Evaluating temporal trends in behavior and demographics to understand the lack of recovery of an endangered whale population

by

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Abstract

Beluga whales (*Delphinapterus leucas*) are critical components of the Arctic marine ecosystem, and they face numerous threats from environmental changes and human activities. Understanding their population dynamics, habitat use, and social structure is crucial for their conservation. The research outlined here investigates the endangered Cumberland Sound beluga whale population using various techniques including drone surveys, aerial surveys, and satellite telemetry. The thesis begins with an overview of beluga whale ecology, behavior, and the threats they face, and explores how many of these aspects vary between populations. Satellite telemetry was used to explore behavioral trends, revealing stable migration timing over several years. Dive behavior analyses suggest a change in prey preference from Arctic cod (*Boreogadus saida*) to capelin (*Mallotus villosus*), which may have negative consequences for the population over time as the distribution and abundance of capelin can be less predictable. Drone technology was used to create a photographic identification catalog for the beluga whale population, allowing for detailed monitoring of individual whales, minimizing disturbance, and providing insights into age structure and social dynamics. From 2017 to 2019, drone surveys identified 93 individual whales, revealing many uniquely marked adults and consistent resightings, and the existence of stable social groups over multiple years. Aerial surveys in 2014 and 2017 provided extensive coverage of the beluga whale population and showed a potential contraction in geographical range and a lower proportion of juveniles compared to other populations. The integration of drone and aerial surveys in this study resulted in comprehensive data on demographic trends, crucial for understanding population health. This thesis also examined the long-term impacts of satellite tagging. Two whales were photographed with tag remnants and scars, suggesting although tagging did not result in long-term health issues in these cases, the remnants of tagging may remain long after intended. In summary, this thesis provides a detailed examination of the Cumberland Sound beluga whale population, demonstrating the importance of varied research methods for effective monitoring. Given interpopulation differences in beluga whale ecology, these insights are crucial for developing targeted conservation strategies and ensuring the long-term resilience of the population against environmental and anthropogenic pressures.

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Dedication

To my mom and family for always encouraging my love of science, the ocean, and all its critters.

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Contributions of Authors

Chapter 1

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Chapter 2

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Watt, Brent G. Young, and Kasey P. Ryan conceived the idea and methodology for this study. William R. Koski, Brent G. Young, and Kasey P. Ryan conducted fieldwork to collect photographs of beluga whales. Kasey P. Ryan led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Chapter 5

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Introduction

A comprehensive understanding of life history traits, habitat use, and overall ecology is essential to study endangered species and populations, and to identify threats and establish effective recovery programs (Abbitt et al. 2001; Hernández-Yáñez et al. 2022; Murray et al. 2011; Palm et al. 2020). Habitat selection and life history traits can differ greatly among populations of the same species, making it critical to examine these dynamics within each specific system (Bong et al. 2021; Frederiksen et al. 2005; Lambrechts et al. 1997; Murray et al. 2011). Interpopulation differences in life history traits can arise from varying habitats; for example, bird species may exhibit significant differences in fecundity and other reproductive traits, influenced by their habitat and how they respond to different biotic and abiotic conditions within that habitat (Frederiksen et al. 2005; Lambrechts et al. 1997). Other variables such as age structure, mortality rates, and foraging behavior can contribute to a lack of growth or recovery in endangered species, and population-specific knowledge of these variables is needed to understand how the species might respond to changing environmental and biological conditions, including climate change or changes in prey availability (Bong et al. 2021; Frederiksen et al. 2005; Hernández-Yáñez et al. 2022; Lambrechts et al. 1997; Murray et al. 2011).

Habitat selection theory, which posits that animals use specific strategies to select habitats that maximize their fitness, is fundamental in understanding ecology and behavior (Mayor et al. 2009; Morris, 2003; Rosenzweig 1981). Insights into habitat selection and use are particularly important for endangered species, which are often vulnerable to environmental changes and human activities given their previous population declines and small population sizes (Abbitt & Scott 2001; Halpern et al. 2007). Habitat protection becomes even more crucial as anthropogenic activities such as development and resource extraction expand and overlap with critical habitats (Ragen et al. 2008; Laidre et al. 2015). Understanding migration patterns, including the timing and routes of seasonal movements, is also critical for identifying these key habitats (Cherry et al. 2013; Snell et al. 2019). By recognizing that certain species require specific habitats for migrating and other activities including breeding and calving, conservationists can implement measures to protect these critical areas, thereby enhancing reproductive success and long-term survival (New et al. 2013; Sternecker et al. 2010). The choice of habitat also ultimately affects an

individual's survival and reproductive success, thereby influencing overall population viability (Morris, 2003).

The loss of a species from an ecosystem can trigger detrimental cascading effects, impacting other species within the ecosystem (Bowen, 1997; Estes et al. 2011; Ferretti et al. 2010). The disappearance of key predators can result in overpopulation of prey species, which may in turn disrupt vegetation and habitat (Estes et al. 2011; Ferretti et al. 2010). This disruption can also lead to shifts in biodiversity, reducing ecosystem resilience and making it more vulnerable to invasive species (Estes et al. 2011; Wallach et al. 2010). For example, the removal of apex predators, like dingoes in Australia, disrupted ecosystem resilience and allowed invasive mesopredators like foxes and cats, as well as herbivores like rabbits, to increase in abundance and further reduce native species while allowing invasive species to take over (Wallach et al. 2010). Relaxing predator control, however, allowed dingoes to re-establish top-down regulation, leading to the recovery of biodiversity and ecosystem productivity (Wallach et al. 2010). The effects of the removal of a species from an ecosystem can even impact the cultural and socio-economic dynamics of human communities (Bowen, 1997). For instance, in coastal regions, the removal of marine mammal species can affect fisheries and disrupt traditional practices, particularly in regions that rely heavily on natural resources for sustenance and cultural identity (Bowen, 1997).

Marine mammals, most being high trophic level species, are integral parts of their ecosystems and are thought to be a stable component of the marine environment similar to trees in a forest, taking up and storing large amounts of nutrients (Bowen, 1997). The removal of millions of whales during the 19th and 20th centuries when commercial whaling reached its peak led to the decline and near-extirpation of many populations and species (Clapham et al. 1999; Tulloch et al. 2019). The effects of these removals are still being investigated but are thought to include reducing biodiversity, preventing carbon sequestration that occurs when whale carcasses fall to the seafloor, and disrupting nutrient cycling (Butman et al. 1995; Clapham et al. 1999; Pershing et al. 2010; Roman et al. 2014; Tulloch et al. 2019). While some whale species have shown signs of recovery, others are stagnant or declining further (Clapham et al. 1999; White et al. 2022). The lack of recovery in these species has often been attributed to continued anthropogenic impacts such as ship strikes and entanglements in fishing gear, and various effects of climate change such

as changes in prey distribution and availability, and increasing interspecific competition as the ranges of species shift (Clapham et al. 1999; Tulloch et al. 2019).

As one of only three cetaceans endemic to the Arctic, beluga whales (*Delphinapterus leucas*) are an integral part of the Arctic ecosystem as predators of many fish and invertebrate species, prey of killer whales and polar bears, and nutrient recyclers (Bowen, 1997; Kiszka et al. 2015; Matley et al. 2015; Shelden et al. 2003). The ecological importance of beluga whales extends to their cultural significance for Indigenous communities who harvest them for subsistence and cultural practices (Kilabuk, 1998). Beluga whales are experiencing significant shifts in their ecosystem associated with climate change (Jahn et al. 2024; Laidre et al. 2008; Skovrind et al. 2021). The Arctic is warming four times as fast as the rest of the planet, and as such, the suitable habitat for beluga whales is declining and projected to decline further with a decline in beluga whale population sizes occurring as a result (Jahn et al. 2024; Rantanen et al. 2022; Skovrind et al. 2021). Predicting the responses of species such as beluga whales to climate change is difficult, especially when much of their ecology remains relatively poorly understood. Several beluga populations are classified as endangered or threatened, largely due to historical overhunting, and many are still harvested by local Indigenous communities (Hobbs et al. 2020). Some communities near endangered beluga populations such as in Cook Inlet and St. Lawrence Estuary have suspended hunting (both Indigenous and non-Indigenous) since 2008 and 1979, respectively (Mosnier et al. 2015; Rugh et al. 2010), but neither population has shown significant signs of recovery since (Mosnier et al. 2015; Norman at al. 2015).

The beluga whale population in Cumberland Sound, Nunavut is currently assessed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) due to historical overhunting and ongoing subsistence harvesting (COSEWIC, 2004; Stewart, 2018). A quota of 41 whales per year has been in place for the local Inuit hamlet of Pangnirtung since 2002 to try to prevent further population declines (COSEWIC, 2004). Despite these efforts, a 2017 aerial survey estimated only 1,381 whales (95% CI = 760–1,744), far below the pre-whaling estimate of 8,500 (COSEWIC, 2004; DFO, 2019). Population models suggest the Cumberland Sound beluga whale population may continue to decline under this quota (Watt et al. 2021). As one of the few “resident” populations with short migrations and a relatively small home range, further declines could lead to local extirpation (Richard & Stewart, 2009; Watt et al. 2021). Given these

threats, understanding the population dynamics, health, and social structure of beluga whales is critical for developing effective conservation strategies.

The primary aim of this research is to improve understanding of beluga whales through the integration of various methodologies, including drone technology, aerial surveys, and satellite tagging. Specifically, the objective is to assess how aspects of beluga whale life history, habitat use, and overall ecology relate to the Cumberland Sound population and its conservation, and to identify differences between the whales in Cumberland Sound and those in other populations. By employing these techniques, this research seeks to provide comprehensive insights into the behavior and the specific conservation needs of Cumberland Sound beluga whales, and to better understand why the population has not recovered. To provide background information about beluga whales, Chapter 1 offers a broad review of beluga whale life history focusing on aspects such as habitat use, diet, social structure, reproductive behavior, and threats that beluga whales face such as climate change and hunting. Throughout the chapter, interpopulation differences in life history are identified. For example, reproductive and mortality rates of populations, prey preferences, and migration timing and drivers can vary among beluga whale populations, and notably, many of these variables were unknown for the Cumberland Sound population.

In Chapter 2, the focus is on the migration timing and changes in dive behavior over time in Cumberland Sound. For beluga whales, habitat selection throughout the year involves interactions and tradeoffs between several factors such as targeting prey and environmental changes such as the buildup and breakup of ice (Bailleul et al., 2012; Goetz et al., 2012; Hauser et al., 2014, 2017, 2018; O'Corry-Crowe et al., 2016). This chapter employs long-term satellite tagging data to analyze migration patterns and dive behaviors of Cumberland Sound beluga whales. The objective of the chapter is to understand how beluga whales navigate and use their habitat, which is essential for their conservation. Chapter 3 details the use of drone photography to identify individual whales, offering a non-invasive method for monitoring the endangered Cumberland Sound beluga whale population in more detail. The chapter describes the development of a photographic identification catalog, which allows for the identification and tracking of individual whales over time. This approach provides high-resolution data on the whales' physical conditions and social interactions. Chapter 4 combines the previous drone survey analysis with aerial surveys to examine the social organization and age structure of the

Cumberland Sound beluga whale population. These two methodologies enable detailed examination at both fine and broad scales: at the individual level using drones, they offer insights into aspects such as social complexity, while at a broader scale using aerial surveys, they provide a thorough examination of a larger portion of the population, including its age structure and how it compares to other populations. Finally, Chapter 5 presents photographic evidence of the long-term impacts of satellite tagging on two beluga whales, one from Cumberland Sound and one from western Hudson Bay. This chapter underscores the need for ongoing monitoring to understand the health implications of tagging.

The integration of various methodologies such as drone technology, aerial surveys, photographic identification, and satellite tagging results in a detailed approach to studying the Cumberland Sound beluga whale population, providing a thorough understanding of how the ecology of this population aligns with and differs from other beluga whale populations. This combination of methods also allows for the exploration of both broad-scale population trends and fine-scale individual behaviors, resulting in a more in-depth examination of the population as a whole. The insights gained from these studies shed light on some of the possible challenges beluga whales face and have important implications for the management and protection of beluga whale populations, particularly in the face of rapid environmental changes and increasing anthropogenic pressures. These insights are crucial for developing management strategies that can respond to the threats faced by the Cumberland Sound population and has implications for other beluga whale populations facing similar threats.

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Chapter 1 – An overview of beluga whale life history, behavior, and the threats they face

Excerpts from a book chapter on beluga whales published in the *Handbook of the Mammals of Europe*

1.1 Current distribution

Beluga whales inhabit Arctic and sub-Arctic waters primarily between latitudes of 47° N and 82° N (Fig. 1.1) (Hobbs et al. 2020). Their distribution varies seasonally because of biannual migrations that are linked to the extreme seasonality of northern latitudes, primarily the dynamic nature of sea ice. In some beluga whale populations, the migrations are extensive and their summer and winter habitats are thousands of kilometers apart. Others have a coastal distribution and migrate only short distances in winter in order to avoid ice buildup along the coast (Hobbs et al. 2020; Suydam et al. 2001; Vacquié-Garcia et al. 2018). About one-quarter of all beluga whale populations are considered year-round residents in their respective geographic areas; these include Cook Inlet (USA), Cumberland Sound (Canada), Svalbard (Norway), the White Sea (Russia), and the St. Lawrence estuary (Canada), which is also the southernmost beluga whale population globally at 47° N latitude (Fig. 1.1) (Hobbs et al. 2008; Hobbs et al. 2020; Richard and Stewart 2009). The southernmost extralimital records of beluga whales include those as far south as New Jersey (39° N, USA) and Southern California, (32° N, USA) (Fox 2020; Reeves and Katona 1980).

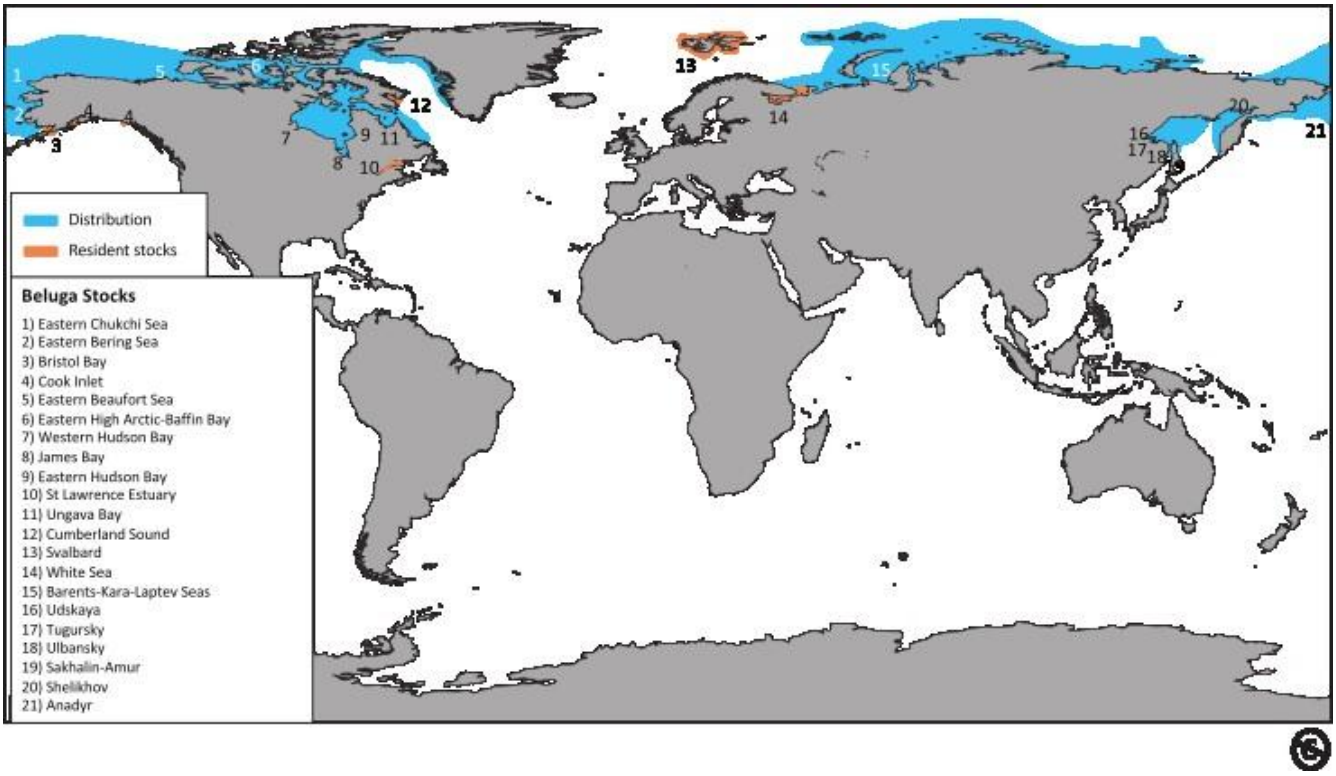


Figure 1.1: Global distribution (blue) and resident stocks (orange) of beluga whales (*Delphinapterus leucas*), delineated by stock. (Distribution is based on Hobbs et al. (2020))

1.2 Description

1.2.1 Morphology and Coloration

Beluga whales are medium-sized toothed whales. The pure white color of adults is a distinguishing feature of the species (O'Corry-Crowe 2018). They lack a dorsal fin and instead have a narrow ridge on their back (Fig. 1.2), which is thought to be an adaptation for breaking through sea ice and possibly to conserve heat (O'Corry-Crowe 2018). Beluga whales also have unfused cervical vertebrae, which give them the ability to move their head and neck laterally, and likely contribute to their ability to inhabit extremely shallow water (O'Corry-Crowe 2018). Their flippers are relatively small and square in shape (O'Corry-Crowe 2018). The beluga whale head has a distinct bulging melon and a short and broad beak, both of which can change shape and create different facial expressions (Fig. 1.2) (O'Corry-Crowe 2018).



Figure 1.2: Beluga whales (*Delphinapterus leucas*). (Photograph courtesy of Beluga Bits/Explore.org 2021)

The pure white color of beluga whales is unique among cetaceans but is not present from birth. Beluga whale calves are approximately 1.5–1.7 m in length at birth, weigh 80–100 kg, and are gray-tan but change quickly to a dark brown, blue-gray, or black color (Alekseeva et al. 2013; Heide-Jørgensen and Teilmann 1994; O'Corry-Crowe 2018; Reeves et al. 2002). They continue to turn a lighter gray during their juvenile years, and then from gray to white (Fig. 1.3), roughly around the age of their sexual maturation, which can begin at age five and eight in females and males, respectively. Most whales are completely white by age 14 in females and 18 in males, although traces of gray may still be present at 22 years of age or later, most often in females (Jefferson et al. 2011; O'Corry-Crowe 2018; Suydam 2009). Beluga whales exhibit sexual dimorphism by the age of sexual maturity, and by physical maturity males are 25% larger than females (Doidge 1990; Jefferson et al. 2011; Robeck et al. 2005). The size of adult beluga whales typically ranges from 700 to 1600 kg and 3.1–5.5 m in length but varies by population (see Table 1.1) (Doidge 1990; O'Corry-Crowe 2018; Reeves et al. 2002; Sergeant and Brodie 1969).



Figure 1.3: Mother and calf beluga whale (*Delphinapterus leucas*), demonstrating the color difference between white adult and gray juvenile whales. (Photograph courtesy of Stephen Petersen 2021)

Table 1.1: Maximum length (cm) of adult beluga whales from several populations where data has been collected

Population	**Length (cm)**		**Sources**
	Female	**Male**	
White Sea	330	400	Sergeant and Brodie (1969)
Kara and Barents Seas (excluding Laptev Sea area)	340	400	Sergeant and Brodie (1969)
Eastern Hudson Bay	340	390	Luque and Ferguson (2010)

St Lawrence Estuary	350	430	Sergeant and Brodie (1969)
Western Hudson Bay	360	410	Luque and Ferguson (2010)
Bristol Bay	360	420	Burns and Seaman (1986)
Ellesmere Island (High Arctic – Baffin Bay)	370	450	Sergeant and Brodie (1969)
Sea of Okhotsk (several eastern Russian populations)	380	420	Heide-Jørgensen and Teilmann (1994)
Eastern Beaufort Sea	380	430	Luque and Ferguson (2010)
Cumberland Sound	390	440	Luque and Ferguson (2010)
Sakhalin-Amur	390	470	Sergeant and Brodie (1969)
West Greenland (extirpated)	390	480	Heide-Jørgensen and Teilmann (1994)

1.2.2 Life History

The life history characteristics of beluga whales vary by sex and population. Male beluga whales reach sexual maturity between ages 8 and 18, the majority by 12–14 years of age, and females reach sexual maturity between ages 5 and 14, the majority by 8–11 years of age (Ferguson et al.

2020; Heide-Jørgensen and Teilmann 1994; Jefferson et al. 2011; Suydam 2009). The weight and length of beluga whales at this stage of development, and after physical maturation (Table 1.1), vary greatly among populations (Fig. 1.4). At sexual maturity, males are approximately 300 cm long and weigh 350–400 kg (Doidge 1990). Females reach sexual maturity around 270 cm length and 300–350 kg weight (Doidge 1990; Ferguson et al. 2020; Suydam 2009). Adult females typically weigh 700–1200 kg at physical maturity and are shorter in length than males (Table 1.1), while males range from 1100–1600 kg (Doidge 1990; Reeves et al. 2002; Sergeant and Brodie 1969).

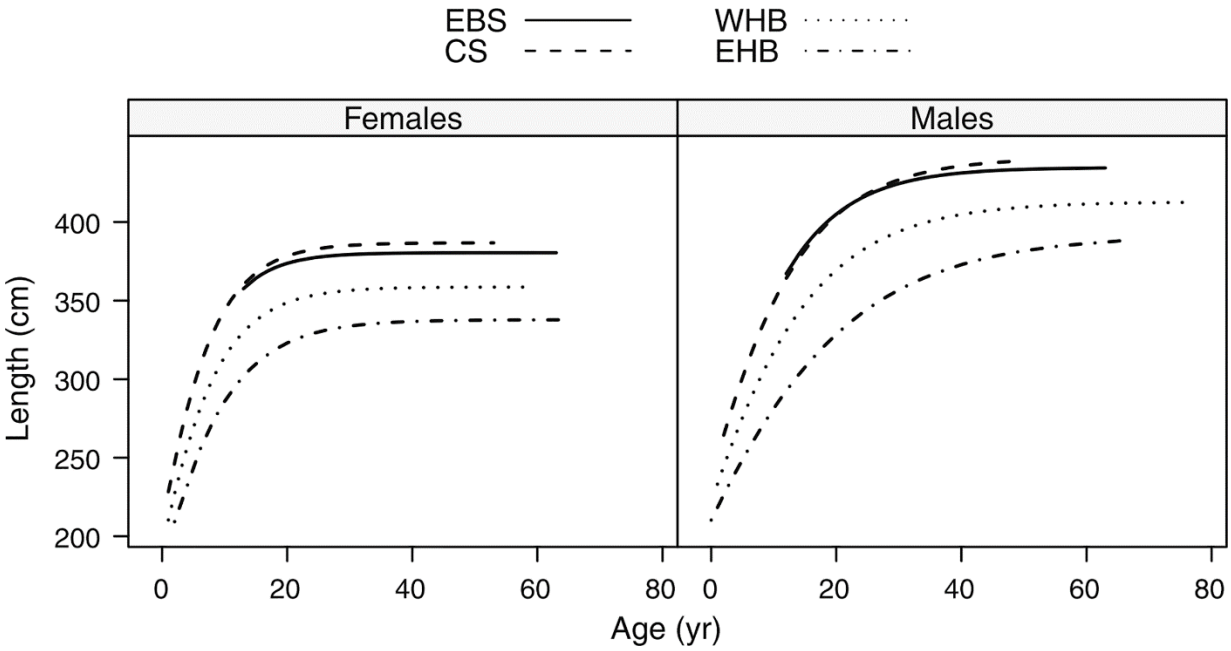


Figure 1.4: Beluga whale (*Delphinapterus leucas*) growth curves showing sexual dimorphism, growth rates of juveniles, and the difference in body lengths (cm) among populations in Canada, representing the global trend of varying body sizes in different populations. Cumberland Sound (CS) and Eastern Beaufort Sea (EBS) whales were largest, followed by Western Hudson Bay (WHB) and the smallest in Eastern Hudson Bay (EHB). (Figure reproduced with permission from Luque and Ferguson 2010)

The sex ratio of beluga whales is 1:1 based on harvested whales, including fetuses or newborn calves collected during harvests. Mating takes place from March to May, with geographical variation (Burns and Seaman 1986; Robeck et al. 2005). It is currently unknown if beluga whales have delayed implantation (O'Corry-Crowe 2018). In addition to geographic variability, there can be high temporal variation in pregnancy rates. Generally, pregnancy rates range from 0.26 to

0.41 annually (approximately 26–41% of females within a population are pregnant in any given year, including new pregnancies and whales about to give birth), while reproductive (calving) rates are between 0.04 and 0.12 (Burns and Seaman 1986; Heide-Jørgensen and Teilmann 1994; Hobbs et al. 2016; Suydam 2009). Pregnancy rates start to decline when females are approximately 25 years old, and at approximately 40 years the rate of pregnant females is halved, which may indicate menopause in the species (Burns and Seaman 1986; Ellis et al. 2018; Ferguson et al. 2020; Suydam 2009).

Gestation lasts 12–15 months, and a single calf is born between April and early September depending on the population (Burns and Seaman 1986; O'Corry-Crowe 2018; Suydam 2009). Lactation lasts for approximately two years, with individual variation ranging from 1 to 3 years (Matthews and Ferguson 2015). Milk is important during the first year and during its second year is supplemented with prey that the calf captures (O'Corry-Crowe 2018). Beluga whales at the approximate age of weaning can range in size from 200 to 350 cm and 200–450 kg depending on sex and population (Burns and Seaman 1986; Doidge 1990; Heide-Jørgensen and Teilmann 1994; Robeck et al. 2005). After weaning, whales may remain with their mothers for several more years (Krasnova et al. 2014).

Estimation of the maximum lifespan and natural mortality rate of beluga whales is difficult, in part because much of what we know comes from harvested whales that were predominantly healthy when hunted. The maximum reported lifespan (obtained from aging of teeth) for beluga whales is 77 years of age, though age may frequently be underestimated because as beluga whales age their teeth become worn down and growth layer groups are lost (Burns and Seaman 1986; Luque and Ferguson 2010; Suydam 2009). The narwhal, their closest living relative, similarly has a long lifespan of up to 115 years (±10 SE) (Garde et al. 2007). Annual mortality estimates range from 4% to 8% for males and 3–5% for females for populations in Canada, and up to 9% in Northwest Alaska, though these estimates include mortality from subsistence harvests and not every population is currently harvested (Burns and Seaman 1986; Luque and Ferguson 2010). In a population that is not harvested, the minimum mortality rate is 2% (SD = 1.2%), although this estimate is based solely on the number of carcasses found each year and therefore underestimates total mortality (Hobbs et al. 2016).

