

Beluga Whale Habitat Selection and Distribution
in the Mackenzie Estuary and
the Tarium Niryutait Marine Protected Area

by

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Abstract

The Eastern Beaufort Sea (EBS) beluga population migrates to the Mackenzie Estuary and the Taimur Nirvutait Marine Protected Area every summer and the reasons behind this selection are not fully understood. Once in the Estuary, beluga whales (*Delphinapterus leucas*) are harvested by Inuvialuit communities of the Inuvialuit Settlement Region for whom they represent an essential country food, contributing to their health and cultural well-being. In the last decade, community members voiced their concerns and identified research priorities pertaining to belugas resources, baselines and habitats in the Estuary. To enhance our understanding of belugas habitat and further anticipate effects of a changing climate, it is crucial to understand why belugas select these habitats and what features are driving habitat selection. With that in mind, we created a habitat model based on aerial surveys observations from the late summer 2019 paired with remote sensing imagery to establish a baseline of environmental and spatial conditions selected by belugas. Then we assessed the baseline against historical data. We finally evaluated the habitat model with concurrent tagged observations to integrate the inferences made at a larger spatio-temporal scale. High turbidity and warm water temperatures were the two most important factors explaining beluga presence and were associated with the inshore waters of the Mackenzie River channels and along unprotected coastlines. Comparisons with past observations suggested that the observed beluga distribution had shifted from the baseline and was probably the results of the influence of changing environmental conditions on beluga response, either on a temporary (i.e., acclimatisation) or permanent basis (i.e., adaptation). The evaluation of the habitat model showed mixed results. We interpreted that variability by several factors, specific to the nature of belugas, to the coastal estuarine environment, or to the model itself. The inferences of selection, created in combining quality of environmental conditions and belugas mechanisms of selection, explained the intertwined patterns of beluga habitat distribution. Those findings enhanced our understanding of EBS beluga ecology and highlighted the complexity in defining and predicting beluga habitat distribution. This complexity, by preventing an accurate assessment of the changing beluga habitat distribution, represents new challenges for harvesters that who may have to switch the timing and location of their harvest in response. If we want to improve our understanding of belugas highly complex relationship with their environment, we should keep on building the habitat model aiming to create an integrated model.

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Inuvialuit Game Council (Inuvialuit Settlement Region) for their contributions in providing the 2019 satellite telemetry data as part of the Eastern Beaufort Sea Beluga Tagging Program. I would like to the NASA GSFC for providing free access to MODIS satellite data and to SeaDAS software and the Ocean Monitoring and Observation Section at the Fisheries and Oceans Canada Bedford Institute of Oceanography (Halifax, Canada) for their collaboration with the access and the processing of the imageries. The satellite dataset was generated under the DFO Arctic Science Fund project: “Measuring the impact of permafrost thaw and river export on the health of the coastal arctic ecosystem using satellite observation of Ocean Colour and hydrodynamic simulation: case study of MPAs in the Southern Beaufort Sea”.

Finally, thanks to this amazing opportunity, my own perceptions were challenged and brought me a new sense of awareness about different systems of knowledge and inquiry. I was able to define my positionality and acknowledge my own reflexivity, allowing me to be critical, cautious and transparent in my understandings, and guiding me in being a better scientist. Additionally, as I was an outsider of the community and a treaty person, it took me some time to find the place where I belonged, teaching me incidentally, to be a better person.

Contributions of Authors

The research reported in Chapter Two was conducted by Aurelie Noel (conceptualisation, methodology, data curation, formal analysis, writing – original draft, writing - reviewing and editing). This chapter has been reviewed by Lisa Loseto (Department of Fisheries and Oceans, University of Manitoba; also involved in the conceptualisation and methodology), Emmanuel Devred (Department of Fisheries and Oceans; who provided part of the data), John Iacozza (University of Manitoba; also involved in the methodology), Claire Hornby and Marianne Marcoux (Department of Fisheries and Oceans; who also provided part of the data). Douglas Esagok (Inuvik Hunters and Trappers Committee) participated at the conceptualisation and part of the investigation. The manuscript was submitted in the open-access journal Arctic Science for the Special Issue on the TN MPA as a manuscript for which I am the corresponding author on January 15, 2022. The manuscript was accepted under the condition of minor revisions on February 17, 2022, and is pending publication. Revised version was submitted on March 31, 2022.

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The research reported in Chapter Three was conducted by Aurelie Noel (conceptualisation, methodology, analysis and interpretation, writing, reviewing and editing). This chapter has been reviewed by Lisa Loseto (Department of Fisheries and Oceans, University of Manitoba) and John Iacozza (University of Manitoba; also involved in the methodology). Luke Storrie (PhD student at University of Manitoba) participated in the conceptualisation, methodology and part of the interpretation. This manuscript is in preparation for submission.

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CHAPTER ONE:

INTRODUCTION AND BACKGROUND

1.1 Beluga whales in the Mackenzie Estuary

The beluga whales (qilalugaq in Inuvialuktun or *Delphinapterus leucas* in Latin, hereafter belugas) are aquatic marine mammals distributed across Arctic and sub-Arctic ocean regions. Belugas are medium sized odontocetes, reaching an adult size between 3.5 (female) to 4.5 meters (male) and sexual maturity between the ages 5 (female) and 7 years (male) old. Belugas are born dark grey to become white as they mature and can live between 15 and 40 years. Belugas feed on a great variety of prey species including fish and invertebrates and are mainly preyed by polar bears or killer whales. The other causes of mortality are ice entrapments and subsistence hunting. Belugas are gregarious and demonstrate culturally-transmitted or learnt behaviours. Based on their distribution and genetics, belugas are currently divided in eight distinct populations (i.e., designatable units) in Canada. Most populations exhibit repetitive migrative patterns from partially ice-covered regions, where they overwinter, to river estuaries in the spring and summer (COSEWIC 2016).

The Eastern Beaufort Sea (EBS) beluga population has a wide circumpolar distribution (Laidre et al. 2008) and migrates seasonally to the Mackenzie Estuary in the Northwest Territories, Inuvialuit Settlement Region (ISR). EBS belugas seasonal movements are greatly influenced by sea ice conditions (Fraker et al. 1979a; Hornby et al. 2016; Citta et al. 2017). Belugas migrate along the Alaskan North Slope from their wintering areas in the Chukchi and Bering Seas (Citta et al. 2017) under thick pack ice and through deep offshore leads (Barber et al. 2001) to arrive in the Beaufort Sea in late May and June, waiting for the landfast sea ice to free the Mackenzie Estuary (Fraker et al. 1979a; Hornby et al. 2016). Belugas cluster in the Mackenzie Estuary in specific areas during the summer (Harwood et al. 2014) although some belugas seem to stay only intermittently (Richard et al. 2001). In late August, belugas move offshore and eastward into areas such as Viscount Melville Sound and the Amundsen Gulf (Fisheries Joint Management Committee – FJMC 2013; Hauser et al. 2017) and then return northwest to their wintering habitat (Citta et al. 2017). In the Mackenzie Estuary, belugas occupy specific areas recognized for their significance (Fraker et al. 1979a; FJMC 2013; Harwood et al. 2014), and protected under the Canada's Oceans

Act of 1997 by the designation in 2010 of the Tarium Niryutait Marine Protected Area (TN MPA; Canada Gazette 2010). The TN MPA is composed of Niaqunnaq, Okeevik and Kittigaruit sub-regions, located in Shallow Bay, West Mackenzie Bay and Kugmallit Bay respectively. These relatively shallow bays are shaped by the mouth of the Mackenzie River channels, respectively the West Channel, the Middle Channel and the East Channel (Macdonald and Yu 2006) and define the Mackenzie Estuary. The Mackenzie Estuary experiences strong season dynamics mainly related to the flow of the Mackenzie River and the sea ice fluctuations (Macdonald and Yu 2006). In summertime, the Mackenzie Estuary waters are generally fresh, highly turbid (suspended load around $375 \text{ g} \cdot \text{m}^{-3}$; Macdonald and Yu 2006) and much warmer than offshore (up to 18°C ; Fraker et al. 1979b). Those specific environmental conditions, associated with low winds, and featureless and flat or shoal-sandy seabed, have been suggested as favourable for belugas aggregation, justifying potentially the belugas fidelity for the Mackenzie Estuary (Fraker et al. 1979a; ISR-TK 2006; Scharffenberg et al. 2019; Whalen et al. 2020).

During their migration, EBS belugas occupy a wide variety of habitats; yet their summering site fidelity to the Mackenzie Estuary remains not fully understood (COSEWIC 2016). Various hypotheses of use have been proposed related to the specific environmental conditions of the Mackenzie Estuary. The water low salinity and warm temperature might contribute to epidermal moulting (St. Aubin et al. 1990) and shoal-sandy seabed might support the mechanical rubbing and removal of moulted skin (Scharffenberg et al. 2019; Whalen et al. 2020). Warm waters might promote calving or at least calf rearing, lowering the heat loss younglings might experience as their blubber has not been fully grown yet (ISR Traditional Knowledge report [ISR-TK] 2006; Waugh et al. 2018). Turbid waters have been suggested as refuge for predator avoidance, especially for juveniles protection, tempering with predators visualisation (Anderson et al. 2017). Opportunistic or low-energetic feeding might occur (Norton and Harwood 1986; Ostertag et al. 2019; Choy et al. 2020), even though foraging is thought to happen offshore (Storrie et al. 2022). Finally, it is also probable that belugas conduct simple activities such as resting, socialising or resting (Lemieux Lefebvre et al. 2017). Measuring the fundamental connections between belugas and their environment in the Mackenzie Estuary would corroborate some of the beluga philopatry hypotheses.

Rapid climate shifts occurring in the Arctic (Waugh et al. 2018; Bush and Lemmen 2019; Worden et al. 2020) strongly impact estuarine ecosystems (Pörtner et al. 2019) already affecting beluga summer habitat and habitat selection in the Mackenzie Estuary and TN MPA (Inuit Observations of Climate Change [IOCC] project 1999; ISR-TK 2006; Loseto et al. 2018; Scharffenberg et al. 2019; Worden et al. 2020; Ovitz et al. in-prep). Ascertaining impacts of environmental changes on beluga distribution patterns would continue serving as guidance in conservation and management decisions (Redfern et al. 2006), especially in the TN MPA.

1.2 Methods to Understand and Model Species Habitat Selection

Modelling approaches such as descriptive statistical techniques in the form of species distribution models (SDM) have been successfully used to describe the spatial distribution of a species, to understand the reasons of the species spatial patterns, and to predict conditions where the species may occur (Guisan and Thuiller 2005; Matthiopoulos et al. 2020).

To effectively apply models to ecological studies, some definitions are necessary. SDM are methods that relate species field observations to environmental variables (Guisan et al. 2017 – p. 11). A habitat is a description of environmental conditions at a discrete spatial location at a particular scale of space and time where a species either actually or potentially occur (adapted from Kerney et al. 2006 and Morris 2003). Species select a habitat because of its environmental characteristics, such as environmental conditions, resources and risks, that meet the species demands for population success and satisfy the species fitness needs (Guisan and Thuiller 2005). The association and interaction between the habitat and the species define the patterns of distribution (Matthiopoulos et al. 2020).

The choice of the model approach is based on the question asked, the ecology of the species, and the availability and the significance for the species of the environmental variables selected (Johnson et al. 2006). In this thesis, the relationships between belugas (i.e., the species) and their habitat were explored to assess and predict effects of climate change on the belugas and their habitat (Robinson et al. 2017; Northrup et al. 2022). A habitat model was consequently created in the form of a Resource Selection Function (RSF). RSF have been widely used in ecology and specifically with cetaceans, such as the Eastern Beaufort Sea beluga whales population (Loseto et al. 2006; Goetz et al. 2007; Hauser et al. 2017; Hornby et al. 2017; Whalen et al. 2020). RSF

mainly consist in regression techniques such as generalized linear models and accommodate polynomial and interaction terms, allowing flexibility in the modelling (Johnson et al. 2006; Guisan et al. 2017). A RSF is any function that relates likelihood of species occurrence with defined environmental variables, conditional on habitat availability (Johnson and Gillingham 2005; Redfern et al. 2006; Guisan et al. 2017). In this thesis, the species occurrences were surfaced belugas sampled from aerial surveys (Chapter Two) and tagged belugas followed by satellite telemetry (Chapter Three) during the summer of 2019. The environmental variables were the sea surface temperature, the suspended particulate matter concentration and the chlorophyll-*a* concentration extracted from satellite remote sensing images. The inferences of selection made at the third order (i.e., home range; Johnson et al. 1980). Due to drastically evolving terminology in this field, the fundamentals of selection functions will not be addressed in great detail (Northrup et al. 2021 and references therein) however the terminology chosen will be specified. The term probability of selection was used as defined in Lele and Keim (2013), based on a binary decision an animal of a species make depending only on the environmental conditions encountered: “as an animal encounters available habitat, it selects a habitat and uses it in some ways” (Northrup et al. 2022 – p. 3). A RSF calculates a relative probability of selection, considering what is available and accessible in terms of environmental conditions for the beluga to encounter but not knowing what the probability of encounter is. The term preference was avoided as it is defined as the disproportionality of selection compared to availability, considering availability being equal in terms of frequency and access for the whole area, which was not this case (Johnson 1980), and it was adding a notion of population density (and consequent competition) as a factor influencing selection (Northrup et al. 2022), which was not included.

Additionally, two different aspects of a RSF will be approached and combined to analyse habitat selection (HSA) and model habitat distribution (HDM) as species such as cetaceans are challenging to monitor (Redfern et al. 2006; Derville et al. 2018). HDM represent a different way of looking at species distribution as they do not predict where the species will occur but rather predict the spatial distribution of environmental conditions (included in the model) that are of quality for the species, defining habitat for the species that are likely to be selected (adapted from Guisan et al. 2017; Fieberg et al. 2018). HSA further that inference in emphasising the mechanisms by which species differentially select available habitats (Morris 2003), consequently generating patterns of habitat selection.

1.3 Multi-faceted context

This project, as every research project, is context dependent and I wanted to acknowledge that the results presented here are related to that very specific context.

1.3.1 Rationale – Inuvialuit Context

Belugas are an essential country food for the Inuvialuit communities of the ISR, contributing to their health and cultural well-being (Hoover et al. 2016). Through the Inuvialuit Final Agreement (IFA 1984), the co-management of belugas, notably in the Mackenzie Estuary, is shared between the Inuvialuit Hunters and Trappers Committees (HTC) and Fisheries and Oceans Canada through the FJMC and follows the Beaufort Sea Beluga Management Plan (FJMC 2013). In the last decade, community members voiced their concerns and identified research priorities. In 2013, the TN MPA working group reported several missing trends on indicator data such as ice cycle, oceanography and physical habitat (FJMC 2013). In 2016, during the Beluga Summit in Inuvik (Beluga summit 2018), research needs on beluga habitat use in the Mackenzie Estuary were identified by the communities of the ISR. In 2019, the FJMC highlighted several priorities to be addressed, notably the inventory of existing marine mammal resources and their habitats, the identification of their baselines and natural variation (Worden et al. 2019), and the enhancement of community involvement. The Inuvialuit Game Council gave its support, the same year, to gather Traditional Ecological Knowledge on beluga movement in the Beaufort Sea, notably to pursue knowledge co-production using the interpretation of spatial data.

This thesis was designed to address some of Inuvialuit concerns about belugas. The goal was to enhance our understanding of how belugas currently interact with their inshore summer environment with respect to key environmental features in the Mackenzie Estuary (and TN MPA) to better predict how belugas will respond to rapid environmental changes (Stafford et al. 2018) and to further inform conservation and management strategies of belugas in the TN MPA. This thesis endeavoured to sustain the dynamic foundation laid by the Fish and Marine Mammal Community Monitoring Program (FJMC 2013).

1.3.2 Community Engagement – Global Context

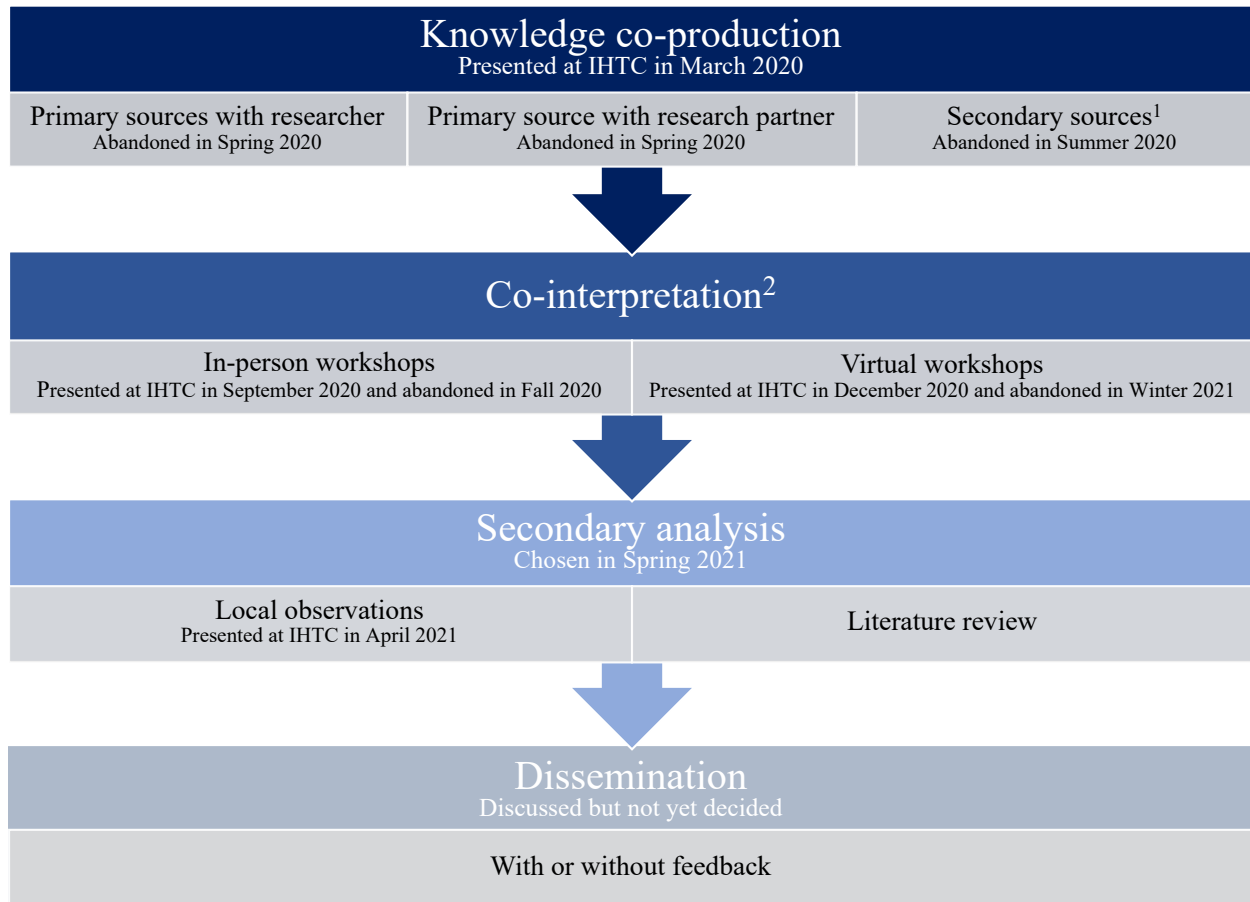
The thesis has seen a lot of changes from its conception and through its elaboration. Indeed, with the COVID-19 pandemic, travel restrictions challenged engagement with communities as initially envisioned and it was important to still present the work that was done, and which had to be cancelled multiple times over the course of the master's program.

The second part of the thesis (Chapter Two) was originally dedicated to a partnership with Inuvialuit beluga harvesters embracing quantitative and qualitative sciences in a mixed-methods fashion (Creswell 2009), and providing the opportunity to involve beluga knowledge holders from all systems of inquiry and knowledge. That partnership laid its foundations on the IFA that states “the relevant knowledge and experience of both Inuvialuit and the scientific communities should be employed in order to achieve conservation” (IFA 1984: article 14.5) and on the Inuvialuit communities identified concerns and needs (see section 1.3).

The initial objective was to gather Inuvialuit perceptions about belugas and their interactions with their summer habitat to further understand how climate change has, is, will impact the beluga summer habitat and habitat use, and identify threats and opportunities for traditional harvesting. This gathering would have informed our habitat model which results would have been brought back in the community to exchange expertise, gaining an enriched, accurate and sustainable understanding of beluga movement. The process was envisioned more particularly with the harvesters from Inuvik who have a broad knowledge of beluga habitat as harvesters traditionally reside in coastal whaling camps (Baby Island, Kendall Island, East White Fish and Kittigaruit), located around traditional beluga concentration locations.

This partnership was supported in December 2019 by the Inuvik Hunters and Trappers Committee (IHTC) (Appendix 1). However, acknowledging the reality linked to travel restrictions, flexible and evolving community engagement strategies were considered and several contingency plans were created (Figure 1.1, Appendix 2) in a sequential fashion. IHTC was involved at every step of the thesis, at the level they wanted, and was informed about all the contingency plans for them to either give guidance to tailor plans based on interests and suggestions, or even just support. Douglas Esagok, Director of the IHTC also served as our Research Advisor starting in April 2020.

Figure 1.1: Community engagement contingency plans



Notes: The contingency plans were abandoned one after the other as the COVID-19 pandemic progressed.

¹ The secondary sources knowledge co-production scenario envisioned a collaboration with the Inuvialuit Joint Secretariat/Shared Services Unit “A Beluga Traditional Knowledge Project”. ² The workshops would have been organized with an Inuvialuit facilitator.

Ultimately, a pragmatic approach was used, as seen on section 1.2, and this thesis, while following basic ethical guidelines and framework (Huntington 2000; TCPS-2 2018 (Appendix 3); Bartlett et al. 2012; Djenontin and Meadow, 2018 – Appendix 2 for details; Reid et al. 2020; Wilson et al. 2020; Pedersen et al. 2020), was mainly based on interdisciplinary content of natural sciences, social sciences and accessible literature encompassing Inuvialuit Knowledge, from peer-review publications and grey literature.

Finally, I conducted most of this work from home, like most of researchers during this challenging time, and consequently missed opportunities of meetings and open conversations with experts and mates.

