding period during which animals may seek to minimize energy expenditure (Alerstam & Lindström, 1990). Habitat preferences and patterns of resource selection often varies between migratory and residency periods when the two are directly compared (B. B. Allen et al., 2020). Resource selection functions could be used to examine how individual belugas respond to variable sea ice conditions during the migration period, and how these responses vary among individuals with different traits like reproductive status or body size that may impose physiological constraints on habitat use.

4.4 Conclusion

In this thesis, I demonstrated approaches for integrating historical datasets with differing error structures and sampling regimes, enabling analyses across decades. Using a combined dataset from three decades of EBS beluga collaborative satellite telemetry studies, I re-established seasonal ranges and high-use areas and identified distinct summering groups that differ in space use and migration timing, indicating that subgroup-specific movement patterns structure much of the observed variability. Building on this foundation, the combined decadal dataset archive can support further inquiry to advance our understanding of EBS beluga movements and their responses to environmental change.

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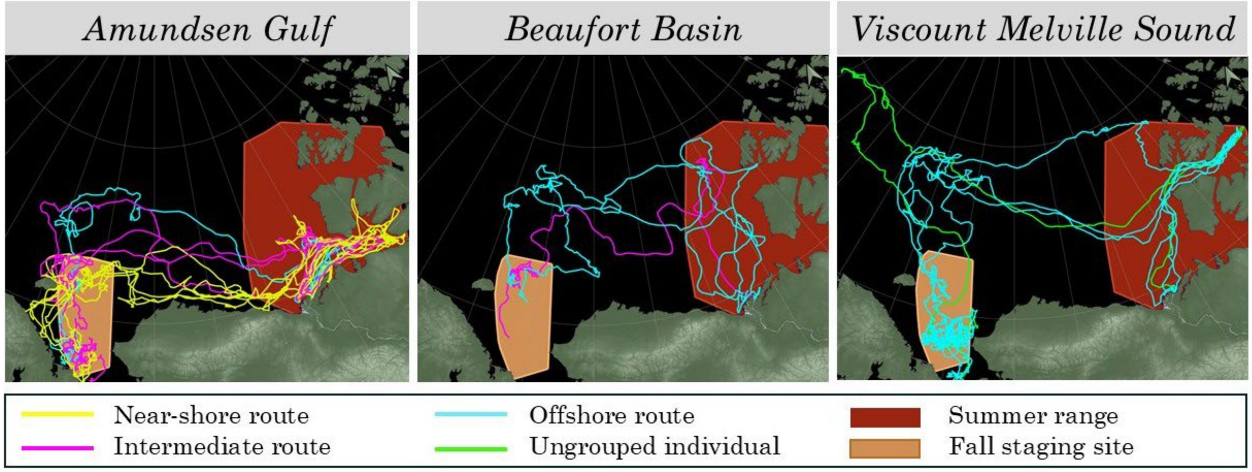
Appendix 1: Influence of summering groups on fall migration routes

While I identified several groups exhibiting distinct summer movement patterns, it was unclear whether these group associations persist during subsequent stages of the annual migration. I identified belugas that transmitted locations until they arrived to the staging sites in the Chukchi Sea, with no gaps >72h between subsequent locations for the entire duration of the fall migration (n=16). I used a state-space model (Jonsen et al., 2005) to interpolate locations to 8-hour intervals. I created an occurrence distribution with a spatial resolution of 10 km^2 for each beluga using dynamic Brownian Bridge Movement Models (dBBMMs) (Kranstauber et al., 2012), then quantified the similarity between each pair of belugas using Earth Mover's Distance, which compares two raster images and computes the effort required to transform one distribution into the other (Kranstauber et al., 2017). I then grouped belugas that were more similar than the average inter-individual distance using hierarchical clustering (Barbour et al., 2023)

Belugas were clustered into four fall migration routes (Appendix 1. Figure 1). Cluster 1 ("nearshore route") included individuals that remained near or south of the continental shelf throughout their migration, travelling along the coast of Canada and Alaska. Cluster 3 ("offshore route") travelled past the deepest areas of the Canada Basin, spending time above the Chukchi Plateau and Mendeleev Ridge. Cluster 2 ("intermediate route") travelled at latitudes between the other two or travelled along the nearshore route before veering offshore midway through their migration. One individual ("unclustered individual") travelled further north than any of the other individuals, venturing into the East Siberian Sea.

Belugas in the Amundsen Gulf summering group (Chapter 3), which exhibited the greatest range of individual traits, followed a mix of individual, intermediate and offshore routes (Figure 4.2), including all the belugas that followed a nearshore route, three males that followed the intermediate route and one large male that followed the offshore route (Appendix 1. Table 1). Of the four belugas that spent the summer along the coast of the Beaufort Sea shelf, three transmitted locations for the entire fall migration, of which the two males followed an offshore route and the female veered south to follow an intermediate route. Of the eight mature male belugas that summered in Viscount Melville Sound, four transmitted locations for the full migration, of which three followed an offshore route and one veered further north than the other ("ungrouped individual").