1.3 Ecology

1.3.1 Habitat Use

The reports of extralimital sightings of beluga whales in Europe do not provide detailed descriptions of habitat use given their infrequency and usual brevity of the sightings (Evans et al. 2003; van der Meij and Camphuysen 2006). The remainder of this section, and several of the following sections, will therefore describe data from beluga whale populations globally, or in the populations from which these beluga whales in Europe most likely originated (i.e., Svalbard, the Barents-Kara-Laptev Seas, and the White Sea). In general, the habitat use of beluga whales is highly dependent on the season because of their migrations between defined summering and wintering grounds. Beluga whale habitat preferences incorporate factors including tides, temperature, river discharge, water depth, and ice cover (Moore et al. 2000). It is poorly understood whether these factors influence beluga whale distribution because of their physiological needs or because they are affecting the distribution and abundance of their prey (Moore et al. 2000).

During summer, beluga whales often aggregate around sources of freshwater, in river estuaries, deltas, bays, and fjords. These areas are usually characterized by low salinities, high temperatures, and shallow depths relative to other available habitats. Beluga whales likely select these habitats for shelter from predators or weather (Goetz et al. 2012a; Lydersen et al. 2001), calving (Goetz et al. 2012a), foraging (Shulezhko et al. 2018), or molting (St. Aubin et al. 1990). Specifically, the warmer estuarine water may be chosen for calves because they have yet to build up blubber stores and would experience significant heat loss in colder waters. In terms of molting, Arctic endemic cetacean species (i.e., the bowhead whale [*Balaena mysticetus*], narwhal, and beluga whale) are unique among cetaceans in that they shed the outer layers of their epidermis each summer (Fortune et al. 2017; St. Aubin et al. 1990). The high temperature and low salinity of estuarine water promotes the shedding of dead skin and stimulates the growth of new epidermal cells (St. Aubin et al. 1990). Offshore movements and deep diving outside the typical coastal habitats have been observed during the summer, and are more frequently observed in males, with evidence of sexual segregation and segregation based on size and reproductive stage in some populations (Loseto et al. 2006; Louis et al. 2021). Males have higher energetic demands due to their larger body size, and because of their body size they are able to target

deeper areas, such as offshore areas and deep ocean basins (Loseto et al. 2006; Louis et al. 2021; Szpak et al. 2020). Males have a higher trophic level and larger ecological niche than females, targeting more diverse prey including high trophic benthic species (Louis et al. 2021; Szpak et al. 2020).

Migrations from summering grounds to wintering grounds are thought to be a response to increased ice coverage in the autumn and winter that pushes them out of their summering habitats, and usually begin between August and October. In most populations the timing of this migration is based on water temperature or the formation of ice (Hauser et al. 2017; Smith and Martin 1994). This relationship between migration timing and ice formation is evident in populations where whales delay their autumn migrations until the freeze-up date; their migrations can vary by several weeks each year as a result (Hauser et al. 2017). However, other populations seem unaffected by freeze-up dates and may instead be influenced by another factor, such as foraging opportunities, or may be inflexible to altering the timing of their migrations (Hauser et al. 2017; Smith et al. 2017). There are reports of the autumn and spring migrations occurring at the same time each year in some populations with remarkable consistency on decadal scales, despite significant changes in sea ice (O'Corry-Crowe et al. 2016; Smith et al. 2017).

During winter, ice limits beluga whale distribution, restricting their access to coastal habitats or parts of their migration routes (Goetz et al. 2012b; Shulezhko et al. 2018). Thus, beluga whale habitat selection in winter depends on sea ice conditions such as the formation of polynyas and leads in the pack ice (Fig. 1.5) (Hobbs et al. 2020; Richard and Stewart 2009). Beluga whales do not require completely ice-free habitats during winter, however, as some populations do travel for hundreds of kilometers in areas with greater than 90% ice cover (Suydam et al. 2001). There are also reports of beluga whales preferentially selecting habitats with heavy ice over winter despite ice-free habitats being available, potentially because they prefer to remain inshore even when doing so means inhabiting ice-covered areas. This strategy may be to avoid predation or for foraging opportunities (e.g., Arctic cod [*Boreogadus saida*]) (Goetz et al. 2012b; Laidre et al. 2008).

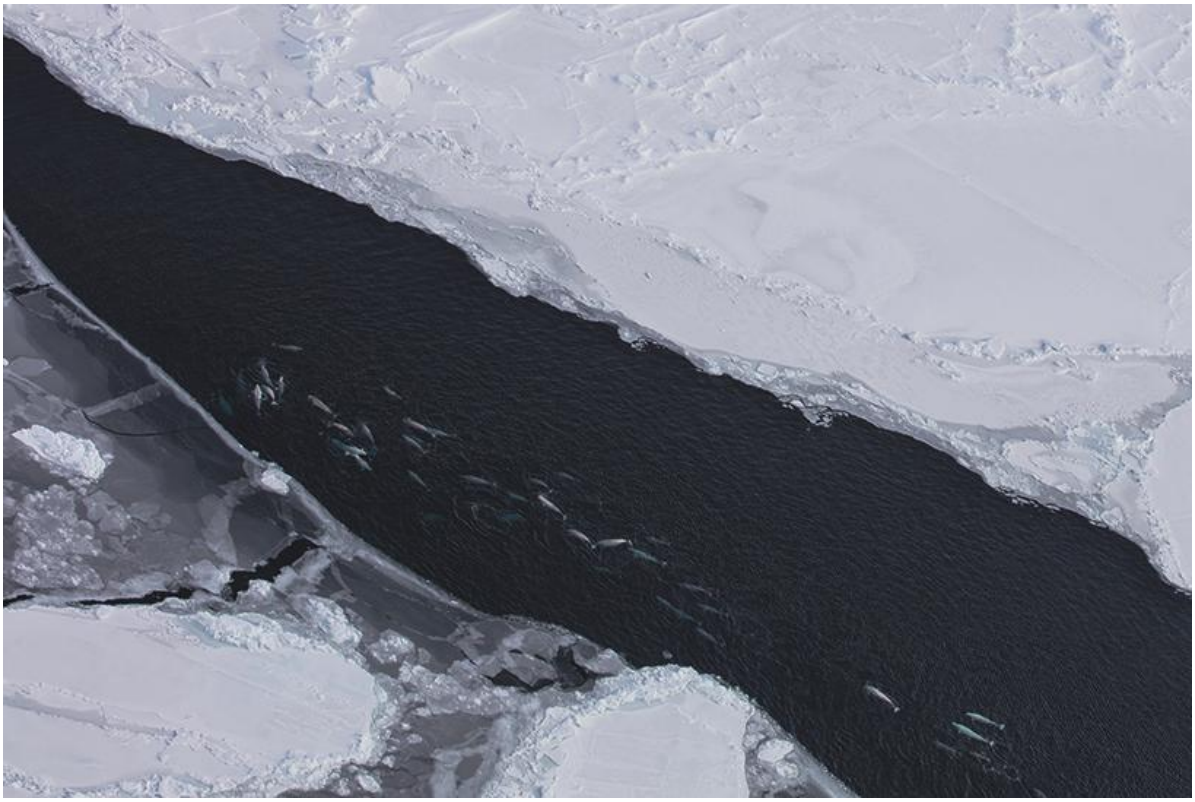


Figure 1.5: Beluga whales (*Delphinapterus leucas*) traveling through leads in ice. (Photograph courtesy of Carsten Egevang 2021)

Habitat use of the beluga whale populations bordering Europe is diverse. While relatively little is known about the Barents-Kara-Laptev Seas population, the timing of their migrations and their coastal distribution in rivers, bays, and inlets in the summer are thought to be linked to prey distribution and availability (Boltunov and Belikov 2002; Hobbs et al. 2020). In the White Sea, females and calves remain coastal and their distribution is linked to tidal movements (Alekseeva et al. 2013). Migrations of whales in the White Sea are likely correlated with ice dynamics in autumn and the migration of Atlantic salmon (*Salmo salar*) in spring (Kuznetsova et al. 2016). In Svalbard, the rivers are too shallow for beluga whales to use and they spend the majority of their time in summer near the faces of glaciers and in fjords instead (Hobbs et al. 2020;Lydersen et al. 2001; Vacquié-Garcia et al. 2018). Similar to rivers, these areas are huge sources of freshwater and have an abundance of prey species (Lydersen et al. 2001; Vacquié-Garcia et al. 2018). When sea ice forms in the winter, the whales are pushed offshore but remain in the Svalbard area,

occupying areas with drifting ice or areas with more than 90% ice cover, which provides protection against weather and predators (Hobbs et al. 2020).

1.3.2 Diet and Feeding

The diet of beluga whales is highly variable, both geographically and on short and long temporal scales (Boltunov and Belikov 2002; Quakenbush et al. 2015). The prey species listed here are primarily those consumed during spring, summer, and autumn. Identifying the winter prey of beluga whales is more difficult because whales are typically harvested in summer and autumn, and the standard methods of identifying prey species (e.g., stomach samples and stable isotope analyses from harvested whales) only represent recent trends in diet (Marcoux et al. 2012). Arctic cod are likely the main prey of beluga whales in Svalbard, while capelin (*Mallotus villosus*), copepod (*Calanus hyperboreus*), and shrimps (*Pandalus borealis*) are also important prey items (Dahl et al. 2000). Arctic cod is also the main prey of populations in Western Russia, with whitefish (Coregonidae) and Arctic cisco (*Coregonus autumnalis*) also being exploited by some populations in coastal waters during the summer (Boltunov and Belikov 2002). In the Barents Sea, in addition to Arctic cod and whitefish, Arctic char (*Salvelinus alpinus*), herring (*Clupea harengus*), and navaga (*Eleginus navaga*) are important prey species (Boltunov and Belikov 2002).

Alaskan beluga whale populations are illustrative examples of the geographic diversity and seasonal changes in beluga whale diet. Quakenbush et al. (2015) found that fish were found in only 30–34% of beluga whale stomachs in the Beaufort Sea and Eastern Chukchi Seas, while in other Alaskan populations fish were found in 95–100% of stomachs. Within a population, the diet of the whales also varies seasonally. In Cook Inlet, for example, beluga whales consumed eulachon (*Thaleichthys pacificus*) and gadids (Gadidae) during spring. In summer Pacific salmon (*Oncorhynchus* spp.) became the primary prey, and as the salmon runs declined in the fall they switched back to cod and other benthic species (Hobbs et al. 2008). In addition to seasonal changes in diet, there have been reports of long-term shifts in prey preferences in a number of populations; Arctic prey species are being replaced by Atlantic species in beluga whale diets as a result of climate change (Hobbs et al. 2020; Vacquié-Garcia et al. 2018; Watt et al. 2016). In some populations there has been a marked shift in preferred prey, while in others it is likely that the whales are using a more generalist foraging strategy, and targeting more species (Hobbs et

al. 2020; Vacquié-Garcia et al. 2018; Watt et al. 2016). In the waters around Svalbard, for example, there has been a decline in the predation of Arctic cod, and an increase in the predation of Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring as a result of significant changes in the hydrographic conditions (Hobbs et al. 2020; Vacquié-Garcia et al. 2018).

1.4 Behavior

1.4.1 Migrations and Movements

Beluga whales undertake two seasonal migrations each year, though the length of these journeys varies significantly among populations. Generally, whales spend summer in coastal grounds where they forage, calve, and undergo a seasonal molt (see Habitat Use). The whales then migrate in late summer or autumn, typically southward and ahead of the advancing sea ice, to wintering grounds at the ice front that are often located offshore (Citta et al. 2016). In some cases, interbreeding among populations may occur on shared wintering grounds or during the spring or early summer when beluga whales migrate back to traditional summer habitats, though they are considered separate populations/stocks and defined by the location of their summering grounds. Some populations travel thousands of kilometers on migration (Hobbs et al. 2020; O'Corry-Crowe 2018; Suydam et al. 2001). Other populations remain within smaller geographic ranges throughout the year, typically in subarctic regions with less extensive seasonal variation in ice cover. These include the Cook Inlet (USA), Svalbard (Norway), White Sea (Russia), St. Lawrence estuary (Canada), and Cumberland Sound (Canada) populations (Fig. 2) (Hobbs et al. 2008; Hobbs et al. 2020; Richard and Stewart 2009). Genetic and satellite telemetry studies have recently revealed that genetically distinct subpopulations of beluga whales follow traditional migratory routes that have been maintained over multiple generations, and that some routes overlap in space if not in time (Citta et al. 2016; O'Corry-Crowe et al. 2018). The whales develop migratory cultures via social learning of migration routes and destinations, which enables population genetic and evolutionary divergence over time (O'Corry-Crowe et al. 2018).

1.4.2 Swim and Dive Behavior

The amount of time beluga whales spend diving varies by region and depends on behavioral activity, season, and time of day (Heide-Jørgensen et al. 2001; Kingsley et al. 2001), and the

depth that they target is based on prey distribution (Citta et al. 2013; Hauser et al. 2015). Whales typically spend >40% of their time below the surface, though this value can be significantly lower in shallow estuarine habitats (<10%) or much higher during presumed active foraging events (>80%) (Citta et al. 2013; Heide-Jørgensen et al. 2001; Kingsley et al. 2001). During migration seasons, surface times may change because of the need to devote more time to traveling (Heide-Jørgensen et al. 2001). There can also be differences in dive behavior based on age and sex, with males likely making deeper dives than females and smaller, younger whales spending more time at the surface (Heide-Jørgensen et al. 2001; Loseto et al. 2006; Louis et al. 2021). Dives typically last 1–18 min but dives greater than 22 min have been reported (Citta et al. 2013; Kingsley et al. 2001). The greatest recorded depth of beluga whale dives was greater than 950 m in the Eastern Chukchi Sea (Hauser et al. 2015). Typical travel speeds range from approximately 1–4 km/h when whales are making short, local movements and 4–6 km/h during sustained long-distance travel (Lydersen et al. 2001; Smith and Martin 1994; Suydam et al. 2001; Vacquié-Garcia et al. 2018). High speeds of 10–20 km/h have been reported in the Canadian High Arctic over shorter durations (Richard et al. 2001).

1.4.3 Foraging

The foraging behavior of beluga whales is usually inferred from movement or acoustic data, with few direct observations of foraging (Alekseeva et al. 2013; Castellote et al. 2020). Typically foraging is identified from dive data under the assumption that whales spend time and energy targeting certain depths to benefit from the foraging opportunities found there (Citta et al. 2013; Hauser et al. 2015; Kingsley et al. 2001; Watt et al. 2016). During behavioral observations at the surface, foraging is inferred when prey is seen and beluga whales make rapid “chase” movements, or, similar to other cetacean species, from observations of fluke-up displays preceding a dive (Alekseeva et al. 2013; Shulezhko et al. 2018). Acoustic monitoring can also be used to identify foraging; as toothed whales, beluga whales use echolocation to find and target prey (see Acoustics section) (Au et al. 1985; Bel’kovitch and Sh’ekotov 1993). Castellote et al. (2020) monitored beluga whale foraging by using passive acoustic monitoring of echolocation clicks. They identified the "terminal buzz," a rapid burst of clicks produced when whales are near their prey, likely helping them pinpoint its exact location during capture (Bel’kovitch and Sh’ekotov 1993).

1.4.4 Social Behavior

Beluga whales display some of the highest levels of social structure, including cooperative foraging, extended association between mother and calf after weaning, and allomaternal care (wherein adult females other than the mother temporarily care for the calf) (Krasnova et al. 2009; Krasnova et al. 2014; Shulezhko et al. 2018). There is also evidence of long-term bonds between individuals, such as the coordination of diving and surfacing in tagged whales that had been captured together, and of whales separating and then converging at the same places over time (Kingsley et al. 2001; Smith and Martin 1994). Beluga whales are most often found in group sizes of 2–20 individuals, and usually no more than 50 animals (Bel'kovitch and Sh'ekotov 1993; Boltunov and Belikov 2002; O'Corry-Crowe et al. 2020). However, multiple groups can also aggregate into larger herds, comprised of over a thousand individuals (O'Corry-Crowe et al. 2020). When solitary individuals are seen, they are usually in close proximity to another group (Alekseeva et al. 2013; Boltunov and Belikov 2002). Though solitary individuals are rare within their normal ranges, when beluga whales are sighted in Europe they are most often traveling alone; there have been 20 sightings of beluga whales around the UK (16 sightings since 1900; Evans et al. 2003) and Belgium (4 sightings since 1970; van der Meij and Camphuysen 2006), and all 20 were solitary animals.

Although relatively understudied, beluga whale social systems were hypothesized to center around mothers and their offspring, with females remaining with their maternal pod and males dispersing to join other male pods, similar to other toothed whale social systems such as killer whales (*Orcinus orca*) (Krasnova et al. 2009; Rendell et al. 2019). The fact that beluga whales undergo early reproductive senescence (whereby pregnancy rates significantly decline by age 40 [Ellis et al. 2018; Ferguson et al. 2020]) provided support for this hypothesis; only humans, killer whales, short-finned pilot whales (*Globicephala macrorhynchus*), and narwhals are known to have a long postreproductive lifespan, and the role of the postreproductive female is thought to share ecological and social knowledge with younger related individuals, rather than compete with them (Croft et al. 2017; Ellis et al. 2018). However, a recent genetic study of beluga whale group structure and kinship revealed that social groupings were made up of both kin and nonkin (O'Corry-Crowe et al. 2020). In fact, many group members were paternally related, rather than structured around maternal relatives as had been predicted (O'Corry-Crowe et al. 2020). It

appears that beluga whale societies are quite complex, and fitness benefits from living in such societies may be achieved through mutualism, reciprocity, and kin selection (O'Corry-Crowe et al. 2020).

Play and agonistic behaviors are most often described from observation of whales in captivity, but have also been observed in wild populations (Hill et al. 2015; Krasnova et al. 2014). In the White Sea, beluga whale calves are frequently seen engaging in "tag" behavior, whereby one calf chases another and upon catching it, the calf then pursues another calf (Krasnova et al. 2014). This behavior has also been observed between mothers and calves (Krasnova et al. 2014). Juvenile and adult whales in the White Sea population also frequently play with strands of algae by pushing it on their head or body and swimming with it for up to an hour at a time (see Krasnova et al. 2014). Agonistic behaviors, including biting and open mouth threats, are thought to be related to maintaining or establishing some form of social hierarchy (Krasnova et al. 2014). In captivity, agonistic behaviors also include head jerks, charges, jaw pops, and melon thrusts (Hill et al. 2015).

Relatively little is known about social interactions between beluga whales and their closest living relative, the narwhal, despite overlapping distributions in some regions. The limited observed interactions between the two include surveys in Northern Hudson Bay where narwhal and beluga whale have been seen in close proximity to each other (Fisheries and Oceans Canada, unpublished data 2018), and a narwhal that was found to travel with a pod of beluga whale in the St. Lawrence estuary population in 2016 and for several years after (Katz 2018). The two species are also known to interbreed based on the discovery of a hybrid skull in West Greenland (Fig. 4) (Skovrind et al. 2019).

1.4.5 Reproductive Behavior

Mating likely occurs in March–June, with geographic variability (Burns and Seaman 1986; Heide-Jørgensen and Teilmann 1994; Robeck et al. 2005). In the White Sea, however, mating behavior is observed from late June to early August (Krasnova et al. 2014). Socio-sexual behavior has been observed in Cook Inlet (Alaska) in April and May during aerial surveys; the mating behavior included ventral side presentations, pelvic thrusting, and contact swimming, which are similar to behaviors observed in captivity during mating (Hill et al. 2015; Lomac-

Macnair et al. 2015). The mating system of beluga whales is unknown but their large testes size (relative to body size and compared to narwhals) indicates the need for large amounts of sperm, suggesting that their mating system is promiscuous (i.e., multimale and multifemale) (Kelley et al. 2015).

The birth of calves and nursing (for 1–3 years) after birth are rarely observed in the wild (Matthews and Ferguson 2015; McGuire et al. 2020a). In the White Sea, calving has one peak in April–May and another in July–August (Krasnova et al. 2014). Mothers remain in constant contact with newborn calves for the first few days visually, acoustically, and tactically, and usually join with other mother/calf pairs for at least a few days after the birth of their calf, likely for protection from predators (Krasnova et al. 2009). Similar to other odontocete species, calves usually remain at the mother's side or at her fluke (Krasnova et al. 2009). One-month old and two-month old calves typically associate with other calves in their age group, spending increasing amounts of time with cohorts as they age (Krasnova et al. 2009). Nursing has also been observed in this population and lasted 3–24 s (average 8.4 s); in captivity, nursing occurs approximately every 35 min (Krasnova et al. 2014; Russell et al. 1997).

1.5 Acoustics

Beluga whales are highly vocal and produce a diverse range of calls, hence their nickname the "sea canary" (O'Corry-Crowe 2018). Generally, acoustic signals can be assigned to one of five categories based on aural and visual analysis (see Garland et al. 2015 for an example of spectrogram analysis): tonal signals (whistles), pulsed calls, noisy calls, combined calls, and click series (Table 1.2) (Garland et al. 2015; Panova et al. 2012). Whistles are narrowband signals, classified by their shape (Alekseeva et al. 2013). Pulsed calls are more broadband, complex signals that consist of pulses, and measuring the pulse repetition rate (PRR) distinguishes these calls from one another (Alekseeva et al. 2013; Garland et al. 2015). Noisy calls are characterized by so much "noise" or static that determining the PRR is not possible (Sjare and Smith 1986). Combined calls have two components within the same call, such as tonal and pulsed components (Chmelnitsky and Ferguson 2012). Clicks are broadband pulses that are individually short in duration but are emitted in succession, known as a click series (Alekseeva et al. 2013; Sjare and Smith 1986). Overall, the PRR of clicks ranges from 5 to 400 pulses per second, but typically 200–400 pulses per second represent the "terminal buzz" when the whale is

capturing prey (Table 1.2) (Bel'kovitch and Sh'ekotov 1993). The peak frequency and source level of clicks can be adapted to different settings and adjusted for ambient noise (Au et al. 1985).

Table 1.2: Characteristics and function of beluga whale acoustic signals

Call type	**Frequency range**	**PRR (pulses/second)**	**Function**	**Sources**
Tonal signals	Narrowband (contoured line)	NA	Communication, social, and foraging	2, 3, 4, 7
Pulsed tones	Intermediate (1–8 kHz band)	20–1400	Social, maintain contact and group cohesion	4, 5, 8
Noise signals	Intermediate (1–4 kHz band)	NA	Poorly understood	4, 5
Combined calls	Intermediate (1–8 kHz band)	50–700	Social and vocal signature	4, 7, 8
Click series	Broadband (0.2–120 kHz band)	5–400	Foraging, navigation, and exploration	1, 2, 3, 6, 7

Pulse repetition rate (PRR) is unique to calls that have a pulsed component and is therefore not applicable (NA) to some call types. Values represent the combined range from several sources (and populations) where possible.

[1] Au et al. (1985); [2] Sjare and Smith (1986); [3] Bel'kovitch and Sh'ekotov (1993); [4] Chmelnitsky and Ferguson (2012); [5] Panova et al. (2012); [6] Castellote et al. (2013); [7] Garland et al. (2015); [8] Vergara and Mikus (2019)

The specific function of acoustic signals and how often they are used can vary depending on location (Table 1.2) (Karlsen et al. 2002; Panova et al. 2012; Sjare and Smith 1986). In general, pulsed calls have a social function; contact calls, for example, identify a group or individual, and are used to maintain contact and group cohesion between individuals or between mothers and their calves (Vergara and Mikus 2019). Some calls with a pulsed and tonal component (a type of combined call) are classified as contact calls as well, and preliminary findings suggest that these may be vocal signatures, unique to individual whales (Vergara and Mikus 2019).

Because some beluga whale populations are so vocal, they can be monitored long term using passive acoustics, and this method has been used to identify beluga whale distribution patterns in Cook Inlet and the St. Lawrence estuary (Castellote et al. 2020; Giard et al. 2020). Whales in Svalbard, however, differ from many other populations because they are uncharacteristically quiet (Castellote et al. 2013; Karlsen et al. 2002). This may be a defensive response, either long term due to potential killer whale predation or short term due to the presence of boats in the area (Karlsen et al. 2002). Castellote et al. (2013) noted that the reduced detection of echolocation click trains in Svalbard may also be related to water turbidity; in the clear waters around Svalbard the whales might use visual cues instead of relying on echolocation for navigation.

As a highly communicative species, beluga whale hearing is quite sensitive (Mooney et al. 2018). Beluga whales have a U-shaped audiogram that is also common to other odontocetes (Mooney et al. 2018). Wild beluga whales in Bristol Bay (Alaska) had sensitive hearing (<80 dB) at frequencies ranging from 16 to 100 kHz, with relatively high variation among individuals (30–70 dB) (Mooney et al. 2018). The most sensitive hearing range was 45–80 kHz, though 80–100 kHz range was also sensitive and most (76% of individuals) responded to sounds of at least 120 kHz (Mooney et al. 2018). Auditory and morphological analyses of hearing in a 21-year-old captive whale showed bilateral high-frequency hearing loss probably related to an infection; however, age-related hearing loss needs to be explored further (Morell et al. 2020). Overall,

since only one wild population has been studied thoroughly, hearing variability and hearing loss are still poorly understood in beluga whales.

1.6 Conservation

1.6.1 Human Threats

Historically, hunting caused a significant reduction in the abundance of many beluga whale populations, with commercial whaling beginning in the nineteenth and twentieth centuries in several populations (Boltunov and Belikov 2002; Mahoney and Shelden 2000). In some areas, harvesting of beluga whales had occurred traditionally for several centuries before (e.g., Russia since the fifteenth century) (Boltunov and Belikov 2002; Hobbs et al. 2020). In the Barents and Kara Seas, commercial hunting reached its peak from 1960 to 1965, when an average of 3500 whales were taken annually; the size of this population, both pre- and post-hunting, is unknown, but is likely depleted from these large removals (Boltunov and Belikov 2002; Hobbs et al. 2020). Overharvesting has had a lasting effect on other populations, including extirpations of populations off Southwest Greenland and in Ungava Bay (Canada), from high rates of both commercial and subsistence hunting (Hobbs et al. 2020).