1.3.3 Positionality – Personal Context

Defining my positionality and acknowledging my reflexivity (Kovach, 2009) brought me awareness and allowed me to be critical to my research and how my understanding might be biased, leading me to (dis)miss, misinterpret or overlook the nuances and complexity of a story that will be shared with me (Smith, 2006). It also created transparency by recognizing that the researcher and the research participants were reflected in the meanings being made (Kovach, 2009). I am an immigrant originally from Belgium, French-speaking and a mother of two. I moved to Canada in 2011, in Winnipeg/on Treaty One territory, following my husband's career. I am a natural scientist, the only University-graduate of my family. I am a geographer working mainly in Earth Observation using remote sensing and Geographic Information System, educated in a system of knowledge following a positivist and materialist epistemology. I have experience in collaborating with local communities on risk mitigation projects and wanted to pursue further work in that direction. Being a foreigner and a settler, and not speaking the language (Uummarmiutun), made me an obvious outsider (Smith, 2006) to this project. Yet it also made me a valuable partner, aware of my own limitations, of my responsibilities as a treaty person, and with experience finding solutions to cross those barriers and to be cautious with what I would experience. This project was the start of a new journey for me, growing and shifting my ability to see the world in different ways.

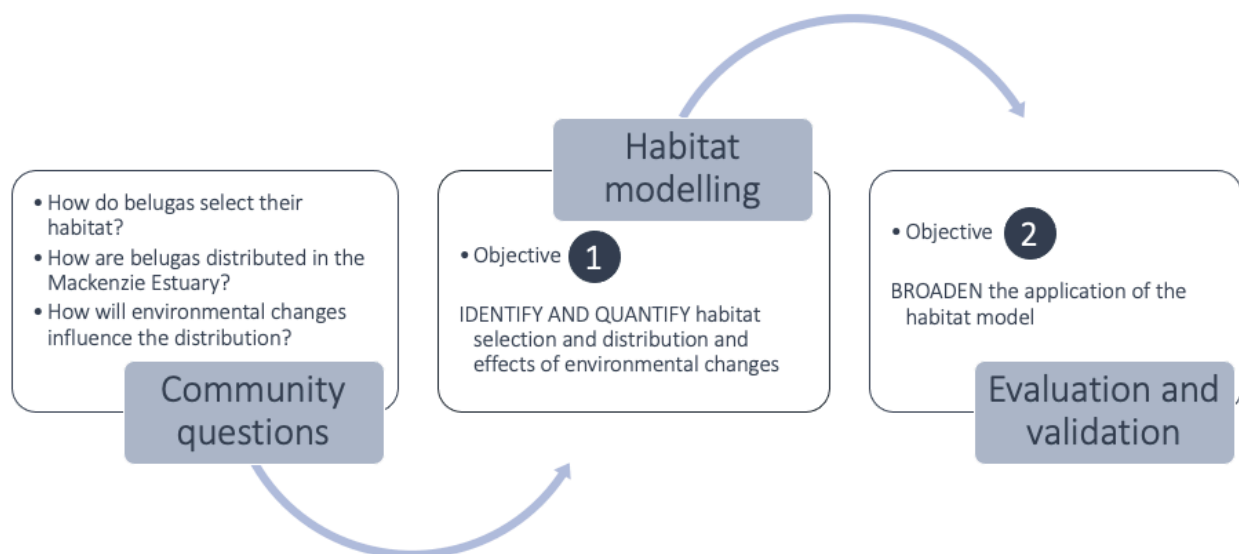
1.4 Thesis objectives and structure

This thesis is structured as “manuscripts within a thesis”, with Chapters One and Four being the Introduction and Conclusions respectively, and Chapters Two and Three written following the scientific manuscript structure (Abstract, Introduction, Methods, Results, Discussion and Conclusion).

Chapter One offers an introduction to the content, a description of the rationale and two consequent objectives, followed by an additional item that underlines the importance of the multi-faceted context around this project and concludes with an overview of the thesis structure. The overarching goal of this thesis was to enhance our understanding of Eastern Beaufort Sea beluga whale habitat to further anticipate effects of climate changes and was addressed in Chapters Two and Three. **Chapter Two** addresses the objective 1: to identify, quantify and qualify late summer

beluga habitat in terms of environmental conditions, spatial selection and variations over time in relation with climate change with a habitat model. It focuses on exploring beluga habitat distribution in the Mackenzie Estuary considering current environmental conditions, then on analyzing beluga distribution shifts in relation with climate change. Aerial surveys data from the Department of Fisheries and Oceans (DFO, Winnipeg and Inuvik) population abundance estimate from the summer of 2019 and remote sensing data processed in collaboration with DFO (Bedford Institute, Dartmouth) were used. **Chapter Three** is directly linked with Chapter Two and its limitations, and addresses the objective 2: to broaden the application of the habitat model created in the Chapter Two, aiming to give the model predictions a larger temporal and spatial scale. Satellite telemetry data from the EBS beluga tagging program led by DFO, the Fisheries Joint Management Committee (FJMC) and Inuvialuit Game Council (IGC) in the summer of 2019 and remote sensing data processed in collaboration with DFO were used. Finally, **Chapter Four** includes a summary of the findings, contributing to the body of knowledge existing about beluga whales, and general conclusion leading to future work and dissemination of the findings. Three appendices detailing community support, engagement and framework, and ethics requirement were also added.

Figure 1.2: Thesis structure



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CHAPTER TWO:

BELUGA DISTRIBUTION IN A CHANGING CLIMATE: A CASE STUDY OF INSHORE REGIONS IN THE MACKENZIE ESTUARY AND THE TARIUM NIRYUTAIT MARINE PROTECTED AREA

Abstract

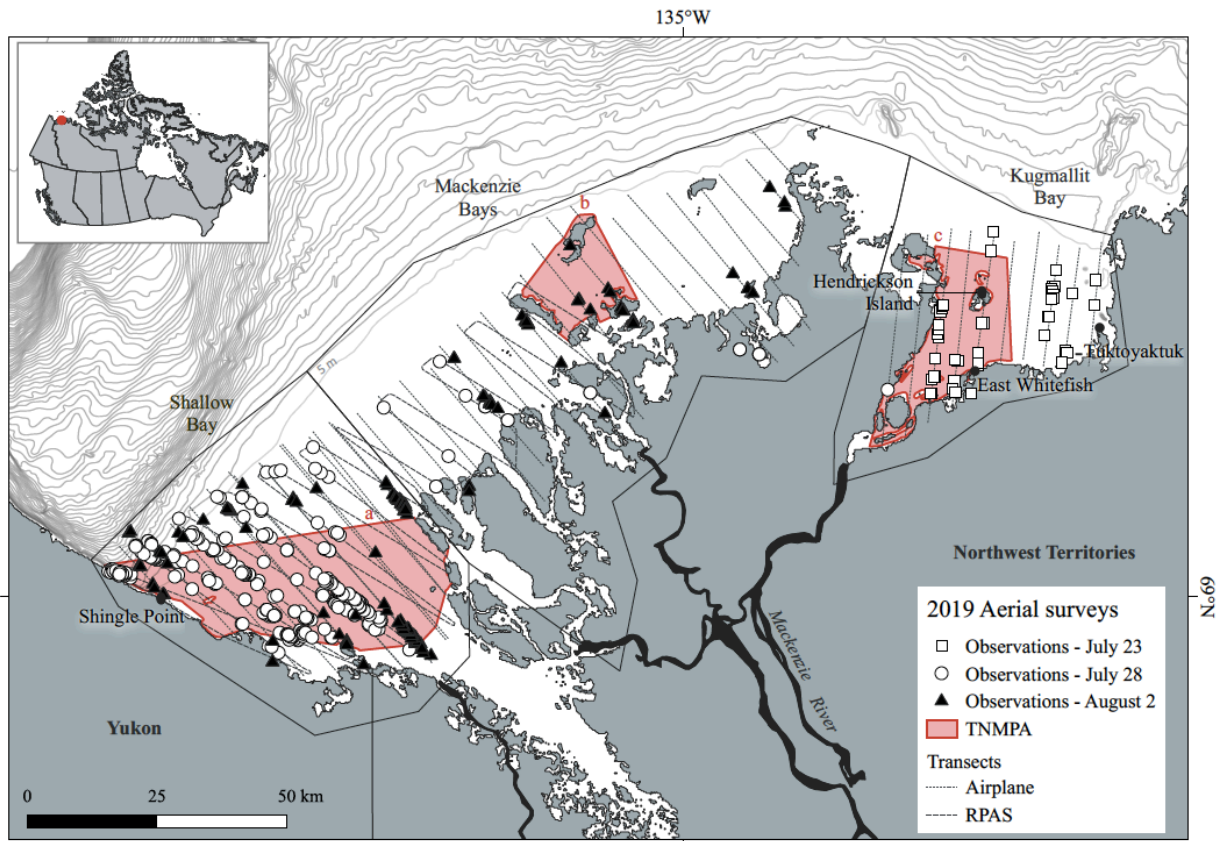
During summer, the Eastern Beaufort Sea beluga whale population aggregates in the inshore waters of the Mackenzie Estuary and Tarium Niryutait Marine Protected Area (TN MPA). Climate change impacts to late summer beluga habitat in this region are expected to influence seasonal movement, habitat selection and distribution. Guided by local communities' perspectives, this study aimed to better understand beluga habitat selection by quantifying and qualifying summer beluga habitat, and further examining whether shifts in beluga distribution are expected under a changing climate. We used a resource selection function based on beluga aerial survey data to estimate the likelihood of beluga presence as a function of environmental conditions. The suspended particulate matter concentration (SPM) and sea surface temperature (SST) were mainly driving beluga habitat selection, especially with SPM and SST ranging above average estuarine values. Subregions featuring these specific conditions included the mouth of the Mackenzie River channels and unprotected coastlines, which are experiencing increasing freshwater flows and accelerating coastal erosion. Using a diachronic analysis, we found a general distribution shift towards coastal areas. This finding provides insight into current and evolving beluga habitat and habitat selection under a changing climate, which could help inform future beluga management in the TN MPA.

2.1 Introduction

Beluga whales, *Delphinapterus leucas* (Pallas, 1776) or *qilalugaq* in Inuvialuktun (hereafter belugas), are distributed across the Arctic and sub-Arctic regions with eight distinct populations spending all or part of the year in Canadian waters (COSEWIC 2016). Belugas occupy a wide variety of habitats; however, many populations exhibit high site fidelity to estuaries in the summer for reasons not fully understood (COSEWIC 2016). Estuarine environments host important and diverse ecosystems, and serve multiple purposes (Costanza et al. 1997; Dunton, Schonberg and Cooper 2012). Rapid climate shifts occurring in the Arctic (Nichols et al. 2004; Waugh et al. 2018; Bush and Lemmen 2019; Worden et al. 2020) strongly impact estuarine ecosystems (Pörtner et al. 2019). Therefore, it is crucial to understand why belugas select these habitats and what features are driving habitat selection.

The Eastern Beaufort Sea (EBS) beluga population migrates from its wintering habitat in the Bering and Chukchi Seas to the Beaufort Sea in late May and June (Harwood et al. 1996; Citta et al. 2017). In late June, following the break-up of land-fast ice in the Southern Beaufort Sea, belugas enter the Mackenzie River estuaries including the Tarium Niryutait Marine Protected Area (TN MPA) (Figure 2.1; hereafter referred to as the estuary) (Hornby et al. 2016) and form one of the world's largest summer aggregations (Norton and Harwood 1986). Key areas of recurring clustering across the estuary have been identified based on historical aerial surveys from 1977 – 1985 and 1992 (Harwood et al. 2014). Some environmental conditions have already been identified as favourable for beluga aggregation, such as warm (water temperature $> 2\text{ }^{\circ}\text{C}$ and up to $18\text{ }^{\circ}\text{C}$; Fraker, Sergeant and Hoek 1979; Hornby et al. 2016) and turbid waters (suspended matter concentration $\sim 375\text{ g}\cdot\text{m}^{-3}$; Macdonald and Yu 2006), low salinity ($< 1\text{‰}$; Fraker et al. 1979), and low wind conditions ($< 40\text{ km}\cdot\text{h}^{-1}$; Scharffenberg et al. 2019a). Furthermore, it has been suggested that belugas choose particular spatial features, such as sheltered areas (Fraker, Sergeant and Hoek 1979; Scharffenberg et al. 2019b) or shoal-sandy substrates (Whalen et al. 2020). Altogether, these recent studies underline the complexity behind habitat selection, combining spatial features and environmental conditions under multiple distinct circumstances.

Figure 2.1: Study area for the beluga late summer habitat selection modelling.



Notes: Study area from Shingle Point (Tapqaaq) moving east to Tuktoyaktuk, with the subsections of Shallow Bay, Mackenzie Bays (encompassing East Mackenzie Bay and West Mackenzie Bay) and Kugmallit Bay, including in red the TN MPA regions in light red Niaqunnaq (a), Okeevik (b) and Kittigaryuit (c) respectively, flown during the 2019 aerial surveys. The Mackenzie River (Kuukpak) main tributaries, moving east are the West Channel and Reindeer Channel flowing in Shallow Bay, the Middle Channel flowing in Mackenzie Bays and the East Channel, flowing in Kugmallit Bay. The grey dot lines are the transects flown by plane and the dash lines flown by the RPAS during the three days of the survey. The belugas identified during the summer 2019 aerial surveys on July 23 are symbolized by white squares, on July 28 by white circles and on August 2 by black triangles. The light grey lines are the 5 m isolines for the bathymetry. The traditional names were referenced from Inuvialuit Settlement Region Traditional Knowledge Report (ISR-TK 2006). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

In summer, EBS belugas are harvested by Inuvialuit communities located in the Inuvialuit Settlement Region (ISR) (McGhee 1988). For Inuvialuit, belugas remain an essential traditional food source and continuing to harvest belugas is central to Inuvialuit food security, well-being and cultural survival (Byers and Roberts 1995; Hoover et al. 2016). To promote the conservation and sustainable management of the EBS beluga population and their habitat, the co-management of

belugas in the ISR is shared between the Inuvialuit and Fisheries and Oceans Canada (DFO) through the Fisheries Joint Management Committee (FJMC; Inuvialuit Final Agreement 1984) and follows the Beaufort Sea Beluga Management Plan (FJMC 2013). This cooperative effort has led to the creation of beluga management zones in the estuary, and the TN MPA was designated in August 2010 under Canada's Oceans Act of 1997 (Canada Gazette 2010).

The estuary, like many other Arctic coastal regions, is facing considerable physical and biogeochemical stresses due to climate change impacts (Pörtner et al. 2019). Seawater temperature is rising (Bush and Lemmen 2019) and larger sedimentary inputs (Solomon, Forbes and Kierstead 1994; Lantuit, Overduin and Wetterich 2013; Worden et al. 2020) are affecting seawater turbidity and primary production (Carmack and Wassmann 2006; Wang et al. 2013) with unknown impacts on EBS beluga and their habitat. Further investigation has been recommended to understand how belugas may respond to ecosystem changes (Loseto et al. 2018). Additionally, community members, through the TN MPA working group monitoring plan in 2013 (DFO-FJMC 2013) followed by the Beluga Summit in 2016 (Beluga Summit 2018), identified several research priorities, specifically to establish baselines and indicators to assess changing conditions related to beluga inshore habitat under a changing climate.

To respond to these community priorities and to quantify the influence of a changing climate on late summer beluga distribution in the estuary the following study aimed at: i) identifying and quantifying beluga environmental habitat conditions; ii) identifying and qualifying spatial areas of selection; and iii) evaluating variations in beluga distribution over time. The first step was to assess current habitat selection (i.e., why and how belugas choose specific locations) using a habitat model in the form of a Resource Selection Function (RSF) applied to environmental conditions. The RSF was used to test if the likelihood of beluga presence in the estuary in late summer was a function of specific environmental variables. Beluga presence was estimated from aerial surveys conducted in the late summer of 2019 and the environmental variables (sea surface temperature, suspended particulate matter concentration and chlorophyll-*a* concentration) were derived by ocean colour satellite remote sensing. The second step was to determine how beluga distribution may have shifted by analysing current and past aggregation areas, and lastly, to link beluga distribution shifts with habitat selection processes in relation to a changing climate. Together, our

findings can help to inform guidance for future TN MPA monitoring given the recent environmental changes across the region.

2.2 Methods

2.2.1 Study design

In addition to responding to community research priorities derived from the long standing co-managed Fish and Marine Mammal Community Monitoring Program (FJMC 2013), this study aimed to engage beluga knowledge holders across multiple stages of the study. Observations and knowledge gathered for generations by harvesters represent an essential part in understanding interactions between belugas and their habitat in summer, and how those interactions have been changing over time (Inuvialuit Settlement Region Traditional Knowledge Report – ISR-TK 2006). In December 2019, the Inuvik Hunters and Trappers Committee (IHTC) supported this work and the engagement of beluga harvesters. The study design and methods were further discussed during in-person meetings with IHTC members, IHTC board members and Joint Secretariat members in March 2020, as well as virtually during meetings, once with IHTC Director and Research Advisor D. Esagok in September 2020, and then with the IHTC board in April 2021 (along with written updates on the study). However, the level of engagement with harvesters and community members evolved with the COVID-19 pandemic. The habitat model was initially envisioned to be the starting point of a broader conversation with local harvesters and community members about changes in beluga habitat distribution through participant observation and experiential learning. We had planned to bring the results of the habitat model to an expert knowledge working group to hold discussions on the observed outputs. Specifically, we had hoped to co-interpret the habitat model outputs by bringing together beluga experts for different ways of knowing in an ethical space and equitable way. Due to the pandemic travel restrictions and requests by regional boards to not hold these specific gatherings over virtual media (so, as to honour and respect the knowledge), the design and structure of the habitat model were instead developed based on previous EBS beluga habitat modelling (Loseto et al. 2006; Hauser et al. 2017; Hornby et al. 2017; Whalen et al. 2020) and conversations with Research Advisor D. Esagok (harvester and knowledge holder). The discussions around changes in beluga habitat and model interpretation were then based on secondary sources (i.e., interdisciplinary content of natural sciences, social sciences and accessible literature encompassing Inuvialuit Knowledge, in peer-review publications and grey

literature, and discussions with D. Esagok), in place of discussions with beluga harvesters. Changes in beluga habitat distribution were evaluated by comparing aggregation areas from this study to decades-old baseline data detailed in Harwood et al (2014).

2.2.2 Study area

The study area, referred to as the estuary, encompasses the submerged delta of the Mackenzie River and its two estuaries located within the waters of the ISR in the Northwest Territories of Canada. This area extends from north of Shingle Point (137.8°W) to north of Tuktoyaktuk (132.8°W) and expands from the coasts to approximately the 5-m isobath (from 68.7 to 69.8°N). The study area includes the TN MPA regions Niaqunnaq, Okeevik and Kittigaryuit, located in the subsections of Shallow Bay, Mackenzie Bays and Kugmallit Bay respectively, all areas where belugas are observed and harvested during the summertime (Harwood et al. 2002) (Figure 2.1).

From October to June, the estuary is primarily covered with grounded landfast sea ice and is inaccessible to belugas (Harwood and Smith 2002). During the spring freshet, the large riverine discharge from the Mackenzie River channels, associated with sea ice meltwater, forms a pool of freshwater trapped nearshore by the floating landfast sea ice (Macdonald and Yu 2006). Once this ice bridge breaks, belugas enter the estuary (Norton and Harwood 1986) and remain in the warm (water temperature > 12°C; Mulligan and Perrie 2019) and turbid (concentration in suspended particulate matter > 10 g·m⁻³; Doxaran, Devred and Babin 2015) freshwater forming the Mackenzie River plume (Fraker et al. 1979). The plume rapidly extends offshore displaying, on average, a descending gradient of suspended particulate matter concentration and surface temperature (Doxaran, Devred and Babin 2015; Mulligan and Perrie 2019). The Mackenzie River represents an important source of nutrients to the estuary for primary production (Emmerton, Lesack and Vincent 2008) and contributes to the plume turbidity by supplying organic and inorganic suspended particulate sediments (i.e., silt and sand; Doxaran, Devred and Babin 2015). High plume turbidity is also supported by the release of suspended particles from coastal erosion, resuspension and thawing permafrost underlying the entire area (Solomon, Forbes and Kierstead 1994; Hill et al. 2001; Lantuit, Overduin and Wetterich 2013). By late summer, the sea surface temperature is mostly influenced by solar radiation (Mulligan and Perrie 2019). Since the estuary is 2-m-deep on average (Macdonald and Yu 2006), warm surface waters display a horizontally homogenous distribution within the estuary (Supporting information 2.1).

2.2.3 Beluga sightings from aerial surveys

In summer of 2019, aerial surveys were carried out by DFO and Inuvialuit partners to update the EBS beluga population abundance estimate in the Beaufort Sea (DFO – unpublished data). The systematic assessment of inshore and offshore regions occurred during ten days between July 21 and August 2, 2019. This study only focused on the three inshore photographic surveys within the estuary conducted on July 23, July 28 and August 2 (i.e., the study period). Photos were taken either from a Twin Otter aircraft or from a SeaHunter Remotely Piloted Aircraft System (RPAS, unmanned aircraft piloted from a remote station), and were geotagged and georeferenced respectively along with systematic NW-SE line transects (Figure 2.1). Photos were taken along survey transects covering a defined area in which belugas were expected to be present based on previous aerial surveys (Harwood et al. 1996) and ISR community consultation (Table 2.1). Photo dimensions, from both the Twin Otter and the RPAS, were 875 m x 583 m, covering an area of 0.51 km². Photos were automatically taken every seven seconds by a Nikon D850 camera with a 25 mm lens at 610 m (2,000 feet) altitude. All belugas appearing in the photos, regardless of their size or estimated maturity, were identified and digitized in shapefiles (.shp) by a researcher specializing in whale identification, using a local CRS NAD83 Lambert Conic Conformal projection and resulted in a dataset of 611 spatial observations.

Table 2.1: Summary of aerial surveys information and associated RSF model details.

Date of survey	Subsections	Survey type	Number of transects	Total length of transects (km)	Number of belugas identified in photos	Selected resource units	Available resource units
July 23	Kugmallit Bay	Airplane	10	291	58	9	305
July 28	Shallow Bay	RPAS	11	537	339	233	6712
July 28	Mackenzie Bays	RPAS	11	358	17	6	4459
August 2	Shallow Bay	Airplane	10	379	144	17	1369
August 2	Mackenzie Bays	Airplane	19	522	53	0	1373
Total			61	1958	611	265	14218

2.2.4 Habitat variables and remote sensing imagery processing

Ocean colour satellite remote sensing provides imagery on the distribution and variability of relevant biophysical features, such as sea surface temperature SST (in °C), suspended particulate matter concentration SPM (in $\text{g}\cdot\text{m}^{-3}$) and chlorophyll-*a* concentration CHL (in $\text{mg}\cdot\text{m}^{-3}$). These environmental variables represent dynamic seawater surface properties related to beluga habitat and were chosen based on prior knowledge of physiological drivers of beluga distribution (Fraker et al. 1979; Norton and Harwood 1986; Scharffenberg et al. 2019a).