Appendix 1. Figure 1 Fall migration routes employed by belugas in each of the three summering groups established in Chapter 3.

Appendix 1. Table 1 Summering groups, sex and body size of belugas on each fall migration route.

Fall migration route	**Summering group**			**Sex**		**Length (m)**	
	AG	**BB**	**VMS**	**M**	**F (calf)**	**Mean**	**SD**
Nearshore (n= 5)	5	0	0	3	2 (1)	3.80	0.65
Intermediate (n= 4)	3	1	0	3	1	4.07	0.29
Offshore (n= 6)	1	2	3	6	0	4.06	0.30
Ungrouped (n=1)	0	0	1	1	0	4.20	n/a

Multiple fall migration routes were employed by belugas in each summering group, and in particular, the Amundsen Gulf group included belugas that employed a variety of routes. Since the AG group included a mix of males, females without calves and females with calve, this subsequent partitioning during the fall may be influenced by individual traits. It could also suggest that the AG group encompasses several smaller groups that would be resolved with larger sample sizes. The VMS group included several mature males instrumented in 2018 that later followed an offshore route; however, these belugas diverged after crossing the Arctic basin and targeted a variety of areas along the Chukchi Plateau. This suggests that fall movements are influenced by a combination of factors including group associations, real-time responses to environmental conditions, or individual variability. Future work could examine the strategies associated with this different summer and fall movement patterns based on characteristics like migration timing, swimming speed or stopover site use.

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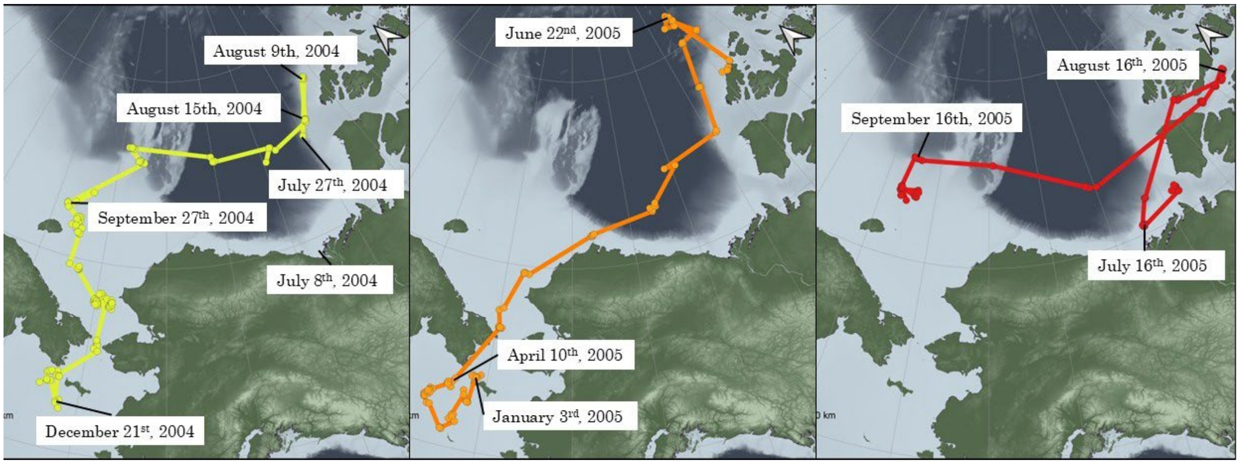
Appendix 2: Repeatability of long-distance movements

A single male beluga (body length = 4m) transmitted locations during two subsequent fall migrations (Appendix 2. Figure 1), which, to my knowledge, has not been documented elsewhere for belugas.



Appendix 2. Figure 1 Raw locations and tracks for beluga 04-37023.

The beluga was instrumented on July 8th, 2004, at Hendrickson Island. It began transmitting locations on July 27th, 2004 then again on August 9th, west of Banks Island. While it was not recorded inside Viscount Melville Sound in 2004, it could have travelled east between late July and early August, like some of the other tagged whales described in this thesis (see chapter 3.3 and S3). During the second summer, the beluga was recorded in Viscount Melville Sound in mid-August. During both years, the beluga travelled along an offshore route during its fall migration and targeted the edge of the Chukchi Plateau before continuing south to the Chukchi Sea. Spring movements for this individual are discussed in chapter 2. These movements suggest some interannual fidelity to summering areas and fall migration routes, with interannual variation in the timing of these movements. Further analyses could examine the environmental conditions encountered across the two subsequent years to evaluate whether the beluga may have modulated its movements in response to external drivers like weather, temperature or sea ice.