Other populations have been depleted but are now protected, including the St. Lawrence estuary, which was impacted by sport and commercial hunting, as well as a cull that was initiated to protect fish stocks (Hobbs et al. 2020; Kingsley 2002). The Cook Inlet population was similarly affected by commercial and sport hunting, followed by a relatively high rate of subsistence hunting in the 1990s (Mahoney and Shelden 2000). However, even with the prohibition of hunting decades ago, neither of these populations has shown signs of recovery (Hobbs et al. 2020; Shelden and Wade 2019). Most beluga whale populations are now harvested sustainably by Inuit and aboriginal communities or not at all, with the exceptions of Cumberland Sound where harvests are significantly above suggested sustainable levels, and possibly the Eastern Bering Sea and Eastern Hudson Bay populations where more information is needed to evaluate the sustainability of harvests (DFO 2019; Hobbs et al. 2020; Lowry et al. 2019). The frequency of unauthorized hunting is unknown but may be a concern in some populations, especially those that are currently endangered (Hobbs et al. 2020; Shelden and Wade 2019).

Captures and mortalities of beluga whales also occur in relation to live displays by aquaria. Russia has been the primary source of beluga whale exports to other countries such as the USA, Japan, and Canada since the 1990s (Fisher and Reeves 2005). Live captures may be affecting the Sakhalin-Amur population, where over 80 whales were captured in one year for educational/cultural display and research, and at least 40 additional whales died during and after capture (Hobbs et al. 2020; Reeves et al. 2011; Shpak and Glazov 2014). Further concern comes from the specific targeting of 2- to 3-year-old female whales (Shpak et al. 2019), likely because they are weaned, small in size, and close to reproductive maturity. This practice could skew the sex ratio of the population and affect the sustainability of such removals (Hobbs et al. 2020; Reeves et al. 2011; Shpak et al. 2019) because the population is relatively small at fewer than 4000 whales (Shpak and Glazov 2013). In recent years, pens holding close to 100 beluga whales and killer whales that had been caught for the aquarium trade garnered worldwide attention; these beluga whales were illegally captured in the Sakhalin-Amur area (Hobbs et al. 2020; Nechepurenko 2019; Shpak et al. 2019; Shpak and Glazov 2014). Beluga whales have recently been caught in the White Sea as well for cultural display and research, but the numbers are believed to be small compared to Sakhalin-Amur (e.g., 5–6 whales per capture) (Hobbs et al. 2020).

The Arctic is warming four times as fast as the global average, causing a massive loss of sea ice and changes in entire ecosystems (Laidre et al. 2008; Rantanen et al. 2022). Some concerns for beluga whale populations include potential competition from southern marine mammal species as their distribution extends northwards, changes in prey and predator distribution and abundance, changes in sea ice conditions, and introductions of novel parasites and diseases (Hobbs et al. 2020; Laidre et al. 2008). There is evidence of beluga whales preferentially selecting habitats with a high density of ice, and although it is not fully understood why they choose these areas, loss of sea ice may have a detrimental impact on beluga whales (Goetz et al. 2012a). Decreases in sea ice are also facilitating increasing vessel traffic in formerly inaccessible areas of the Arctic, which may disturb beluga whales, especially if they overlap with critical habitats like calving and foraging areas (Hobbs et al. 2020; Norman et al. 2016). There is also already evidence of a shift in preferred prey in recent decades as southern prey species such as capelin moves north and displaces prey such as Arctic cod in beluga whale diets, which may have negative effects on body condition (Marcoux et al. 2012; Watt et al. 2016).

Ecotourism is not a concern for most beluga whale populations given their Arctic and subarctic distribution, but does occur in areas such as Churchill (Western Hudson Bay), the St. Lawrence estuary, and the White Sea. In general, when beluga whales are disturbed, they show avoidance behavior such as increasing speed, shorter and less frequent surfacing, changing behavior (i.e., stop feeding), or leaving the area (Krasnova et al. 2012). As tourism develops in the White Sea, Krasnova et al. (2012) reported that beluga whales show strong avoidance to human activity, sometimes resulting in 70–80% of whales leaving the area after a disturbance. Anthropogenic disturbance in the St. Lawrence estuary is also of concern because of the overlap of commercial tourism and beluga whale critical habitats (i.e., calving areas), which may have contributed to a high level of calf mortalities in the population (Ménard et al. 2014). Tourism (and boat traffic in general) elicits an entirely different response from whales in Churchill, where they frequently show no reaction or actively approach and interact with boats (Malcolm and Penner 2011); this difference may be the result of several factors, such as less shipping traffic than other populations, no live capture and very rare hunting incidents in the past few decades, and a larger population size than any other beluga whale population (Hobbs et al. 2020; Malcolm and Penner 2011).

Beluga whales accumulate a wide range of contaminants likely due to a lower contaminant metabolism than other marine mammals (Wolkers et al. 2006). A high rate of cancer in the St. Lawrence estuary beluga whale population is thought to be related to contaminants such as polycyclic aromatic hydrocarbons (PAHs) (Martineau et al. 2002). High levels of persistent organic pollutants (POPs) have been found in the Russian Arctic at river mouths, bays, and other coastal areas frequented by beluga whales (Boltunov and Belikov 2002). POPs are likely a threat to beluga whales in the Russian Arctic because they have a high degree of lipid solubility and because, as a predator, beluga whales experience biomagnification, or the buildup of toxins at increasing trophic levels (Boltunov and Belikov 2002; Loseto et al. 2015). Because beluga whales experience biomagnification, they also have relatively high mercury contamination (Loseto et al. 2015). It is not fully understood what impacts high mercury burdens have on beluga whale health, but it is known that it can reduce their resistance to disease (Frouin et al. 2012).

Noise is of concern for many beluga whale populations, as whales exhibit strong avoidance to high shipping traffic and may be displaced from critical habitats such as foraging and calving grounds (Hobbs et al. 2020). Of particular concern are the anthropogenic noise levels in the Barents and Kara Seas, Cook Inlet, and the St. Lawrence estuary (Castellote et al. 2018; Hobbs et al. 2020). Noise comes from shipping activity, military activity, land use and development, and oil and gas exploration, among others (Hobbs et al. 2020). Specifically, these noises may mask beluga whale communication and hearing, especially since noise is exceeding behavioral harassment levels every day in areas such as the Cook Inlet beluga whale critical habitat (Castellote et al. 2018; Castellote et al. 2020). The Barents, Kara, and Laptev Seas have heavy shipping that could have considerable impacts since the population is likely already depleted from historic commercial hunting; however, the extent to which these shipping corridors overlap with beluga whale ranges is largely unknown (Hobbs et al. 2020).

Entanglement in fishing gear, incidental takes in fisheries, conflict with fishermen, and ship strikes have been reported in several populations as a cause or probable cause of injury or mortality (Lair et al. 2016; McGuire et al. 2020b; Moore et al. 2000). However, there is a low occurrence of beluga whale entanglement in populations that have a high overlap with fisheries, which may be a result of their high maneuverability compared to other cetaceans, allowing them to avoid or escape entanglement (Reeves et al. 2011). Competition with fisheries may also have an impact and is of concern in many populations, but the effect of competition is hard to quantify (Hobbs et al. 2020; Moore et al. 2000).

1.6.2 Natural Impacts

Strandings of beluga whales and ice entrapments can cause mass mortalities. Strandings usually occur in areas with extreme tides or because groups are driven toward the shore while fleeing predators. Tens to hundreds of individuals can strand at a time, but not all strandings result in mortality (McGuire et al. 2020b; Moore et al. 2000; Norman et al. 2016). Beluga whales also periodically become trapped in ice when weather conditions change suddenly and ice shifts (Siegstad and Heide-Jørgensen 1994). These are referred to as ice entrapments, known as sassats by the Inuit, and are natural occurrences that can cause hundreds to thousands of whales to perish in a single incident, which could significantly impact populations (Richard and Stewart 2009; Shpak et al. 2019). An increase in unpredictable and extreme weather events with a changing

climate may result in more ice entrapments of beluga whales (Norman et al. 2016). Natural disasters could also impact habitat or prey, but the effects of those have not been quantified for beluga whales (Moore et al. 2000).

Long-term monitoring of beluga whale carcasses in more accessible populations has provided new insights into beluga whale mortality. According to data gathered under the St. Lawrence estuary beluga whale carcass monitoring program, infectious diseases caused by parasites (20.0%) or bacteria (17.7%) were the most frequent causes of death (see above) (Lair et al. 2016). Nine beluga whale mortalities were recorded in 1 month in the St Lawrence estuary during an algal bloom, and though only one whale was examined, it was determined to have died by saxitoxin intoxication (Lair et al. 2016). Although beluga whale mortalities during algal blooms have not been reported elsewhere, these events may occur more frequently in this and other populations as ecosystems shift in a changing climate (Lair et al. 2016).

Competition for food resources (both intraspecific and interspecific) and rates of predation are difficult to quantify. In West Greenland, where beluga whale and narwhal overlap in distribution, there is evidence of resource partitioning, with beluga whales feeding at higher trophic levels than narwhal (Louis et al. 2021). In terms of predation, killer whales and polar bears are the only natural predators of beluga whales, but they do not occur in every population. Because polar bears often feed on beluga whales when they surface at the ice edge or at holes, the extent to which they feed on beluga whales is linked to sea ice extent, which can vary significantly from year to year (Mckinney et al. 2017). In the Canadian High Arctic, polar bear diets vary by individual with beluga whales making up the majority of some individual diets, and approximately 15–20% of polar bear diets overall (Galicia et al. 2015). It is unknown to what extent killer whales currently prey on beluga whales, but there have been reported incidents in several populations, and killer whales can also cause mortality by eliciting stranding events (Moore et al. 2000; Norman et al. 2016). With the range of killer whales expanding north as sea ice decreases, their impacts on some beluga whale populations could be significant.

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Chapter 2 – Stable decadal migration timing and temporal variation in dive behavior of an endangered whale population

2.1 Abstract

Understanding migration timing and movement behavior is critical for predicting how populations may respond to environmental threats or changes. The beluga whale (*Delphinapterus leucas*) population in Cumberland Sound, Nunavut, is currently assessed as endangered due to historical and ongoing overharvesting. By comparing satellite telemetry data from two distinct time periods (1998–1999 and 2006–2008), we evaluated the timing of the beluga whales' annual autumn migration in relation to ice cover, foraging habits, potential sex-based behavioral differences, and move persistence. We examined the proportion of dives below 100m to detect possible changes in prey from Arctic cod to capelin, as indicated by shallower dives to match capelin's distribution. Additionally, we fitted a move persistence model to the telemetry data. We employed generalized linear mixed models to both the dive and move persistence data to analyze influences of age, sex, ice cover, bottom depth, time period, month, and their interactions on the whales' movement patterns. We used both move persistence and a latitudinal threshold to determine migration timing, and found that migration precedes any buildup of ice in the whales' summer and autumn habitats by more than six weeks. We found significant seasonal and temporal variation in diving behavior, with more shallow dives in summer than in autumn and winter. Additionally, there was a notable shift to more shallow dives in the second time period compared to the first, suggesting a change in foraging from Arctic cod to capelin. This shift likely occurred due to changes in prey distribution driven by climate change and warmer ocean temperatures, which may have negative long-term impacts on the population. Some of the trends identified in this study differ from those observed in other beluga whale populations, emphasizing the need for distinct management strategies to ensure the long-term survival of the Cumberland Sound beluga whale population.

2.2 Introduction

Migration is a fundamental biological process that affects the distribution and abundance of species and can have significant implications for their survival and reproductive success (Aidley, 1981; Seebacher & Post, 2015; Shaw, 2016). Understanding the migration timing and movement

behavior of species can help to predict changes in population dynamics and ecosystem interactions, and understanding migration is particularly important in the context of climate change, as climate often mediates migratory behavior (Aidley, 1981; Anderson et al., 2013; Horton et al., 2020; Kuletz et al. 2024; Seebacher & Post, 2015; Shaw, 2016). Thus, knowledge of migratory behavior is vital for the development of effective conservation strategies and for ensuring the long-term sustainability of biodiversity (Seebacher & Post, 2015; Shaw, 2016). For instance, by analyzing the migratory patterns of birds, conservationists can protect key stopover sites that are crucial for refueling during long journeys (Gavin et al., 2018). Additionally, identifying critical habitats and migration corridors for mammals can help mitigate the impacts of habitat fragmentation (Mönkkönen et al., 2011). For endangered species, collecting this information becomes even more important because accurate data on migration and movement patterns can aid in identifying critical habitats, migration corridors, and potential threats, thereby informing targeted conservation efforts (Goetz, Montgomery, Hoef, et al., 2012; Runge et al., 2014; Seebacher & Post, 2015; Shaw, 2016).

In the rapidly warming Arctic, where species already face extreme conditions and rapid environmental changes, the opportunity to study migration and movement behaviors offers unique insight into how these species respond to their environment (Laidre et al., 2008; Rantanen et al., 2022; Wassmann et al., 2011). As species' ranges expand into Arctic ecosystems and native species experience and respond to novel challenges, including competition by southern species and the introduction of new predators and prey, the overall dynamics of traditional Arctic food webs are changing (Campana et al., 2020; Yurkowski et al., 2018). These shifts in Arctic ecosystems can have cascading effects on other species, triggering complex interactions and potentially leading to unexpected consequences for both native and invasive species alike (Laidre et al., 2008). For example, seasonal behaviors, movements, and migration routes are being altered in response to changes in ice cover and ocean temperature or to match shifts in food availability as warmer temperatures concurrently affect the timing and distribution of prey species (Hamilton et al., 2015; Hauser et al., 2017; Laidre et al., 2008).

Beluga whales (*Delphinapterus leucas*) are one of few Arctic resident marine mammals, and therefore are subject to climate-mediated ecosystem alterations (Hauser et al., 2017; Marcoux et al., 2012; Watt et al., 2016). There has been evidence of beluga whales preferentially selecting

areas with high ice density, whether to avoid predators such as killer whales (*Orcinus orca*) or to find ice-associated prey such as Arctic cod (*Boreogadus saida*) (Goetz, Robinson, et al., 2012; Loseto et al., 2009; Suydam et al., 2001). Arctic cod and several other prey species of beluga whales are susceptible to population declines associated with a reduction in sea ice and an increase in temperature, indicating that the loss of sea ice may have detrimental effects on beluga whale foraging and survival (Carscadden et al., 2001; Choy et al., 2020; Hop & Gjøsæter, 2013; Huse & Ellingsen, 2008; Huserbråten et al., 2019). As the Arctic warms, suitable habitat for beluga whales, calculated based on depth, sea surface temperature, and ice cover, is declining and projected to decline rapidly by the year 2100, with a predicted concurrent decline in population size (Jahn et al., 2024; Skovrind et al., 2021). However, beluga whales, with their relatively generalist diet and flexible distribution in some populations, may exhibit a degree of flexibility compared to other cetaceans in response to climate change (Heide-Jørgensen et al. 2010; Laidre et el. 2008).

The distribution of beluga whales in summer tends to be concentrated near sources of freshwater, often characterized by lower salinity, higher temperatures, and relatively shallow water (Ezer et al., 2012; Litovka, 2002; Scharffenberg et al., 2019; Shulezhko et al., 2018; Smith et al., 2017; Westdal et al., 2022). Beluga whales may preferentially use these areas for different reasons depending on the population and the ecology of the whales; the warmer water is good for newborn calves that do not yet have blubber stores (Goetz, Montgomery, Ver Hoef, et al., 2012), the warm and freshwater may promote shedding and new growth of skin while the whales molt over the summer (St. Aubin et al., 1990), the shallow water offers protection from predators and weather events (Goetz, Montgomery, Ver Hoef, et al., 2012; Lydersen et al., 2001), and there may be prey associated with fresh or brackish water (Shulezhko et al., 2018). Beluga whales may also select habitat based on age or size, with larger males being able to, or needing to, exploit different resources due to their larger body size and higher energetic demands than females or younger whales who tend to spend more time at the surface and in shallower water (Heide-Jørgensen et al., 2001; Loseto et al., 2006; Louis et al., 2021).

Beluga whales undergo biannual migrations between summer and winter habitats. In some populations these migrations occur over thousands of miles (Hobbs et al., 2020; O'Corry-Crowe, 2018; Storrie et al. 2023; Suydam et al., 2001), while in other populations, migrations are

relatively short (Richard & Stewart, 2009; Rugh et al., 2010; Simard et al., 2023). The migration routes are learned from the mother, so it is likely whales follow the same route for their entire lives (Brodie, 1969; Citta et al., 2016; Hauser et al., 2017; O'Corry-Crowe et al., 2018). Beluga whales maintain associations with a network of relatives during migration, indicating that relatives beyond mother-calf pairs play a significant role in maintaining social structure and culture in migratory behavior (Colbeck et al., 2013). The migration timing of beluga whales varies by population, where some populations are flexible and respond to environmental changes and others migrate at or around the same time each year regardless of ice conditions and other environmental factors (Bailleul et al., 2012; Hauser et al., 2014; Hauser et al., 2017; O'Corry-Crowe et al., 2018; Smith & Martin, 1994). The late summer/autumn migration is typically ahead of advancing sea ice and towards offshore, ice front, or lower concentration ice areas (Citta et al., 2016).

For populations using the formation and breakup of ice as a cue for migration timing, long-term changes in ice formation and breakup may result in altered migration timing or routes (Cherry et al. 2013; Moline et al. 2008; O'Corry-Crowe et al. 2016). If beluga whales rely on cues associated with changes in weather, such as ice formation or breakup, they may be able to adapt to long-term climatic changes. The effect of these climatic changes on beluga whale populations is largely unclear but could be detrimental, especially in populations where winter foraging is crucial, as the time spent in winter habitats could be reduced by earlier spring and later autumn migrations (Watt et al., 2016). Conversely, for populations where summer foraging is essential, these changes might be beneficial, provided their prey species remain abundant throughout the extended summer season. If the timing of their migration is not weather-based, belugas could become out-of-sync with ecosystem processes that are responding to weather patterns, such as the availability of food sources.

Diving patterns play a crucial role in inferring beluga whale foraging behavior, as variations in dive duration and depth are used as indicators of their search for prey because foraging opportunities are likely providing benefits that outweigh the time and energy costs of diving (Citta et al., 2013; Hauser et al., 2015; Kingsley et al., 2001; Watt et al., 2016). Dive behavior can also vary depending on the population, largely due to the depths of different prey species and bathymetry that is available (Citta et al., 2020; Goetz, Robinson, et al., 2012; Heide-Jørgensen et

al., 1998, 2001; Lemieux Lefebvre et al., 2018; Martin et al., 2001; Storrie et al., 2022). The maximum recorded depths of beluga whale dives are approximately 1,400m (Storrie et al. 2022). Dive behavior in beluga whales can vary depending on behavioral activity, season, and time of day. Typically, beluga whales spend more than 40% of their time below the water's surface, although whales can spend less than 10% of their time diving in shallow estuarine habitats to over 80% during active foraging events (Citta et al., 2013; Heide-Jørgensen et al., 2001; Kingsley et al., 2001). Understanding dive patterns can provide insight into the foraging ecology and habitat use of beluga whale populations and their broader implications for ecosystem dynamics and conservation strategies.

The beluga whale population in Cumberland Sound, Nunavut, is currently assessed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC, 2004), a designation resulting in part from extensive commercial whaling activities dating back to the mid-19th century (Stewart, 2018). To prevent further population decline, a quota of 41 whales landed per year has been in place for the local Inuit hamlet of Pangnirtung since 2002 (COSEWIC, 2004;). However, despite these conservation efforts, the most recent aerial survey in 2017 estimated only 1,381 whales in the population (95% CI = 760–1,744), indicating that the population has not yet recovered to its pre-whaling estimated size of 8,500 whales (COSEWIC, 2004; DFO, 2019). While the most significant historical population decline has already occurred, population models suggest that the Cumberland Sound beluga whale population may continue to decline under the current quota (Watt et al., 2020). The Cumberland Sound population is one of the few beluga whale populations to undergo short migrations and is relatively isolated from other populations, so continued population declines could result in local extirpation of this species (DFO, 2022; Richard & Stewart, 2009).

Environmental changes in Cumberland Sound may be impacting the habitat of beluga whales and their prey, which may impact the whales' ability to forage. Stable isotope analyses have indicated that the targeted prey of the Cumberland Sound beluga whale has changed over time as a result of climate change in the Arctic; Atlantic species such as capelin (*Mallotus villosus*) have been replacing traditional prey species such as Arctic cod (Hobbs et al., 2020; Marcoux et al., 2012; Vacquié-Garcia et al., 2018; Watt et al., 2016). During fall and winter, Arctic cod are typically found lower in the water column than capelin, so changes in dive behavior to shallower

depths may indicate a change in foraging strategies over time (Benoit et al., 2014; Falk-Petersen et al., 1986; Forster et al., 2020; Geoffroy et al., 2011; Jansen et al., 2021; McGowan et al., 2019). Dive behavior can be used to infer the targeting of prey and to detect a possible shift in foraging from Arctic cod to capelin. Arctic cod are a deeper-dwelling species than capelin, with adults typically found below 200m while capelin are more shallowly distributed (<100m) (Benoit et al., 2014; Bohn & McElroy, 1976; Brown, 2002; Falk-Petersen et al., 1986; Forster et al., 2020; Geoffroy et al., 2011; Jansen et al., 2021; McGowan et al., 2019; Thors, 1981). Thus, a trend toward shallower dive behavior would indicate a shift from Artic cod to capelin. Shifts in prey consumption has implications for the health (e.g., abundance) of Cumberland Sound beluga whales, as capelin may be lower in dietary quality and more unpredictable in its distribution and abundance than other species (Choy et al., 2019, 2020; Leu et al., 2011; Marcoux et al., 2012; Thiemann et al., 2008). These factors highlight the complex interplay between changing prey dynamics, foraging behavior, and the overall health and survival of Cumberland Sound beluga whales in a rapidly evolving Arctic environment.

In this study, we addressed several key objectives to better understand the behavior and dynamics of the Cumberland Sound beluga whale population. A primary focus was to gain insight into the annual migration patterns of these beluga whales (i). Our objective was to estimate the timing of the autumn migration each year and to investigate whether the migration timing has changed over time. We tested the hypothesis that the timing of the whales' migration was dependent on the formation of ice, and whether any delayed formation of ice in the autumn would trigger a delayed start to their migration. Secondly, we analyzed their foraging behavior using dive data and compared dive depths with known prey species specific to this population (ii). This analysis allowed us to examine whether there were specific times of the year when foraging activity was more prevalent. To detect any potential shifts in dive behavior and prey use, we compared dive data from the only two distinct periods when beluga whales from this population have been satellite tagged, 1998–1999 and 2006–2008. We hypothesized that the whales responded to changes in prey availability and because the geographic range of capelin expanded north to Cumberland Sound between our study periods, in the second time period, Cumberland Sound beluga whales would target depths associated with capelin more than those associated with Arctic cod, resulting in shallower dives in 2006–2008. Furthermore, we aimed to identify potential sex-based differences in beluga whale behavior, such as males diving deeper

than females, that could indicate resource partitioning (iii). By examining these differences in behavior, we aimed to gain insight into how males and females may respond differently to the prey and bathymetric features available to them in their environment. Additionally, we sought to explore the general distribution and habitat use of Cumberland Sound by the beluga whale population through move persistence analyses (i.e., estimating highly directional travel versus area-restricted searches by their movement patterns) (iv) to provide an overview of their habitat preferences and use throughout the year, identify factors impacting their move persistence, and explore an alternative approach to estimate migration timing, as high move persistence indicates the directional travel typical of migration.

2.3 Methods

Study Area and Population

The study was conducted in Cumberland Sound, located on Baffin Island, Nunavut (Figure 2.1). This sound encompasses an area approximately 100 miles long and 50 miles wide. The Cumberland Sound beluga whale population migrates biannually between a summer habitat in the northernmost extents of the sound and a winter habitat near the southeastern most extent of the sound (Richard & Stewart, 2009).

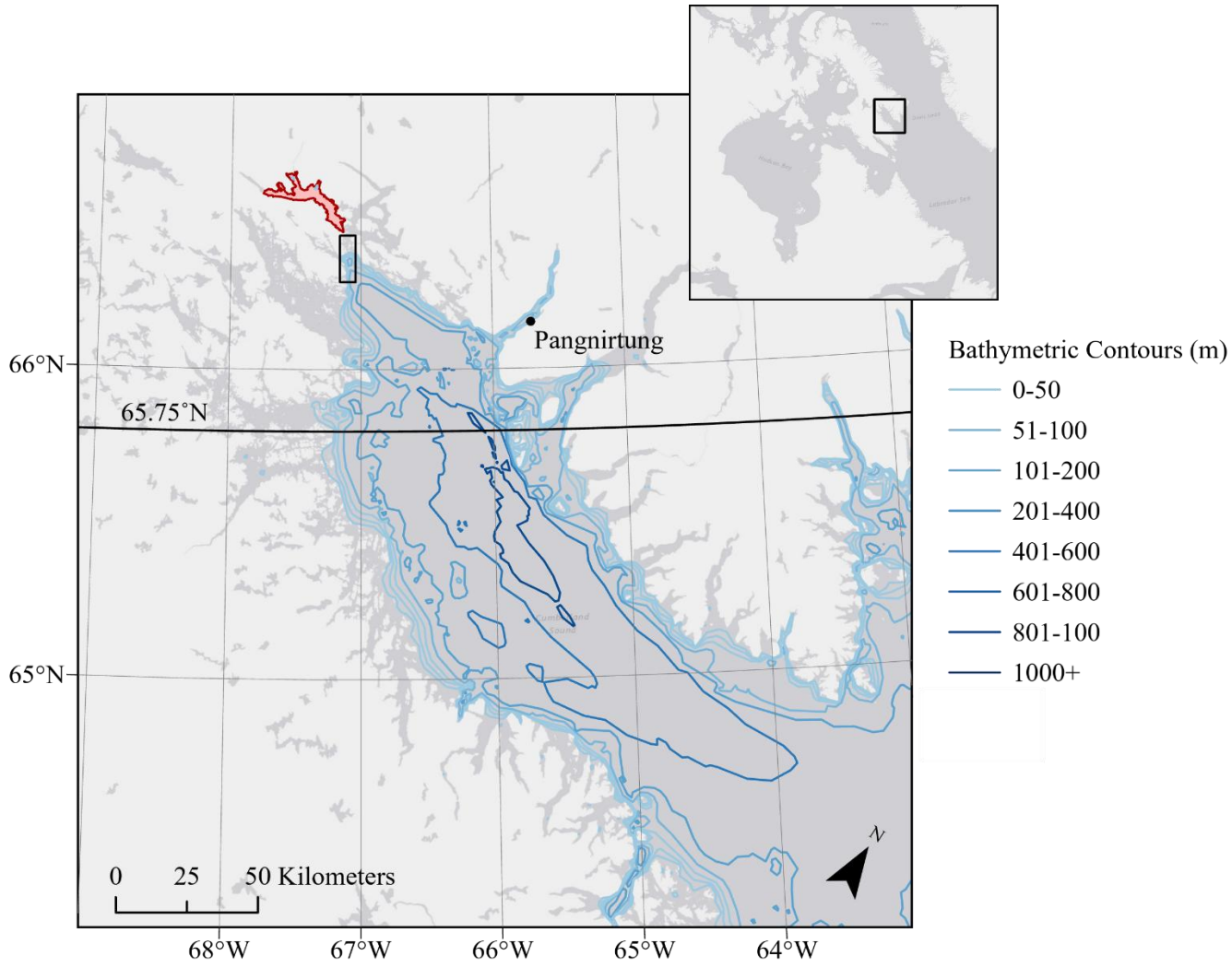


Figure 2.1: The study area with bathymetric contours (m) in Cumberland Sound, Nunavut, Canada. The Pangnirtung community is denoted with a black dot. Clearwater Fjord, the primary summer range of the beluga whales is shaded in red, and the approximate tagging areas of the whales are outlined in black. The latitudinal threshold we used to define migration at 65.75˚N is denoted with a black line.