SST, representing the temperature of the first few micrometers of the water column, was selected since the estuary is thought to offer belugas a thermal advantage (Scharffenberg et al. 2019a). SPM, the concentration of suspended solid organic and inorganic particles found in the water column, was selected as belugas are commonly found in turbid waters (Fraker, Sergeant and Hoek 1979; Fraker et al. 1979; Hornby et al. 2016), with a high level of suspended particulate matter indicating a higher turbidity (Gippel 1995; Klein et al. 2019). Also, the organic content of suspended particles enriches the nutrients content of the estuary (Emmerton, Lesack and Vincent 2008) that may promote local biological uptake contributing to coastal preys such as white fishes and ciscos (*Coregonus autumnalis*, *Coregonus nasus*, *Coregonus sardinella*; Brewster et al. 2016) some of which have been identified in beluga diets (Loseto et al. 2009; Harwood et al. 2015). CHL, the concentration of the dominant type of chlorophylls contained in the chloroplast of phytoplankton, was selected as it is an indicator of algal biomass (Perrette et al. 2011) and primary productivity (Carmack and Wassmann 2006; Wang et al. 2013). Phytoplankton productivity determines zooplankton abundance (Legendre and Michaud 1999) and, may identify biologically productive areas of importance to belugas (Loseto et al. 2009; Ostertag et al. 2019; D. Esagok pers. comm., Sept. 17, 2020; suggesting food availability as variable).

Open-source daily satellite images from the multi spectral Moderate Resolution Imaging Spectroradiometer (MODIS) instrument onboard the Aqua satellite were downloaded from NASA website (<https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/>) for the area and period of interest and were processed (e.g., geophysical products) using SeaDAS (version 7.5.3, Baith, Lindsay and McClain 2001) as described in Doxaran, Devred and Babin (2015). For each image, SST was calculated with the long-wave algorithm (Walton et al. 1998), SPM with the algorithm developed by Doxaran, Devred and Babin (2015) and CHL using the O'Reilly standard band ratio OC3/OC4

(O'Reilly et al. 1998) combined with the Hu color index algorithms (Hu, Lee and Franz 2012), representing the upper optical depth of the water column. When several images were available for one day, the median values for SST, SPM and CHL were calculated to obtain only one daily composite. Daily composite grid files were created in GMT (version 5.4.5, Wessel et al. 2013) at 300 m resolution. When the coverage of the daily composite was poor, averaged composites based on the previous and next day were used.

2.2.5 Habitat modelling

An RSF was used to model habitat selection by belugas. An RSF is a species distribution model based on regression techniques that relates likelihood of species occurrence (i.e., relative probability of selection of an area by a beluga) with defined environmental variables, considering habitat availability (Johnson and Gillingham 2006; Redfern et al. 2006; Guisan, Thuiller and Zimmermann 2017). The RSF model assumes that the resource selection is a linear and additive function of environmental conditions found within a resource unit and is represented by a statistical model used to estimate the relative probability of selecting that resource unit by comparing to any other resource unit available (Manly et al. 2002).

To run the RSF, a specific dataset of resource units was created. All transect lines were buffered at 875 m on each side in QGIS (version 3.10.8, QGIS Development Team 2021), representing the maximum width of the photograph, and accounting for uncentered photographs and transect inaccuracy. Those buffered areas covered one third of the study area and were divided in discrete units called resource units. A resource unit is an area of water whose spatial extent and scale were defined to match the environmental variable grid file extent and cell size (300 m x 300 m), lowering spatial inaccuracy between the point observations and the polygonal environmental variable (Guisan, Thuiller and Zimmermann 2017). All resource units within the buffered areas were considered “available” for a beluga at the time of the surveys and any available resource unit where a beluga was identified was considered “selected” (Lele et al. 2013; Northrup et al. 2013). Each resource unit centroid was given a binary value of either “1” if the unit was encountered and selected by the beluga, or “0” if the unit remained unselected. Values of SST, SPM and CHL, characterising each resource unit, were extracted from the satellite imagery grid files. Only resource units with a value for each of the variables were included in the analysis. There were 14,218 available resource units of which 265 were selected by belugas (Table 2.1). A

bivariate correlation analysis (Pearson's product moment correlation) was completed for each pair of variables (normalised with a log10 base for CHL and SPM). A correlation between two variables could lead to biases in terms of variable contribution to the model. If the correlation coefficient was significant ($p\text{-value} < 0.05$) and greater than $|0.7|$ (Ratner 2009), the pair was considered strongly correlated and the variable that contributed the least was removed.

The SST, SPM and CHL density distributions were examined and showed skewedness and multi-modality (Supporting information 2.2). To avoid compromising the linearity assumption of the RSF, the environmental variables were transformed. The transformation consisted of adding polynomial terms to the environmental variables using a generalized linear model (GLM) to simulate multimodal distributions (Guisan, Thuiller and Zimmermann 2017). A GLM is a flexible form of linear regression relating the combination of environmental variables to the response variable (e.g., beluga presence) by a link function commonly used in RSF modeling (Guisan, Thuiller and Zimmermann 2017). A polynomial GLM was run with the function `glm` from the `stats` package (version 4.0.2, Hastie, Tibshirani and Friedman 2009) in RStudio (version 1.4.1106, RStudio Team 2020). An automated forward stepwise procedure was followed to build the multi-model inference with the function `stepAIC` from the `MASS` package (version 7.3-53, Venables and Ripley 2002) in RStudio, considering various combinations of the three continuous environmental variables ordered with a polynomial of a degree that is less than or equal to 3. This process ranked and selected the most descriptive models based on the Akaike Information Criteria (AIC, Akaike 1973) and contribution to lowering the deviance. The best model had the lowest AIC. Akaike weights were calculated to estimate the contribution of each environmental variable to the overall performance of the model based on multi-model inference, by summing the Akaike weight of each model containing that environmental variable (Guisan, Thuiller and Zimmermann 2017). The environmental variable with the highest Akaike weight was the one that contributed the most (Burnham and Anderson 2004).

The relative probability of selection of a resource unit was given by the value fitted by the best RSF model (Lele and Keim 2006) and reflected the relative likelihood of presence of a beluga (Philipps et al. 2009), from 0 (very unlikely) to 1 (very likely). Those fitted values are interpreted as the probability of selection by a beluga of a resource unit, characterized by specific environmental variable values, relative to all other available resource units being freely and equally

accessible. The univariate response curves displayed the distribution of belugas along a range of environmental variable values in terms of relative probability of selection, while keeping the other variables at their mean value (Guisan, Thuiller and Zimmermann 2017). The range of values for the environmental variable corresponding to the highest relative probability of selection by a beluga was given by the optimum represented by the peak of the concave part of the curve. The slope of the curve indicated the importance of the influence on selection when encountering a certain range of values. A steep curve indicates a strong influence of the range of values on selection.

The fitted values for each resource unit were classified in 6 quantile bins, attributed a mapping colour (blue: [0-0.05[, green: [0.05-0.25[, light green: [0.25-0.5[, yellow: [0.5-0.75[, orange: [0.75-0.95[, red: [0.95-1]) to ease visualisation and interpretation, then mapped to assess areas of habitat selection. A resource unit with a fitted value lower than the 0.25 quantile value was qualified of low relative probability of selection and corresponded to a spatial location of lower quality for belugas compared to other available units. A resource unit with a fitted value higher than the 0.75 quantile value was qualified of high relative probability of selection. When several resource units displayed the same quality, areas of selection were defined.

2.2.6 Temporal distribution analysis

The spatial distribution analyses were conducted using a Kernel Density Estimates (KDE) based on aerial survey spatial observations for each subsection of the estuary similarly to Harwood et al (2014) for purpose of comparison. This analysis was completed using QGIS. The raster files resulting from the probability density distribution fitted by the KDE were reclassified into contoured areas of spatial aggregation that represent 50 percent of the volume of spatial observations (i.e., core area; Fieberg and Börger 2012). To explore potential shifts in beluga distribution over time, these aggregation areas were compared to the 50 percent volume contours based on 30 to 45-year-old late summer observations made approximately during the same period as this study period, between July 21 – 31 of 1977, 1978, 1980, 1981, 1982, 1985 and 1992, outlined in Harwood et al (2014).

2.3 Results

2.3.1 Environmental conditions

The Pearson correlation coefficient was 0.51 for the pair SPM-CHL (p-value < 0.05), 0.32 for SST-CHL (p-value < 0.05) and 0.47 for SST-SPM (p-value < 0.05). The variables were therefore considered independent. Model development conducted by the stepwise procedure resulted in three steps (Table 2.2). Based on the AIC, the combination of SPM at the third degree and SST at the third degree was estimated the best RSF model to reflect beluga habitat selection, dismissing CHL as a significant explanatory variable.

Table 2.2: Best candidate models describing habitat selection by Eastern Beaufort Sea belugas in the late summer, based on a forward stepwise selection process.

Step	Candidate model	AIC ^a	Δ AIC ^b	Deviance	Deviance residuals
1	Intercept only (null model)	2637.8	116.9	2635.8	0
2	SPM³	2532.7	11.8	2524.7	111.1
3	SPM³ + SST³	2520.9	0	2506.9	17.8
4	SPM³ + SST³ + CHL	2522.1	1.2	2506.1	0.8

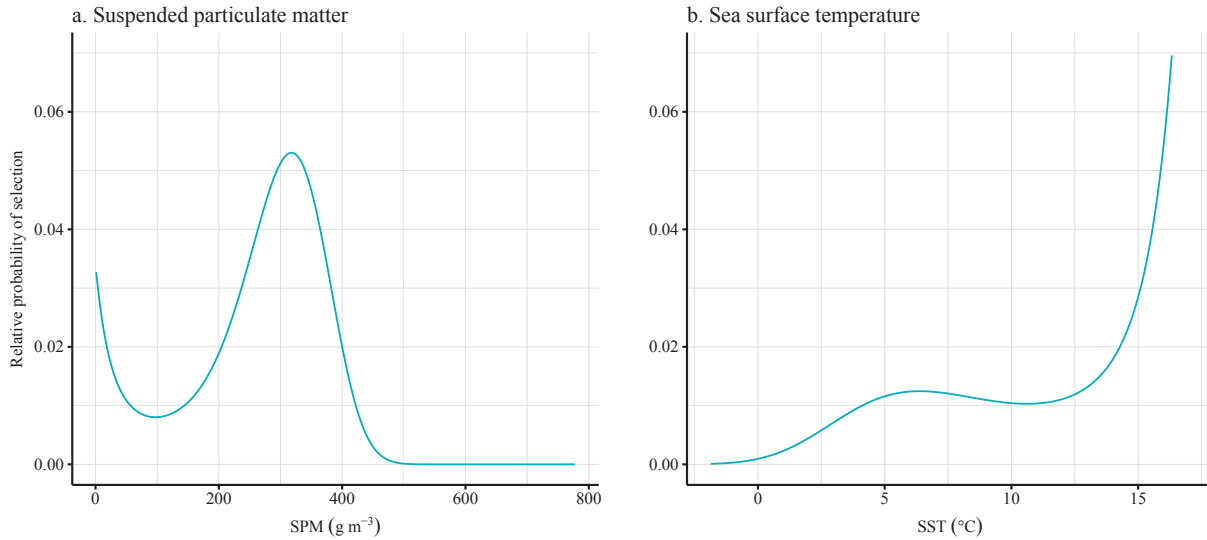
Notes: Variables in bold have a significant p-value. Deviance residuals represent the contributions of the candidate model to the deviance. a. AIC is the Akaike Information Criteria based on log likelihood of the model (Akaike 1973). b. Δ AIC is the difference between the AIC value of the model and the lowest AIC value of all models.

Akaike weights summation values were 0.505 for CHL, 1.001 for SPM, 0.995 for SST. As SPM and SST Akaike weights had similar values, they contributed almost equally to the explanatory power, turbidity and temperature influencing equally beluga selection (Supporting Information 2.3).

The RSF response curves displayed a cubic shape as a third-degree polynomial function was used for fitting the model (Figure 2.2). The RSF response curve for SPM (Figure 2.2a) reached a local minimum for SPM around $150 \text{ g}\cdot\text{m}^{-3}$, increased to the maximum for SPM around

$350 \text{ g} \cdot \text{m}^{-3}$, to finally decrease to 0 beyond $400 \text{ g} \cdot \text{m}^{-3}$, representing the limit of the data. The RSF response curve for SST (Figure 2.2b) steadily increased from -1.8°C to reach a first maximum at 6°C , then decreased to a minimum for SST around 12°C , to increase exponentially at about 13°C .

Figure 2.2: Responses curves for the best RSF model.

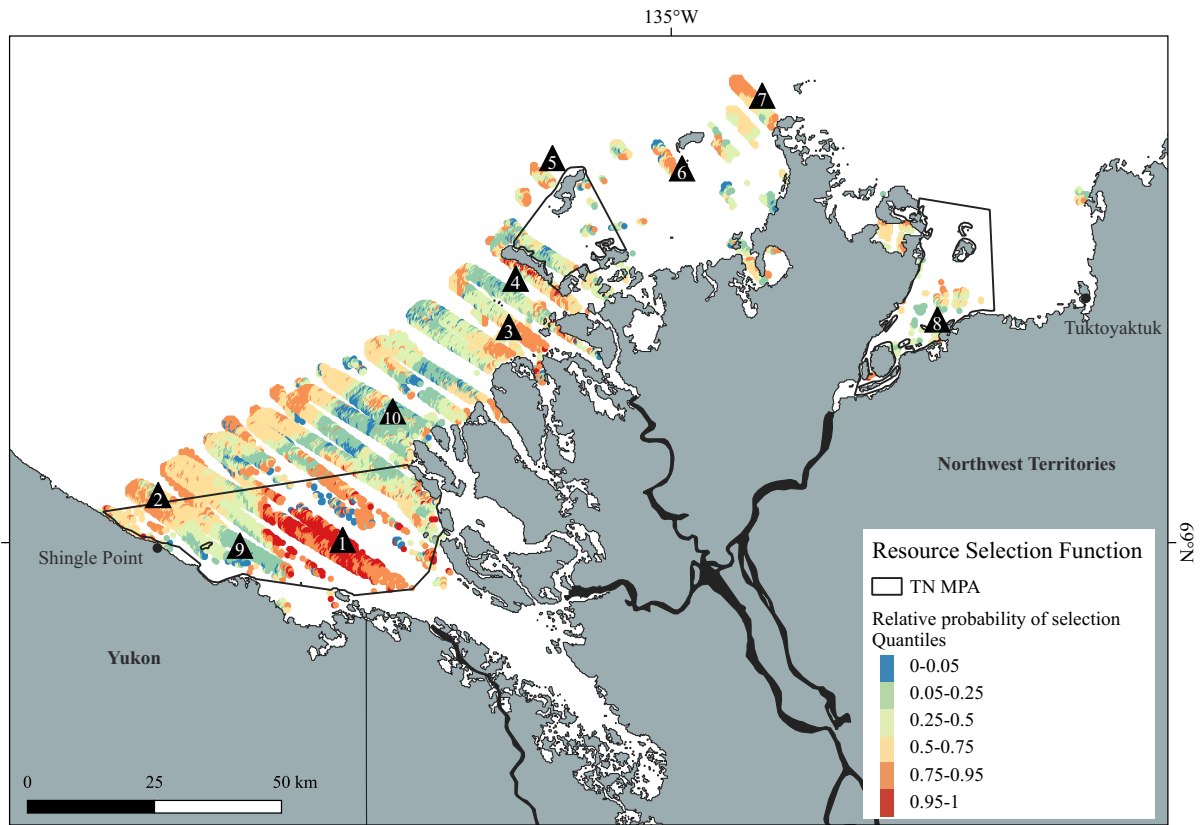


Notes: The response curves are fitted with the polynomial glm for SPM (a) and SST (b). The plots were created with the ggplot2 package (version 3.3.2, Wickham 2016) in RStudio (version 1.4.1106, RStudio Team 2020).

2.3.2 Spatial selection

The relative probability of selection values ranged from 0 to $2.93 \cdot 10^{-1}$ (with the highest probability corresponding to SST value of 16.4°C and SPM value of $311 \text{ g} \cdot \text{m}^{-3}$). Resource units with a relative probability of selection value above 0.0196 (0.75 quantile) were qualified of high relative probability of selection and resource units with value under 0.0103 (0.25 quantile) were qualified of low relative probability of selection. Areas with high probability of selection relative to other geographical areas (red/orange, Figure 2.3) were located north of Tent Island in Niaqunnaq Bay at the mouth of the West Channel (#1), north of Shingle Point (#2), at the Middle Channel river mouth (#3), off the west coast of Garry Island (#4), northwest of Pelly Island (#5), southwest of Hopper Island (#6), offshore North Head (#7) and, with values slightly more mixed, southward of Hendrickson Island (#8). Areas of low relative probability of selection (blue/green, Figure 2.3) were located northward of the Blow River delta (#9) and in West Mackenzie Bay (#10).

Figure 2.3: Spatial distribution of fitted values determining areas of selection.

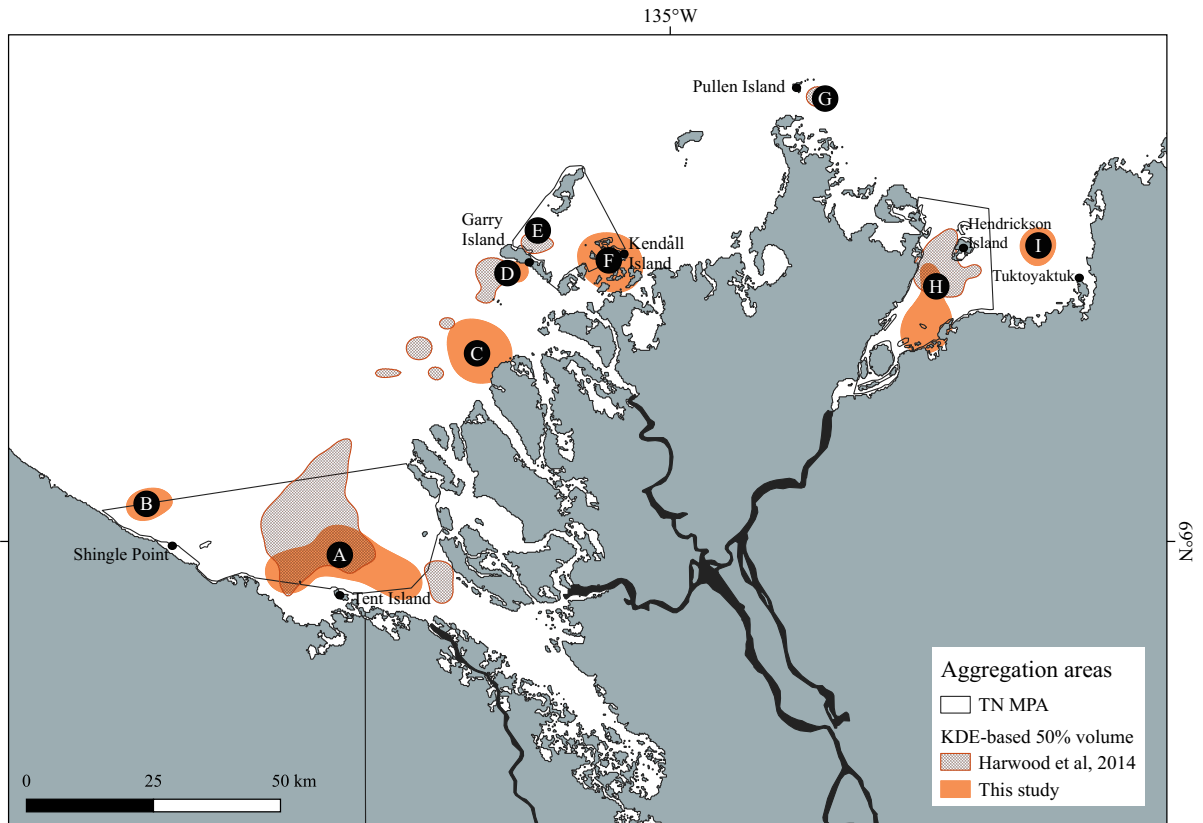


Notes: Areas of high relative probabilities of selection are in red and orange: (1) north of Tent Island, (2) north of Shingle Point (Tapqaq), (3) Middle Channel (Ataagiaq) river mouth, (4) west of Garry Island (Ualligyuaq), (5) northwest of Pelly Island (Igluligyuaq), (6) southwest of Hopper Island (Kamikgik), (7) offshore North Head, (8) southwest of Hendrickson Island (Qikiqtaq), off East Whitefish (Nalruriaq). Areas of low relative probabilities of selection are in blue and green: (9) northward of the Blow River delta (Itiguryaq) and (10) West Mackenzie Bay. The traditional names were referenced from Inuvialuit Settlement Region Traditional Knowledge Report (ISR-TK 2006). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

2.3.3 Distribution analysis

Overall, only 25% of the aggregation areas in 2019 corresponded with the areas identified in Harwood et al (2014) (solid colour and coloured mesh respectively, Figure 2.4). The aggregation areas located north of Shingle Point (B), around Kendall Island (F) and northwest of Tuktoyaktuk (I) were present in 2019, but not identified in Harwood et al (2014). The areas east of Garry Island (E) and south of Pullen Island (G) identified in Harwood et al (2014) were not present in 2019.

Figure 2.4: Aggregation areas containing 50% of the volume of spatial observations interpolated by Kernel density estimation.



The aggregation areas from this study are in solid colour, based on aerial data from 2019 and the aggregation areas from Harwood et al (2014) are in coloured mesh, based on aerial data from 1977 – 1985 and 1992. The aggregation areas are located north of Tent Island (A) north of Shingle Point (B), close to coastline and a tributary mouth (C), southwest (D) and east of Garry Island (E), around Kendall Island (F), south of Pullen island (G), southwest of Hendrickson Island (H) and northwest of Tuktoyaktuk (I). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

Spatially, the aggregation areas in 2019 were located closer to coastlines (areas C and D) and channel mouths compared to Harwood et al (2014). In Shallow Bay, the aggregation area (A) was more compressed in 2019, shorter in latitude but longer in longitude and deeper in the estuary compared to Harwood et al (2014), while showing a superposition northward of Tent Island. The aggregation area at the mouth of the East channel in Kugmallit Bay (H) was located further into the bay in 2019 compared to Harwood et al (2014) while showing superposition southwest of Hendrickson Island. The two areas of superposition A and D matched with the two highest relative

probability of selection areas 1 and 4 respectively, while the area of superposition H matched in a smaller extent with the relative probability of selection area 8.

2.4 Discussion

This study aimed to quantify and qualify beluga habitat in the late summer and provide greater insight to habitat selection and probable beluga distribution shifts under a changing climate. To achieve this, a multi-step approach was used. Current beluga distribution trends were explored for the population size at the time of the study by analysing beluga habitat selection using a RSF model, based on aerial survey observations and satellite derived environmental variables, and then comparing these findings to past beluga distribution patterns to detect any distributional shifts.

2.4.1 Environmental conditions

The RSF model describing beluga habitat selection suggested that the SST and the SPM of an area were the main environmental conditions driving belugas to select that area. More specifically, belugas selected habitat with high SPM (i.e., ranging from 200 and 400 $\text{g}\cdot\text{m}^{-3}$) and high SST (i.e., greater than 13 °C, up until 17 °C, the maximum SST value), noting the average observed SPM and SST ($N = 14,218$) for the estuary during the study period were 92 $\text{g}\cdot\text{m}^{-3}$ ($SD = 90.1$) and 10.35 °C ($SD = 2.58$). The large ambivalent range of SST, from 6 to 13 °C, may reflect their tolerance to large range of temperatures as endotherms, recognizing belugas evolve in offshore and ice-covered regions with water temperature lower than 5 °C (St. Aubin et al. 1990) or considering belugas might select a specific range of temperature (or turbidity) for a specific activity (Lemieux Lefebvre et al. 2017), trading-off optimal conditions. It is also possible that SST influence belugas selection at a broader scale whereas SPM can determine selection at a local scale (Rasmussen et al. 2007).

2.4.2 Habitat selection and current distribution

To examine habitat selection across the study area in relation to beluga spatial distribution, key areas of selection were mapped using the RSF outputs for the specific environmental conditions (Figure 2.3). A total of ten (10) key areas were identified as high or low relative probability of selection within the estuary. Those areas are discussed here in context with spatial features explaining the specific environmental conditions and their potential ecological roles.

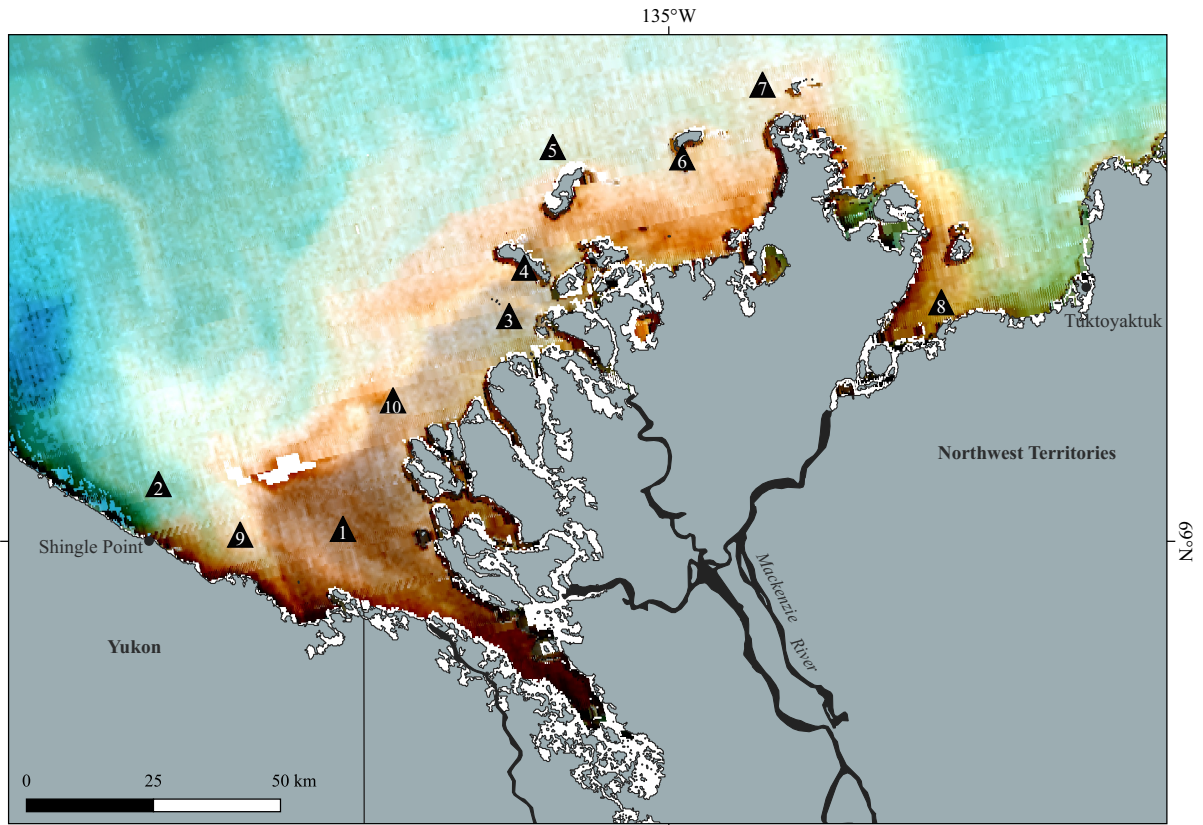
The high relative probability of selection areas 4 and 5 (Figure 2.3) occurred along unprotected coastlines. These areas are subject to coastal erosion (permafrost: Kerfoot 1969; storms: Lim et al. 2020) and responsible for high SPM (Solomon, Forbes and Kierstead 1994; Lantuit, Overduin and Wetterich 2013; Worden et al. 2020). The high relative probability of selection areas 1, 3, and 8 (Figure 2.3) occurred at the mouth of the Mackenzie River channels. These areas are characterised by freshwater discharge responsible for high SPM and high SST (Macdonald and Yu 2006; Doxaran, Devred and Babin 2015). These conditions are favourable to provide a thermal refugia to nurture calves (Fraker, Sergeant and Hoek, 1979) or to facilitate belugas epidermal moulting and regrowth (St. Aubin et al. 1990), similarly to other beluga populations (i.e., Hudson Bay; Sergeant, 1973), supporting hypotheses about the ecological roles of estuaries for belugas. More specifically, the area 8 (Figure 2.3) at the mouth of the East Channel was associated with the silty sand patch mapped by Whalen et al (2020), supporting the hypothesis that belugas may use this location to rub and scrape off moulted skin (Waugh et al. 2018; Scharffenberg et al. 2019a). Waugh et al (2018) also identified this location as favourable for beluga females calving while Ostertag et al (2019) highlighted the abundant presence of calves in the same area in addition to observing belugas feeding.

The low relative probability of selection area 10 (Figure 2.3) occurred in an open area that is subject to ocean-wind perturbation, such as storms causing a high variability in SST (Inuit Observations of Climate Change [IOCC] project 1999; Scharffenberg et al. 2019b). The low relative probability of selection area 9 (Figure 2.3) was spatially associated with the head of the Mackenzie Trough bathymetric canyon, an area subject to low SST due to upwelling (Williams et al. 2006). That spatial feature is also related to oceanographic influences promoting biologically productive areas (Williams et al. 2006) that might be of importance for belugas. For example, the Eastern Chukchi Sea beluga population select their habitat in association with the Barrow Canyon for foraging (Hauser et al. 2015; Hauser et al. 2017). However, as the habitat model was built only on turbidity and temperature, the area 9 presented conditions deemed unfavourable for belugas and modelled as such. Additionally, while EBS belugas have been observed feeding in the estuary (Ostertag et al. 2019), recent findings seem to point to the offshore as favoured foraging areas (Hornby et al. 2017; Storrie et al. 2022). Finally, it was unclear why some areas were of high relative probability of selection (2, 6, 7 in Figure 2.3), but with no apparent specific spatial features related to high turbidity and temperature.

In summary, while considering SPM and SST, it seemed that it was mostly turbid areas with high freshwater input or subject to coastal erosion that were selected. However, other factors not considered in this study may be important in explaining the distribution observed. Indeed, additional environmental variables may also influence beluga presence in the estuary, such as winds and waves (Scharffenberg et al. 2019a), tides (Simard et al. 2014), bathymetry (Hornby et al. 2016), seabed compositions (Whalen et al. 2020), river current or upwelling (Redfern et al. 2006, Hauser et al. 2015). Ecological influences such as predation (Anderson et al. 2017) and competition (Guisan, Thuiller and Zimmermann 2017), or anthropogenic disturbances due to shipping (Halliday et al. 2020) may also represent valid explanations of beluga distribution patterns throughout the season. Finally, beluga presence in the estuary may be explained by their social behaviour (gaming; Fraker et al. 1979) or by their cultural learning and memory (O’Corry-Crowe et al. 2020) rather than optimal environmental conditions. Belugas may also display a certain form of distribution based solely on their group composition (Mayette et al. 2022), or on their physiological characteristics (i.e., age or sex; Loseto et al. 2006; Hauser et al. 2017).

At a broader scale, areas in the nearshore part of the Mackenzie River plume are likely to be selected by belugas due to high SPM and high SST (Gippel 1995; Macdonald and Yu 2006) (Figure 2.5) strengthening the association between the offshore part of the plume with beluga presence in terms of turbidity and temperature (Hornby et al. 2016; 2017). However, the plume extent can be temporally and spatially variable due to surface current, wave action (Hill et al. 2001) and winds (Macdonald and Yu 2006; Klein et al. 2019), resulting in belugas selecting habitat only temporarily favourable (Mulligan and Perrie 2019). Based on previous literature (e.g., ISR-TK report 2006; Anderson et al. 2017), this large-scale pattern may be explained by belugas using highly turbid waters as sheltered areas, escaping from predators, and protecting juveniles (Anderson et al. 2017).

Figure 2.5: Mackenzie Plume in true-colours from July 27, 2019.



Notes: The map displays areas of selection from Figure 2.2. The plume extent follows north-easterly winds (Macdonald and Yu 2006). Darker colours suggest a higher sediment load. The image was composed (RGB from Rrs_667, Rrs_531, Rrs_443 MODIS Aqua L2 image) and projected in SeaDAS (version 7.5.3, Baith, Lindsay and McClain 2001) and imported in QGIS 3.10.8 for mapping. The basemap is open data shapefile (www.gdam.org).

The application of the resource selection model is limited by the study design and inherent to the spatial and temporal availability and accuracy of survey and habitat data. The model results are restricted to areas that were covered by the aerial survey, and where remotely sensed data were available. Consequently, only one tenth (1/10) of the study area was modeled, leaving large areas with unknown probability of selection in Kugmallit Bay, East Mackenzie Bay, and further in the estuary in Shallow Bay. Transferring the model to these regions could have been possible using model projections (Guisan, Thuiller and Zimmermann 2017). However, as the dataset was insufficient to evaluate accurately the predictive power of the model, the model predictions were not valid outside the space or period used to fit the model and uncertainties linked to the model parameters could not be estimated (Guisan, Thuiller and Zimmermann 2017).

Additionally, aerial surveys represent a snapshot in time in a defined space. They were flown under fair weather conditions that could have influenced beluga presence. Indeed, belugas may simply vacate areas experiencing physical disturbances such as storms, characterised by low water temperatures and storm-induced waves (Scharffenberg et al. 2019b). Furthermore, the aerial surveys, on which the model is based, sampled areas of high turbidity, leading to perception and availability biases in beluga counting (Redfern et al. 2006). Adding species observations obtained from different sampling methods, such as passive acoustic monitoring (Scharffenberg et al. 2019a) or telemetry (Storrie et al. 2022), would provide additional information for the model to perform better around certain areas known as highly selected by belugas, notably around East Whitefish Station (Nalruriaq) or Kitigazuit where several traditional whaling camps are located (Harwood et al. 2002).

The choice to work only with remote sensing data also lead to several limitations (Williamson et al. 2019) including cloud coverage and spatial resolution that may hide both spatial and temporal disparities, near-surface observations that may not represent sub-surface properties (Doxaran, Devred and Babin 2015) or creation of averaged composites potentially hiding daily variability. Higher spatial resolution ocean colour sensors, such as the ones onboard Sentinel-2 (10-m) or Landsat-8 (30-m), could provide fine scale environmental details on areas of interest. Regardless of those limitations, models remain a powerful tool to represent the complexity behind natural processes and to further estimate predictions, especially within the context of climate change.

2.4.3 Temporal and spatial shifts in beluga distribution

To detect whether beluga distribution had shifted over time, KDE results from previous beluga distribution, that set a baseline on observations from 30 to 45 years ago (Harwood et al. 2014), were compared to beluga distribution from this study. The results suggested a distributional shift of belugas selecting their late summer habitat areas closer to the coasts and to the mouth of the Mackenzie River channels and this, as a response to environmental changes. These observed shifts may suggest a capacity to adjust to changes, either by a successful acclimatisation to temporary conditions or by adaptation to a changing climate (Moore and Huntington 2008), belugas selecting areas warmer and more turbid. Belugas have already demonstrated plasticity by shifting their prey-base (Choy et al. 2020), the timing of summering location arrival (Loseto et al.

2018), their diving behaviours (Hauser et al. 2018) or, in this case, by selecting different areas, while conserving a general philopatry.

Emerging literature on local environmental changes was examined to extrapolate how beluga distribution could be influenced by changing physicochemical conditions. Increasing storm activity may drive belugas closer to shore where they can find shelter from waves and influxes of cold oceanic waters (IOCC project 1999). Large open-water fetch and decreasing sea ice cover (Stroeve et al. 2012) result in increasing ocean-wind coupling causing more frequent storms in the estuary (IOCC project 1999; Kokelj et al. 2011). In July 2016, following a severe weather event with winds greater than $60 \text{ km} \cdot \text{h}^{-1}$, belugas were found to vacate Kugmallit Bay to search for shelters with lower impact of waves (Scharffenberg et al. 2019b). Greater freshwater discharge from the Mackenzie channels (Doxaran, Devred and Babin 2015) and accelerating coastal erosion (Solomon, Forbes and Kierstead 1994; Jones et al. 2018; Worden et al. 2020) may drive belugas near coasts and further in the channel mouths, supporting the selection by belugas of areas with high suspended particulate content concentration. Additionally, areas in Kugmallit Bay are becoming shallower due to increasing sedimentation (Whalen et al. 2016) and belugas may take advantage of these new features for their epidermal moulting scrape-off.

The model used in this study assumes that current conditions are responsible for current beluga distribution and ignores the possible spatial and temporal mismatch between the change in environmental conditions and the species responses (Redfern et al. 2006; Scharffenberg, MacPhee and Loseto 2020). Creating a climatology would provide more accurate indications on environmental changes that already occurred and may have possibly influenced belugas. The RSF model is also static and can only show a particular instant in time and space, whereas a multi-temporal analysis may better capture this complex distribution (Derville et al. 2018). Gathering observations from harvesters during whaling seasons or collected by the long-term and on-going community-based monitoring would represent an undeniably valuable source of information (Nichols et al. 2004; Brook and McLachlan 2009; Derville et al. 2018; Ostertag et al. 2019) creating expert-based models (Bélisle et al. 2018).

2.5 Conclusions

Similar to several other beluga populations in the Arctic, the Eastern Beaufort Sea population aggregating in the Mackenzie Estuary and in the TN MPA exhibits high site fidelity to estuaries in their summering grounds and the reasons behind this selection are not fully understood (COSEWIC 2016). This study assessed current beluga late summer habitat selection in the Mackenzie Estuary, including the TN MPA, focusing primarily on the influence of estuarine habitat environmental conditions as indicators affecting beluga habitat selection and consequent beluga distribution. Shifts in distribution were further related to possible environmental changes in the study area, which are likely to influence conditions favorable to belugas.

These findings revealed that water turbidity, with a high suspended matter concentration, and warm water temperature explained beluga habitat selection whereby belugas selected regions characterized by this specific combination of environmental conditions (i.e., high SPM and high SST) such as at the mouth of Mackenzie River channels and unprotected coastlines (i.e., specific spatial features). These environmental conditions support further hypotheses on the ecological roles of estuaries for belugas such as providing a thermal advantage for their calves or for belugas epidermal moulting and regrowth (Fraker, Sergeant and Hoek 1973; St. Aubin et al. 1990).

These areas are already experiencing the effects of climate change including more extreme temperature and accelerating coastal erosion. The observation of late summer beluga distribution towards coastal areas and inshore waters, specifically to locations with warmer and more turbid areas, may suggest temporary or permanent influence of changing environmental conditions on beluga selection and consequent distribution. These distributional shifts represent new challenges for harvesters who may have to switch the timing and location of their harvest in response to changing beluga distribution¹ (Loseto et al. 2018).

Continued monitoring of how these spatial features evolve with the changing climate will provide an indication of potential future shifts in beluga habitat selection and consequent beluga distribution. Community-based monitoring remains a critical component to collect timely observations of changes, in order to keep building accurate and appropriate strategies while

¹ Ovitz, K., Matari, K., O'Hara, S., Esagok, D., Loseto, L. L. 2021. Observations of social and ecological change on Kendall Island, a traditional whaling camp in the Inuvialuit Settlement Region. [manuscript in preparation].

promoting knowledge co-production. Several areas of research have also been identified to further this work such as including additional sources of observations (e.g., telemetry, drone, citizen science) and environmental data (e.g., climatology, weather stations), and weaving knowledge of local communities to achieve a comprehensive understanding of beluga movement ecology. With this in mind, creating an integrated model, by adding historical Inuvialuit experts observations to the habitat model, has been envisioned as the next logical step (Isaac et al. 2020).

The results presented here can inform beluga monitoring to serve the sustainable beluga management and conservation in the Mackenzie Estuary and TN MPA. More importantly, this study was initiated by communities needs and perspectives, the results are intended to be disseminated at a later convenient time and can serve as a guidance for anticipating changes to come.

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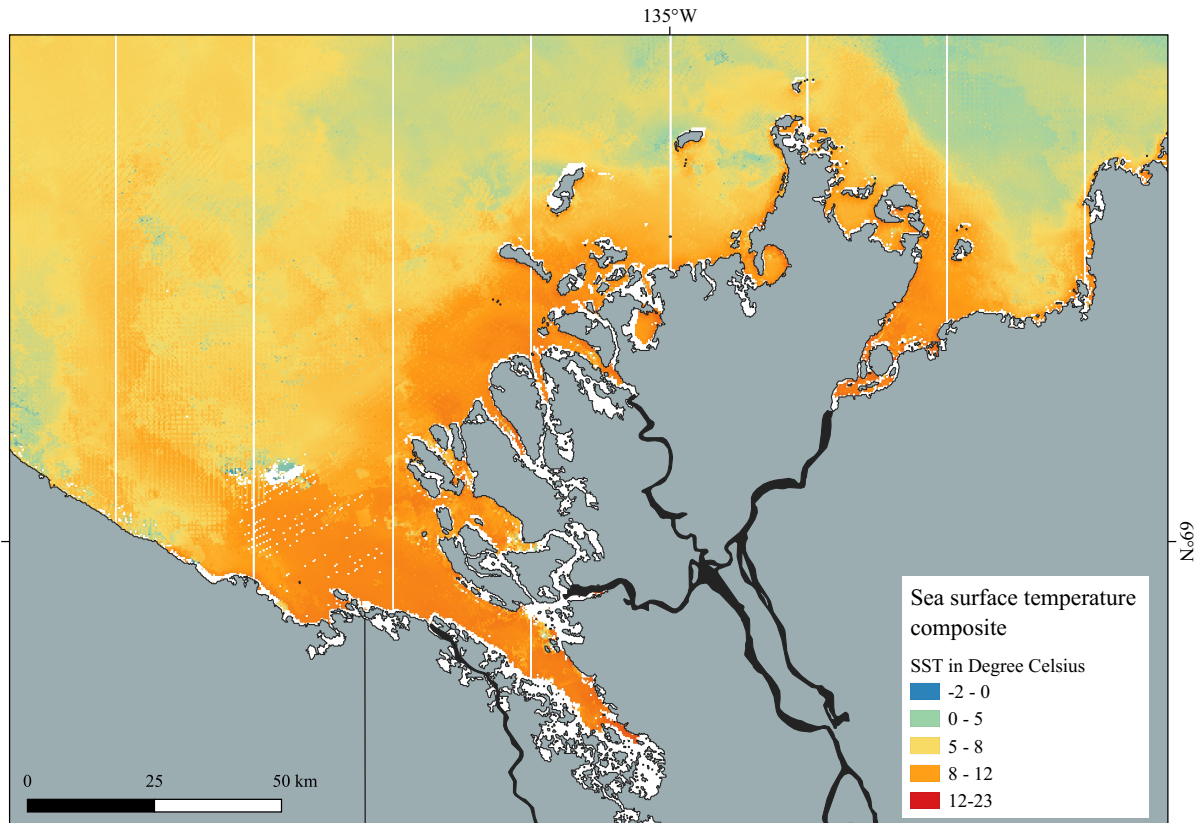
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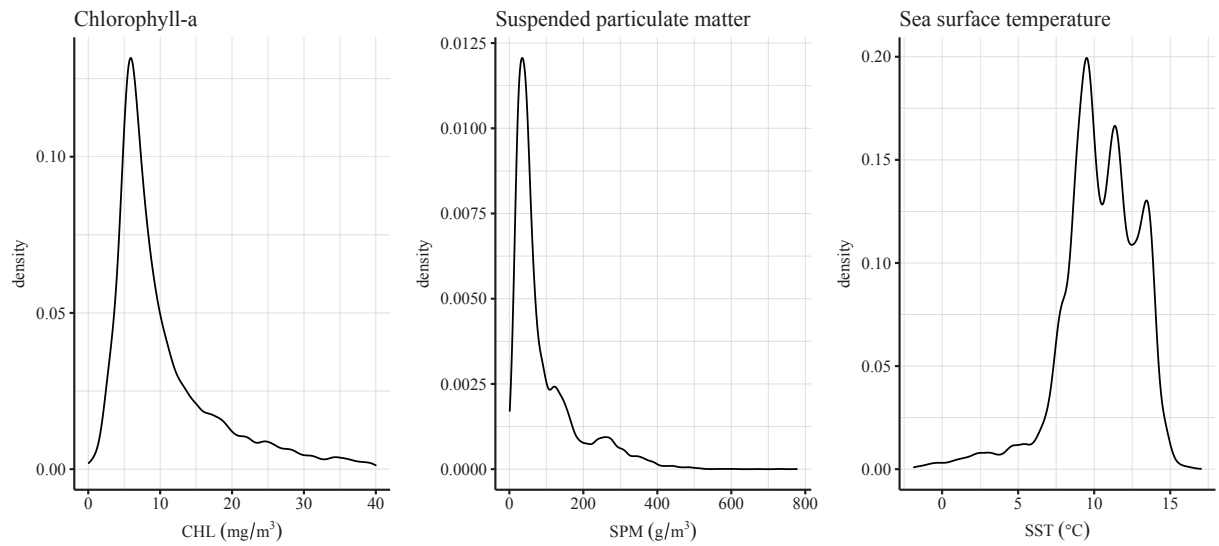
Supporting Information

Supporting Information 2.1: Map of the sea surface temperature (SST) spatial distribution (composite of 6 SST grid files from July 23, 24, 28, 29 and August 2 and 3, 2019) calculated with the long-wave algorithm (Walton et al. 1998) from Aqua MODIS images (<https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/>).



Notes: White lines are artefacts due to compositing. The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

Supporting Information 2.2: Density curves based on kernel density estimate (smoothed frequency histograms) for CHL, SPM and SST for all resource units.