Satellite Tagging and Data Collection

Satellite-linked time-depth recorder tags, specifically SPLASH tags from Wildlife Computers, were used to monitor adult beluga whales. These tags provided daily transmissions of location and dive data. Tags were deployed on 20 beluga whales, 10 female and 10 male (Table 2.1), between July and September across five field seasons in 1998–1999 (n=13) and 2006–2008 (n=7). Sex was determined genetically from biopsy samples (Watt et al. 2023). The approximate

ages of the whales were estimated based on their length and sex, using population- and sex-specific growth rates in Luque and Ferguson (2010). For full-grown adult whales, age estimates are noted as '25+' for females and '35+' for males, reflecting the approximate age at which growth curves level off according to the referenced growth models, beyond which more specific aging cannot be accurately determined (Luque & Ferguson, 2010). The capture and tagging methods employed followed established protocols as described by Orr et al. (2001). Briefly, beluga whales were captured using nets positioned perpendicular to the shore along their migratory path. Once entangled, whales were restrained between two zodiac boats using a combination of hoop nets, straps, and a tailstock rope. The tags were affixed to the dorsal ridge of the whales using three 10 mm nylon pins secured with high-grade stainless-steel wires. This setup minimized the potential for tag loss and ensured reliable data transmission. Tagging may cause stress, behavioral changes, discomfort, inflammation, infection, or localized tissue damage at the attachment site, with potential long-term effects on energy expenditure; in some cases, these impacts may contribute to or result in mortality events (Aubin et al. 2001; Burek-Huntington et al. 2023; McGuire et al. 2021; Ryan et al. 2022).

Table 2.1: Summary of satellite-linked time-depth recorder tag deployments on beluga whales in Cumberland Sound, Nunavut. The notation 'F*' indicates a female whale accompanied by a calf at the time of tagging. Tag longevities with ** denote tags that resulted in insufficient data to be included in analyses.

Year	Tag	Transmission start date	Transmission end date	Tag longevity	Sex	Length (cm)	Approximate age (yrs)
1998	7925	28 Aug 98	14 Oct 98	47	F	302.6	5.5
1998	17000	19 Aug 98	31 Aug 98	12**	M	384.6	14.5
1998	17001	20 Aug 98	27 Oct 98	68	M	302.6	5
1998	20682	25 Aug 98	8 Nov 98	75	M	394.9	16
1998	20683	30 Aug 98	4 Sep 98	5**	M	312.8	5.5
1998	20684	30 Aug 98	25 Oct 98	56	F	394.9	25+
1998	20685	30 Aug 98	3 Nov 98	65	F	335.9	8.5
1999	20162	3 Sep 99	16 Jan 00	135	M	461.5	35+
1999	20682	3 Sep 99	23 Nov 99	81	F*	359.0	12
1999	20683	8 Sep 99	10 Sep 99	2**	F	423.1	25+
1999	20684	3 Sep 99	7 Dec 99	95	M	341.0	8.5
1999	20685	5 Sep 99	11 Dec 99	97	M	430.8	30
1999	7926	8 Sep 99	18 Nov 99	71	M	415.4	22
2006	57594	17 Jul 06	3 Mar 07	229	F	NA	NA
2007	37023	12 Jul 07	3 Nov 07	114	F	315	6.5
2007	57602	12 Jul 07	15 Nov 07	126	F	350	11
2008	39296	5 Sep 08	14 May 09	251	F	290	4.5
2008	39308	6 Sep 08	3 Jun 09	270	F	340	9.5
2008	39323	9 Sep 08	28 Apr 09	231	M	370	13
2008	40623	9 Sep 08	16 Sep 08	7**	M	340	9

The tag location data was collected and categorized with the Argos system. Data included four 6-hour histograms of diving activity, with location accuracy categorized based on transmission accuracy: Location quality classes A and B provided no location accuracy information; Class 0 represented an error of >1500 m; Class 1, 500−1500 m; Class 2, 250−500 m; and Class 3, <250 m (CLS America). We omitted Class Z, which provides an invalid location and no error estimate. Every transmission contained location data, but not all transmissions included dive data. Depths were recorded with a resolution of 0.5 m. Tags were programmed with fewer dive depth categories in 1998–1999, so some depth bins were combined for 2006–2008 (e.g. 20-25m, 25-50m, and 50-100m were pooled to represent 20-100m) to ensure consistency across the datasets.

The bins used were 20-100m and 100m or greater. The number of dives to each of these bins is recorded in a single transmission that represents the last 6 or more hours, depending on when the tag can transmit. The year that the whales were tagged is referred to as 'sampling year' throughout this study, since some tags continued to collect data into the next calendar year. Tags that transmitted for less than two weeks (see Table 2.1) and transmissions with missing data were filtered out. The dataset was also filtered to include only the months from September to December due to limited data outside of these months.

Move Persistence and Migration

We used the fit_ssm function in the aniMotum package v1.1-04 in R v 4.2.2 to fit a move persistence model to each track, and to predict locations at 24hr intervals (Jonsen et al., 2020; R Core Team, 2022). We fitted the model with a speed filter threshold of 7.5m/s (27 km/h) based on the maximum speed of whales recorded in other studies (Lydersen et al., 2001; Richard et al., 2001; Smith & Martin, 1994; Suydam et al., 2001; Vacquié-Garcia et al., 2018) to identify and exclude outlier locations exceeding realistic movement speeds for beluga whales. Land shapefiles from the rnaturalearth package v0.3.2 in R were used to exclude points on land (Massicotte P & South A, 2023; R Core Team, 2022). After the removal of these data, there were 8,622 location data points. We selected the move persistence model to analyze movement patterns by estimating a time-varying move persistence parameter (γ_t) along the track. This parameter provides an index of how the autocorrelation in successive movements varies in space and time, with higher values indicating more persistent, directional movement and lower values indicating less persistent, more variable movement behavior. To investigate the factors influencing move persistence, we fitted multiple generalized linear mixed models (GLMMs) using the glmmTMB package v1.1.9 in R, specifying the beta family for the response variable move persistence proportion data (bounded between 0 and 1) with a Logit link function and without an overall intercept. The candidate models included various combinations of ice cover (continuous on a scale from 0-10), bottom depth (continuous), sex, time period (1998–1999 or 2006–2008), month, and age class, along with interaction terms. Sixteen different models were specified, each incorporating different sets of predictors and interactions. The models were compared using the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) to determine the best fit.

To explore migration timing, we analyzed both the whales' move persistence and their movements past 65.75° latitude. The 65.75° latitude lies between their primary summer and autumn habitats, as indicated by fixed-kernel range estimates (see Richard & Stewart 2009) and their frequent movements north of this boundary in summer and south of it in autumn when observed through animated tracking data. For the latitudinal analysis, we analyzed the location data to identify their migration patterns across the 65.75° latitude boundary, filtering the dataset to include locations where whales crossed the 65.75° latitude threshold from north to south. The date and time of each whale's first southward crossing over 65.75° latitude in the autumn, and their last southward crossing before returning north in the spring, were identified. We used the move persistence data to estimate the start of migration, defined as the first date that move persistence exceeded 25% of the range between the minimum and maximum move persistence values (Shuert et al. 2022). This calculation was based on all move persistence estimates for each individual whale while its tag was still transmitting.

To explore the full duration of the whales' migrations, we also used the location data to map their positions along a diagonal transect within Cumberland Sound, tracking their migration progress throughout the year. Each year from the study period (1998, 1999, 2006, 2007, 2008) was analyzed separately, as were male and female beluga whales, to determine if there were changes over time or any sex-specific differences in migration timing. Using a tilted transect instead of a longitudinal degree line provided a more accurate understanding of the whales' positions along their migration route, as they migrate along the angled eastern portion of the sound rather than following a strictly north-south direction. However, to examine how often the whales moved north, south, and back and forth during their migration, we counted the number of times they crossed the 65.75° latitude line.

Differences between the two time periods were analyzed for the first and last crossings of the latitudinal threshold, the duration between those dates, the number of crossings over the threshold, and the persistent movement migration dates. Additionally, we examined potential differences between males and females for all these metrics. Levene's tests were conducted to assess the homogeneity of variances between the groups, followed by t-tests to identify statistically significant differences in migration timing between the two time periods. Data filtering and processing were conducted in R v 4.2.2.

Ice data was used to test the hypothesis that the timing of the whales' migrations depended on the buildup of ice. Weekly regional ice charts (for summer) and monthly regional ice charts (for winter) for Cumberland Sound were collected from the Canadian Ice Service. The export files (.e00) were converted to shapefiles in R v4.2.2 (R Core Team, 2022). For the generalized linear mixed models, the total ice concentration (i.e., combination of old ice, multi-year ice, young ice, and all other ice types) was extracted from the ice chart data closest to each transmission date and at the location of the transmission. The total ice concentration was also extracted for each polygonal area within the ice chart, with 5/10 representing approximately 50% ice concentration of that area and 10/10 representing 100% concentration of that area. We calculated the percentage of Cumberland Sound covered in 5/10 or greater ice concentration (following Hauser et al. 2017) and 10/10 ice concentration. The percentage of Cumberland Sound covered in 5/10 or greater ice concentration was plotted to determine if the formation or breakup of ice changed between years. Linear regression analysis was performed to assess potential trends in ice formation over time.

Dive Behavior

There were 3,685 dive data records, with the cumulation of dives recorded in the 6 dive bins. Dives in the 0-20m bin were excluded from our analyses given the difference in how the data was binned for each of the two time periods; 1998–1999 data included dives between 8-20m, while 2006–2008 dives included dives between 6-20m. The exclusion of the 0-20m dives, where appropriate, ensured that dives of 6-8m in the 2006–2008 data, but not 1998–1999, would not skew the results. Dives to 0-20m were also more likely to be transiting dives rather than foraging dives, and thus less relevant to our analyses.

The dive dataset was analyzed to determine the proportion of dives exceeding 100 meters across months and years to estimate the dives targeting Arctic cod, a deeper-dwelling species than capelin. Each dive was treated either as a deep dive (>100m) or shallow dive (20-100m). We applied multiple generalized linear mixed models (GLMMs) with a binomial family to the dive data using the lme4 package v1.1-35.3 in R v4.2.2 (Bates et al., 2015; R Core Team, 2022), each incorporating various combinations of bottom depth, month, time period, age, ice cover, and sex, as well as interaction terms. The models were compared using the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) to determine the best fit.

2.4 Results

Move Persistence and Migration

The best-fitting model to explain move persistence included ice cover, bottom depth, sex, time period, month, and the interaction between bottom depth and time period (Model 1, Table 2.2). Individual variation in move persistence was observed (Figure S2.5), and was accounted for by including individual (whale) as a random effect. Although sex was included in the best-fitting model, move persistence did not differ for males and females (Table 2.3). September had significantly higher move persistence compared to October, November, and December (Table 2.3). There were no significant differences in move persistence between December and November, December and October, or November and October. Movements were more persistent in areas with higher ice cover and greater bottom depth, and also in the second time period (2006–2008) compared to the first (1998–1999) (Table 2.3). However, the interaction between bottom depth and time period suggested that the influence of bottom depth on move persistence decreased in later years. Age was not included in the best-fitting model.

Table 2.2: Generalized linear models of Cumberland Sound beluga whale move persistence behavior in 1998–1999 and 2006–2008 considering age, sex, ice cover (ICE), bottom depth (DPT), time period (PER), month (MTH), and their interactions. Individual whale was also included as a random effect in every model.

Model	ΔAIC	AIC	BIC
Model 1: ICE + DPT + SEX + PER + MTH + DPT * PER	0.00	-12451.9	-12378.0
Model 2: DPT + MTH * PER + AGE	266.1	-12185.9	-12105.8
Model 3: AGE + MTH * PER	267.5	-12184.5	-12111.1
Model 4: ICE + DPT + SEX + PER + MTH	342.1	-12109.8	-12042.6
Model 5: ICE + SEX * PER + DPT + MONTH	343.8	-12108.1	-12034.1
Model 6: ICE + SEX + PER + MTH	363.9	-12088.0	-12027.5
Model 7: DPT + MTH + PER	368.5	-12083.4	-12029.7
Model 8: DPT + MTH	369.0	-12082.9	-12035.9
Model 9: DPT + MONTH + PER + SEX * PER	371.9	-12080.1	-12012.9
Model 10: MTH + PER	392.6	-12059.3	-12012.3
Model 11: DPT + PER	713.4	-11738.6	-11704.9
Model 12: ICE + DPT + ICE * DPT + AGE + SEX + PER + MTH	842.8	-11591.9	-11511.8
Model 13: DPT + ICE + AGE + SEX + PER + MTH	889.5	-11546.2	-11472.8
Model 14: DPT + AGE + MTH + PER	956.2	-11495.8	-11435.7
Model 15: SEX * PER + DPT + AGE + MONTH	959.6	-11492.3	-11418.8
Model 16: DPT + AGE + PER	1263.7	-11189.5	-11149.4

Table 2.3: Results from the best generalized linear model to explain move persistence of beluga whales in Cumberland Sound, 1998–1999 and 2006–2008. Significant effects are in bold.

Effect	Estimate	Std. Error	z-value	p-value
Ice cover	**0.039**	**0.011**	**3.485**	**< 0.001**
Bottom depth	**0.017**	**0.007**	**2.569**	**0.010**
Sex: Male	0.225	0.312	0.721	0.471
Time period: 2006–2008	**0.631**	**0.320**	**1.972**	**0.049**
September - October	**-0.281**	**-0.014**	**-20.704**	**< 0.001**
September - November	**-0.244**	**-0.024**	**-10.086**	**< 0.001**
September - December	**-0.311**	**-0.038**	**-8.154**	**< 0.001**
October - November	0.038	0.024	1.556	0.404
October - December	-0.030	-0.038	-0.780	0.863
November - December	-0.068	-0.031	-2.200	0.123
Bottom depth × Time period	**-0.269**	**0.014**	**-18.713**	**< 0.001**

The first southward crossing past 65.75° latitude occurred between 9-27 September of the tagging year for all whales, with the exception of one whale that migrated in July (Table 2.4), and did not change between the two time periods (Table 2.4; $t_{14} = 0.629$, $p = 0.540$). The last southward crossing occurred between early October and early December, again with no difference between the two time periods ($t_{6.08} = 1.223$, $p = 0.267$). The last crossing migration date in 1999 averaged 15 days later than in 1998 ($t_8 = -3.526$, $p = 0.008$). There was no significant difference between the last crossing dates in 2007 and 2008 ($t_3 = -1.929$, $p = 0.149$). Insufficient data prevented the analysis of differences between 2006 and 2007, and between 2006 and 2008.

Beluga whale migration patterns, as examined as the position along a transect against the day of the year, show a relatively consistent pattern in migration timing, beginning on 7 September (ordinal day 250) (Figure 2.3). However, the movements of beluga whales in 1998–1999 were more variable, with more frequent north-south transitions (Figure 2.3). In contrast, during the later years (2006–2008), once migration began, the whales showed fewer transitional movements, indicating a quicker, more direct migration from north to south. Though there was

no difference between the two time periods in the duration between the first and last dates the whales crossed the latitudinal threshold (t_{14} = 0.622, p = 0.544), the number of times whales crossed the 65.75° latitude was significantly higher in 1998–1999 compared to 2006–2008 (t_{14} = 6.013, p < 0.001) (Table 2.4).

The date of migration as defined by high move persistence occurred between 3 August and 19 September for all whales, with no significant difference between the two time periods ($t_{3.055}$ = -0.408, p = 0.71). The persistence of two whales passed the threshold on the day of their tagging (Tag 57594 on 17 July 2006 and Tag 57602 on 12 July 2007) and were not included in the persistent movement analyses due to potential confounding factors, such as the tagging procedure itself eliciting an evasive response from the whales.

No difference was detected between males and females in the first date they cross the latitudinal threshold (t_{14} = -0.242, p = 0.812) or the last (Figure 2.3; $t_{9.19}$ = -1.843, p = 0.098), the duration between first and last crossings, ($t_{9.07}$ = -1.464, p = 0.177), the number of crossings (t_{14} = -1.666, p = 0.118), or the persistent movement dates (t_{12} = -0.638, p = 0.536).

The ice formation followed a relatively stable pattern throughout the study years, with some variations observed but no long-term trends over the study period (Figure 2.2; R^2 = 0.127; $F_{1,3}$ = 0.437; p = 0.556). In general, the ice cover increased steadily from around 27 October (day 300), peaked between 4 February (day 400) and 25 March (day 450), and then gradually decreased.

Table 2.4: Metrics defining Cumberland Sound beluga whale migration timing. "First Crossing" is the initial crossing south of 65.75° latitude, "Last Crossing" is the final recorded crossing, and "Duration" is the number of days between these crossings. * Indicates that the tag stopped transmitting within 5 days of the last crossing, so the actual date may be later. Persistent Movement indicates when a whale's move persistence first exceeded 25% of its move persistence range. Bold dates indicate that the move persistence exceeded the threshold on the day of tagging and were excluded from analyses.

Year	Tag	First Crossing	Last Crossing	Duration	# of Crossings	Persistent Movement
1998	7925	10 Sep 98	11 Oct 98*	31	16	28 Aug 98
1998	17001	09 Sep 98	26 Oct 98	47	17	28 Aug 98
1998	20682	09 Sep 98	6 Nov 98*	58	16	28 Aug 98
1998	20684	10 Sep 98	20 Oct 98	40	20	04 Sep 98
1998	20685	25 Sep 98	18 Oct 98	23	17	26 Aug 98
1999	20162	15 Sep 99	13 Nov 99	59	11	01 Sep 99
1999	20682	19 Sep 99	20 Nov 99*	62	17	01 Sep 99
1999	20684	10 Sep 99	1 Nov 99	52	23	01 Sep 99
1999	20685	10 Sep 99	7 Nov 99	58	21	03 Sep 99
1999	7926	15 Sep 99	8 Nov 99	54	23	05 Sep 99
2006	57594	27 Sep 06	29 Nov 06	63	7	**17 July 06**
2007	37023	14 Sep 07	22 Sep 07	8	3	03 Aug 07
2007	57602	12 Jul 07	23 Sep 07	83	13	**12 July 07**
2008	39296	17 Sep 08	30 Oct 08	43	7	19 Sep 08
2008	39308	17 Sep 08	27 Sep 08	10	5	06 Sep 08
2008	39323	17 Sep 08	31 Oct 08	44	7	19 Sep 08

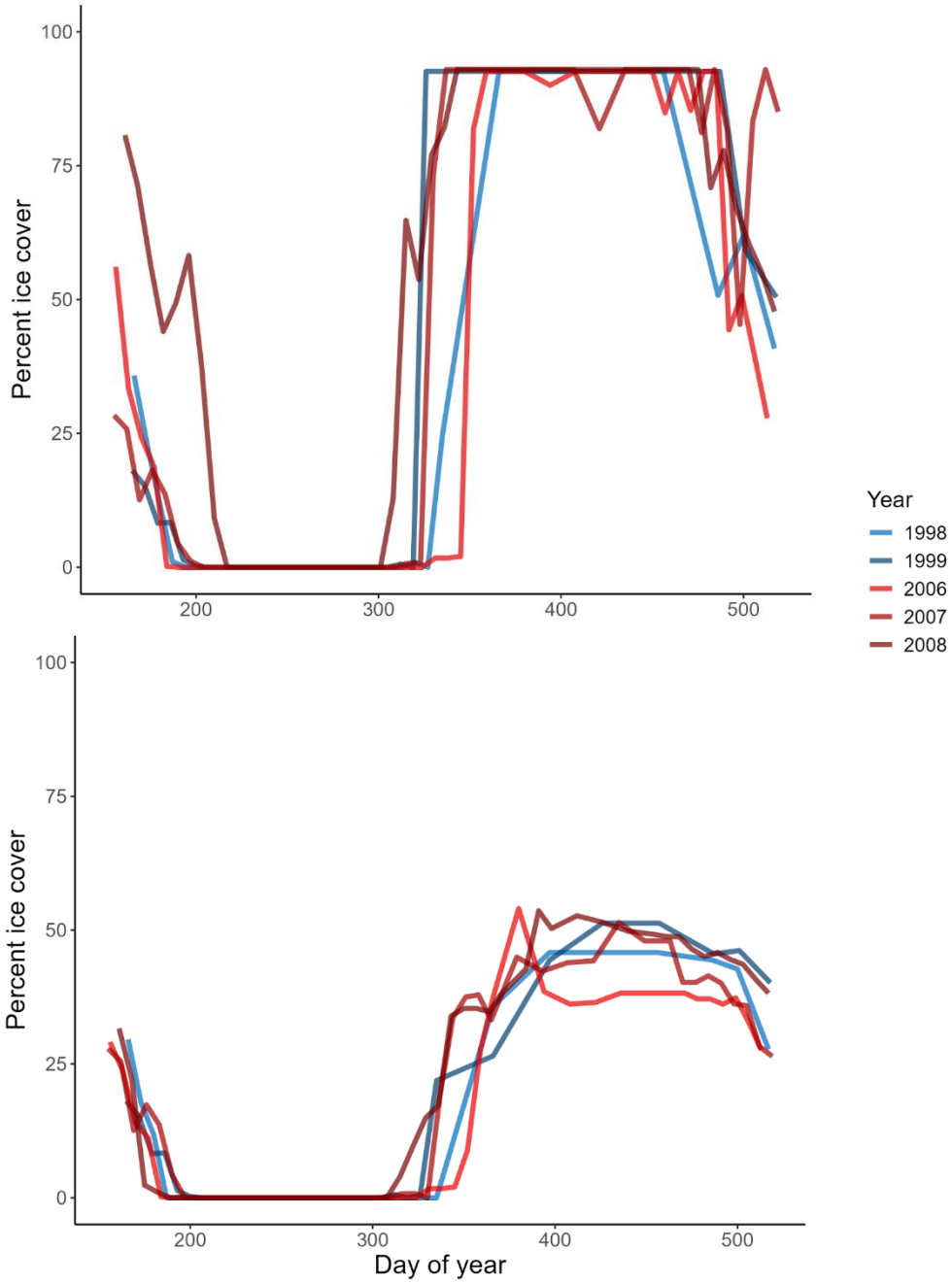


Figure 2.2: Percent of ≥5/10 ice cover (top panel) and 10/10 ice cover (bottom panel) in Cumberland Sound for years whales were sampled, as estimated from Canadian Ice Service weekly regional ice charts.

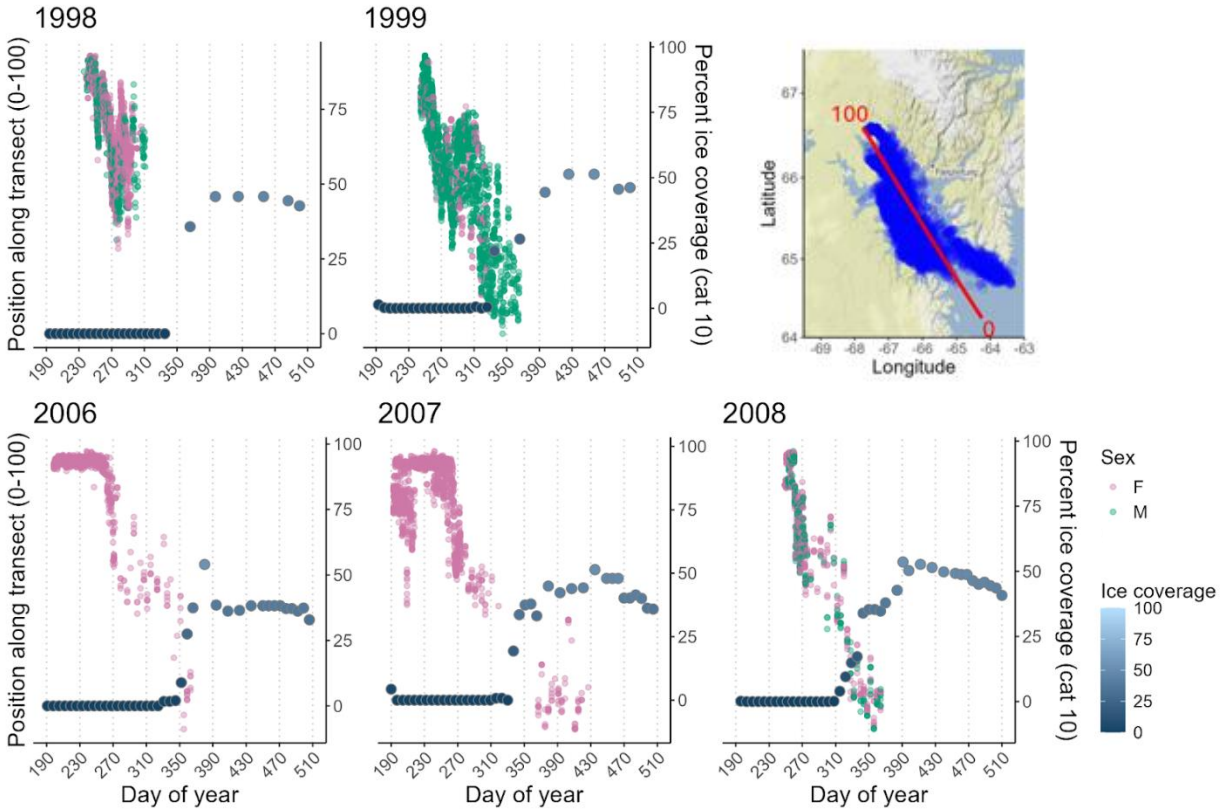


Figure 2.3: The migration trajectory of male (green) and female (pink) tagged beluga whales in Cumberland Sound. The telemetry data for all whales was combined for each sampling year. The y-axis shows the position along the transect (100-0; 100 demarks the start and 0 end of the transect), representing the approximate location of the whales over their range. The secondary y-axis represents the percentage of Cumberland Sound covered in 10/10 or greater ice concentration. The x-axis shows the day of the year, from 9 July (Day 190) to 25 May (Day 510). The map in the top right corner illustrates the study area in Cumberland Sound with the transect line.