Notes: The figures were created with the package ggplot2 (version 3.3.2, Wickham 2016) in RStudio (version 1.4.1106, RStudio Team 2020).

Supporting Information 2.3: Stepwise selection detailed steps for the polynomial GLM.

Candidate model combination	Variable	Df ^a	Deviance	Deviance residuals	AIC ^b	Δ AIC ^c	RL ^d	Akaike weight
Step 1								
none	intercept		2635.8	0	2637.8	116.9	$4.13 \cdot 10^{-26}$	$1.89 \cdot 10^{-26}$
+	sst	1	2612.9	-22.9	2616.9	96	$1.43 \cdot 10^{-21}$	$6.53 \cdot 10^{-22}$
+	chl	1	2607.4	-28.4	2611.4	90.5	$2.23 \cdot 10^{-20}$	$1.02 \cdot 10^{-20}$
+	poly(chl, 2)	2	2605	-30.8	2611	90.1	$2.72 \cdot 10^{-20}$	$1.25 \cdot 10^{-20}$
+	poly(sst, 2)	2	2603.8	-32	2609.8	88.9	$4.96 \cdot 10^{-20}$	$2.27 \cdot 10^{-20}$
+	poly(chl, 3)	3	2597.2	-38.6	2605.2	84.3	$4.95 \cdot 10^{-19}$	$2.27 \cdot 10^{-19}$
+	poly(sst, 3)	3	2588.6	-47.2	2596.6	75.7	$3.65 \cdot 10^{-17}$	$1.67 \cdot 10^{-17}$
+	poly(spm, 2)	2	2586.4	-49.4	2592.4	71.5	$2.98 \cdot 10^{-16}$	$1.36 \cdot 10^{-16}$
+	spm	1	2587.2	-48.6	2591.2	70.3	$5.43 \cdot 10^{-16}$	$2.49 \cdot 10^{-16}$
+	poly(spm, 3)	3	2524.7	-111.1	2532.7	11.8	0.00273945	0.00125517
Step 2								
-	poly(spm, 3)	3	2635.8	111.1	2637.8	116.9	$4.13 \cdot 10^{-26}$	$1.89 \cdot 10^{-26}$
+	poly(chl, 3)	3	2519	-5.7	2533	12.1	0.002357862	0.001080332
none			2524.7	0	2532.7	11.8	0.002739445	0.001255167
+	poly(chl, 2)	2	2520.6	-4.1	2532.6	11.7	0.002879899	0.00131952
+	chl	1	2522.1	-2.6	2532.1	11.2	0.003697864	0.001694298
+	poly(sst, 2)	2	2516.6	-8.1	2528.6	7.7	0.021279736	0.009750011
+	sst	1	2516.7	-8	2526.7	5.8	0.05502322	0.025210696
+	poly(sst, 3)	3	2506.9	-17.8	2520.9	0	1	0.45818286
Step 3								
-	poly(spm, 3)	3	2588.6	81.7	2596.6	75.7	$3.65 \cdot 10^{-17}$	$1.67 \cdot 10^{-17}$
-	poly(sst, 3)	3	2524.7	17.8	2532.7	11.8	0.002739445	0.001255167
+	poly(chl, 3)	3	2503.6	-3.3	2523.6	2.7	0.259240261	0.118779444
+	poly(chl, 2)	2	2505.4	-1.5	2523.4	2.5	0.286504797	0.131271587
+	chl	1	2506.1	-0.8	2522.1	1.2	0.548811636	0.251456085
none			2506.9	0	2520.9	0	1	0.45818286

Note: Deviance residuals represent the contributions of the candidate model to the deviance. Akaike weight is calculated with: RL of the candidate model/sum of all RL (Guisan, Thuiller and Zimmermann 2017) to determine each variable contribution to the model explanatory power, at each step. a. Df: degrees of freedom. b. AIC is the Akaike Information Criteria based on log likelihood of the model (Akaike 1973). c. Δ AIC is the difference between the AIC value of the model and the lowest AIC value of all models. d. RL: Relative likelihood, calculated with $\exp(-0.5 \cdot \Delta$ AIC) (Guisan, Thuiller and Zimmermann 2017).

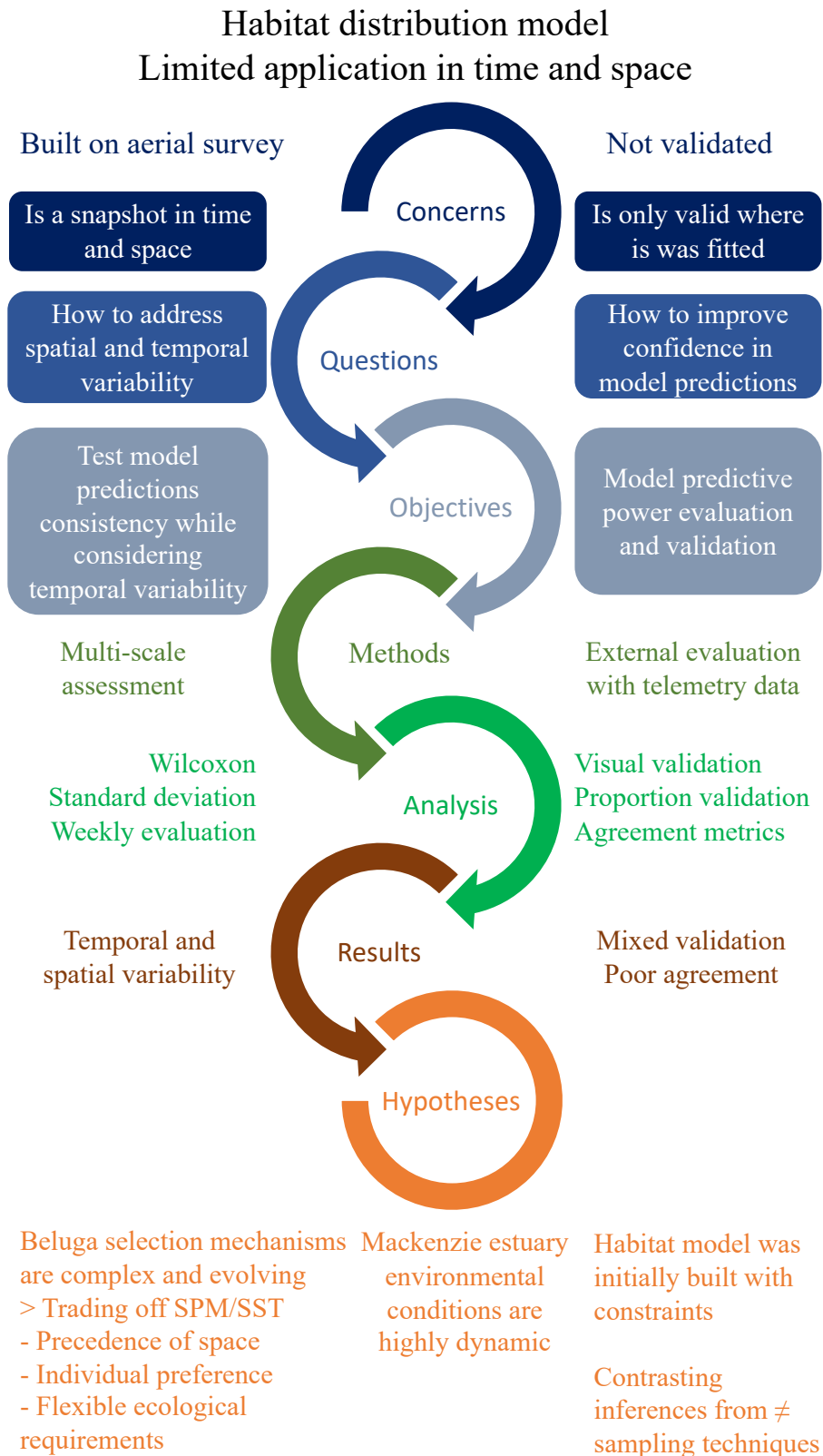
CHAPTER THREE:

HIGHLIGHTING COMPLEXITIES IN DEFINING BELUGA WHALE HABITAT SELECTION AND DISTRIBUTION IN THE MACKENZIE ESTUARY

Abstract

Beluga habitat selection in the Mackenzie Estuary was previously modelled to evaluate the impacts of climate change on beluga distribution in the late summer. This habitat model, based on aerial surveys observations (from 2019) and remotely sensed environmental conditions, represents a snapshot in time and space. To broaden the application of the habitat model, we tested and evaluated the predictions using telemetry data from 7 whales tagged the same year. Based on the intra-estuarine observations, the model correctly predicted beluga presence in Shallow Bay and around Garry Island but failed to predict the presence in Kugmallit Bay and Okeevik, although those regions are well known for belugas abundance in summer. We suggest belugas, by their migratory nature, have a large tolerance to environmental conditions, making habitat selection less predictable. The Mackenzie Estuary is highly dynamic, with rapid fluctuating environmental conditions, making it difficult to model accurately long-term predictions. Finally, the simultaneous data interpretation from aerial surveys, that are static in time and space, and from telemetry, that represent movement over time and space, may lead to contrasting inferences. Those explanations highlight the complexity behind beluga habitat selection and the challenges to create accurate predictions. Simultaneously, we advocated that any additional contribution would bring the model closer to a holistic understanding of the ecology of belugas. We recommended to keep on building the model with observations from other sources such as passive acoustic monitoring or community-based monitoring, allowing to comprehensively assess beluga future management and conservation.

Visual abstract



3.1 Introduction

Understanding the drivers behind habitat selection of marine mammals provides solid background to establish spatial distribution baseline to further monitor changes and consequently predict any variation especially under evolving environmental conditions. Modelling species and habitat distribution has been successfully used to inform species and habitat conservation and management (Goetz et al. 2012), improve knowledge of a species ecology (Hauser et al. 2017; Citta et al. 2017; Storrie et al. 2022), estimate the effects of anthropogenic activities (Halliday et al. 2022) or climate change on habitat selection (Noel et al. *in review*), especially for species such as cetaceans that are challenging to monitor (Redfern et al. 2006; Derville et al. 2018).

Beluga whales (*Delphinapterus leucas*; Pallas, 1776 or *qilalugaq* in Inuvialuktun; hereafter belugas) are an Arctic and sub-Arctic species occupying different types of habitats during their migration, notably estuaries in summer (COSEWIC 2016). There are several hypotheses on belugas estuarine fidelity including epidermal moulting (St. Aubin et al. 1990), calving (Fraker et al. 1979; Ostertag et al. 2019), feeding (Norton and Harwood 1986; Ostertag et al. 2019), predator avoidance (Inuvialuit Settlement Region Traditional Knowledge Report – ISR-TK 2006; Anderson et al. 2017) or socialising (Fraker et al. 1979; Lemieux Lefebvre et al. 2017). The Eastern Beaufort Sea (EBS) beluga population migrates from its wintering grounds in the Bering and Chukchi Seas to enter the Mackenzie estuaries following the break-up of land-fast ice in the Southern Beaufort Sea (Hornby et al. 2016) in the beginning of summer (Inuvialuit Settlement Region – ISR, Western Canadian Arctic; Citta et al. 2017). More particularly, belugas aggregate in the Tarniutit Marine Protected Area (TN MPA; Figure 3.1; Fisheries Joint Management Committee – FJMC 2001) where they represent a key subsistence species, still harvested by Inuvialuit communities as a traditional country food (McGhee 1988; Hoover et al. 2016).

The coastal areas of the Mackenzie Estuary, like most of the Arctic, is experiencing increasing impacts of climate change with expected negative consequences for local ecosystems and communities (Pörtner et al. 2019; Steiner et al. 2021). In order to understand how belugas would respond to such ecosystem changes, a habitat model was designed (Noel et al. *in review*) and resulted in environmental and geographical descriptions of beluga late summer habitat distribution in the Mackenzie Estuary during the summer of 2019. However, modelling approaches are bounded with limitations and assumptions. The habitat model was built on beluga observed

from aerial photo surveys and on remotely sensed environmental covariates, limiting its application to a snapshot in time and to areas covered concurrently by the surveys and the satellite data. Additionally, the dataset was insufficient to evaluate accurately the predictions, leading to potential bias (such as no estimates of precision; Johnson and Gillingham 2005) and making predictions invalid outside the space or period used to fit the habitat model (Guisan et al. 2017). This resulted in the inability to project the habitat model in future time periods or space to assess the possible impacts of climate change on belugas (Guisan et al. 2017). Finally, using aerial survey sampling with elusive species such as belugas in highly turbid areas like the Mackenzie Estuary leads to perception and availability biases (Redfern et al. 2006) that could limit the results, however, could be managed by complementing different sampling methods such as satellite telemetry.

Use of satellite telemetry recently increased to monitor marine mammals movements (i.e., the displacement in space and time) and behaviours (i.e., response to stimuli) using animal-borne electronic tracking devices especially EBS belugas (Richard et al. 2001; Loseto et al. 2006; Hauser et al. 2017; Citta et al. 2017; Storrie et al. 2022). Such techniques offer the advantages of not being visually, temporally or spatially bounded, offsetting aerial survey sampling design limitations for habitat modelling.

To broaden the application of the habitat model, this study aimed to evaluate and validate the habitat model outside of its initially trained conditions, and to address the role of variability in space and time to create accurate predictions. Assessing a model performance (i.e., ability of the model to predict the occurrence of habitat; Johnson and Gillingham 2005) based on a distinct dataset that the one used to fit the model has notably been successfully conducted in Smith et al. (2012), with humpback whales satellite tag data. Additionally, telemetry data, by their nature, are mobile observations in space and time, and were used to test if the model predictions were consistent while considering spatial and temporal variability. To overcome the limitations of the habitat model, an independent telemetry dataset, encompassing the same study period and study area, was used i) to improve confidence in the existing habitat model predictions with evaluation, and ii) to highlight agreements and discrepancies between static model predictions and mobile tagged observations. Variability was also considered to iii) test the habitat model performance at multiple temporal and spatial scales. The goal was that, once the habitat model would be evaluated

and validated by the tagging data, the predictions would be more accurate and could be extended spatially (e.g., entire estuary) and temporally (longer period).

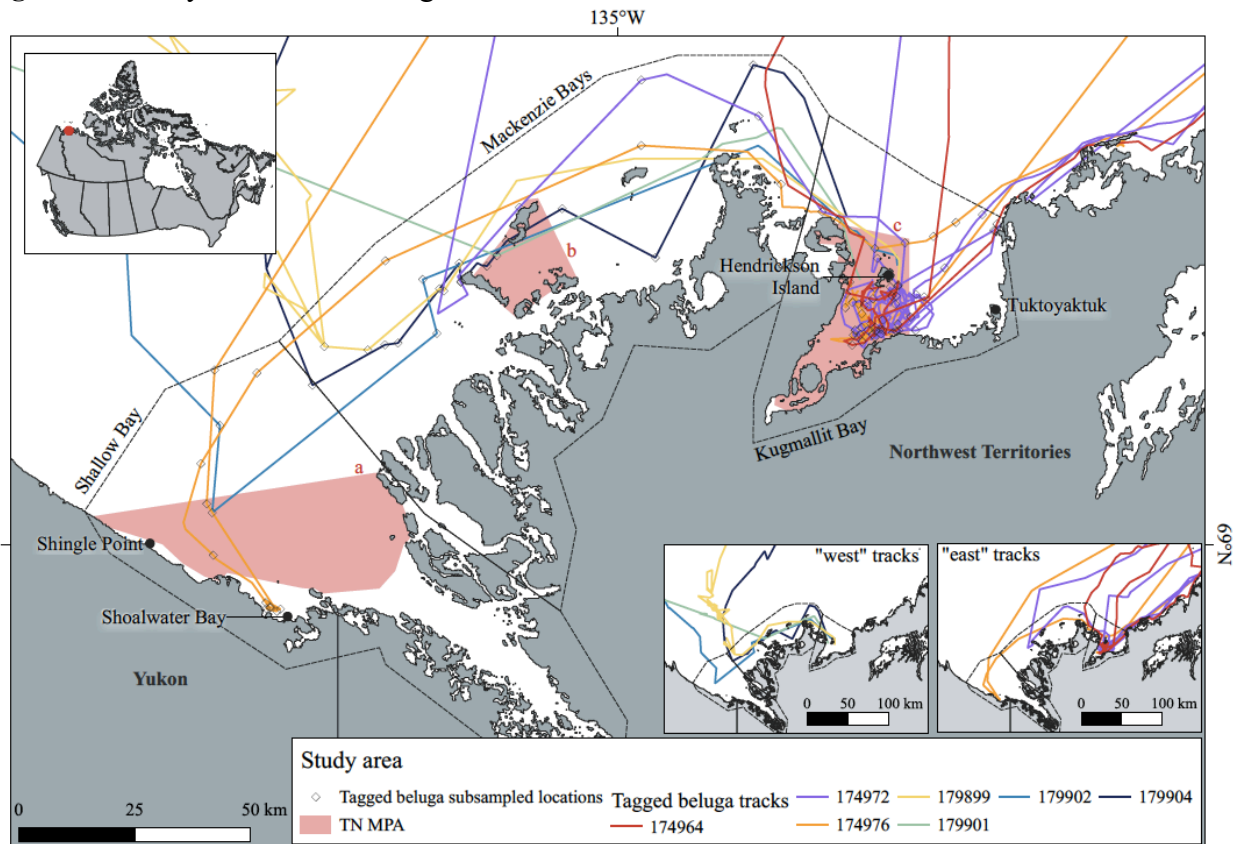
3.2 Methods

3.2.1 Study design

The habitat model developed in Noel et al. (*in review*) was based on a Resource Selection Function (RSF). It estimated the likelihood of beluga presence in the Mackenzie Estuary (i.e., relative probability of selection of an area by a beluga) as a function of chosen environmental conditions in the late summer of 2019, considering habitat availability. The dataset consisted of 611 surfaced belugas observed during 3 days of aerial survey in the Mackenzie Estuary. The relevant environment covariates were derived from ocean colour satellite remote sensing (Aqua MODIS; <https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua>) and consisted of aerial survey-based transect buffers from grid files at 300-m spatial resolution of the sea surface temperature SST (in °C), the suspended particulate matter concentration SPM (in $\text{g}\cdot\text{m}^{-3}$) and the chlorophyll-*a* concentration CHL (in $\text{mg}\cdot\text{m}^{-3}$) (the methods are detailed in Noel et al. *in review*). The habitat model revealed SPM and SST were mainly driving beluga habitat selection, especially with values above estuarine averages: SPM ranging from 200 and 400 $\text{g}\cdot\text{m}^{-3}$ while the average observed SPM ($N = 14,218$) for the Mackenzie Estuary during the study period was 92 $\text{g}\cdot\text{m}^{-3}$ ($SD = 90.1$), and SST greater than 13 °C, up till 17 °C (the maximum SST value) while the average observed SST ($N = 14,218$) for the Mackenzie Estuary during the study period was 10.35 °C ($SD = 2.58$). However, as the dataset was insufficient, the habitat model performance could not be validated. Then, as the habitat model was based on aerial photo survey observations, it only represented a specific space and time, and did not account for any temporal or spatial variability. Consequently, the habitat model was restricted in its building constraints and predictions were valid only in the aerial survey-based transects spatial extent and during the three days of the aerial survey (Guisan et al. 2017). In order to broaden the application of the habitat model (Noel et al. *in review*) in space (i.e., entire estuary) and time (e.g., entire season, across years), two concurrent sets of analysis were envisioned to evaluate the model performance and to test the performance at different scales. First, the habitat model performance was determined at a monthly scale with an external evaluation (Manel et al. 2001; Guisan et al. 2017), consisting in the evaluation and potential validation of the habitat model predictions with an independent satellite telemetry dataset. The methods used were

agreement metrics computation, and visual and proportional evaluation. Then, to test the variability in the predictions at different temporal and spatial scales, a multi-scale assessment was completed by running weekly evaluations, comparing the agreement metrics and proportion validation results on a weekly basis. Model predictions were compared on a weekly basis with variability indicators such as a Wilcoxon test and a standard deviation map. A glossary was provided in Supporting Information 3.1 to clarify the methods nomenclature.

Figure 3.1: Study area for the beluga late summer habitat model evaluation.



Notes: Study area from north of Shingle Point (Tapqaa) moving east to north of Tuktoyaktuk, with the subsections of Shallow Bay, Mackenzie Bays (encompassing East Mackenzie Bay and West Mackenzie Bay) and Kugmallit Bay, including in red the TN MPA regions in light red Niaqunnaq (a), Okeevik (b) and Kittigaryuit (c) respectively. The telemetry tracks of seven belugas tagged from Hendrickson Island (Qitiqtaq) during the summer of 2019 (whose PTT are in the legend, please refer to Table 1 for more information) are symbolized by distinct colours. The hollow black diamond are subsampled locations (please refer to the glossary in Tables S1 in Supplemental material for more information on the nomenclature.). The vignettes represent the two different directions of course. The traditional names were referenced from Inuvialuit Settlement Region Traditional Knowledge Report (ISR-TK 2006). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

3.2.2 Study area

The study area spans the inshore Mackenzie Estuary (Northwest Territories, Canada) including the submerged delta of the Mackenzie River and its two estuaries located within the waters of the ISR, matching the study area used for the habitat model development in Noel et al. (*in review*) with the addition of the deeper estuary in Shallow Bay. This area extends from north of Shingle Point (137.8°W) to north of Tuktoyaktuk (132.8°W) and expands to approximately the 5-m isobath (from 68.4 to 69.9°N). It includes the TN MPA regions Niaqunnaq, Okeevik and Kittigaryuit, located in the subsections of Shallow Bay, Mackenzie Bays (East and West), and Kugmallit Bay respectively, all areas where belugas are commonly observed and harvested in summertime (ISR-TK 2006) (Figure 3.1).

3.2.3 Habitat model predictions

To evaluate the model performance, the habitat model was transferred in the current study area assuming the environmental conditions were comparable in terms of availability and analogy as the ones used to initially train the model. While transferring a fitted model outside of its space and time of training is called a projection (Guisan et al. 2017), for the purposes of convenience, the term prediction will be used in this study, as it is a term commonly used for model outcomes evaluation (Supporting Information 3.1C).

To transfer the habitat model, and create predictions for the entire study area and for the time periods belugas were in the study area (Guisan et al. 2017), the area was divided in discrete units called resource units (Noel et al. *in review*). For each day of the time period, values of SPM and SST, characterising each resource unit, were extracted from the corresponding environmental grid files. Values of SPM and SST were averaged across all dates and multicollinearity was tested with the Pearson's product moment correlation coefficient calculation. If the correlation coefficient was significant ($p\text{-value} < 0.05$) and greater than $|0.7|$ (Ratner 2009), the pair was considered strongly correlated and one of the covariates was excluded. The habitat model was applied on each resource unit of the study area to obtain their relative probability of selection (RPS) as a function of SPM and SST. The RPS values for each resource unit were classified in 6 quantile bins (Morris et al. 2016) with a corresponding mapping colour: blue $[0-0.05[$, green $[0.05-0.25[$, light green $[0.25, 0.5[$, yellow $[0.5, 0.75[$, orange $[0.75-0.95[$, red $[0.95-1]$, then mapped to assess spatial areas of

habitat selection (i.e., habitat distribution). A resource unit with a RPS value lower than the 0.25 quantile value was qualified of low relative probability of selection (LRPS) and corresponded to a space of lower quality for belugas compared to other available units. A resource unit with a RPS value higher than the 0.75 quantile value was qualified of high relative probability of selection (HRPS) and corresponded to a space of higher quality for belugas compared to other available units. When several resource units displayed the same quality, areas of selection were defined, identifying areas that had high and low probability of being selected by a beluga, relatively to what was available for the beluga. To test the influence of the environmental variability in terms of sea surface temperature and turbidity, models were created per time period resulting in one monthly model and five weekly models.

3.2.4 External evaluation

Following the principles of external evaluation that compares probabilities of presence from the habitat model to binary presence-absence data (Guisan et al. 2017), the model performance was assessed using the telemetry data. Similar as Smith et al. (2012), track data were overlayed on a predictive habitat map to evaluate model predictions with a visual and a proportional evaluation, and agreement metrics were estimated.

3.2.4.1 Beluga locations from satellite telemetry

The independent dataset consisted of beluga whale movements from satellite telemetry. From June 29 to July 13, 2019, belugas were tagged from Hendrickson Island in Kugmallit Bay as part of the EBS beluga tagging program (Storrie et al. 2022). The tags featured Fastloc-GPS receiver combined with an Argos transmitter (Wildlife Computers Ltd., Redmond, WA, United States) and additional samplers such as temperature, depth or light sensors. Locations (i.e., geographical positional fix in latitude and longitude) were acquired every time the belugas surfaced. Due to requirement of location data present in, and returning to, the study area during the study period, only 7 adult male belugas were considered for this study (Table 3.1), and only their Fastloc-GPS locations (transmitted via the Argos system) were processed as they presented a higher resolution (Dujon et al. 2014).

Based on their tracking by Fastloc-GPS, the seven belugas were present in the study area during 24 days over a timespan of 34 days (from June 29 to August 1, 2019; study period). Fastloc-

GPS acquire location when the animal surfaces (at 10's of milliseconds), allowing for a rapid tracking of the location with the level of positioning accuracy depending on the number of satellites used in the position calculation (Dujon et al. 2014). To obtain a position accuracy at least equal to the resolution of the environmental grids (300 m), the raw data were filtered in RStudio (version 1.4.1106, RStudio Team 2020) by removing locations calculated with less than 5 satellites (insuring 95% of the locations within 169 m of the true position as per Dujon et al. 2014). Additional filters were applied on the data such as removing double locations, locations with residual values > 35 (Dujon et al. 2014) and locations with an acquisition time within the 24-h following the tagging as belugas might show effects of the capture in their behaviour (Shuert et al. 2021), resulting in 2991 filtered locations. One track per beluga was created based on the filtered locations time sequence with the Points to path tool in QGIS (version 3.10.8, QGIS Development Team 2021) generating seven tracks (Figure 3.1; Supporting Information 3.1B).

Only filtered locations located within the study area were considered, totaling 563 clipped locations. As some belugas travelled from and to the study area, their occupancy time (i.e., time spent in a space) was divided in period of time while in the study area (Table 3.1).

For each period of time a beluga was in the study area, a track was created based on the time sequence of clipped locations with the Points to path tool in QGIS generating 11 periodic tracks. Those tracks were used for the visual evaluation. The same process was followed for each day a beluga was in the study area, creating 39 daily tracks (Table 3.1).

The daily tracks were used to calculate mean daily travelled distances and swimming speeds, and patterns of movement in occupied areas. The mean daily travelled distances and mean swimming speeds between consecutive clipped locations were calculated based on a straight line of travel. The distinction between patterns of movement was based on visual inspection of the daily tracks. The tracks were examined and discriminated by their predominant movement patterns (Table 3.2). The occupied area was estimated by drawing the smallest convex polygon including all the points of a daily track.

Table 3.1: Tagged whales components with the tag identifier and the date of deployment, and details of movement data per location, track, time period, bay and model-sampling in the study area.

PTT ^a	Deployment date	In the study area				
		Number of clipped locations	Number of daily tracks	Time period present	Bays visited ^b	Monthly observations
LC-174972	2019/06/29	310	4	June 29–July 2		8
			6	July 13–July 18	KB	22
			3	July 30–August 1	KB KB/MB	7
LC-174964	2019/06/30	94	2	June 30–July 1	KB/MB	1
			2	July 22–July 23	KB	5
LC-174976	2019/07/03	107	4	July 3–July 6	KB	8
			5	July 25–July 29	KB/MB/SB	18
LC-179901	2019/07/10	10	2	July 10–July 11	KB/MB	1
RD-179899	2019/07/13	13	3	July 14–July 16	KB/MB	4
RD-179902	2019/07/13	16	4	July 13–July 16	KB/MB/SB	4
RD-179904	2019/07/13	13	4	July 15–July 18	KB/MB/SB	11
		563	39			89

Notes: Please refer to the glossary (Tables S1 in Supplemental material) for more information on the nomenclature. a. PTT: satellite platform transmitter terminal unique number. LC: live-capture tagging used SPLASH10-F-238 tag (WC, Wildlife Computers Ltd., Redmond, WA, United States of America) and RD: remote deployment harpooning, operated by Inuvialuit knowledge holders, used SPLASH-F-321 tags (WC, Wildlife Computers Ltd., Redmond, WA, United States of America). b. Bay names abbreviations with KB standing for Kugmallit Bay, MB for Mackenzie Bays and SB for Shallow Bay.

Table 3.2: Surface movement visual inspection (adapted from Lemieux Lefebvre et al. 2017 and Storrie et al. 2022)

Predominant movement pattern	Surface activity	Function ^a
Visual description of the surface movement	The movement belugas do	The reasons belugas do that movement
Concentrated and overlapping short tracks	Milling = dispersion over a small area and a low dynamism	Calving, calf rearing, resting, scrape off skin, pelagic, settling/socializing,
Isolated, with a continuous and undeviating orientation and long tracks	Directional = distribution over a large area and a moderate dynamism	Transiting, travelling, exploring habitat, foraging/exploring or pursuing preys

Notes: a. Defined as surface behaviour in Lemieux Lefebvre et al. 2017 or space use in Northup et al. 2021.

The 563 clipped location points were subsampled to limit the inherent spatial and temporal autocorrelation of the satellite tag data violating the independence assumption needed for statistical inference (Swihart and Slade 1985). The subsampling was based on the calculated hourly average swimming speed of the belugas ($\sim 2 \text{ km} \cdot \text{h}^{-1}$) and the spatial resolution of the environmental grid files (300 m) to insure a representative sampling of the environmental covariate variation (Fieberg et al. 2010). With a subsampling every four (4) hours, a beluga whale would travel 8 km or 26 grid cells, increasing the scale of sampling and lowering the over-representation or replicated sampling of an environmental covariate (Boyce et al. 2010). The 4-hour subsampling generated 90 subsampled locations, with an average of 5.8 hour-lag between each subsampled location (Supporting Information 3.1A).

3.2.4.2 Evaluation and validation

The first evaluation was visual and consisted of plotting the beluga tracks, line and point locations, over the habitat map and describing existing overlaps. The 11 periodic tracks and 90 subsampled locations points were plotted over the monthly model map. If the track and points coincided with a predicted HRPS area, then the monthly model predictions were visually validated.

The second evaluation consisted in a proportion evaluation (i.e., estimation of the sensitivity; Guisan et al. 2017). It consisted of sampling RPS values for each subsampled location (i.e., an observation) from the monthly and the weekly models to estimate the proportion of observations with a HRPS value (i.e., a presence), such as in Smith et al. (2012). The sensitivity gives the percentage of presences correctly predicted. In an RSF, each presence is a selected location and therefore should have a HRPS value, if the model predictions are accurate. If the percentage of presence with HRPS value was high, the model predictions were validated.

Agreement metrics such as the presence predictive power (PPP) or the Cohen's kappa statistic were used to evaluate the model performance in its ability to distinguish between selected and unselected sites (Guisan et al. 2017). To calculate those metrics, a confusion matrix was created based on the number of presence (i.e., an observation with a HRPS value) and absence (i.e., all other observations; Supporting Information 3.1A) and respective equations can be found in Supporting Information 3.2. The PPP calculates the percentage of presence predictions that are presence. The kappa statistic is a measure of agreement between observations and predictions

(Cohen 1960) where $k > 0.75$ means an excellent agreement, $0.4 > k > 0.75$ good, $k < 0.4$ poor and $k < 0$ a disagreement (Landis and Koch 1977). The effects of prevalence (i.e., frequency of occurrences) are only marginal when the kappa is computed, allowing a rather standardized process when the number of presences is disproportionate compared to the absences (Manel et al. 2002).

3.2.5 Multi-scales assessment

To visually observe temporal and spatial RPS variability between weeks, two types of maps were created: 5 weekly predictive maps and one map with the standard deviation (SD) of the RPS values. For each resource unit and each week, a RPS value was calculated and the SD was estimated over the five weeks. The SD values for each resource unit were classified with a corresponding mapping colour: dark grey for low change ($SD < 0.25$ quantile), denoting a consistency in the relative probability of selection (high or low) and consequent stable habitat conditions in terms of turbidity and sea surface temperature, white for moderate change ($0.25 < SD < 0.75$) and red ($SD > 0.75$ quantile), for high change denoting changing habitat conditions leading to a variability of the RPS values.

To estimate if RPS values between weeks are similar, Wilcoxon tests were run on the predictions (i.e., RPS values predicted by the habitat model) and on the observations (i.e., RPS values at tagged beluga subsampled locations). If the p-value was < 0.05 , then each week was different from the other. Finally, to estimate the effects of the environmental variability on beluga selection, external evaluations were also conducted at a weekly scale, computing sensitivity, PPP and kappa statistics for each week.

3.3 Results

3.3.1 Monthly model predictions

The monthly RPS values for the resource units with a value of both SST and SPM were calculated (Table 3.3), binned (Supporting Information 3.2), and mapped, discriminating areas of HRPS (RPS values > 0.75 quantile) from areas of LRPS (RPS value < 0.25 quantile) (Figures 3.2 and 3.3). The Pearson correlation coefficients was under 0.7 with p-value < 0.05 , the covariates were therefore considered independent (Table 3.3).

Table 3.3: Modelling metrics for the predictions and the observations, and for the agreement between them, for the monthly and the five weekly models.

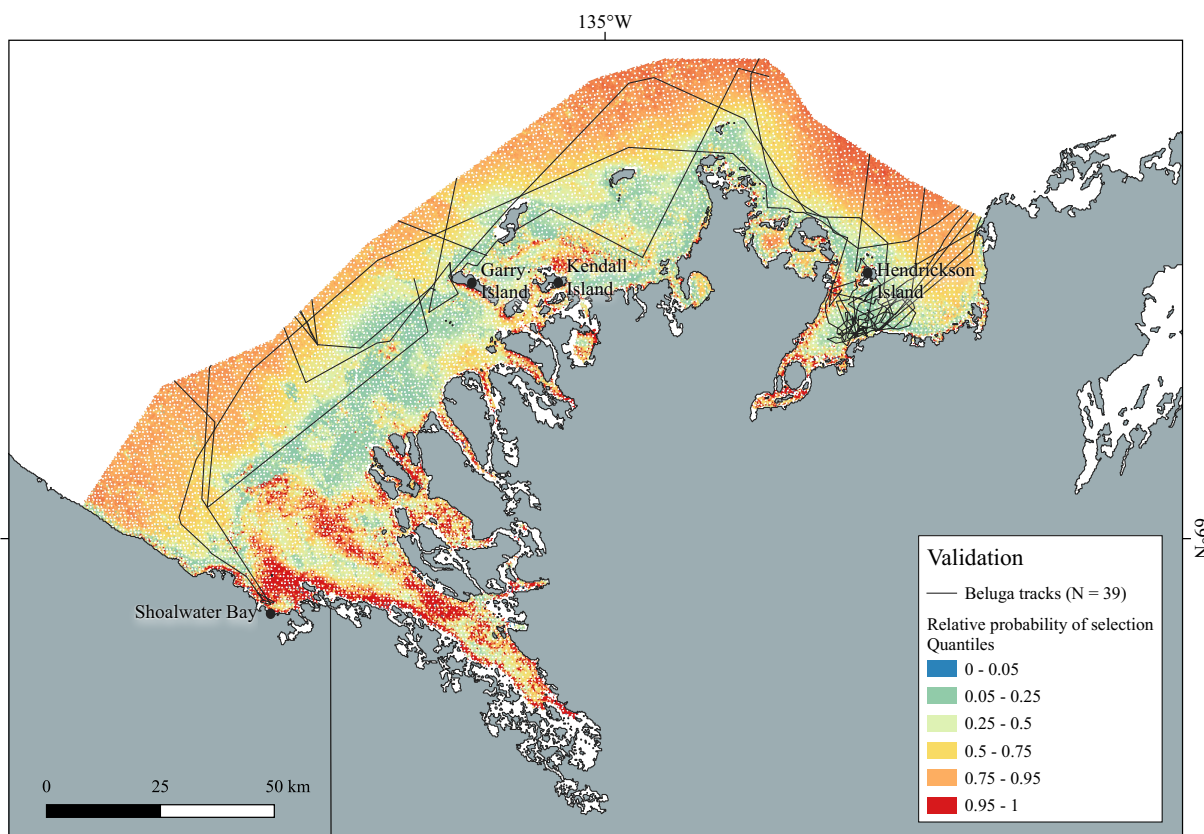
	Monthly Jun 29-Aug 2	Week 1 Jun 29-Jul 5	Week 2 Jul 6-12	Week 3 Jul 13-19	Week 4 Jul 20-26	Week 5 Jul 27-Aug 2
PREDICTIONS^a						
Study area number of resource units	90400	72312	57661	71238	80794	87640
RPS min/max	0/0.992	0/0.790	0/0.994	0/0.999	0/0.483	0/0.997
RPS mean/SD	0.017/0.018	0.019/0.013	0.02/0.031	0.02/0.031	0.019/0.017	0.02/0.018
SPM/SST Pearson correlation coefficient (p-value)	0.627 (<0.05)	0.283 (<0.05)	0.434 (<0.05)	0.354 (<0.05)	0.348 (<0.05)	0.543 (<0.05)
0.75 quantile value = HRPS	0.01864	0.02224	0.02018	0.02129	0.02139	0.02276
0.25 quantile value = LRPS	0.00993	0.01508	0.01361	0.01333	0.01029	0.01226
OBSERVATIONS						
Number of observations	89	10	2	37	12	14
RPS min/max	0.008/0.063	0.0125/0.031	0.008/0.017	0/0.473	0/0.053	0.004/0.025
RPS mean/SD	0.013/0.008	0.017/0.005	0.013/0.007	0.015/0.007	0.018/0.018	0.016/0.005
Number of tracks	39	10	2	13	7	3
AGREEMENT						
Percentage of observations in HRPS = Sensitivity	12.3%	10%	0%	11%	25%	14%
PPP	4.86 10 ⁻⁴	5.52 10 ⁻⁵	0	2.24 10 ⁻⁴	1.48 10 ⁻⁴	9.13 10 ⁻⁵
k	- 9.94 10 ⁻⁴	-5.25 10 ⁻⁵	-1.75 10 ⁻⁵	-5.89 10 ⁻⁴	1.25 10 ⁻⁷	-1.37 10 ⁻⁴

Notes: Please refer to the glossary (Tables S1 in Supplemental material) for more information on the nomenclature. RPS: Relative Probability of Selection; HRPS: High Relative Probability of Selection; LRPS: Low Relative Probability of Selection; PPP: Presence Predictive Power; k: kappa.

In Kugmallit Bay, the model predicted LRPS areas (in green and blue, Figures 3.2 and 3.3) in Kittigazuit Bay, south of Hendrickson Island and north of East Whitefish Station, and HRPS areas (in red and orange, Figures 3.2 and 3.3) along the coastlines and at the East Channel mouth. In Mackenzie Bays, the model predicted HRPS areas west of Garry Island, northeast of Kendall

Island and at the mouth of the Middle Channel and other Mackenzie River channels. In Mackenzie Bays, areas of predicted LRPS were mainly located transversally in the center of the region. In Shallow Bay, HRPS areas were predicted in most of coastal areas of the estuary aside from the centre, including Shoalwater Bay. Overall, 60% of the HRPS areas were in Shallow Bay, 30% in Mackenzie Bays and 10% in Kugmallit Bay (Supporting Information 3.3).

Figure 3.2: Monthly model relative probability of selection (RPS) values projected in the study area for the study period, overlaid by the beluga periodic tracks.



Notes: Areas of high relative probability of selection (RPS value > quantile 0.75) are in red and orange in Shoalwater Bay, west of Garry Island (Ualligyuaq), Kendall Island (Ukiivik) and at the mouths of the river tributaries. Areas of low relative probability of selection (RPS value < quantile 0.25) are in blue and green around Hendrickson Island (Qikiqtaq) and transversally Mackenzie Bays. The traditional names were referenced from Inuvialuit Settlement Region Traditional Knowledge Report (ISR-TK 2006). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

3.3.2 Tracks and subsampled locations data

From June 29 to August 2, 2019, the seven tracks displayed two distinct directions of course (Figure 3.1). Belugas #174964, #174972 and #174976, tagged between June 29 and July 3, stayed in Kugmallit Bay for up to 4 days after being tagged, swam away in the east direction, came back (after 20, 10 and 18 days respectively) into Kugmallit Bay (#174964 for 2 days and #174972 for 6 days), then Mackenzie Bays (less than a day for #174976 and #174972) and Shallow Bay (#174976 for 4 days), to continue their courses back in the east direction. On the other hand, belugas #17899, #179901, #179902, #179904 tagged between July 10 and 14, left Kugmallit Bay immediately after being tagged, swimming west towards the edges of Mackenzie Bays and Shallow Bay (#179902 and #179904) to then head north to not come back in the study area.

In the study area, the tracks showed two different patterns of movement (Figures 3.1 and 3.2). In Kugmallit Bay, the tracks were mainly concentrated and overlapping, covering a mean area of 39.4 km² while in Mackenzie Bays and most of Shallow Bay, the tracks were following a continuous route, covering a mean area of 393 km² to briefly overlap in Shoalwater Bay. The mean daily distance travelled by the tracked belugas in Kugmallit Bay was 33.3 km (SD = 18.2, N = 16) with a mean swimming speed of 1.4 km·h⁻¹ while it was 55.3 km (SD = 41.3, N = 23) for Mackenzie Bays and most Shallow Bay, with a mean swimming speed of 2.3 km·h⁻¹.

53 subsampled locations were in Kugmallit Bay (59.5%), 22 were in Mackenzie Bays (25%) and 14 were in Shallow Bay (15.5%) (Supporting Information 3.3). Only beluga #174976 was present in Shallow Bay inshore waters, while most subsampled locations (80%) in Kugmallit Bay were from beluga #174972 (38/90) (Figures 3.1 and 3.3).

3.3.3 Model evaluation

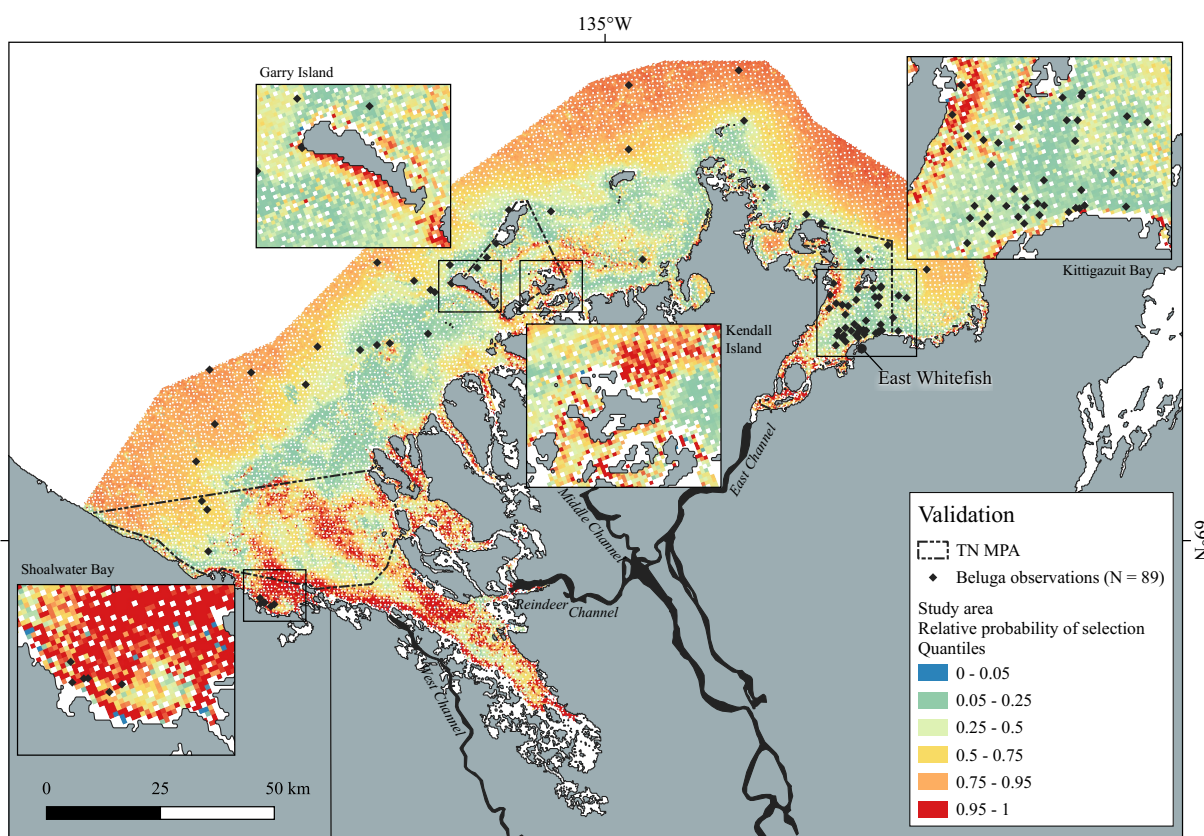
3.3.3.1 Monthly model visual validation

Based on visual inspection, the periodic tracks of the seven satellite-tagged belugas were mainly located in areas of LRPS predicted by the monthly model (blue and green coloured-areas, Figure 3.2) with the exception of Shoalwater Bay and the north tip of the west coast of Garry Island.