Dive Behavior

The best-fitting generalized linear mixed model (GLMM) for explaining the number of dives to depths greater than 100m included bottom depth, age, month, time period, and ice cover as fixed effects, with unique whale ID as a random effect (Model 1, Table 2.5). The number of deeper dives decreased in the second time period (2006–2008) compared to the first time period (1998–1999) (Table 2.6). Dives in September and were significantly shallower compared to those in October, November, and December (Table 2.6). November dives were significantly deeper than those in October and December, and there was no difference between the deep dives in October

and December. An increase in ice cover was associated with a decrease in deep dives (Table 2.6). We also found fewer deep dives in deep water. Age was not significant (Table 2.6), and sex was not a term in the best-fitting model.

Table 2.5: Binomial generalized linear mixed models of Cumberland Sound beluga whale dives to depths greater than 100m in 1998–1999 and 2006–2008, considering age, sex, bottom depth (DPT), time period (PER), month (MTH), ice cover (ICE), and their interactions, with individual whale (ID) included as a random effect.

Model	ΔAIC	AIC	BIC
Model 1: DPT + AGE + MTH + PER + ICE	0	100371.2	100454.4
Model 2: DPT + AGE + PER * MTH	75.7	100446.9	100548.5
Model 3: DPT + AGE + PER + MTH	157.0	100528.2	100602.1
Model 4: AGE + MTH * PER + ICE	356.6	100727.8	100829.4
Model 5: AGE + MTH * PER	501.6	100872.8	100965.2
Model 6: DPT + MTH * PER + ICE	3815.1	104186.3	104288.4
Model 7: DPT + MTH * PER + SEX * PER + ICE	3818.3	104189.5	104310.2
Model 8: DPT + MTH * PER	3952.9	104324.1	104417
Model 9: DPT + MTH + PER + ICE	3956.6	104327.8	104402.1
Model 10: DPT + MTH + PER	4091.7	104462.9	104527.9
Model 11: DPT + SEX + MTH + PER	4093.7	104464.9	104539.2
Model 12: DPT + MTH	4099.7	104470.9	104526.6
Model 13: MTH * PER + SEX * PER	4409.4	104780.6	104882.8
Model 14: MTH + PER	4635.2	105006.4	105062.1
Model 15: SEX + MTH + PER	4637.1	105008.3	105073.3
Model 16: DPT + ICE	4860.5	105231.7	105259.6
Model 17: DPT + PER	5037.9	105409.1	105446.2
Model 18: DPT + SEX + PER	5039.8	105411	105457.5
Model 19: DPT + SEX * PER	5040.7	105411.9	105467.6
Model 20: SEX + PER	6322.7	106693.9	106731.0

Table 2.6: Results from the generalized linear model that best explained the proportion of dives greater than or equal to 100 meters for Cumberland Sound beluga whales in 1998–1999 and 2006–2008. Significant effects are in bold.

Effect	Estimate	Std. Error	z-value	p-value
Bottom depth	**-0.198**	**0.009**	**-22.029**	**< 0.001**
Age	-0.037	0.090	-0.414	0.679
September - October	**-0.398**	**0.020**	**-20.240**	**< 0.001**
September - November	**-0.734**	**0.029**	**-25.838**	**< 0.001**
September - December	**-0.457**	**0.050**	**-9.068**	**< 0.001**
October - November	**-0.337**	**0.028**	**-12.059**	**< 0.001**
October - December	-0.059	0.051	-1.157	0.654
November - December	**0.278**	**0.041**	**6.751**	**< 0.001**
Time period	**-0.504**	**0.159**	**-3.173**	**0.002**
Ice Cover	**-0.072**	**0.014**	**-5.189**	**< 0.001**

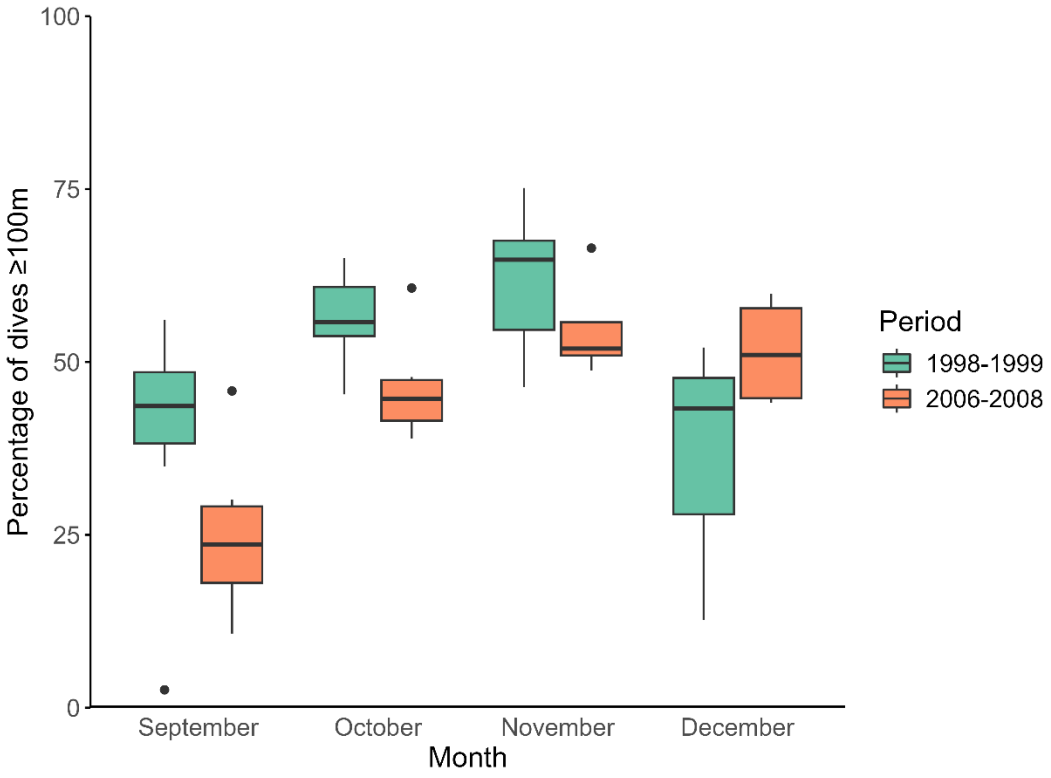


Figure 2.4: Percentage of dives of Cumberland Sound beluga whales greater than or equal to 100 meters in 1998–1999 and 2006–2008. Data collected from January to August were excluded due to insufficient data for one or both of the time periods.

2.5 Discussion

Our study revealed several critical findings regarding the Cumberland Sound beluga whales' diving and movement behavior, migration patterns, and their response to environmental variables. Our research aimed to address key questions about their annual migration patterns by examining the first and last date they crossed a latitudinal threshold and determining if their migration timing was related to the formation of ice in Cumberland Sound, revealing that the start of their migration precedes any buildup of ice in the area. We also sought to detect possible changes to their foraging patterns and noted a decline in the proportion of deep dives in the second time period (2006–2008) compared to the first (1998–1999) that may indicate a shift from Arctic cod to capelin.

The seasonal variation in whale move persistence likely reflects changes in whale behavior related to foraging and migration. The increase in move persistence (i.e., highly directional travel) in September may be due to the whales' migration, since most whales seem to begin their migrations in September based on the first date they cross below the 65.75° latitudinal threshold (Hauser et al., 2014). Ice cover was a significant predictor of move persistence, indicating that whales exhibited highly directional travel in areas with higher ice cover. This behavior could also be related to the whales' search for prey in ice-covered regions, where prey might be more concentrated or accessible. Arctic marine mammals including beluga whales often exploit ice-covered areas for foraging, as these regions can provide refuge and abundant prey (Laidre et al., 2008).

Similarly, whales tended to exhibit more persistent movements in deeper areas. This pattern could be attributed to searching for patchy areas of prey in deep water, resulting in longer movements and higher move persistence. Additionally, the whales may migrate over the central and deepest areas of Cumberland Sound, further contributing to the observed patterns in move persistence. This behavior aligns with findings from other marine mammal studies that highlight the influence of bathymetry on foraging and movement patterns (Cox et al. 2018; Hauser et el. 2017; Laidre et al., 2018). In contrast, shallower areas might see more congregations of prey, leading to more variable and less persistent movements, indicative of lower move persistence. October could have resulted in area-restricted searches (i.e., low move persistence) due to tight turns and short steps during the whales' migrations when they tend to make short but frequent north-south trips, presumably for foraging. November and December may have been characterized by limited movements due to high ice cover in much of Cumberland Sound at this time, which could have resulted in restricted movement and foraging activities (Laidre et al., 2018).

Bottom depth significantly influenced both the move persistence and diving behavior of beluga whales, and when combined, these findings suggest distinct movement patterns in relation to bottom depth. Whales exhibited more persistent movements in deeper areas, likely due to migration or foraging strategies that involve longer movements in search of prey in these regions (Hauser et al., 2018; Heide-Jørgensen et al., 1998; Laidre et al., 2008). The dive behavior analysis showed that whales are less likely to perform deeper dives in areas with greater bottom

depth, suggesting that while whales might move persistently through deeper waters, they are not diving deeply in these regions (Martin & Smith, 1992). The lack of deep dives could be due to the energetic costs associated with them, making them less frequent in deeper waters. Instead, whales may be traveling quickly through these deeper areas, possibly during migrations, where the need for deep dives is reduced (Hauser et al., 2015). Additionally, the interaction between bottom depth and time period was significant and negative, indicating that the influence of bottom depth on move persistence has decreased over time (Laidre et al., 2015). This change might reflect shifts in prey distribution or adjustments in whale foraging strategies, driven by environmental changes (Moore and Huntington, 2008). The higher move persistence combined with lower deep dive frequency in deeper areas underscores the possibility that whales are using these regions as transit routes rather than for intensive foraging (Castellote et al., 2020).

The migration patterns of Cumberland Sound beluga whales did not show significant shifts over the duration of our study period. The data also show that both male and female beluga whales exhibit similar migration timing, starting and finishing their migrations at approximately the same time each year (Richard & Stewart, 2009; Hobbs et al., 2008). This consistency in migration timing across sexes and years suggests stable and synchronized migratory behavior. The migrations of Cumberland Sound beluga whales are much smaller than many other beluga whale populations and it may be harder to detect trends given the short distance between their summer and winter sites. Cumberland Sound, Cook Inlet, the White Sea, Svalbard, and St. Lawrence Estuary are considered resident populations that only move as far as they need to in order to avoid fast ice formation, as opposed to other beluga whale populations that travel relatively long distances between separate summering and wintering sites (Hobbs et al., 2008, 2020; Laidre et al., 2008; Richard & Stewart, 2009). The timing of the formation of landfast ice was relatively consistent over our survey years, but our results indicate that these movements, hypothesized to avoid fast ice, occur well before its formation (Laidre et al., 2008). As such, the early migration may be a learned adaptive response, potentially transmitted culturally from experiences of ice entrapment when the ice formed anomalously early, rather than an immediate response to environmental cues (O'Corry-Crowe et al. 2016; O'Corry-Crowe et al. 2018).

The timing of the start of the migration of Cumberland Sound whales appear to be unrelated to ice cover; the last day that any whale made its first crossing over the 65.75° latitudinal threshold

was 27 September (day 270), while solid ice cover did not begin forming for any of the sampling years until approximately 6 November (day 310). The first ice buildup in Cumberland Sound in 1999, for example, was between 1-7 November (days 305-311) and restricted to the Clearwater Fjord area where the whales spend the summer; the whales had been outside of Clearwater Fjord since approximately 27 September (day 270). There was also no difference between the migration timing of the two time periods, but the 1998 migration occurred approximately 15 days earlier than 1999. In the same years, the buildup of 5/10 total ice concentration over 50% of Cumberland Sound occurred approximately 18 days later in 1998 than 1999. This pattern suggests that ice cover is unlikely to be the trigger for their migration, and other factors that we could not measure in this study, such as the movement and distribution of prey or social factors, might play a role in determining migration timing. Future studies in Cumberland Sound should aim to include more extended periods and explore additional environmental variables that might influence beluga whale migration.

The variability in the timing of the last southward crossing, with approximately seven weeks between the earliest and latest date, reflects individual differences in migration timing, which could be influenced by factors such as prey availability, ice cover, and other environmental conditions. The migration dates based on move persistence, with some exceptions, generally occurred 1-2 weeks before the first crossing of the latitudinal threshold. This aligns with expectations, as move persistence increases when the whales begin migrating, and the latitudinal crossing typically happens after they have been moving for some time. The more varied latitudinal movements during migration with several crossings over the latitudinal threshold that were observed in the earlier time period (1998–1999) may indicate changes in environmental conditions such as water temperature or prey availability that are not immediately apparent from the location and ice data alone (Bailleul et al., 2012). The higher number of crossings in the first time period could be a result of the whales targeting Arctic cod more during that period, since the latitudinal threshold is an area of greater depth than Clearwater Fjord and Arctic cod are typically found in deeper water. While our study found stability in migration timing and ice cover during the study period, the potential for future changes due to climate variability underscores the need for continued monitoring and research to understand the long-term impacts on beluga whale ecology. It is likely that other environmental factors, such as food availability

and temperature, may be influenced by climatic changes, which in turn could affect beluga whales and their migrations (Laidre et al. 2008).

The timing of beluga whale migrations in other populations has been found to be influenced by various factors, including ice cover, but differences between populations have been identified. For example, the Eastern Chukchi Sea beluga whales will delay their autumn migration by several weeks due to later regional sea ice formation, (Hauser et al., 2017) and whales in eastern Hudson Bay changed their migration date by several weeks in response to changes in sea surface temperature (Bailleul et al. 2012), indicating a flexible response to environmental changes. Similarly, variations in sea ice conditions have influenced the migration patterns of beluga whales in the Pacific Arctic where, though the whales show strong site fidelity to certain coastal areas, inconsistent ice cover has led to anomalous migration and residency events (O'Corry-Crowe et al., 2016). Conversely, other studies have found that some beluga whale populations migrate at consistent times each year, regardless of environmental conditions. Eastern Beaufort Sea beluga whales, for example, exhibit a high degree of philopatry, returning to the same summering grounds annually despite varying ice conditions, and bathymetric features were more likely predictors of beluga whale distribution in summer and autumn (Hauser et al., 2014, 2018; Hauser et al., 2017). Similarly, in the Cook Inlet population, whales frequently chose areas of pack ice when there were ice-free portions of their habitat available, suggesting that their fidelity to certain coastal areas is stronger than an avoidance of ice (Goetz, Robinson, et al., 2012). These studies suggest that while some beluga whale populations change their behavior to respond to changing ice conditions, others maintain rigid migratory schedules driven by other factors. Though no significant difference in the timing of ice formation was detected during our study period, the consistency in migration timing also raises concerns about the Cumberland Sound population's ability to shift their behaviors in response to future climate changes. It warrants further investigation to determine if migration timing does change for this population in years with anomalous ice formation or ice breakup timings.

Beluga whale populations in the Arctic face numerous threats, including climate change, overharvesting, habitat degradation, pollution, and increased human activities such as shipping and resource extraction (Carter & Nielsen, 2011; De Guise et al., 1995; Hobbs et al., 2020). One significant threat is the loss of sea ice, which apart from the possible effects on some beluga

whale population migrations, has profound impacts on the distribution and availability of prey, as well as increased predation risk from species such as killer whales that are moving into newly accessible areas (Laidre et al., 2008; Moore et al., 2000; Norman et al., 2016; O'Corry-Crowe et al., 2016). If sea ice continues to decline or form later in the year, beluga whales may face challenges in synchronizing their migrations with optimal foraging conditions. This potential misalignment could affect their access to prey and overall survival, particularly if key prey species are more sensitive to changes in ice cover (Hamilton et al., 2015; Laidre et al. 2008). The flexibility of beluga whale populations in migration timing and routes could be crucial for their resilience to these threats. Flexibility could help mitigate the impacts of climate change and other anthropogenic pressures by enabling beluga whales to adjust their behavior to optimize foraging success and avoid hazards, while those populations that are inflexible may be more at risk (Laidre et al., 2008). The population-specific responses to changes in environmental conditions underscore the need to better understand each population separately and predict how each might be affected by threats such as climate change (Bailleul et al., 2012; Goetz, Robinson, et al., 2012; Hauser et al., 2014; Hauser et al., 2017; O'Corry-Crowe et al., 2016).

Though we do not have depth distributions specific to Cumberland Sound for prey, we can infer their general distribution based on findings in other areas and their affinity for certain depths or bathymetric features. The vertical distribution of Arctic cod varies based on age, time of year, and the oceanography and bathymetry of the area. Medium and full-sized cod can typically be found at depths ranging from 200 to 1,000 meters and often along the seafloor, while juveniles may be found in shallower pelagic water (Benoit et al., 2014; Bohn & McElroy, 1976; Falk-Petersen et al., 1986; Forster et al., 2020). In the Beaufort Sea, they were not recorded above 221m (Geoffrey et al., 2011). Beluga whales will preferentially select larger, schooling adult cod (Matley et al. 2015). Capelin is usually found over banks at depths around 50-100 meters and in shallower waters during younger stages, and during spawning they have been found between 8-90 meters (Brown 2002; Jansen et al., 2021; McGowan et al., 2018; Thors 1981). Though there may be some overlap between the vertical distributions of capelin and Arctic cod at certain life stages, the preference of beluga whales for larger fish would still likely result in a change in dive behavior that would suggest this shift from one prey to another.

We found significant temporal variations in the diving behavior of beluga whales, and there was a notable shift in the diving behavior of beluga whales between the two time periods of our study. In the earlier time period (1998–1999) whales exhibited more deep dives than in the later time period (2006–2008) to depths of 100m and greater. This shift suggests a possible change in prey preference or availability, with beluga whales potentially targeting capelin instead of Arctic cod, as has been substantiated in other studies of Cumberland Sound beluga whales, including fatty acid and stable isotope analyses (Marcoux et al., 2012; Watt et al., 2016). However, beluga whales in the Chukchi Sea spent more time at deeper depths during 2007–2012 compared to 1998–2002 (Hauser et al., 2018), a contrast to our study. In that case, deeper and longer dives could have resulted from more dispersed or deeper prey associated with changes in sea ice, requiring more energy for searching, or more extensive and productive foraging opportunities in recent years (Hauser et al. 2018). These dives may be very costly for whales, such as juveniles, that are already at their physiological limits (Noren & Suydam, 2016, Hauser et al. 2018).

The differences in dive behavior between the two time periods indicate Cumberland Sound beluga whales exhibit a degree of flexibility in their diving strategies, likely in response to varying ecological conditions. Variation in foraging strategies can be seen in other populations, where the whales seem to alter behavior based on differences in prey availability and environmental conditions across different regions and times of the year (Hauser et al., 2015, 2018; Storrie et al., 2022). Whale move persistence also showed a significant increase from 1998–1999 to 2006–2008. This trend suggests that whale movement patterns have changed over time, potentially reflecting changes in environmental conditions such as variations in prey availability or shifts in habitat use. If, for instance, prey became more dispersed or shifted locations, whales may have needed to travel longer distances and exhibit more persistent movements to locate and capture their food (Moore and Huntington, 2008; Laidre et al., 2015). Additionally, shifts in habitat use driven by environmental factors might have necessitated different movement strategies (Kovacs et al., 2011).

The introduction and establishment of capelin in the area could have provided a more accessible and abundant prey source, resulting in shallower dives. However, the ecological implications of this shift from Arctic cod to capelin are potentially significant, if true. Though both species are susceptible to population declines associated with warmer temperatures and a reduction in ice

cover, fluctuations in the abundance and even distribution of capelin may be more variable because of its reliance on specific environmental conditions and the impact these abiotic factors have on their spawning and foraging habitats (Carscadden et al., 2001; Choy et al., 2020; Hop & Gjøsæter, 2013; Huse & Ellingsen, 2008; Huserbråten et al., 2019). Species such as capelin have also been associated with a decline in body condition in beluga whales (Choy et al., 2020). Poor body condition, in turn, can affect the whales' ability to dive, which can result in increased mortality in the event of ice entrapments, encounters with predators, and a decreased ability to capture certain prey (Choy et al., 2019, 2020). Capelin has a smaller body mass than Arctic cod, which could result in increased energetic costs of foraging. The shift from Arctic cod to capelin has contributed to reduced nestling growth rates in Brunnich's guillemots, for example, as the birds must make more frequent foraging trips to compensate for the smaller mass of capelin (Gaston et al. 2005).

Beyond these direct effects on beluga whales, the introduction of capelin could have broader cascading effects on the ecosystem by altering predator-prey relationships and resource competition within the food web. Other species that rely on Arctic cod, such as Greenland halibut (*Reinhardtius hippoglossoides*), Arctic char (*Salvelinus alpinus*), and ringed seals (*Pusa hispid*a), may experience increased competition or dietary shifts if capelin is dominant in the system, potentially altering the availability of these key prey items for beluga whales and affecting the overall stability of the Arctic marine food web (Yurkowski et al. 2018). Fluctuations in the access that beluga whales have to capelin, as well as possible changes to their nutrient, fat, and contaminant intake, could have long-term negative impacts on the population over time (Choy et al., 2019, 2020; Gaston et al. 2005; Leu et al., 2011; Marcoux et al., 2012; Thiemann et al., 2008), especially given its endangered status.

The higher percentage of deeper dives in October, November, and December underline the importance of seasonal factors in shaping diving patterns. Beluga whales generally exhibit distinct seasonal foraging strategies influenced by their habitat and prey availability (Castellote et al., 2020; Hauser et al., 2015; Hornby et al., 2017; Storrie et al., 2022). The shallower dives in September may be related to the bathymetry of Cumberland Sound itself, since their summer habitat is shallower than in autumn or winter. However, the whales have access to deeper areas than they appear to be using in September based on the bathymetry of Cumberland Sound just

outside of Clearwater Fjord and in areas between the fjords where they primarily spend the summer. The lack of use of these deeper areas could be due to a lack of prey at depth or because the whales are targeting more shallow species, as is common in summer in other beluga whale populations (Barber et al., 2001; Kingsley et al., 2001; Martin & Smith, 1992). For example, beluga whales in Cook Inlet display a preference for foraging near river mouths during summer, coinciding with the runs of anadromous fish such as eulachon and salmon (Castellote et al., 2020). This seasonal aggregation in shallow estuarine areas also aligns with the findings from the Mackenzie Estuary, where beluga whales exploit feeding grounds during the summer before moving to offshore and deeper waters in the late summer and autumn for different types of prey (Hornby et al., 2017).

The deeper dives in the winter months may indicate that this season is more important for foraging than summer months or that the whales are targeting deeper-dwelling prey species such as Arctic cod or Greenland halibut (Watt et al., 2016). The deeper dives in November compared to October and December could be due to bathymetry, as the habitat in November, located towards the eastern side of the central portion of Cumberland Sound, includes deeper areas. During the winter months, beluga whales in the Eastern Beaufort Sea demonstrate shallower and more frequent dives than in the summer when they are likely targeting Arctic cod, but the whales are likely foraging throughout the year (Storrie et al., 2022).

Both male and female whales exhibited similar diving behaviors and move persistence. This contrasts with other studies that have found sex-specific differences in marine mammal movement and foraging patterns, often due to differing energetic requirements and reproductive roles (Breed et al., 2006; Kovacs et al., 2011; Beck et al., 2003; Gowans et al., 2007; Loseto et al., 2007). Based on findings in other populations, we would expect males to have significantly more deep dives and possibly distinct strategies for move persistence due to potential sex-specific resource partitioning (Choy et al., 2020; Loseto et al., 2006, 2008; Szpak et al., 2020). However, findings have also shown that both sexes of beluga whales have comparable deep-diving capabilities (Martin & Smith, 1992). Sex-specific differences in dive behavior may not be clear in Cumberland Sound because although a small area of the sound extends deeper than 1000m, the majority of the whales' habitats throughout the year are under 400m. In other

populations, males can dive in excess of 1000m likely in search of deeper-dwelling prey. In our population, they might not have the need or opportunity to dive to such depths.

There were some uncertainties associated with our analyses, including our sample size of 20 whales spanning only five years of data collection, which limits the generalizability of our findings. The duration of the tags transmitting was also relatively short, with an average of only 125.5 days, which may have constrained our ability to capture the full foraging and autumn migratory behaviors of the population, and did not allow for exploration of the spring migration. Furthermore, the sea ice metrics used in our study were relatively coarse, being collected only weekly or monthly depending on the season, which may have missed finer-scale changes in ice cover that could influence beluga whale behavior. Another source of uncertainty in our analyses involves the classification of dive depths. Dives to depths between 0-20m were presumed to be transiting rather than foraging dives, but it is possible that we missed some shallow foraging dives, especially if prey was present near the surface. However, we attempted to address this issue by excluding these shallow dives for both time periods, providing consistency in our approach across the datasets. Additionally, our models relied on available covariates (e.g., ice cover, bottom depth), but unmeasured environmental factors (e.g., predation risk, prey availability) may also influence movement behavior.

Although males and females were represented in both time periods, the first time period (1998–1999) was predominantly comprised of males while the second time period (2006–2008) was predominantly female whales. Notably, no male whales were sampled in 2006 or 2007 and only one male whale in 2008 with sufficient data. The significantly higher number of crossings over the latitudinal threshold in the first time period may be a result of males being more exploratory than females, especially juvenile males. These sampling biases may also have confounded differences in the dive data if, as in other beluga whale populations, males forage in deeper water than females and calves (Choy et al., 2020; Loseto et al., 2006, 2008; Szpak et al., 2020). More deep dives due to the sex of the whales in 1998–1999 would have made it harder to see overall population differences if the whales preferred prey shifted from shallow-water capelin to more mid-water Arctic cod between the two time periods, but the lack of a significant difference between the sexes in the 1998–1999 data, with four female whale tags transmitting for a significant time during that time period, discounts that potential bias.