3.3.3.2 Monthly model proportion validation

Only subsampled locations with a RPS values were considered resulting in 89 observations. The 89 observations were analysed for the model validation and were mapped (Figure 3.3), producing mixed results: only 12.3 % of the observations were found in HRPS areas ($N = 11/89$) which represented 25% of the study area (Table 3.3).

Figure 3.3: Monthly model relative probability of selection (RPS) values projected in the study area for the study period, overlaid by the beluga observations.



Notes: Belugas observations are in plain black diamonds and the TN MPA outlined in dashed lines. Zoomed-in areas of interests for the validation were areas of high relative probability of selection (RPS value > quantile 0.75, in red and orange) in Shoalwater Bay, west of Garry Island (Ualligyuaq), Kendall Island (Ukiivik) and areas of low relative probability of selection (RPS value < quantile 0.25, in blue and green) north of East Whitefish (Nalruiaq), in Kittigazuit Bay. The traditional names were referenced from Inuvialuit Settlement Region Traditional Knowledge Report (ISR-TK 2006). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

The results differed per bay (Table 3.3; Supporting Information 3.3 and 3.4). 10% of Kugmallit Bay was predicted as a HRPS area, considering what was available, yet displaying the most observations (59.5%, $N = 53/89$). 60% of Shallow Bay was predicted as a HRPS area considering what was available, and while counting the least observations (15.5%, $N = 14/89$), most of them were located in Shoalwater Bay, predicted as a HRPS area. Displaying moderate conditions, 30% of Mackenzie Bays was predicted as a HRPS area, considering what was available and included 25% of the observations ($N = 22/89$). Additionally, the area northwest of Kendall Island could not be validated due to the absence of observations. The west coast of Garry Island, predicted as a HRPS area was indeed selected, validating the predictions.

3.3.3.3 Agreement metrics

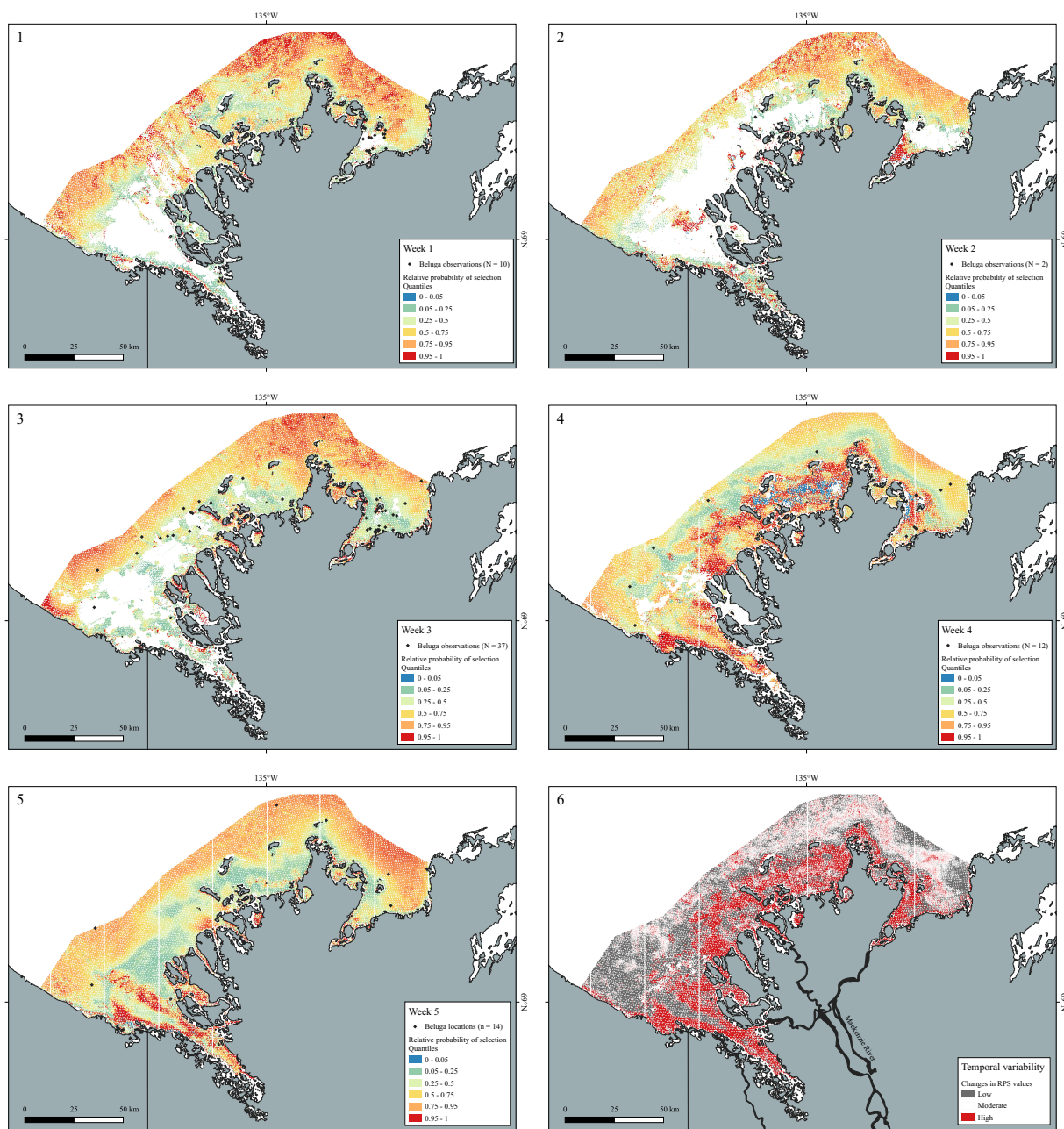
Based on the monthly contingency and confusion matrices (Supporting Information 3.2), the sensitivity, with a value of 12.3%, the PPP, with a value of 0.05% and a kappa of -0.001 showed a general poor agreement between model predictions and observations (Table 3.3).

3.3.4 Multi-scales assessment

3.3.4.1 Variability indicators

The spatial and temporal variability of RPS areas was pronounced between weeks (Table 3.3 and Figure 3.4). While weeks 1 to 3 (maps 1 to 3, Figure 3.4) had a lower coverage in the bays (Table 3.3), weeks 4 and 5 (maps 4 and 5, Figure 3.4) covered the entire study area and allowed complete visual comparisons. Weeks 4 and 5 had the most HRPS areas. Week 4 (map 4, Figure 3.4) showed the greatest spatial contrast between regions of the study area, especially in Mackenzie Bays, with HRPS areas spatially close to LRPS areas. On weeks 2 and 4, the region at the mouth of the East Channel south of Hendrickson Island was predicted as a HRPS area, while on weeks 3 and 5, the region was predicted as a LRPS area. The temporal variability (map 6, Figure 3.4) demonstrated high values around coastal areas and at the mouth of the Mackenzie River channels, while the centre of Shallow Bay and the regions west of Tuktoyaktuk showed low to moderate variability. The Wilcoxon tests confirmed the temporal variability in predictions (p -values < 0.05 for all pairs), showing that the weekly RPS varied considerably (Supporting Information 3.5).

Figure 3.4: Temporal variability.



Notes: Temporal variability represented by the five weekly models (maps 1 to 5) relative probability of selection (RPS) values projected in the study area (with areas of high relative probability of selection [RPS value > quantile 0.75] in red and orange and areas of low relative probability of selection [RPS value < quantile 0.25] in blue and green) overlaid by the respective beluga observations in plain black diamonds; and the standard deviation map (map 6) depicting the spatial variability in terms of RPS between weeks (with high variability in red and low in grey). The basemap is open data shapefile (www.gdam.org). The map was created in QGIS 3.10.8.

3.3.4.2 Weekly external evaluation

Only subsampled locations with a RPS values were considered resulting in 75 observations. The 75 observations were analysed for the weekly models validation (Table 3.3) and were mapped (Figure 3.4). Weeks 3 and 5 had the most observations ($N = 37$ and 14 , respectively). Week 3 saw most observations being in Kugmallit Bay while being predicted as a LRPS area, and in Mackenzie Bays, with a couple of notable observations around the north tip of Garry Island. Week 4, with the most spatial variability in predictions, saw most of the observations at the edge of the study area, and a quarter of the observations in HRPS areas in Kugmallit Bay.

The percentage of presences being correctly predicted (i.e., sensitivity) remained the same whether it was averaged weekly or monthly, with 12% ($N = 5$) and the mean RPS value for the observations also stayed stable (Table 3.3). The Wilcoxon test results on observations displayed the same stability, showing that belugas seem to select the same range of RPS values week after week (p -values > 0.05 for all pairs) even if the predictions change considerably between weeks.

Based on the weekly contingency and confusion matrices (Supporting Information 3.2), the sensitivity, with an averaged value of 12% , the PPP, with an averaged value of 0.02% and the averaged kappa of -0.00032 showed a general poor agreement between model predictions and observations (Table 3.3).

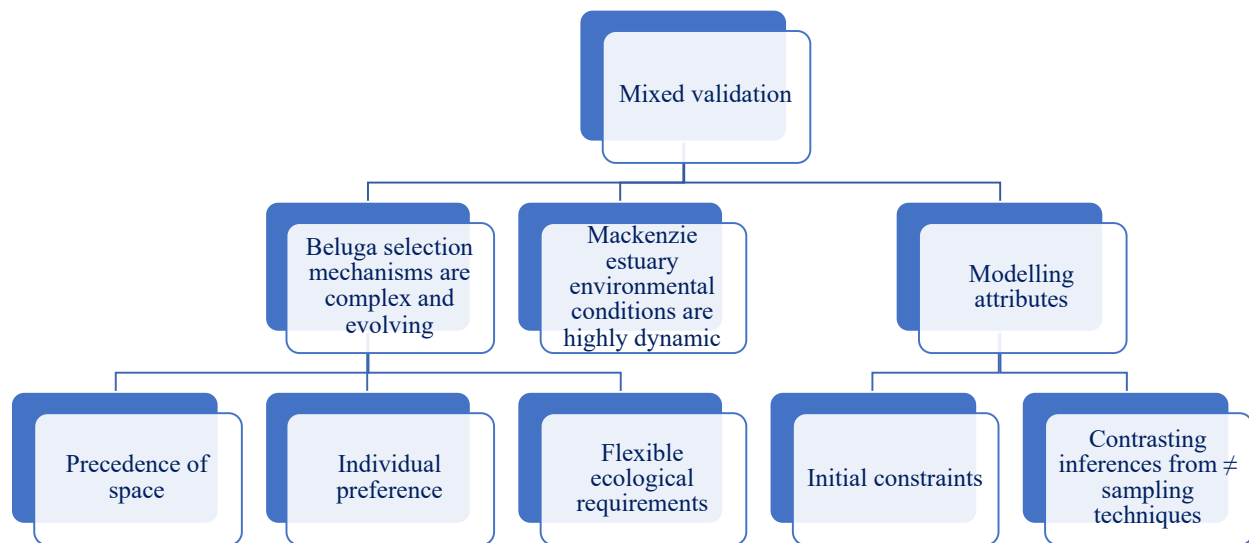
3.4 Discussion

To support the evaluation and validation of the habitat model performance and to account for temporal and spatial variability, we matched observations (i.e., beluga presences from telemetry), with predictions (i.e., areas of predicted high relative probability of selection). We first evaluated the capacity of the model to predict accurately the selection of specific areas by tagged belugas. Then we validated the model where beluga presences matched areas of high relative probability of selection.

The model predictions have been mostly evaluated in disagreement with observations, yet we found variability in agreements and disaccords between model predictions and observations, in space and in time, resulting in a mixed validation. Indeed, some areas were validated by HRPS areas matching beluga presence. The monthly model was validated based on the beluga tracks and

locations for areas in Shallow Bay around Shoalwater Bay, west of Garry Island and at the mouths of the Mackenzie River channels, with beluga presence matching HRPS areas. Some areas were not validated either by lack of beluga presence in HRPS areas or by beluga presence in LRPS areas. The monthly model was not validated around Kendall Island as there was no beluga at that time to match the predicted HRPS area. The monthly model was not validated throughout Mackenzie Bays, as the tracks perfectly overlaid predicted LRPS areas. Similar in Kugmallit Bay, the monthly model was not validated as the large proportion of beluga locations were located around Kittigazuit Bay, a predicted LRPS area. However, temporally, Kittigazuit Bay could have been validated if the model would have been based on weekly conditions instead of monthly. In both cases, Kittigazuit Bay and Kendall Island, fully integrated in the TN MPA, are widely recognized for their belugas concentration, even in a smaller proportion than Shallow Bay (Fraker et al. 1979; FJMC 2001; Harwood et al. 2014; Scharffenberg et al. 2019), and were expected to be validated.

Figure 3.5 Habitat selection analysis schematics.



The goal was not to question the veracity of the habitat model but rather to evaluate the habitat model spatial performance, as the habitat model can perform better in some areas and less in others, making it only partially but still valid (Guisan et al. 2017). Using the habitat model, we conducted a habitat selection analysis to explain the mixed validation. This analysis emphasised

on the mechanisms of selection by which species differentially select available habitats (Morris 2003), consequently generating patterns of habitat selection.

3.4.1 Beluga habitat selection mechanisms

The habitat model created predictions based only on sea surface temperature and turbidity, yet the selection of an area by a beluga might likely vary amidst other ecological influences and factors, justifying a precedence of the space over environmental conditions. We examined proxies such as surface activity obtained from movement data to tentatively untangle the mechanisms of selection, every location being the result of selection (Northrup et al. 2022).

Belugas might select a space independently from the environmental conditions in terms of temperature or turbidity. Lemieux Lefebvre et al. (2017) classified surface activities of belugas in several categories including milling, defined by a dispersion over a small occupied area and a low dynamism, and directional (-D) characterised by a distribution over a large occupied area and a moderate dynamism. We used those definitions to classify the two different patterns of movement observed in Kittigazuit Bay and in Mackenzie Bays/Shallow Bay and to relate those with specific activities. In the LRPS area in Kittigazuit Bay, the overlapping tracks and the long occupancy time seemed to indicate a milling activity, and might be an indicator of a core area (as defined in Noel et al. *in review*), associating functions (Lemieux Lefebvre et al. 2017) such as socialising, resting after feeding, settling or foraging on preys that might not be optimal but low in energetic costs (e. g., capelin; Choy et al. 2020), and this, regardless of the environmental conditions. The long and continuous tracks in LRPS area and the short occupancy time, especially in Mackenzie Bays, may be explained by the fact that belugas might have been travelling and consequently not selecting specifically those areas but using the region to transit (Fraker et al. 1979; Ostertag et al. 2019). In any case, those activities and functions might be completely independent from the turbidity or the temperature of the water and consequently not appear as a HRPS area as defined by the model (oppositely to Shoalwater Bay).

Additionally, belugas might select only a specific range of temperatures/turbidity for a specific function, reflecting a flexibility in their ecological requirements by trading off optimal environmental conditions (Northrup et al. 2022). Belugas, being migratory and endotherms, cope with a large range of temperatures (St. Aubin et al. 1990) and might select a habitat because it is

favourable only temporarily and only for a certain type of function (Northrup et al. 2016). For example, the area near East Whitefish situated at the mouth of the East Channel features a sandy seafloor and pebbles and was correlated positively with beluga presence (Whalen et al. 2020) for they potentially use the area to rub and scrape-off moulted skin (St Aubin et al. 1990; Waugh et al. 2018), making the area attractive for reasons only partially linked with environmental conditions.

Finally, belugas might select a space for individual reasons (Leclerc et al. 2016). Most subsampled locations in Kittigazuit Bay were from beluga #174972, and only beluga #174976, out of the seven tagged belugas, was present in Shoalwater Bay, denoting perhaps a personal preference for a specific bay. Even though, the high occupation in Kugmallit Bay might also be an artifact from the tagging being conducted from Hendrickson Island. Similarly, cultural trait could explain the diverging courses, with some courses heading to the west and others to the east, suggesting that belugas with similar tagged dates may have been part of a group following a specific migrating pattern (O’Corry-Crowe et al. 2018), completely independent of turbidity or water temperature. The role of memory, linked with the general philopatry, was also considered as three of the seven belugas actually returned in the Mackenzie Estuary shortly after leaving (Oliveira-Santos et al. 2016). Lastly, as the tagged belugas were all adult males, it is possible that physiological characteristics might have influenced the mechanisms of selection (Loseto et al. 2006; Northrup et al. 2022).

Belugas might also select a space following the variability in habitat quality, some weeks displaying environmental conditions that might have been more adequate for certain type of activity, justifying selection, than others.

3.4.2 Variability in habitat quality

By comparing weekly predictions, we demonstrated that belugas experienced habitats with high spatio-temporal variability, highlighting the strong dynamism of the environmental conditions in terms of turbidity and sea surface temperature specific to this coastal and estuarine environment (MacDonald and Yu 2006), especially near the coasts and at the mouth of the Mackenzie River channels. While some areas were predicted HRPS one week and LRPS the other week, belugas seemed to select the same range of environmental conditions based on constant RPS

values week after week. This revealed that, even with changing conditions, belugas showed acclimatisation to environmental conditions, temporarily following their optimal habitat at the time. This plasticity and capacity to adapt while conserving a general philopatry was already highlighted assessing the resilience of belugas facing climate change (Hauser et al. 2018; Moore and Huntington 2008), and more particularly in observing shifts in beluga summer distribution within the geographic boundaries of the species with changing conditions (Noel et al. *in review*).

While we saw that the bays displayed a similar variability with the standard deviation of the RPS map, we focused the following discussion on Kittigazuit Bay as the bay demonstrated the more obvious and unexpected disagreement. We saw that the bay displayed HRPS areas two weeks out of the five weeks but became eventually a LRPS area in the monthly model. As implied, the monthly model was built on averaged SST and SPM conditions, and consequently masked the temporality of quality in Kittigazuit Bay by that calculation. Using a monthly model, while enhancing the spatial coverage in terms of environmental conditions and number of locations, limited the inference by hiding some temporal disparities such as storms, leading to eventual mismatch between environmental covariates and beluga locations (Guisan et al. 2017; Milanese et al. 2020).

We also recognized that the variability experienced by some spatial factors was more important to define short-term selection at a larger spatial scale. It is possible that belugas select to follow the Mackenzie River plume (Hornby et al. 2016; Noel et al. *in review*), whose extent is highly sensitive to winds (MacDonald and Yu 2006). Additional to these short-term dynamics, the Mackenzie Estuary experiences interannual variations notably in terms of sea ice conditions, dictating the belugas timing of arrival (Hauser et al. 2017; Loseto et al. 2018). Belugas first enter Shallow Bay, where the landfast ice bridge breaks the earliest, followed by Kendall Island then Kugmallit Bay (ISR-TK 2006; Hornby et al. 2016), explaining by itself the selection of a certain bay by belugas. In both cases, the desired level and type of inference should dictate the adequate scale to use (Johnson et al. 1980; Boyce 2006; Guisan et al. 2017) while considering the option to create multi-scale habitat selection modelling as belugas might select some resources differently at different scales (McGarigal et al. 2016).

The inherent variability, whether coming from beluga habitat selection mechanisms or from the environmental conditions predicting habitat quality, prevents an already limited habitat model to perform ideally for medium to long term predictions.

3.4.3 Modelling attributes

The habitat model foundations were contrasted per bay as already underlined in Noel et al. (2022, *in review*). Especially in Kugmallit Bay, and consequently Kittigazuit Bay, where the coverage was not ideal to fit accurately a habitat model, in terms of satellite imagery and beluga locations. Indeed, Kugmallit Bay was only flown once. During the night of July 20 to 21, two days before the survey of Kugmallit Bay, the weather station in Tuktoyaktuk (69.43°N, 133.02°W; Environment and Climate Change Canada and Meteorological Service of Canada 2019) recorded a weather event with an averaged wind speed of 55 km·h⁻¹ for more than six hours. Those conditions were similar to what was described in Scharffenberg et al. (2019) where belugas were found to temporarily vacate Kugmallit Bay to shelter away from the impact of waves. It is possible that this weather event made belugas abundance potentially lower than expected (Scharffenberg K., DFO – unpublished data) with possibly presence of smaller groups (Mayette et al. 2022 - accepted). The satellite imagery coverage associated with the storm was nonexistent, making it impossible to estimate environmental conditions at that time, hampering the fitting of the model for that bay. Finally, as most of the tagged locations were in Kittigazuit Bay, the gap between the predictions and the observations was actually amplified.

Besides, remotely sensed data mostly provide surface environmental conditions, failing to account water column properties (Doxaran et al. 2015). Using temperature data from the tags or temperature and turbidity data from seafloor moored hydrophones in Kugmallit Bay (Scharffenberg K., DFO – unpublished data) could alleviate that limitation by providing an additional way of validating model-based covariates such as the SST and SPM.

The data acquired from aerial survey and telemetry are very distinct at many levels and the framework of modelling differs accordingly (e.g., availability and accessibility definitions, uncertainty and measurement errors or modelling approach; Guisan et al. 2017; Northrup et al. 2022), bringing caution when building multi-data model in terms of pertinence of the inferences. The habitat model was fitted with 611 observations while telemetry data 89 observations were

coming from only seven belugas, not necessarily representing the same subset of population, potentially computing distinct population-level inferences. Furthermore, the habitat model was built on static surfaced locations while the telemetry data described movement, particularity that remained unexplored during the validation while supporting most of the discussion. Additionally, dive types could be associated with surface movement (Lemieux Lefebvre et al. 2017) and potential functions (Storrie et al. 2022), translating activities not visible if considering only the horizontal component of the movement. Further work on analysing the dives in the Mackenzie Estuary would corroborate or at least improve our understanding of beluga shallow vertical movement, and eventually link those with the fine-scale bathymetry.

While being practical, external validation should be used with caution as each sampling technique has its own inherent issues, assumptions and limitations. It would be insightful to create a habitat model based on telemetry data (e.g., step selection function; Fieberg et al. 2021), passive acoustic monitoring data or harvesters observations (e.g., Bayesian models; Bélisle et al. 2018), and to either test if there is good concurrence between inferences of habitat predictions between these different types of data or to create simultaneous inferences in order to validate further the current habitat model. Different modelling techniques accounting for variability can also be envisioned to validate further the habitat model, such as adding interaction terms, creating multi-temporal modelling (with decades-old data such as in Harwood et al. 2014 or projecting the model back in time using a climatology), hierarchical modelling using mixed-effects approach (Muff et al. 2020), or multi-species modelling (Northrup et al. 2022).

3.5 Conclusions

Understanding the drivers behind an animal habitat selection provides important knowledge to establish spatial distribution baselines. Those baselines enable to monitor changes and to consequently predict any variation especially under evolving environmental conditions. We previously created a habitat model based on observations from aerial surveys to estimate the environmental requirements behind the selection of the Mackenzie Estuary and TN MPA by belugas from the Eastern Beaufort Sea population. This present study aimed to broaden the application of the habitat model by estimating the quality of the model predictions with satellite telemetry data. By evaluating, and tentatively validating the model, the baseline established would be corroborated and predictions inferred with a higher confidence.