2.6 Conclusion

The endangered Cumberland Sound beluga whale population faces conservation challenges, including overharvesting and the impacts of climate change. Our analysis of the population, spanning the two periods 1998–1999 and 2006–2008, provides valuable insights into their migration patterns, diving behavior, and response to environmental changes. The start of migration preceded ice buildup by approximately 40-117 days depending on the whale and year, and appeared relatively stable over the study period. The lack of variation in migration timing could exacerbate the impacts of climate change, particularly if prey species dependent on ice cover become less predictable in their distribution and abundance. Understanding whether or not migration timing aligns with prey availability is crucial for effective population management, especially considering the natural challenges these whales may face. Dive behavior analysis revealed a notable shift in the proportion of deep dives between the two study periods, with whales exhibiting fewer deep dives in 2006–2008 compared to 1998–1999. This shift suggests a potential change in prey preference or availability, with whales possibly targeting capelin instead of Arctic cod. The ecological implications of this shift are significant, as capelin's smaller body mass and reliance on specific environmental conditions could impact the whales' overall foraging success and the energetic costs associated with foraging. Future research should aim to extend the monitoring period and incorporate additional environmental variables to better understand the factors influencing beluga whale migration and diving behavior. The potential for future changes in ice cover, prey availability, and environmental conditions highlights the need for a better understanding of these population-specific behavioral patterns and their drivers. Assessing how environmental changes affect foraging strategies and habitat use is essential for effective conservation planning and to better predict and mitigate the pressures faced by marine mammal populations.

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Supplementary Material

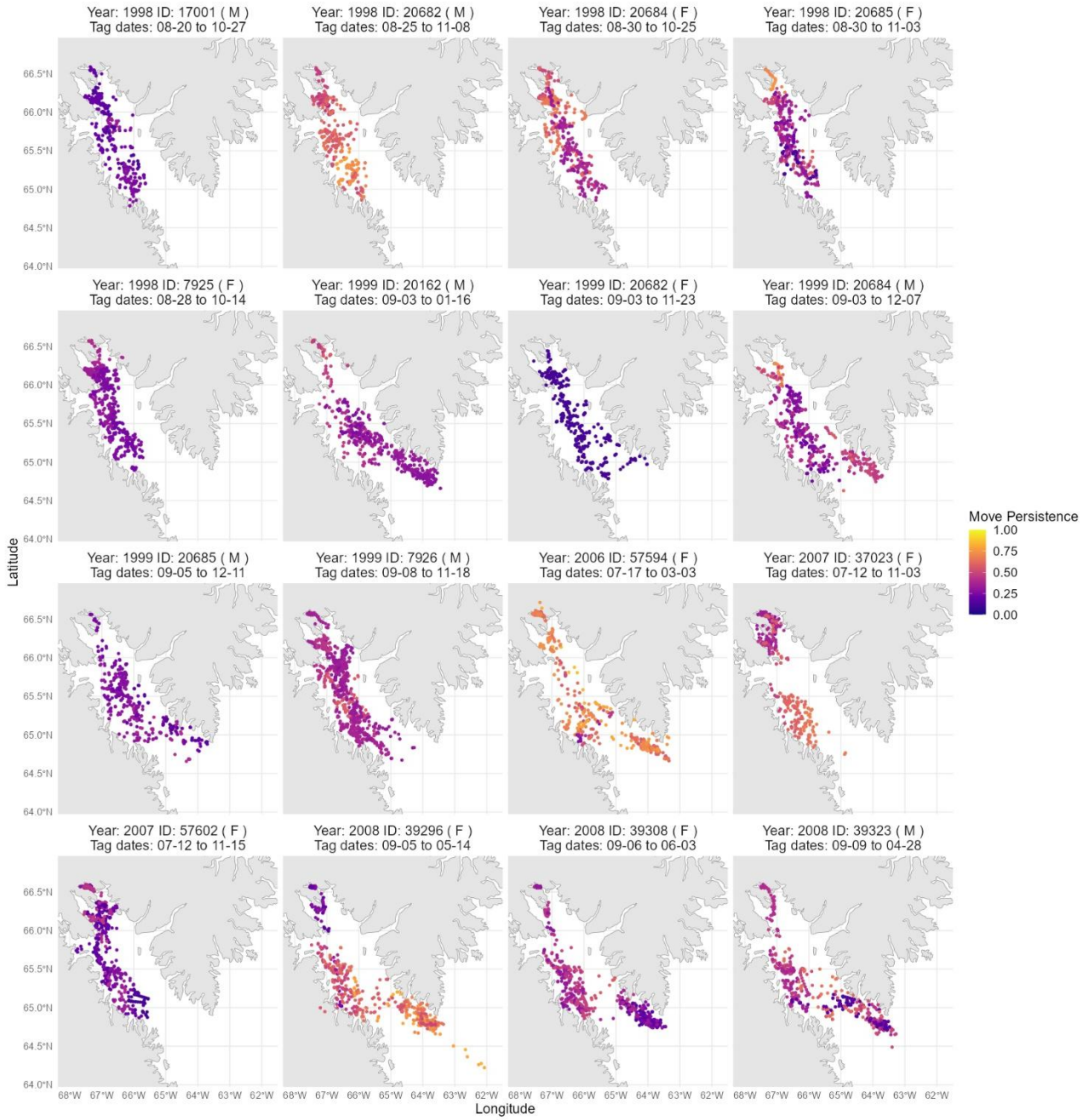


Figure S2.5: Move persistence models fitted to the movement data of 16 beluga whales in Cumberland Sound. Each panel represents a unique whale, denoted by the year it was tagged (Year), its tag identification number (ID) with sex (M or F), and the dates the tag was equipped and fell off or stopped transmitting (Tag dates). Move persistence is denoted on a color scale, with 0.00 (purple) representing area-restricted searches characterized by short distances and tight turns, and 1.00 (yellow) representing highly directional travel characterized by long distances in the same direction.

Chapter 3 - Use of drones for the creation and development of a photographic identification catalogue for an endangered whale population

3.1 Abstract

Photographic identification is increasingly being used as a cost-effective and minimally invasive method to monitor species, which is of particular importance for endangered populations that are vulnerable to intrusive research methods. The purpose of our study was to collect photographs of an endangered population of beluga whales (*Delphinapterus leucas* (Pallas, 1776)) in Cumberland Sound, Nunavut, Canada, for use in photographic identification. Rather than pursuing the whales with boats to collect photographs, drones were used to minimize disturbance. We analyzed drone photographs from 2017 to 2019 for distinctive markings on the whales, which were used to develop a photographic identification catalogue. In total, 93 individuals were identified, with 24 resightings of uniquely marked individuals over the survey period. Approximately 43.4% (standard error 3.3%) of the adult beluga whale population was uniquely marked. The beluga whale population has been harvested at a rate of 41 whales per year, not including struck and lost, since 2002. The markings were from unknown origins (61%), scars/wounds from gunshots (27%), anthropogenic or predatory given the size and severity (11%), or a satellite tag (1%). The continuation of the photographic identification program will allow for the estimation of important population demographics, such as abundance and calving interval, which are important parameters for population conservation and management.

3.2 Introduction

Photographic identification (photo-ID) is a non-invasive and frequently used method of monitoring species, providing insight into reproductive history, estimating mortality and survival, collecting social and age structure data, and monitoring the health of individuals over time (Würsig and Jefferson 1990; Elliser et al. 2018; Raoult et al. 2020; McGuire et al. 2021*b*). Resightings of identified individuals can also be used to estimate abundance using mark–recapture techniques. Photo-ID can be used for populations that are endangered and vulnerable to invasive sampling techniques or that are otherwise difficult to monitor (Meekan et al. 2006; Gamble et al. 2008), including those in the marine environment (Wickman et al. 2021).

The feasibility of using such methods to monitor populations has been established for several marine species including mysticete whales such as the humpback whale (*Megaptera novaeangliae* (Borowski, 1781)) (Constantine et al. 2012), whale sharks (*Rhincodon typus* Smith, 1828) (Schofield et al. 2020), and loggerhead sea turtles (*Caretta caretta* (Linnaeus, 1758)) (Holmberg et al. 2009). The identification of individuals in these studies is based primarily on naturally occurring markings, patterns, or unique colouring.

The individual identification of cetaceans using natural markings in research began in the early 1970s (Würsig and Würsig 1977; Würsig and Jefferson 1990), and photo-ID research conducted since then typically utilizes similar methods including the use of unique markings and colouration, or notches in the dorsal fin or fluke (Gowans et al. 2000; Matthews et al. 2001; Young et al. 2011; Bassos-Hull et al. 2013). Our objective was to use a similar approach to build a photo-ID catalogue for a population of beluga whales (*Delphinapterus leucas* (Pallas, 1776)) in Cumberland Sound, Nunavut, Canada. Identifying individual beluga whales posed a unique challenge because skin colour changes from dark gray to white over the lifetime of a whale and whales often lack unique or permanent pigmentation. They also lack a dorsal fin, a feature that is common in other ice-inhabiting whales. Their flukes are proportionately smaller than larger cetacean species and are generally not exposed above the water surface compared to species for which this method of identification is typically used, such as sperm whales (*Physeter macrocephalus* Linnaeus, 1758) (Matthews et al. 2001) and humpback whales (Constantine et al. 2012). Scarring on the body has also been used in the identification of some marine mammal species (Koski et al. 2013, 2015; Landeo-Yauri et al. 2020), including in other beluga whale populations. Photo-ID studies of beluga whales are being conducted in Cook Inlet, Alaska (McGuire et al. 2020*a*, 2020*b*, 2021*a*), the White Sea, Russia (Chernetsky et al. 2011), and the St. Lawrence estuary, Canada (Michaud 2014), and typically involve collecting boat- and shore-based photographs in areas where the whales are easily accessible.

The Cumberland Sound beluga whale population remains within a relatively small geographic area throughout the year and they are thought to be geographically isolated from nearby populations in the eastern High Arctic, Hudson Bay (including the western Hudson Bay, James Bay, eastern Hudson Bay populations), and Ungava Bay (Richard and Stewart 2009; Hobbs et al. 2020). The population was severely depleted from commercial and subsistence harvests, reduced

from a historic level of over 8500 whales to fewer than 1500 in 2017 (DFO 2019). Currently, the population is hunted for subsistence purposes, and there has been a quota of 41 whales per year since 2002 (COSEWIC 2004; Stewart 2018; DFO 2019). Population models indicate that the Cumberland Sound beluga whale population may continue to decline under the current quota (Watt et al. 2021). In 2017, the population was listed as threatened by the Species at Risk Act, and in 2020 the population was listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (DFO 2019; COSEWIC 2020; Watt et al. 2021).

Monitoring of the endangered Cumberland Sound beluga whale population has been limited due to their remote location. Although aerial surveys were conducted approximately every 3–9 years to monitor abundance from 1990 to 2017, and satellite tagging occurred from 1998–1999 and 2006–2008, additional long-term monitoring of the population was needed (Richard and Stewart 2009; DFO 2019; Watt et al. 2021). The purpose of this study was to determine the feasibility of using drones to identify individual whales in the endangered Cumberland Sound population. If the method proved successful, the photo-ID catalogue could ultimately be used to estimate reproductive rates and population size using mark–recapture techniques. Drones have successfully been used in photo-ID studies of terrestrial and marine species and offer advantages over boat- or shore-based photography. For example, drone photography eliminates the need for separate right- and left-side catalogues, allows for more accurate group size estimates, and minimizes disturbance to whales (Durban at el. 2015; Koski et al. 2015; Pomeroy et al. 2015). Drones have been used to monitor beluga whales in Cook Inlet (P. Wade, personal communication, 2020) and the St. Lawrence estuary (R. Michaud, personal communication, 2021) as a means of supplementing long-term boat-based photo-ID programs, but the efficacy of using drone photography alone to identify individual whales was unknown when the study began. The key objectives of this study were to determine what proportion of the Cumberland Sound beluga whale population had identifiable and permanent markings and to assess whether a long-term photo-ID program would be useful for monitoring the population.

3.3 Methods

Photographic surveys were conducted in Clearwater Fjord, an area within Cumberland Sound, in August 2017–2019 over 1–2 survey days per year. The study area was chosen based on previous aerial survey and telemetry data, which documented an aggregation of Cumberland Sound

beluga whales in Clearwater Fjord in August, approximately 100 km from the nearest community, Pangnirtung, Nunavut, Canada (Fig. 3.1) (Richard and Stewart 2009). Phantom 3 (2017, 2019) and (or) 4 (2018, 2019) drones (DJI, China) equipped with cameras (specifications at https://www.dji.com/ca/phantom-3-pro/info and https://www.dji.com/ca/phantom-4/info, respectively) were operated by an experienced pilot and images were collected as stills. In 2017, the drone pilot was a former US military drone pilot with extensive experience in flying small and large drones, including a DJI Phantom 3, and experience in training drone pilots. Starting in 2018, the drone was operated by an experienced pilot who was trained by the former military pilot and at that time had over 2 years of experience as a local recreational drone operator and had worked in Cumberland Sound the previous 3 years on whale projects. Photographs of the whales were collected under Animal Use Protocol permit numbers FWI-ACC-2018-27 and FWI-ACC-2019-17, following guidelines to minimize the disturbance on the whales.



Figure 3.1: Survey area of the beluga whale photo-ID program in Cumberland Sound, Nunavut, Canada, from 2017 to 2019, denoted by a crosshatch pattern, and the local community of Pangnirtung. Map was generated using ArcGIS 10.7 (ESRI Inc., Redlands, CA, USA). Coordinate system: WGS 1984 Web Mercator Auxiliary Sphere. Projection: Mercator Auxiliary Sphere.

Launch and recovery of the drone took place from a 25-ft-long boat running two 125 hp gas engines. At least two observers were present, one to maintain visual contact with the drone and one to observe the whales. Whales were typically several hundred meters from the boat during surveys due to high avoidance of boats, which is likely a result of their being hunted, but exact

distances were not recorded. During the 2017 survey, whales were photographed from a minimum altitude of 30 m and there were no discernible behavioral responses to the drone seen by the drone pilot. Avoidance of the boat when its engines were running was observed (B. Young, W. Koski, and K. Ryan, personal observation, 2017), so the engine was turned off as frequently as possible during surveys in subsequent years. In 2018–2019, the drone was flown at an altitude of 25 m to approach the whales and the pilot gauged the animals' response to the drone. When no behavioral changes were seen, the drone was lowered to an altitude of 10–20 m. Some avoidance behaviors such as diving or changing direction and speed were hard to distinguish from normal behavior. However, when whales dove out of view the protocol was to orient the drone over a new group of whales.

Data processing involved editing photographs to make any markings on the whales more visible and reduce glare using Adobe Lightroom. Notations were made about which section of the whale was visible (anterior, dorsal ridge, or posterior) (Fig. 3.2) and the direction of the drone relative to the whales (directly above, or right/left if the drone was approaching the whales from the side before orienting above them). The number of markings on each whale was recorded, as well as the shape, location on the body (Fig. 3.2), colour, and size of the markings. The presumed cause of each marking was noted where possible. Possible causes of scars included a gunshot, grazing bullet, or satellite tag. Unknown was assigned if the likely cause could not be determined from the characteristics of the marking and could potentially be attributed to gunshots, predators, or other causes. Here, we refer to open injuries as wounds and healed injuries as scars, and refer to them collectively along with other types of unique identifiers (e.g., atypical dorsal ridge and discolorations) as markings. Gunshot wounds and scars were characterized by a small entry point and a large, usually jagged exit, while bullet grazing markings were lines that usually had a narrow end that widened across the marking (Read and Murray 2000; Moore and Barco 2013).

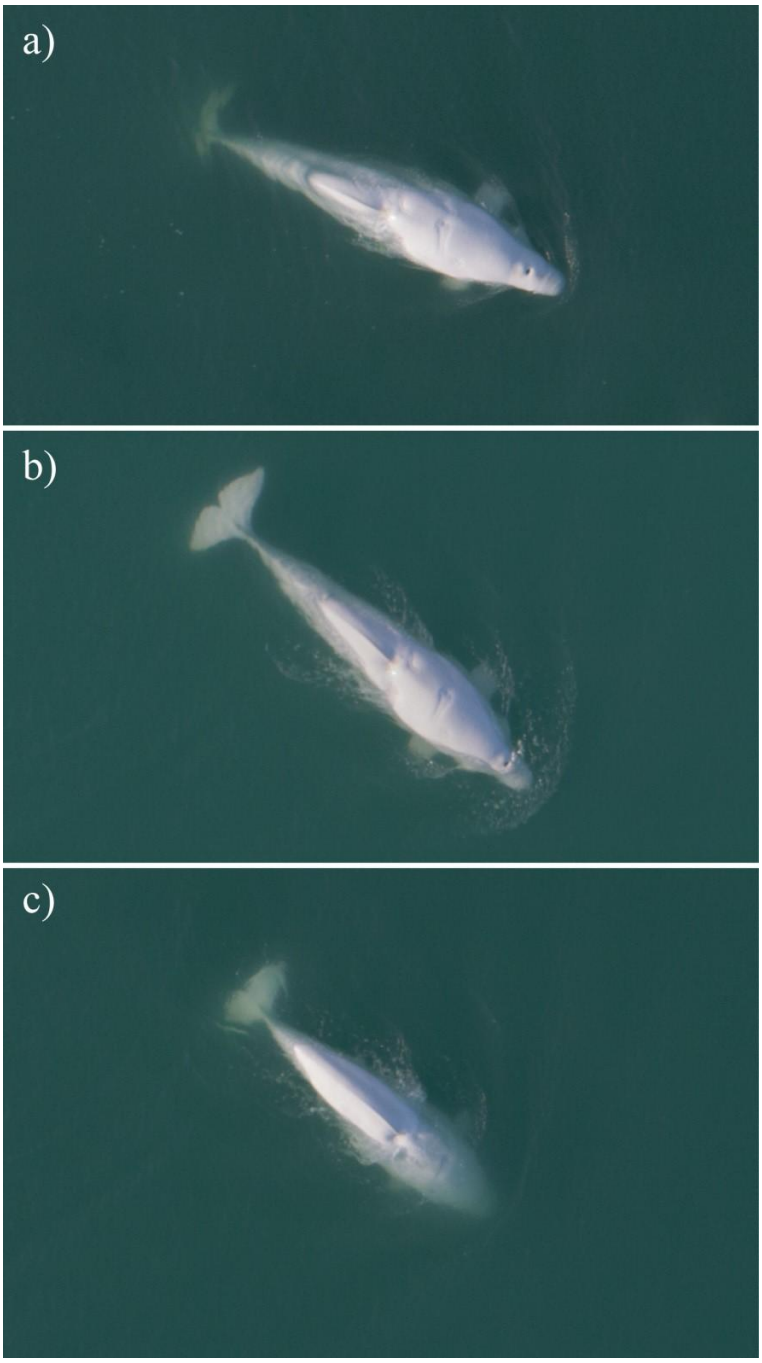


Figure 3.2: Sections used for the photo-ID of beluga whales in Cumberland Sound, divided into (a) anterior, (b) dorsal ridge, or (c) posterior. The right and left sides of the whale were also used to describe locations of markings.

Following the recommendations of Urian et al. (2015), markings were assigned ratings of distinctiveness (i.e., high (very distinct), intermediate (moderately distinct), or low (not

distinct)). The distinctiveness rating was based on shape, color, and size. An individual was considered "identified" if all three sections of the body (i.e., anterior, dorsal ridge, and posterior) were completely photographed or if there were markings in the dorsal ridge section and either anterior or posterior sections; whales without the dorsal ridge section visible were excluded (Fig. 2) (Chernetsky et al. 2011; McGuire et al. 2020*b*). Photographs of all markings and photographs of the entire body of each whale (when possible) were entered into a catalogue in Microsoft Excel and organized into sheets by the location of the marking (i.e., anterior, dorsal ridge, and posterior). Markings from additional survey years were manually compared to historic markings based on size, location, and shape to identify resightings.

Group size was also estimated for each photograph, as well as the number of whales visible, above or below water. Individual groups were differentiated by having at least four body lengths between them (O'Corry-Crowe et al. 2020) and each group of whales was targeted to attempt to capture the entire group within a single photograph, even if this required flying at a slightly higher altitude or taking multiple photographs to ensure capture of all group members. The maximum total size for each group was estimated using the maximum number of whales seen in any one photograph taken during the series of the encounter. Whales were assigned to an age class based on color and size relative to adults: adult (white/white-gray, full size), sub-adult (light gray, >3/4 size of adult), calf (gray, ~2–4 years old, 2/3–3/4 size of adult)[1], yearling (mottled gray, ~1 year old, 1/2–2/3 size of adult), or neonate (brownish-gray with or without fetal folds, <4 months, <1/2 size of adult) (Charry et al. 2018; Vergara and Mikus 2019; McGuire et al. 2021*b*). The proportion of uniquely marked whales was estimated by dividing the number of whales with large or unique markings in a group by the maximum total group size, and then averaged for all encounters (Gerrodette et al. 2019; Wickman et al. 2021). The majority of the Cumberland Sound beluga whale population is found in Clearwater Fiord (Watt et al. 2021), and within this fiord we attempted to photograph all groups of whales encountered during each survey. This represented a random sample of the whales present, which we believe is representative of the majority of the population. Although whales were missed, we have no reason to believe that those whales would be more or less marked than the random sample.

[1] *The older animals in this category are likely dependent on their mothers for social and learning reasons.*

3.4 Results

Over the survey period from 2017 to 2019, 1651 drone photographs were taken of beluga whales in Cumberland Sound. Low-quality photographs (drone altitude too high, drone camera angled, etc.) were discarded to avoid sampling errors, leaving 1137 photographs for analysis (Table 3.1). We photographed 571 beluga whales in 158 groups, including possible repeat sightings. For example, if an individual or group was photographed multiple times in different sessions throughout the day, each session was considered a new group because group membership of unmarked whales may have changed. Mean group size was 3.61 (±2.90 SD), ranging from 1 to 16 whales. There were 93 unique individuals photographically identified over the survey period (Table 3.1); this value does not include marked whales that could not be considered completely identified because a portion of their body was not photographed during the surveys or those in poor-quality photographs. There were 24 resightings of the uniquely identified whales throughout the survey: 8 whales photographed in both 2017 and 2018, 10 whales in 2017 and 2019, and 6 whales in 2018 and 2019. Five whales were sighted during all three survey years (Fig. 3.3). Most whales with unique markings were adults (97%), and the remainder were gray and likely sub-adults based on size (3%). No calves, yearlings, or neonates with scars were observed.

Table 3.1: The number of photographs taken and used during the Cumberland Sound beluga whale photo-ID survey period from 2017 to 2019, and for each survey day: the mean group size with standard deviation (SD), mean number of whales identified with a unique, permanent marking per group and standard error, the total number of whales identified per year, and the number of identified whales that were recaptured in following years, with the number of whales recaptured within the same year reported in parentheses.

Survey	Photographs taken	Photographs used	Group size (SD)	No. of whales identified per group (SE)	No. of new whales identified	No. of recaptured whales
18 August 2017	224	120	3.65 (3.70)	1.39 (0.39)	29	–
11August 2018	367	262	3.59 (2.70)	1.19 (0.23)	21	8
14 August 2019	554	428	3.56 (2.80)	1.11 (0.28)	26	7
22 August 2019	506	327	3.66 (2.81)	0.69 (0.17)	17	6 (4)

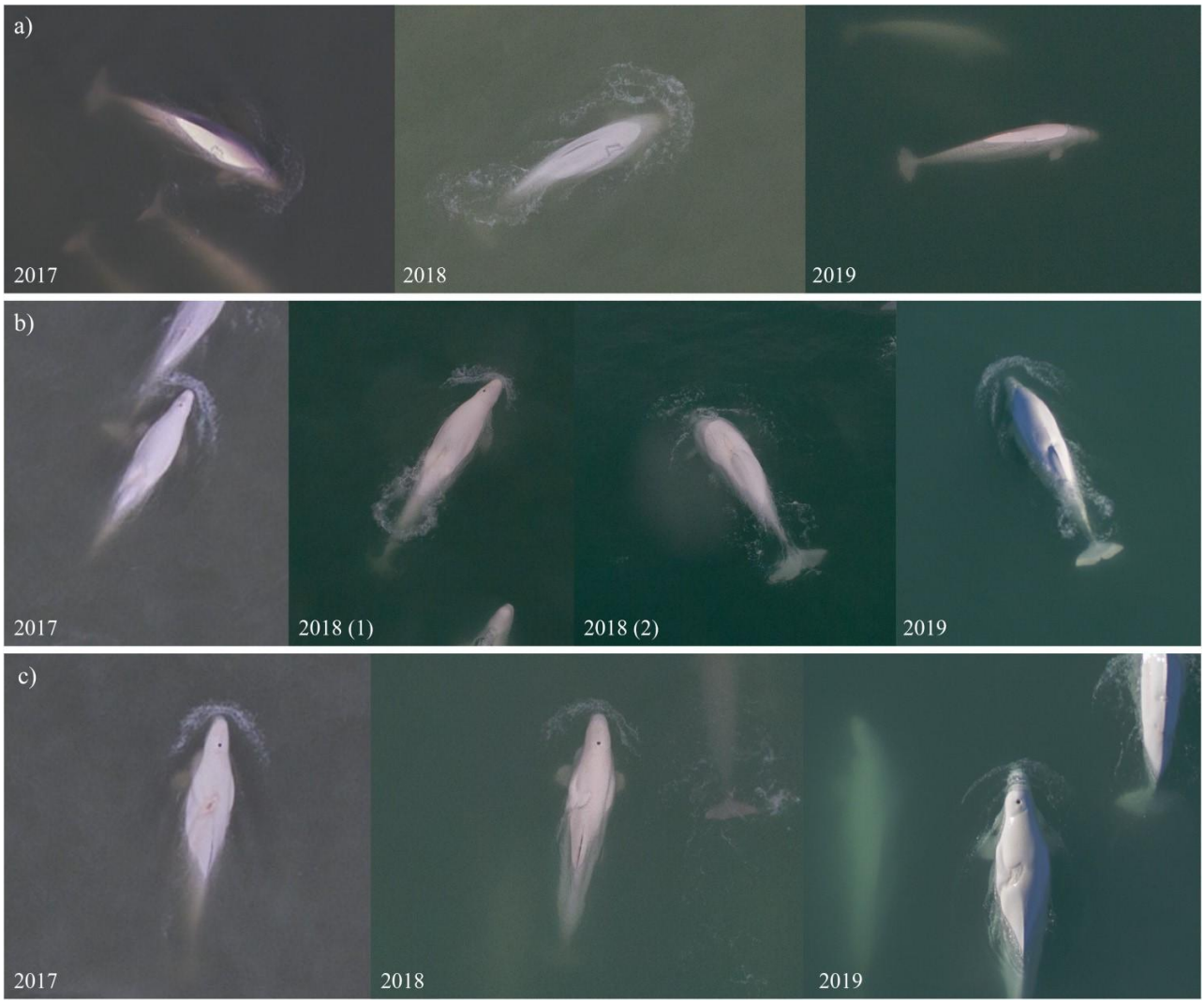


Figure 3.3*:* Three beluga whales identified over three survey years (2017–2019) in Cumberland Sound, Nunavut, Canada. The causes of the markings were (a) unknown, (b) unknown but likely anthropogenic or predatory, and (c) gunshot scar.

We categorized markings based on probable cause as scars from gunshots (representing 11% of marks), scars from bullet grazes (12%), fresh gunshot wounds/grazes (5%), fresh wounds from unknown causes (2%), or scars from unknown causes (59%) (Fig. 3.4). Only one whale with satellite tag scars (1%) was observed, and it had pins from the tag still embedded in the body (Ryan et al. 2022). The remaining markings (10%) were classified as unknown but likely due to anthropogenic or predatory incidents given their large size and the severity of the trauma. Small indentations to the dorsal ridge and surface were common (several in Fig. 3.4*a*), but these were

usually categorized as from an unknown cause unless bullet entry and exit sites could clearly be seen (Fig. 3.4*b*), or if it had the typical shape of a bullet graze decreasing in size along the marking (Fig. 3.4*c*). Larger indentations to the dorsal ridge could not always be classified as scars from gunshots for a similar reason, with clear trauma but no definitive entry and exit (Fig. 3.3*b*). Most markings were scars that appeared to be fully or close to healed (93%). Fresh wounds (7%) were most often observed in 2019 (9% of all markings from that year), compared to 2017 (2%) and 2018 (5%) (Figs. 3.4*b*–3.4*d*), so the full progression of wound healing has not yet been documented. However, a whale with a partially open wound sighted in 2017 was resighted in 2018 with a fully closed scar and again in 2019 with a similar scar (Fig. 3.3*c*). Overall, the percentage of adult whales in the population that were marked with unique scars that are likely permanent given their location or size was 43.4% (SE = 3.3%).

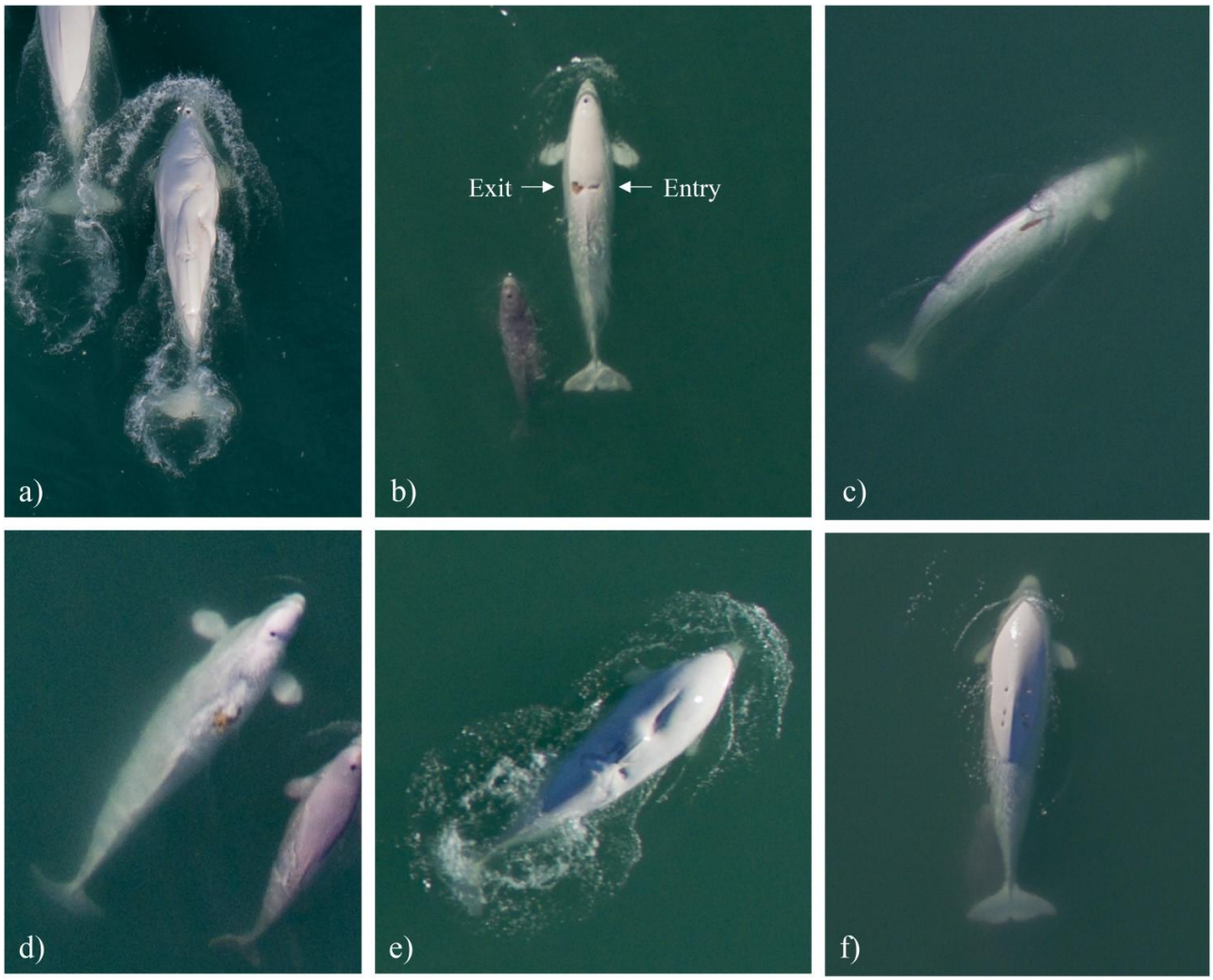


Figure 3.4: Beluga whale markings used for photo-ID in Cumberland Sound from 2017 to 2019. Examples of markings include (a) multiple unknown and bullet graze, (b) gunshot wound (entry and exit), (c) bullet graze wound, (d) gunshot wound, (e) multiple gunshot scars, and (f) satellite tag pins that have been inserted in the whale for 11–21 years at the time the photograph was taken.

3.5 Discussion

The results of this study demonstrated that using drones for photo-ID and monitoring of beluga whales in Cumberland Sound is feasible. Building a photo-ID catalogue of the whales using a minimally invasive method was especially important given the population's small size and research restrictions associated with its endangered status (DFO 2019; COSEWIC 2020). Beluga whales in Cumberland Sound are important in the ecosystem both as a top predator and as a dietary and culturally important species for the local community of Pangnirtung (Stafford et al. 2016; DFO 2019). Since the population is still harvested, some whales are heavily marked with

gross trauma scars that make them easy to identify in drone photographs, but this may be a contributing factor to the strong reactions of the beluga whales to our survey boat and any other anthropogenic activity. The stress levels of beluga whales in Cumberland Sound (as measured by blubber cortisol concentration) are significantly higher than those of other populations (Trana 2014), which may also be contributing to their avoidance behavior. Boat-based photographs were collected in 2018 and 2019 to compare the quality of photographs from this method to the drone photographs. However, the whales were frequently several hundred meters from the boat and typically farther if the engine was on, thus limiting our ability to actively pursue them. Due to these factors, the quality of the drone photographs and the number of whales we could photograph using the drone were superior to boat-based methods.

We found that using drones instead of attempting shore-based photography or pursuing the whales with the boat was not only necessary to minimize the disturbance on the population, but also had several advantages. The drone photographs eliminated the need for separate right- and left-side catalogues; separate catalogues make it difficult to identify a whale completely unless both sides can definitively be linked in the field during photograph collection (Gowans et al. 2000; McGuire et al. 2020*b*). Maintaining separate catalogues also yields two estimates for all variables, such as mortality and population size, instead of one representing the entire population (Gowans et al. 2000; Chernetsky et al. 2011; McGuire et al. 2020*b*). Drone photographs allow for more accurate measurements of group size compared to counts made by boat-based observers, which will yield more accurate abundance estimates in future mark–recapture models (McClintock et al. 2009; Gerrodette et al. 2019; Wickman et al. 2021). Using a drone, especially one that can be launched from a vessel, is an effective alternative to shore-based photography in areas where whales are not close enough to shore to photograph, the shore is not suitable for setting up camp, or in areas where shore work may be dangerous (bears, etc.), including in Cumberland Sound.

Photo-ID as a tool is more successful and robust when a large proportion of the population is marked (Gowans and Whitehead 2001; Wickman et al. 2021). The proportion of marine mammals that are marked varies among species, by location, and depending on the methods used (Gowans et al. 2000; Landeo-Yauri et al. 2020; Feyrer et al. 2021). For example, as few as 10% of individuals were marked in a population of Hector's dolphins (*Cephalorhynchus hectori* (P.-J.

van Bénéden, 1881)) (Gormley et al. 2005), 21% of Antillean manatees (*Trichechus manatus manatus* Linnaeus, 1758) (Landeo-Yauri et al. 2020), and 34% of long-finned pilot whales (*Globicephala melas* (Traill, 1809)) (Ottensmeyer and Whitehead 2003), while as many as 48% of northern bottlenose whales (*Hyperoodon ampullatus* (Forster, 1770)) (Feyrer et al. 2021) and 88% of sperm whales were identifiable (Matthews et al. 2001). In beluga whales, because photo-ID has been used relatively rarely, there are few estimates of the proportion of marked whales. However, in an area of the White Sea, the proportion ranged from 13% to 47%, depending on the year, and was less than 30% in five of seven survey years (Chernetsky and Krasnova 2018). The relatively high rate (43%) of unique markings we found that are likely permanent given their size or location and the number of resightings (24) over the three years of study in Cumberland Sound suggest this may be a viable method to monitor the population size using mark–recapture techniques.

The permanence of scarring in beluga whales is less well known than for other species. It has been suggested that the longevity of scars in beluga whales is reduced by the molting process whales undergo each year, shedding the outermost layers of their skin during summer (St. Aubin et al. 1990; Krasnova et al. 2015). However, some markings that appeared to be small have persisted and remained unchanged over all 3 years of the study, which merits further investigation. It is difficult to establish the depth of wounds from drone photographs, so it is possible that small markings that are deeply embedded will last longer than those that are small and superficial, such as rake marks. Longevity of markings and scars has also been noted in Cook Inlet, where scars did not appear to change over time or changed in ways in which the scar was still recognizable (e.g., debris accumulation in the scar and roughening of the scar surface) (McGuire et al. 2021*b*). These results align with our observations, reinforcing the need to determine whether smaller markings can be reliably used for long-term identification. As the photo-ID catalogue continues to develop, closely monitoring both large, likely permanent scars and smaller markings on the same individuals will help assess their feasibility for identification. The proportion of scarred individuals is also expected to increase over time, both as more is learned about which markings are unique and permanent—allowing for more confident classifications—and as the harvest continues, leading to new scarring each year.

Most markings were the result of unknown causes or gunshot scars, grazes, and open wounds. Although sightings of killer whales in the eastern Canadian Arctic, including Cumberland Sound, have increased in recent years (Higdon et al. 2012; Young et al. 2019) and predation may have an impact on the small population, killer whale interactions were not identified as the definitive cause of any of the markings. This may be because rake marks were rarely seen in the drone photographs, and larger evidence of predation was not observed or could not definitively be determined (and thus was categorized as unknown anthropogenic/predatory). Markings from conspecifics, including rake marks, were also uncommon, likely because they were too small or shallow to be seen in the drone photographs. Some of the unknown markings, especially to the dorsal region, might have been caused by sharp edges of ice when whales travel through heavy ice areas (Suydam et al. 2001; Kaplan et al. 2009; Krasnova et al. 2015). There is also evidence that beluga whales rub their skin on the seafloor substrate during molting to promote the shedding of dead skin, which may produce markings as well (Krasnova et al. 2015; O'Corry-Crowe 2018). Many of the unknown markings were located along the dorsal ridge and could be from ice or substrate, or from glancing gunshot wounds. Indentations to the dorsal ridge are particularly helpful in the photo-ID of beluga whales because these markings are likely permanent (Krasnova et al. 2015).

Other types of markings, such as hypopigmentations (a portion of skin lighter than the surrounding skin) and hyperpigmentations (darker), were hard to distinguish from scars due to the aerial view of the photographs and the difficulty in judging the depth of markings, and were therefore classified as unknown; some of these markings could still be used to identify the whales. Krasnova et al. (2015) suggested that pigmented markings might last over the lifetime of a beluga whale; they documented a hyperpigmented spot that was unchanged on a whale over a period of 12 years. These types of markings also lasted 3 years or greater in light-gray and gray individuals, suggesting that some juveniles may be able to be reidentified over more than one season (Krasnova et al. 2015). Infections and lesions were either not visible or not present in the photographed whales in Cumberland Sound, though some of these (e.g., herpes virus) disappear within a year, and therefore would not be useful for reidentification (Krasnova et al. 2015).

Anthropogenic sources, apart from gunshot-related markings, were not identified as the apparent cause of any of the markings. There were no confirmed occurrences of vessel strike or

entanglement that are more common in heavily trafficked populations (Krasnova et al. 2015; McGuire et al. 2021*b*), though they could have caused some of the larger deformations in the dorsal ridge that were categorized as unknown anthropogenic/predatory. Deformations in the dorsal ridge were rare but were always accompanied by a scar near the deformity. Given the relatively remote location of Cumberland Sound beluga whale habitat, a low occurrence of vessel strikes would be expected. Only one whale with evidence of satellite tagging was observed during our study, with the pins from the tag still inserted in the whale's dorsal ridge. The Cumberland Sound population was tagged intermittently from 1998 to 2008, meaning that at the time the whale was photographed in 2019 the pins had been retained in the whale for at least 11 and up to 21 years (Watt et al. 2016; Ryan et al. 2022). Signs of infection around the tag site were not observed in this whale, but have been documented in other populations (McGuire et al. 2021*b*). Potential recaptures of this whale, which was accompanied by a yearling, and other tagged whales in the population over the course of the program, could provide additional information about the long-term effects of satellite tags.

The high rate of gunshot scars, bullet grazing, and fresh wounds from gunshots has not been documented in any other beluga whale population. One probable reason for this high rate is that the populations with long-term photographic monitoring are currently not harvested regularly or at all, and whales with gunshot scars from previous years of hunting are aging out of the population (Krasnova et al. 2015; McGuire et al. 2021*b*). In Cook Inlet, for example, only 3% of re-identified whales had one or more markings from gunshots, likely because hunting was limited to five whales from 1999 to 2005 and then ceased altogether beginning in 2006 (NMFS 2016; McGuire et al. 2021*b*). Similarly, in the St. Lawrence estuary, crater-like scars present in some whales may be the result of gunshots but were more common in older whales and were detected less frequently over time, which may be attributed to the whales being protected from hunting since 1979 (Le Net et al. 2021). Gunshots were also mentioned as a cause of scarring in beluga whales from the White Sea, but an estimate for the proportion of the population with these markings was not provided (Krasnova et al. 2015).

Gunshot wounds can vary depending on the type of firearm and ammunition used, the angle of the shot, and the distance between the firearm and whale (Moore and Barco 2013); thus, identifying which markings were created by gunshots was not always possible. Some of the

indentations in the dorsal ridge may have been caused by bullets shot perpendicular to the whale that grazed the area. These marks were hard to distinguish from the aforementioned naturally occurring indentations from ice or substrate, and were therefore classified as unknown if they were lacking the typical bullet graze tapering shape. Similarly, holes created by bullets, when the exit wound is not visible, are almost impossible to classify as gunshot wounds because there are no identifying features associated with them (Moore and Barco 2013). For these reasons, the number of all types of gunshot-related markings is likely higher than estimated in our study.

Although commercial hunting of whales ended in 1966, the Cumberland Sound beluga whale population has not recovered to historic levels (DFO 2019). The current subsistence harvest of beluga whales in Cumberland Sound is considered unsustainable and is likely contributing to a lack of population growth over the past 60 years (DFO 2019), though changes in prey composition and competition with fisheries may also be contributing to the lack of population growth (Watt et al. 2021). The estimated number of whales struck by a gunshot and assumed lost during the annual hunt, given the quota of 41 landed whales, is 15 whales (Watt et al. 2021). During drone surveys, the identification of fresh gunshot wounds that are likely from the harvest of the same year may provide information on numbers, persistence, and likelihood of mortality of wounded animals. Over the 3-year study, most fresh wounds were observed during 2019 (including five from gunshots and three from unknown causes), so if wounded whales are resighted in future drone surveys, monitoring the progression of wound healing should be a high priority. Only two gray individuals had scars, and based on size, they were at least sub-adults if not adults. No calves, yearlings, or neonates had scars. This may be due to low survival rate of juveniles when shot, and could be a contributing factor to the lack of growth in the population over time (McGuire et al. 2021*b*).

The research outlined here are the first published results of a photo-ID program developed for a beluga whale population using solely drone photographs. The majority of markings identified in this study were of unknown cause or resulted from gunshots. The applicability of drone photo-ID to other beluga whale populations where harvesting does not occur is undetermined, but warrants further investigation. However, the use of drones to create a photo-ID catalogue can certainly be adapted to other species and environments. The flexibility of following the animals while minimizing the disturbance to them was one of the key benefits of this study. Other benefits

included capturing both sides of the animal in photographs and obtaining more accurate estimations of group size; the latter is important when estimating abundance using mark–recapture methods, and abundance estimation is a long-term objective of this study as more data are collected (Wickman et al. 2021). The continuation of the Cumberland Sound beluga whale photo-ID program will also provide insights into their biology (e.g., calving interval, period of dependence, and wound healing), social structure, and distribution, which are important parameters to assess for endangered populations (Suydam 2009). Overall, drone photography offers a cost-effective, minimally invasive, and long-term strategy to monitor the Cumberland Sound beluga whale population and will help inform sustainable management decisions.

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Chapter 4 - Assessing age structure and social organization in an endangered whale population through aerial and drone surveys

4.1 Abstract

Social systems play a crucial role in the development of social species, influencing their interactions within ecosystems and responses to environmental shifts and threats. Understanding how members of a population distribute themselves in their habitat, interact with conspecifics, and use resources is vital for predicting resilience. As an Arctic resident species, beluga whales (*Delphinapterus leucas*) are facing threats including shifting prey distribution and environmental changes. Despite these challenges, our understanding of beluga whale population dynamics and social systems, especially in the endangered Cumberland Sound population, remains limited. To address this gap, we conducted aerial surveys in 2014 and 2017, complemented by drone focal follows from 2017 to 2019, to quantify the social organization and structure of this population. Aerial surveys indicated a potential contraction in the geographical range of the population. Furthermore, we observed a lower proportion of juveniles, particularly subadults, compared to other populations. Single whales were most commonly observed in aerial surveys, but were also frequently seen in drone surveys, alongside larger groups with multiple adult whales and mixed groups with at least one calf. We noted stable associations between individuals across days and years, indicating the persistence of social groups. Our dual approach used drone surveys for high-resolution data, enabling detailed analysis of age class and group composition, and aerial surveys for extensive photographic coverage of the majority of all social groups, though at a lower resolution. These complementary methods enhanced our understanding of beluga whale social dynamics and population health in Cumberland Sound. Such knowledge is imperative for creating effective conservation strategies in the face of escalating environmental change and anthropogenic pressure.

4.2 Introduction

Social systems are largely shaped by the benefits and costs of group living, such as predator defense contrasted with increased conspicuousness, and the ability to find resources versus increased competition (Alexander, 1974; Brakes, 2019; Silk, 2007). These trade-offs differ not only among species but also across environments, and can be extremely complex (Brakes, 2019;

Kappeleret al., 2013). The social system of a species consists of four parts: social organization (i.e., the size and composition of groups), social structure (i.e., aspects of social interactions and relationships between group members), mating strategy (i.e., set of behaviors and tactics employed to maximize individual reproductive success), and the care system (e.g., parental care, allo-parental care) (Hinde, 1976; Kappeler, 2019; Kappeler et al., 2013; Kappeler & van Schaik, 2002; Wilson, 1975). These components are influenced by various factors, including life history parameters, ecological conditions, and demographic traits (Kappeler, 1999; Kappeler et al., 2013; Trivers, 1985). Social systems directly affect the biology and ecology of species, influencing mating systems, genetic structure, how environments are used, and the transmission of social information and behavior (Brakes, 2019; Cantor et al., 2021; Kappeler et al., 2013; Lusseau et al., 2006). Understanding species' social systems and their components is imperative because of their role in the survival of individual animals and the resilience of populations (Brakes, 2019; Cantor et al., 2021).

In odontocetes, larger body size correlates with more stable social groupings, a trend that reflects extended life-history processes such as lactation and post-weaning maternal care (Rendell et al., 2019). For example, small dolphins (*Tursiops* spp.) form fission-fusion societies with groups that rapidly form and fracture and have highly variable group membership, while larger odontocetes, such as killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*), have multilevel stable societies based on kinship with the mother's family line (hereafter referred to as matrilineal) (Brent et al., 2015; Connor et al., 2000; Mahaffy et al., 2015; Rendell et al., 2019; Williams & Lusseau, 2006). Odontocete calves require a relatively long learning period to develop the necessary skills for independent foraging compared to other marine mammals because their foraging tactics are generally complex and involve group pursuit of prey (Brodie, 1969; Rendell et al., 2019). Additionally, juveniles benefit from the transmission of other types of knowledge such as inherited social networks or matrilineal migration routes (Rendell et al., 2019). Within odontocetes, as in other species, intraspecific variation occurs in social systems; this variation is sometimes due to environmental variability, resulting in diverse adaptive strategies (Kappeler et al., 2013).

In ecosystems undergoing significant transformations, such as the Arctic, which is experiencing rising temperatures and habitat alterations, understanding social systems is critical. Understanding these systems can provide insight into how species native to these environments, like beluga whales (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*), interact with conspecifics and care for their offspring. This knowledge becomes even more crucial as Arctic sea ice, ice-associated habitats, and prey species continue to be affected by climate change (Burek et al., 2008; Laidre et al., 2008; Bailleul et al., 2012; Choy et al., 2020; Heide-Jørgensen et al., 2010; Williams et al., 2021). Beluga whales and narwhals, the only odontocetes endemic to the Arctic, play vital roles in the Arctic ecosystem as nutrient recyclers, predators, and prey. Despite their importance, our understanding of their social systems remains limited (Bowen, 1997; Kiszka et al., 2015; Laidre & Heide-Jorgensen, 2005; Shelden et al., 2003). Understanding these dynamics is vital for conservation efforts aimed at mitigating the impacts of environmental changes on these species.

The social organization of beluga whales is not yet fully understood; it could be as stable and structured as that seen in larger odontocetes like sperm whales and killer whales, or as variable as that of smaller dolphins, or it may display elements of both (Brodie, 1971; Garde et al., 2015; Gowans, 2019; Michaud, 2005; Newsome et al., 2009; Ortega-Ortiz et al., 2011; Rendell et al., 2019; Sergeant, 1973; Williams & Lusseau, 2006). Related beluga whales have been found to be closely associated during migration and across several years and even decades within herds at their summering grounds, suggesting stable associations between kin (Colbeck et al., 2013; O'Corry-Crowe et al., 2018; Ryan et al., 2022). Since beluga whales can migrate hundreds to thousands of kilometers to and from their summering grounds, these associations may be important for transmitting and maintaining migratory culture (Hobbs et al., 2020; O'Corry-Crowe et al., 2018). Beluga whale social systems differ from sperm and killer whales, however, as groups may be comprised of both kin and non-kin, many kin are paternal rather than maternal relatives, and group size and composition can be more variable (Krasnova et al., 2012; Loseto et al., 2006; O'Corry-Crowe et al., 2020). There may also be differences between the sexes, with males potentially forming long-term bonds, and females having looser and more fluid networks (Michaud, 2005). There is also evidence of seasonal, cyclical, and geographic variation in important life-history parameters that could differentiate beluga whales from other odontocete

species and even differentiate individual beluga whale populations. This population variation can include differences in the timing of calving and changes in birth rate over time (Beck et al., 1994; Burns & Seaman, 1986; McGuire et al., 2020; Michaud, 2014; Mosnier et al., 2015; Sergeant, 1973).

The beluga whale population in Cumberland Sound, Nunavut, is classified as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and listed as threatened under the Species at Risk Act (SARA), with ongoing considerations to elevate its status to endangered under SARA (COSEWIC, 2004; COSEWIC, 2020; Fisheries and Oceans Canada, 2024). These designations come in part as a result of extensive commercial whaling dating back to the mid-19th century (DFO, 2016; Stewart, 2018). There has been a quota of 41 whales landed per year for the local Inuit hamlet of Pangnirtung since 2002 in an attempt to avoid further population decline (COSEWIC, 2004; COSEWIC, 2020; Watt et al., 2020). The most recent aerial survey in 2017 estimated 1,381 whales in the population (95% CI = 760–1744), indicating that the population has not recovered to the pre-whaling estimated size of 8,500 whales (COSEWIC, 2004; DFO, 2016, 2019). Population models indicate that the Cumberland Sound beluga whale population may continue to decline under the current quota (Watt et al., 2020). Although the most significant decline in the population occurred during commercial whaling, the population continues to be overexploited and shows elevated signs of stress compared to other populations (Kucheravy et al., 2022; Watt et al., 2020). As such, this population may experience other consequences associated with overexploitation and stress such as a lower birth rate and a contraction in range (Davidson et al., 2012; Wade et al., 2012; Worm & Tittensor, 2011). While satellite tagging (Watt et al., 2016) and aerial surveys conducted using people and/or cameras in aircraft (hereafter referred to as aerial surveys or aerial photographs) (DFO, 2019; Watt et al., 2020) have been used every few years over the past two decades to monitor the population, few studies have evaluated detailed aspects of the Cumberland Sound population's demographics and social system.

The Cumberland Sound beluga whale population is one of only five resident beluga whale populations worldwide that remains within a relatively small geographic area throughout the year (Richard and Stewart, 2009; Hobbs et al., 2020; although see DFO, 2022). Evidence from Inuit

Qaujimaningit (IQ, also referred to as Inuit traditional knowledge), satellite tagging, and aerial surveys indicates that in the summer they remain towards the northern extent of the sound largely concentrated in a small area called Clearwater Fjord and overwinter approximately 200 miles south towards the mouth of Cumberland Sound (Kilabuk, 1998; Richard & Stewart, 2009; Watt et al., 2020). During aerial surveys in summer, 52–86% of the population was found in Clearwater Fjord. The population may also be smaller than previously estimated based on the presence of whales from another population in Cumberland Sound as determined using genetic assignment (DFO, 2022). The presence of other whales, which could be either temporary or permanent residents in Cumberland Sound, would likely have been incorporated in the aerial surveys and thus overinflated the abundance estimate (DFO, 2022). The whales summering in Clearwater Fjord, however, are considered to be genetically isolated from other populations (DFO, 2022). Factors such as geographic isolation and patchy food resources can promote social stability and group fidelity because a lack of immigration/emigration promotes associations between relatives (Acevedo-Gutiérrez 2018; Lusseau et al. 2003). If the Cumberland Sound population is geographically separate from others, their social structure may be more stable than in populations that overlap and breed with others.