While the model predictions have been mostly evaluated in disagreement with observations, we found variability in agreements and disaccords between model predictions and beluga presence, in space and in time. We refined some local areas of selection, confirming predictions of the model were accurate in terms of presence of belugas linked with water temperature and turbidity. Kendall Island was predicted as relatively highly probable to being selected but did not welcome any belugas, so we could not confirm those predictions. Kugmallit Bay, and more specifically Kittigazuit Bay, was not validated as the area was predicted not likely to be selected while considering what was available for the belugas, but displayed the most observations of belugas. That contradiction could have multiple potential explanations. Belugas are a migratory and social species, they experience a wide range of environmental conditions during their annual journey and certainly have flexible habitat requirements based on the space they select, based on the function they have of the space or based on their individual experience, belugas selecting one area serving multiple purposes, and probably selecting several areas serving the same purpose. Additionally, the Mackenzie Estuary is highly dynamics in terms of environmental conditions and belugas might adapt to that variability by selecting habitat that are optimal only at one particular time, period or space but may not transfer to any other time or area under different conditions. The variability in the mechanisms of selection and in the experienced environmental conditions over relatively short time scale raises difficulties in assessing adequately habitat selection and reveals the complex philopatry of belugas in specifically selecting the Mackenzie Estuary despite being harvested annually.

Additionally, the initial model itself was built with imperfections and with a distinct modelling framework. While building supplementary habitat models, based on different types of data could lead to further validation and consequent better predictions, the relevance of modelling a species with complex selection mechanisms is legitimately controversial. Therefore, we wanted to insist that a model remains an approximation, a simple representation of the reality and will never be a perfect agreement. Any additional contribution, while adding complexity, will bring the model closer to a more holistic understanding of the ecology of EBS belugas, allowing Inuvialuit communities to comprehensively assess beluga future management and conservation.

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Supporting Information

Supporting Information 3.1: Glossary

A. Beluga locations in relation with the data processing

Nomenclature	Processing	Number
Locations	Raw data, geographical positional fix	
Filtered locations	All locations filtered by number of satellites and tidied	2991
Clipped locations	Locations located within the study area	563
Subsampled locations	Clipped locations subsampled every 4 hours	90
Observations	Subsampled locations with a value of RPS	89
Presences	Observations with a HRPS (RPS value > quantile 0.75)	11
Absences	Observations with a HRPS (RPS value < quantile 0.75)	78

B. Tracks in relation with the data processing

Nomenclature	Processing	Number
Tracks	All tracks from location points	7
Periodic tracks	Tracks when belugas were in the study area, per beluga	11
Daily tracks	Tracks for each day each beluga was in the study area	39

C. Model outcomes in relation with data processing (Adapted from Guisan et al. 2017)

Nomenclature	Definition for our study	Processing
Resource unit	Area of space	None
Aerial survey-based model RSF model Fitted/trained model	Model fitted with one partition of aerial survey dataset in the environmental space and in the trained geographical space (Noel et al. <i>in-review</i>).	Fitting/training/calibration Transfer
Predictions	Model outcomes validated with a second partition of aerial survey dataset <u>in</u> the study area and time period used to train the model ^a .	Evaluation/Validation
Projections	Any prediction made <u>outside of</u> the study area or time period used to train the model ^b .	Projection

Notes: a. Fitted model transferred and applied to the SST and SPM values of each resource unit of the study area during the period of the aerial surveys. b. Fitted model transferred and applied to the SST and SPM values of each resource unit of the study area during the period tagged belugas were present. In this study we 1) evaluate the model on independent data, creating predictions, but as 2) the evaluation is conducted outside of the time and space used to train the model, the term projection should have been used to strictly define the current model outcomes. However, as the term prediction is more commonly used, we will use it while bringing attention to the fact that technically we evaluated model projections in this study.

Supporting Information 3.2 : Contingency and confusion matrices

A. Contingency matrix: Matrix with counts of observations and predictions relative probability of selection (RPS) values, binned per quantiles values for each temporal model. In this context, observations with a RPS value $> Q0.75$ are considered presence and with a RPS value <0.75 , absence

Counts	Q0.05	Q0.25	Q0.5	Q0.75	Q0.95	Max	Total
Monthly							
Quantile value	0.0083	0.00993	0.01368	0.01864	0.03171	0.9917	
Total	4534	18041	22614	22596	18095	4520	90400
Observations	4	42	16	16	7	4	89
Predictions	4530	17999	22598	22580	18088	4516	90311
Week 1							
Quantile value	0.00974	0.01508	0.01899	0.02276	0.02806		
Total	3620	14461	18087	18046	14484	3614	72312
Observations	3	5	1	0	1		10
Predictions	3617	14456	18086	18046	14483	3614	
Week 2							
Quantile value	0.00894	0.01361	0.01748	0.02139	0.03297		
Total	2888	11532	14428	14383	11547	2882	57661
Observations	1		1				2
Predictions	2887	11532	14427	14383	11547	2882	
Week 3							
Quantile value	0.00952	0.01333	0.01739	0.02129	0.02879		
Total	3575	14234	17818	17786	14261	3564	71238
Observations	3	15	13	2	3	1	37
Predictions	3572	14219	17805	17784	14258	3563	
Week 4							
Quantile value	0.00806	0.01029	0.01357	0.02018	0.05362		
Total	4082	16113	20192	20217	16150	4040	80794
Observations	2	3	3	1	3		12
Predictions	4080	16110	20189	20216	16147	4040	
Week 5							
Quantile value	0.0863	0.01226	0.01805	0.02224	0.03703		
Total	4360	17559	21914	21914	17511	4382	87640
Observations	1	3	6	2	2		14
Predictions	4359	17556	21908	21912	17509	4382	

True absence = TA	False presence = FP
False absence = FA	True presence = TP

B. Confusion matrix: Matrix used to compare the count of resource unit predicted selected and observed selected (1/1 – true presence: salmon) and observed unselected (1/0 – false presence: blue) and the count of resource unit predicted unselected but observed selected (0/1 – false absence: yellow) and observed unselected (0/0 – true absence: green) for each temporal model.

Monthly		Observed	
		1	0
Predicted	1	21893	2
	0	65747	12
Week 1		Observed	
		1	0
Predicted	1	1	18097
	0	9	54205
Week 2		Observed	
		1	0
Predicted	1	0	14429
	0	2	43229
Week 3		Observed	
		1	0
Predicted	1	4	17821
	0	33	53380
Week 4		Observed	
		1	0
Predicted	1	3	20187
	0	9	60595
Week 5		Observed	
		1	0
Predicted	1	2	21891
	0	12	65735

Based on the confusion matrix, we can calculate t

- the sensitivity with: $TP/(TP+FA)$;
- the PPP (presence predictive power) with : $TP/(TP+TA)$,
- the kappa with: $=((TP+TA)-(((TP+FA)*(TP+FP)+(FP+TA)*(FA+TA))/TOTAL)))/(TOTAL-(((TP+FA)*(TP+FP)+(FP+TA)*(FA+TA))/TOTAL))$

as seen on Table 2.

Supporting Information 3.3: Monthly modelling metrics for the predictions and the observations, per bay. Please refer to the glossary (Tables S3.1 in Supporting Information) for more information on the nomenclature.

	MONTHLY MODEL	Kugmallit Bay	Mackenzie Bays	Shallow Bay	Total
OBSERVATIONS					
1	Number of observations	53	22	14	89
2	Percentage of observations	59.5%	25%	15.5%	
3	Number of HRPS observations	1	5	5	11
4	Percentage of HRPS observations	9%	45.5%	45.5%	
5	Percentage of observations predicted as HRPS	2%	22%	36%	
6	Percentage of total observations predicted as HRPS	1%	5.65%	5.65%	12.3%
PREDICTIONS					
7	Number of resource units	14166	45940	30294	90400
8	Percentage of resource units	15.7%	50.8%	33.5%	
9	Number of resource units with a HRPS value	4460	9106	9049	22615
10	Percentage of total area predicted as HRPS	5%	10%	10%	25%
11	Percentage of area predicted as HRPS	30%	20%	30%	
12	Percentage of total HRPS area	10%	30%	60%	100%

Notes:

Line 4 is line 3 divided by the total of line 3

Line 5 is line 3 divided by line 1

Line 6 is line 3 divided by the total of line 1

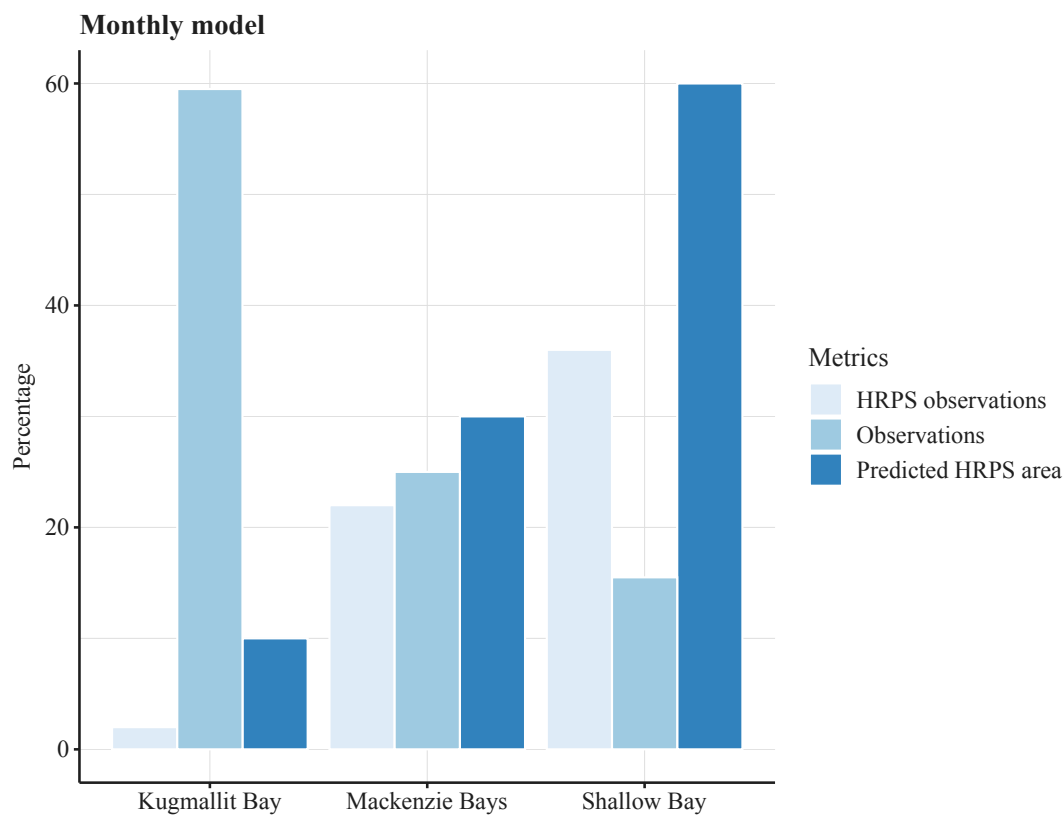
Line 10 is line 9 divided by the total line 7

Line 10 reads “5% of the total area is HRPS located in Kugmallit Bay”

Line 11 reads “30% of Kugmallit Bay was predicted as HRPS”

Line 12 reads “10% of the totality of HRPS areas is in Kugmallit Bay”

Supporting Information 3.4: Validation metrics in percentage for the monthly model.



Notes: Diagram to inspect at a glance the difference between Shallow Bay having the least total observations but most of its observations have HRPS values while Kugmallit Bay, having the most total observations has almost none of its observations with HRPS values.

Supporting Information 3.5: Wilcoxon test p-values on relative probability of selection (RPS) values

Weeks compared	Observations	Projections
1/2	0.06061 (N = 10/2)	< 0.05 (N = 72312/57661)
2/3	0.78 (N = 2/37)	< 0.05 (N = 57661/71238)
3/4	0.2943 (N=37/12)	< 0.05 (N = 1238/80794)
4/5	0.2312 (N = 12/14)	< 0.05 (N = 80794/87640)

Notes: Values per couple of weeks for the observations and the predictions, with respective count (N) for each week included in the comparison. A p-value > 0.05 indicates the belonging of each sample to the same population, in this context, it would mean that there is no significant difference between the RPS values from week 1, 2, 3, 4 and 5. Please refer to the glossary (Tables S3.1 in Supporting Information) for more information on the nomenclature.

CHAPTER FOUR:

SYNTHESIS AND GENERAL CONCLUSIONS

4.1 Synthesis

In order to enhance our understanding of Eastern Beaufort Sea beluga whales habitat and habitat selection to further anticipate effects of climate changes, two objectives were pursued. The first objective was to identify, quantify and qualify late summer beluga habitat in terms of environmental conditions, spatial selection and variations over time in relation with climate change, and was addressed in Chapter Two. First, the spatial distribution was analysed by determining the features driving beluga habitat selection with a habitat model in the form of a Resource Selection Function. Then, potential beluga distribution shifts were evaluated by comparing current aggregation areas with a past baseline. And lastly, beluga distribution shifts were linked with habitat selection mechanisms in relation to environmental changes. The habitat model paired beluga observations from a 3-days late summer 2019 aerial survey with estuarine habitat environmental conditions influencing beluga habitat selection. The second objective was to broaden the application of the habitat model, aiming to give the predictions a larger temporal and spatial scale, and was addressed in Chapter Three. First the habitat model was projected on the entire study area and over a monthly time period. Then, the habitat model was evaluated by adding satellite telemetry observations from late summer 2019 and estimated the agreement with the predictions. Finally, evaluations were run at monthly and weekly scales to determine the contribution of variability inherent to the estuarine environment and the migratory nature of belugas while trying to create long-term predictions.

The results of the Chapter Two revealed that water turbidity, with a high suspended particulate matter concentration (i.e., from 200 and 400 $\text{g}\cdot\text{m}^{-3}$) and warm water temperature (i.e., greater than 13 °C, up to 17 °C) defined beluga habitat selection. The results also showed belugas would select regions characterized by this specific combination of environmental conditions, defining a habitat distribution at the mouth of Mackenzie River channels and along unprotected coastlines. The comparison between the current beluga distribution and historical observations (Harwood et al. 2014) showed a distributional shift closer to the coasts and deeper in the mouth of the Mackenzie River channels. As these selected regions are already experiencing environmental

changes such as more extreme temperature and accelerating coastal erosion (Bush and Lemmen 2019; Lim et al. 2020), these regions potentially displayed conditions more favourable for belugas as defined by the habitat model (i.e., warmer and more turbid waters). Consequently, it was suggested that the observed beluga distribution, shifted from the baseline, was probably the results of the influence of changing environmental conditions on beluga selection and consequent distribution, either on a temporary (i.e., acclimatisation) or permanent basis (i.e., adaptation). To investigate further the influence of environmental changes on beluga distribution, the habitat model performance needed to be consolidated. The results of the Chapter Three showed that the habitat model, built on water turbidity and temperature and as assessed by the tagged data, correctly predicted habitat of quality for belugas in Shoalwater Bay and Garry Island but not in Kugmallit Bay or Kendall Island, if the predictions were computed monthly. However, if the model was built at a shorter timescale, predictions changed, indicating a clear variability explicable by several factors. Belugas experiencing a wide range of environmental conditions during their migration certainly have flexible habitat requirements based on the space they select (Hornby et al. 2016), based on the function they have of the space (Choy et al. 2020) or based on their individual experience (O’Corry-Crowe et al. 2018). Additionally, the Mackenzie Estuary is highly dynamics in terms of environmental conditions (MacDonald and Yu 2006) and belugas might adapt to that variability by selecting habitat that are optimal only at one particular time, period or space but may not transfer to any other time or area under different conditions (Northrup et al. 2022).

By using two concurrent datasets, covering the same study area during the same period, but obtained from distinct sampling methods, a habitat distribution model bound with a habitat selection analysis was run. Inferences of selection were generated considering quality of environmental conditions and belugas mechanisms of selection – both creating intertwined patterns of beluga habitat distribution. Together, the two chapters findings have highlighted the complexity in defining and predicting beluga habitat distribution, hindering accurate assessment of beluga habitat selection while enhancing our understanding of EBS beluga ecology.

4.2 Conclusions and Future Work

The Eastern Beaufort Sea beluga population migrates to the Mackenzie Estuary and to the TN MPA every summer and the reasons behind this selection are not fully understood (COSEWIC

2016). Rapid environmental changes occurring in the Arctic strongly impact estuarine ecosystems (Pörtner et al. 2019), including the Mackenzie Estuary (Nichols et al. 2004; Waugh et al. 2018; Worden et al. 2020). Therefore, it is crucial to understand why belugas select these habitats and what features are driving habitat selection to further inform beluga monitoring and sustainable beluga management and conservation in the context of climate change.

This thesis provides new evidence that belugas are flexible species, capable to adjust to changes. The findings showed that belugas may exhibit two strategies as a response to environmental changes. Belugas may trade-off their optimal environmental conditions and adjust their selection to where they already are either temporarily or permanently. Belugas may also shift their inshore distribution, following more favourable conditions, representing new challenges for harvesters who may have to switch the timing and location of their harvest in response (Loseto et al. 2018). Continued community-based monitoring remains a critical component to collect timely observations of changes, in order to keep building accurate and comprehensive conservation and management strategies for belugas.

This thesis underlines the difficulties to create an accurate habitat model. We showed that adding data to the model increased complexity in inferences made but simultaneously allowed to reflect on mechanisms of selection. Whereas models remain an approximation, they still represent a valuable insight on habitat selection. To achieve a comprehensive understanding of beluga movement ecology, additional sources of observations from passive acoustic monitoring, telemetry, drone, or citizen science should be added, environmental data from past climatology or current weather stations should be included, and knowledge of local communities should be weaved, to create an integrated model (Isaac et al. 2020). The next step in this work is to re-analyse historical beluga harvesters observations. From 2013 to 2016, a beluga monitoring program in partnership with the harvest program called Local Ecological Indicators of beluga health and habitat use was conducted by S. Ostertag notably in Kugmallit Bay at East Whitefish and Hendrickson Island. Ostertag gathered harvesters observations about belugas that could be looped in the current habitat model, contributing to designing an expert-based habitat model (Brook and McLachlan 2009; Bélisle et al. 2018; Skroblin et al. 2021). We already have the IHTC support and our ethics approved by the Joint-Faculty Research Ethics Board at University of Manitoba, Fort Garry Campus (REB R2-2021:044).

More importantly, this project was initiated by communities needs and perspectives, and this thesis showed the iterative process followed while recognising the challenges of the multi-faceted context that precluded our initial engagement approach. The results and new limitations identified are intended to be reported and disseminated following interests at a convenient time. The IHTC suggested to set up a final exchange of ideas by presenting the thesis findings in a personalised and visual form using boundary objects such as interactive maps or circulating illustrated pamphlets. We hope, by this dissemination, to open space for discussions and gather feedback, building a knowledge exchange cycle. The Northern Scientific Training Program granted me funding to present the findings in-person. Additionally, the first part of the thesis is already submitted for publication in an interdisciplinary open-access journal, appended by a plain language summary in order to reach a broader and diverse audience.

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APPENDICES

1. Letter of Support for IHTC and Aurelie partnership.



Laura Murray
Arctic Aquatic Research Division
Fisheries and Oceans Canada

RE: Letter of Support for Aurelle

To Laura,

The Inuvik Hunters and Trappers Committee (IHTC) held their regular board meeting on Wednesday, December 4, 2019. The board of directors agreed on giving support for the project proposal for Aurelle Noel.

If you have any questions or concerns, please contact our office at (867)-777-3671 or email inuvikhtc@hotmail.com

Thank you,



2. Steps towards a successful project

Our initial approach followed the framework of practises detailed in Djenontin and Meadow (2018) for a successful transdisciplinary and collaborative research project in terms of logistic and institutional factors, development and design, and setting-up components. In terms of outputs management and dissemination component, the details are in the section 4.2.

I applied and was successful for additional funding, notably to Northern Science Training Program (NSTP) and to the Oakes-Riewe Environmental Studies Research Award. Initially, the idea was to allow me to go on the field multiple times for in-person discussions, but also for reporting and dissemination. I also envisioned during my time in Inuvik to meet with the local high school or technical college, to be able to train interested community members in my expertise (remote sensing). For planning purpose, we asked the IHTC about when to come to make sure we would take advantage of the time they have as they will be busy “on the land” and/or with their daily job.

I followed a course of Methodology and Research Issues in Native Studies at the department of Native Studies at University of Manitoba (UM). During this course, I learnt about the Indigenous history in Canada and in the Arctic, the attempts of reconciliation and the processes of Indigenous recovery, reconnection and self-determination from the Indigenous peoples. This course provided essential paths to follow when conducting research with a decolonizing eye (Smith, 2006). I also followed an online course about qualitative research and one about Human Environment Relations in the Arctic (UM). I followed numerous workshops and webinars notably about two-eyed seeing, Arctic resilience, reconciling ways of knowing, country foods, community-based monitoring and positionality and reflexivity.

I started my program in September 2019 and started building relationship and involving different stakeholders at multiple stages in December 2019. We sent a letter to the Inuvik Hunters and Trappers Committee (IHTC) and we got their support in December 2019 (Appendix 1) making sure to align this project with their priorities (section 1.3.1). In January 2020, during FJMC meeting, in February over the phone and from February 29th to March 11th 2020, during the DFO Winter 2020 Beluga Community Tour, we met with DFO based in Inuvik and with the Joint Secretariat coordinators from the Shared Services Unit (JS/SSU). We discussed about opportunities for synergies, integrated work and partnership to make their and our projects as

complementary as possible with the community-based monitoring program already in place. During this time, we also hosted a community lunch during which IHTC members were provided with an overview of this project, leaving space for feedback and discussion. Finally, we also met with local community members, harnessing on pre-existing personal and professional relationships from my supervisor Dr. Loseto, participating in community activities and spending time in the community. Following this *in-person* meetings and over the course of the master, we sent several letters to IHTC, updating on challenges, suggesting new approaches (Figure 1.1) and asking for guidance. In April 2021, we virtually met with IHTC to discuss the latest plan about re-analysis of historical observational data, consequent ethics request and dissemination of findings (section 4.2).

In regard to being ready to use remote sensing data, following a proposal from DFO – Bedford Institute of Oceanography (BIO) linking beluga to remote sensing, I went to Halifax (Nova Scotia) from November 25th to 29th 2019 to work with two Ocean Colour radiometry experts Emmanuel Devred and Andrea Hilborn. I also seized the opportunity to meet with a coastal erosion professional Dustin Whalen from Natural Resources Canada (NRCan) to share our points of view and pursue a partnership.

3. Certificate of completion for the Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans – Course on Research Ethics (TPCS 2: CORE).