Photographic identification (photo-ID) can be a powerful and cost-effective means to monitor populations (Beck et al., 2020; Landeo-Yauri et al., 2020; Schofield et al., 2020; Wickman et al., 2021). The minimally-invasive methods used to capture photographs are ideal for populations that are at risk of being disturbed by traditional research methods (Beck et al., 2020; Koski et al., 2015; Ryan et al., 2022; Schofield et al., 2008; Young et al., 2011). Drones offer an additional advantage for studying marine mammal populations that are not easily accessible or show high avoidance behaviors, in that they can be followed and photographed for a longer period of time with less disturbance than traditional boat-based surveys (Álvarez-González et al., 2023; Landeo-Yauri et al., 2020); because of these advantages, the use of highly-detailed drone photography allows for more detailed group membership analyses. The photo-ID of individuals also enables the reidentification of individuals and examination of social structure and group membership over a day, weeks, and several years when whales are opportunistically resighted. This approach allows for the detection of associations between identified individuals over time.

Here, we combined drone focal follows (hereafter referred to as drone surveys) (Ryan et al., 2022) and aerial surveys to examine the social organization of the Cumberland Sound beluga whale population. Specifically, our objectives were to 1) evaluate trends over time in beluga whale group size and composition, including the proportion of calves; 2) examine the distribution of the population within Clearwater Fjord and identify any possible contraction in distribution that may be associated with an overexploited population undergoing stress; and 3) examine associations between individual whales over time.

4.3 Methods

The Cumberland Sound beluga whale population remains within or just outside of the sound throughout the year (Richard & Stewart, 2009), with the majority of the population within a small area called Clearwater Fjord during the summer (Figure 4.1) (Kilabuk, 1998; Marcoux & Hammill, 2016; Richard & Stewart, 2009; Watt et al., 2020). We focused photographic surveys in the summer on the Clearwater Fjord area to capture as much of the population as possible. These surveys aimed to investigate the distribution of age classes across different years and survey methods, assess any significant changes or trends, and compare the results from each method. Beluga whales are long-lived; individuals have been aged up to 77 years using tooth growth layer groups (Luque & Ferguson, 2010), though they may live longer given natural wear on teeth that may affect the ability to accurately count growth layer groups. Also, their closest relative, the narwhal, had a 107-year-old individual identified using aspartic acid racemization (Garde et al., 2022).

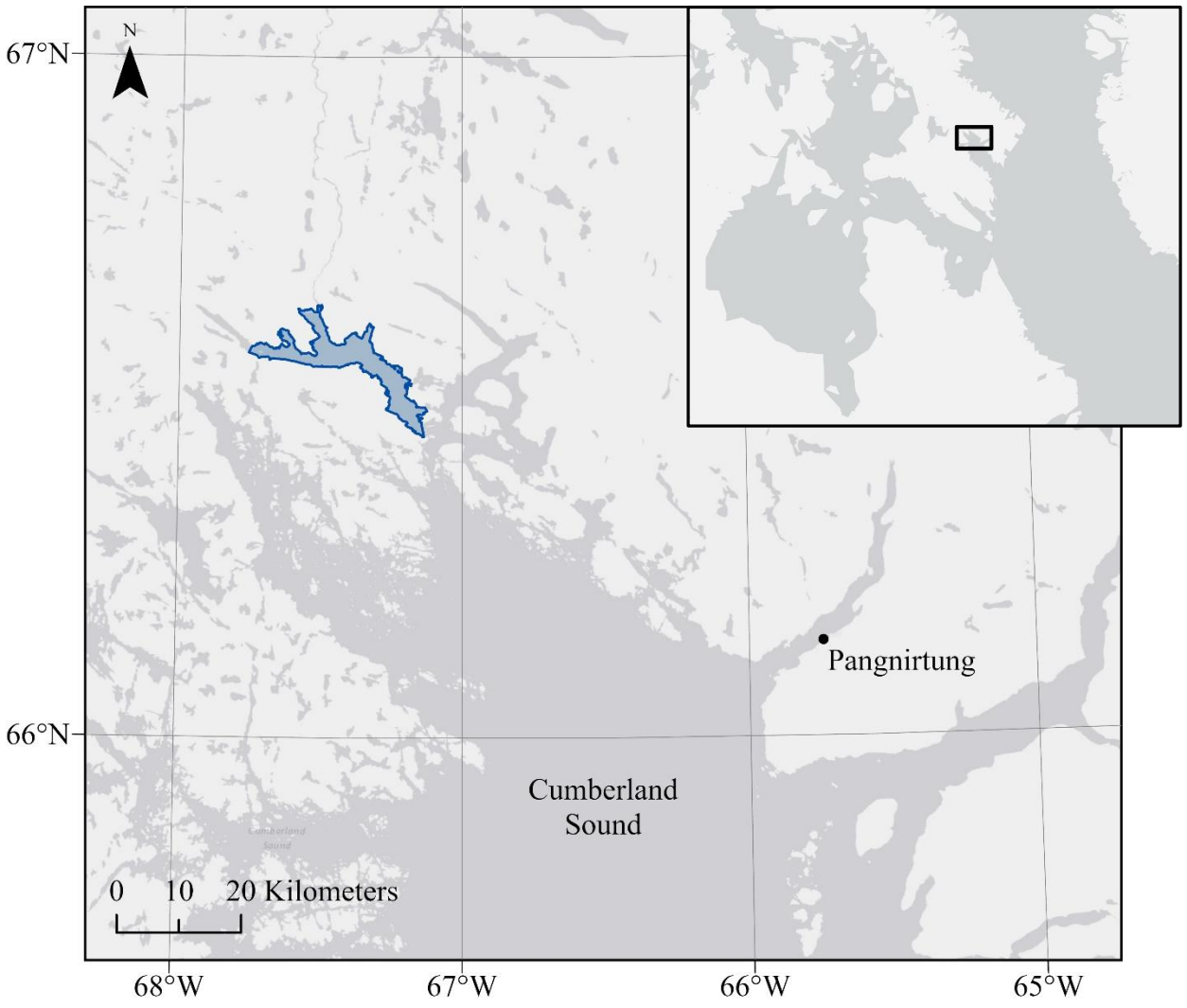


Figure 4.1: The study area in Cumberland Sound, Nunavut, Canada. The approximate area of Clearwater Fjord is marked in blue shading, and the Pangnirtung community is denoted with a black circle.

The calving season of beluga whales usually spans a few months between March and October, with variation between populations (Krasnova et al., 2014; McGuire et al., 2020). The calving season in Cumberland Sound was reported to be late July to early August (Brodie 1971) but with a lack of recent data this estimate warrants further investigation. Beluga whales are born gray and become more white over time, allowing the assignment of approximate age classes based on size and color (Burns & Seaman 1986; Hobbs et al. 2016). Beluga whales usually attain sexual maturity between 5 and 14 years old, with females generally maturing earlier, beginning around age 5 (Heide-Jørgensen and Teilmann 1994; Suydam 2009; Jefferson et al. 2011; Ferguson et al.

2020). In contrast, male beluga whales typically start maturing at age 8 (Heide-Jørgensen and Teilmann 1994; Suydam 2009; Jefferson et al. 2011; Ferguson et al. 2020). Color was not used as a proxy for sexual maturity here, since some beluga whales remain gray well after reaching sexual maturity while others turn white before they are sexually mature (Jefferson et al. 2011; O'Corry-Crowe 2018; Suydam 2009).

Aerial surveys

Aerial surveys were conducted in 2014 and 2017 in a de Havilland Twin Otter (DH-6) (see Watt et al., 2020 for detailed methods). Four surveys were conducted in August 2014 and five surveys were conducted in July and August 2017 (Table 4.1), and all nine surveys had full photograph coverage of the Clearwater Fjord area (approximately 130 km^2) (Figure 4.1). These flights were conducted at an altitude of 610 m and a speed range of 100–110 knots (185–204 km/h). Photographic data were captured using two Nikon D810 cameras, each fitted with a 25 mm lens and mounted at the aircraft's rear, pointing directly downward. This setup ensured a ground coverage of 875.4 m by 585.2 m for each photograph, achieving a 20% side overlap between adjacent transect photographs. When the photographic overlap captured the same group of whales in multiple images, the photograph that depicted the largest group and/or provided the clearest view for determining age classes was selected for analysis. Any duplicate sighting in another photograph was excluded from the dataset. The cameras were georeferenced through a GPS receiver (Bad Elf GPS Pro+) connected to a Foolography Unleashed D200+ Bluetooth Module, allowing for precise location tagging of each image. To maintain the necessary overlap amidst varying flight conditions such as speed, altitude, and pitch adjustments, photographs were taken at intervals of 7–8 seconds. Optimal conditions for water clarity were targeted by coordinating flight times with high tide phases in Clearwater Fjord.

Table 4.1: Data on aerial and drone surveys conducted on beluga whales in Clearwater Fjord within Cumberland Sound, Nunavut.

Survey type	Date	Time (EDT)	# Groups observed	Mean group size (±SE)	Range of group sizes	Proportion single whale	Time of nearest high tide*
Aerial survey	3 August 2014	08:15 - 11:56	198	1.8 ± 0.1	1-18	59%	10:46
	4 August 2014	12:47 - 16:11	168	2.6 ± 0.2	1-19	51%	11:42
	10 August 2014	07:55 - 11:38	173	1.4 ± 0.06	1-5	71%	05:44
	11 August 2014	08:38 - 12:17	118	1.8 ± 0.1	1-11	64%	06:30
	29 July 2017	15:47 - 18:50	55	1.7 ± 0.2	1-10	75%	09:16
	4 August 2017	15:05 - 18:00	308	2.1 ± 0.1	1-15	48%	15:24
	7 August 2017	13:45 - 17:10	292	3.1 ± 0.1	1-16	23%	17:23
	8 August 2017	14:15 - 17:35	360	2.4 ± 0.1	1-17	38%	17:58
	12 August 2017	09:35 - 13:00	363	2.0 ± 0.09	1-14	55%	08:12
Drone survey	18 August 2017	12:23 - 18:46	23	3.7 ± 0.8	1-16	43%	14:59†
	11 August 2018	12:49 - 16:52	37	3.6 ± 0.4	1-14	24%	18:28
	14 August 2019	08:14 - 13:55	45	3.6 ± 0.4	1-11	20%	08:13
	22 August 2019	08:04 - 14:11	53	3.7 ± 0.4	1-12	25%	15:56

* The tidal prediction data are from The Tides, Currents, and Water Levels Website (DFO).
† Tidal prediction data are from Historic Tide and Tidal Current Tables (NOAA).

The density of beluga whales within Clearwater Fjord was estimated using the kernel density tool in ESRI ArGIS Pro (Version 3.1.0), based on all sightings of whales on all days in the 2014 and 2017 surveys. The boundaries of the photographic survey coverage in the aerial surveys were used as a barrier feature in the kernel density calculation for both years to avoid low density values that would have occurred on the borders of the survey area and outside the survey area, including areas on land. These methods were repeated to calculate the kernel density of juvenile whales, as well as neonates only, in order to identify potentially important calving and nursery grounds for the population (see methods for determining age class below).

Drone surveys

Drones were used to collect photographs for the photo-ID program in August 2017–2019 over 1–2 survey days within the same geographic area as the aerial surveys but covering a smaller area (Table 4.1; Figure 4.2) (see Ryan et al., 2022 for detailed methods). During the drone surveys, groups were opportunistically photographed using focal follow methods in Clearwater Fjord each year. The groups were followed with the drone until all group members had been photographed or until the group dove out of view, with each of these sessions being considered a separate encounter. This approach allowed us, in most cases, to examine group membership more thoroughly than traditional boat-based survey techniques. We captured photographs for an average of 36.5 seconds per group, ranging from single photograph (1s) of one individual to several photographs and videos of large groups (3min). The maximum group size was recorded for each group, with the goal of counting each whale, whether marked or unmarked, only once within that group. Even poorly marked whales could sometimes be identified as the same or different individuals during these series of photographs based on size, color, small scars, or other temporary scars or markings. Approximately 2.7 km^2 of Clearwater Fjord was photographed on August 18, 2017, 3.5 km^2 on August 11, 2018, 3.0 km^2 on August 14, 2019, and 4.9 km^2 on August 22, 2019. Although we scanned a larger area during the drone surveys, these values represent the areas where whales were both encountered and photographed, and where the photographs were of high enough quality to be used for analysis. To delineate group membership, we used the same distance between individual whales for both drone and aerial

surveys, with groups defined as all individuals within four adult body lengths of another whale (O'Corry-Crowe et al., 2020).

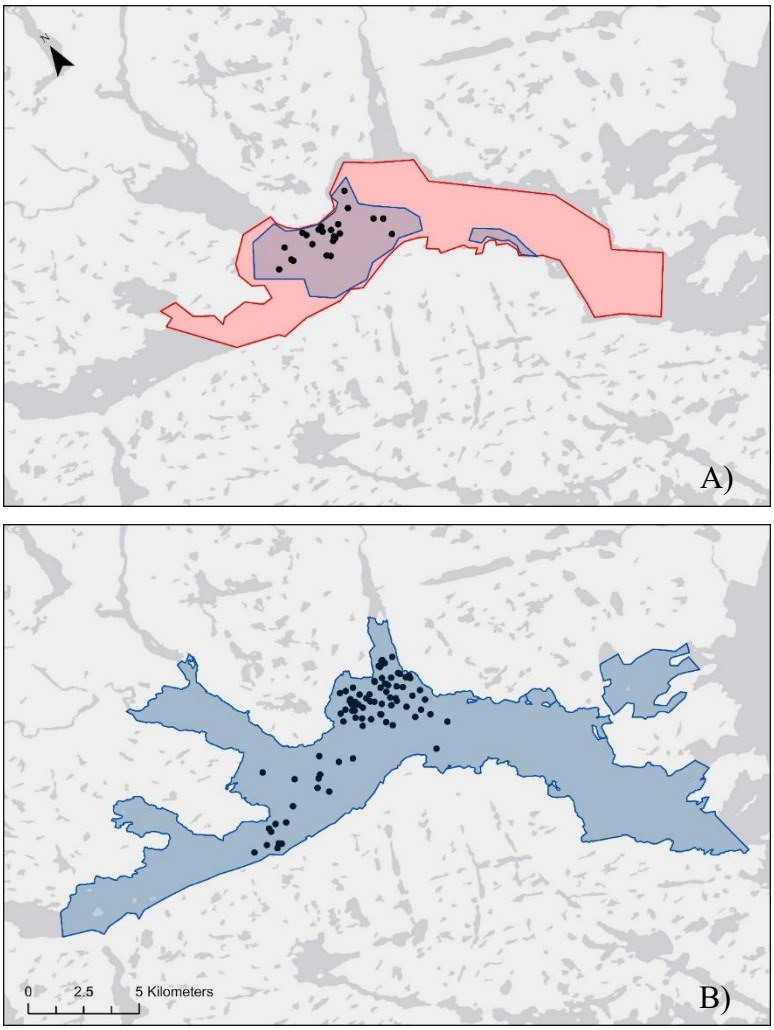


Figure 4.2: Neonates observed in Clearwater Fjord, Cumberland Sound in the drone surveys from 2017, 2018, and 2019 (A) and aerial surveys in 2014 and 2017 (B). The approximate visual coverage of the drone survey is outlined in red, and based on opportunistic sightings within this area, the photographic coverage is outlined in blue (A). Complete photographic coverage of Clearwater Fjord from the aerial survey is outlined in blue (B).

Individual adult whales were uniquely identified in the drone photographs, primarily using markings from unknown origins, scars/wounds from gunshots, and markings that were likely

either anthropogenic or predatory given their size and severity (Ryan et al., 2022). Only unique marks that were likely to be permanent were used in the photo-ID catalog, which allowed us to identify individual whales and reidentify them over multiple years (Figure 4.3). These marks were usually large scars along the dorsal surface of the whale. Although beluga whales do molt the outer layers of their skin each summer and lose more superficial scars, even small scars appear to be long-term and scars in the dorsal ridge are thought to be permanent (Krasnova et al., 2015; McGuire et al., 2021). Photograph quality was also considered to avoid sampling errors, where only photographs of sufficiently high quality to distinguish scars and markings were used (Ryan et al. 2022). Using the photo-ID recapture data, we examined associations between individual whales within a day, a week, and across multiple years. We estimated the total number of whales seen each day by estimating the maximum size of each group. Each encounter was considered a new group, even if some of the same group members were identified earlier in the survey, because group membership may have changed over the course of the day.

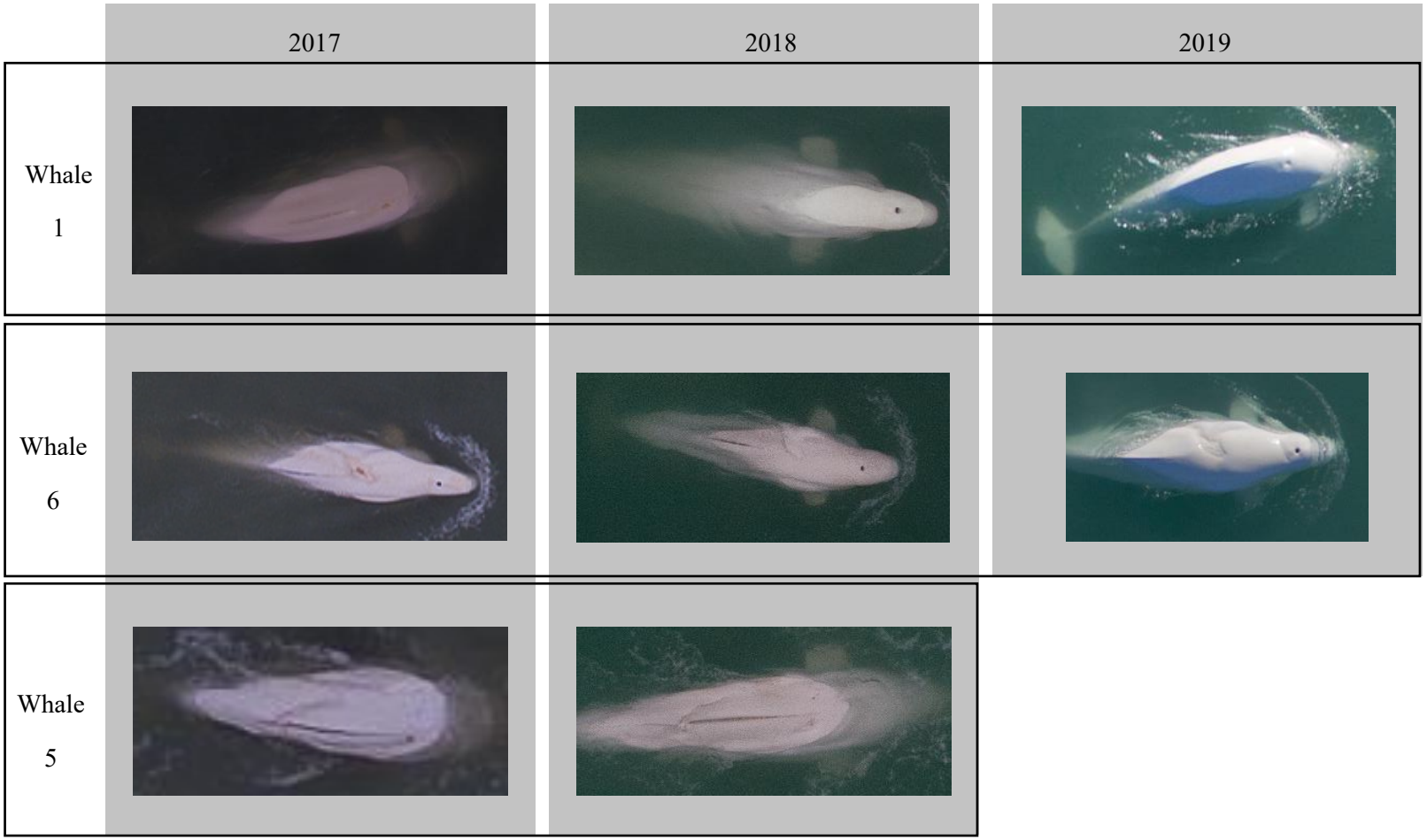


Figure 4.3: Identified beluga whales associated in the same group from drone surveys in 2017, 2018, and 2019. Whales 1 and 6 were in the same group every year, including on two separate occasions approximately two hours apart in 2019, while Whale 5 was seen in the same group in 2017 and 2018, but not in 2019. The whale ID numbers used here correspond to the whale numbers used in Table 4.2. Whale 6 demonstrates healing over time, where in 2017 the wound had begun healing though had not yet finished scarring over, had closed by 2018, and remained unchanged in 2019 due to the severity of the scar.

Data analysis

The approximate age class of each whale was recorded whenever possible for both the aerial and drone photographs (Figure 4.4). We defined six age classes: 1) neonates (born during the current summer season, 1/3–1/2 the size of an adult, and often gray or brown in coloration), 2) yearlings (born during the previous season, 1/2–2/3 the size of an adult and usually darker in color, often with dark mottled patches), 3) subadults (2/3–4/5 adult size, and light gray in color), 4) juveniles of unknown age class (i.e., potentially belonging to any of the 3 previous age classes), 5) adults (white in color) (McGuire et al., 2020; Michaud, 2014), and 6) whales of an unknown age (Figure 4.4). Fetal folds, which are prominent after a calf is born but become less pronounced over a period of about 2 months (McGuire at al. 2020), were used where possible to help identify neonates in the drone photos but were not usually visible given the aerial view of the photographs. Neonates, yearlings, subadults, and juveniles of an unknown age class were grouped together as "juveniles" for some analyses.

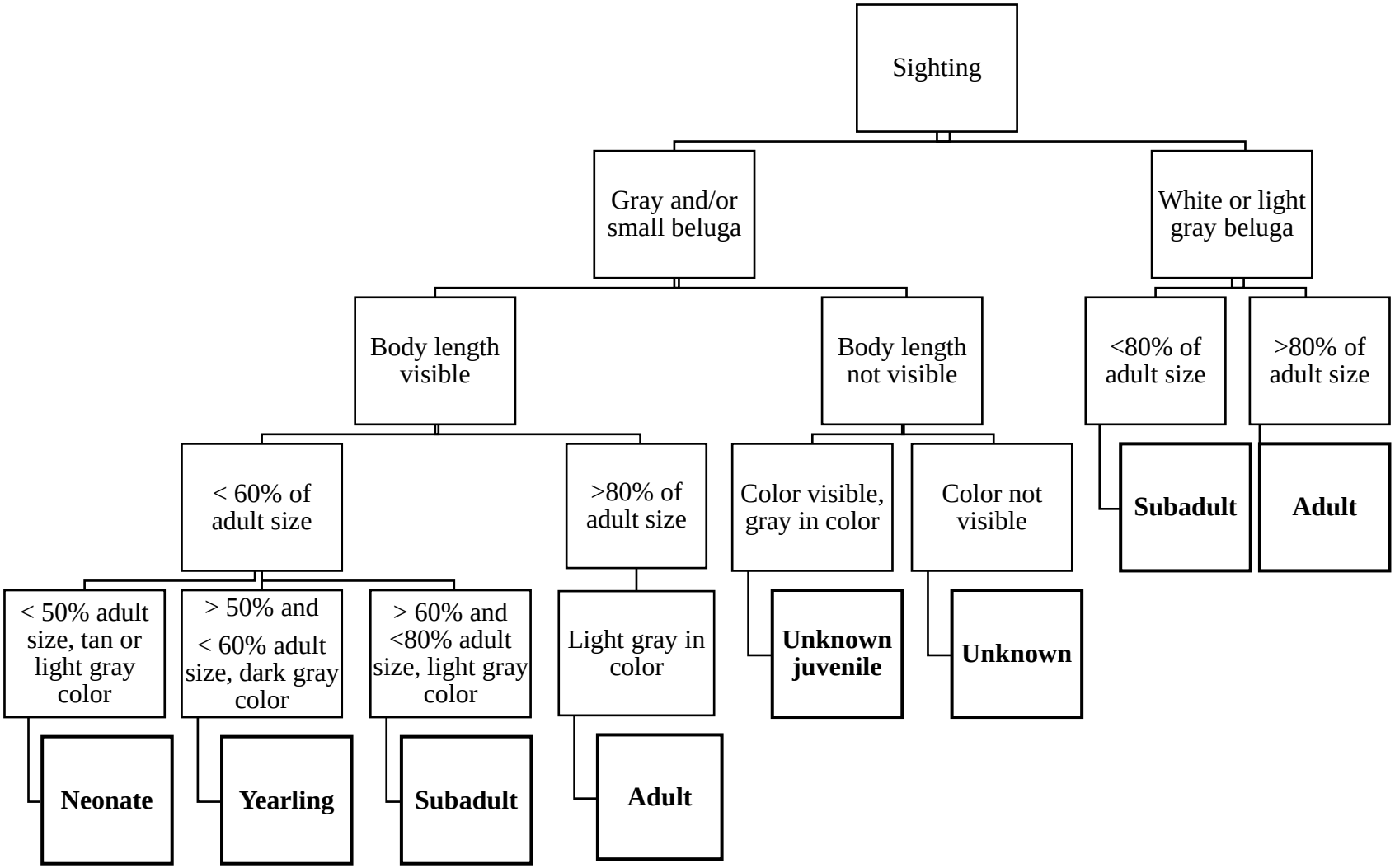


Figure 4.4: Decision tree used to designate beluga whales into one of six age classes: neonate, yearling, subadult, unknown juvenile, adult, or unknown. Whales that are smaller (<80%) than the average size of adults or have dark coloration are categorized as juveniles, which is a grouping composed of neonates, yearlings, subadults, and unknown juveniles.

We investigated the distribution of age classes across years and survey methods to identify any significant changes, and to compare the results from each survey method. We compared the distribution of observed age classes over years within each survey type using Fisher's exact test due to the low sample size in some age classes observed. We also used Fisher's exact test to identify significant differences between age classes in the aerial and drone surveys for 2017, since both survey types were conducted that year. For this comparison, unknown and unknown juvenile age classes were included in the first test to determine if the aerial surveys resulted in higher unknown age classes. In the second test, the counts of four age classes (adults, neonates, subadults, and yearlings) were included, and we excluded the unknown and unknown juvenile classes. Pairwise Fisher's exact tests were used to compare each age class in the 2014 and 2017 aerial surveys by comparing one age class against all other age classes combined. Since multiple comparisons were performed on the same dataset, we applied a Bonferroni adjustment (i.e., for eighteen age class comparisons the critical p-value was 0.0028).

Group types were classified as one adult with juvenile(s) and juveniles only (one adult with one or more juveniles or a group with juveniles only), mixed group (at least two adults and at least one juvenile), multiple adults, and single adult. The group type classifications between the two survey methods, both with all years combined and between the methods using 2017 data only, were also compared using Fisher's exact test with the Bonferroni adjustment (i.e., for six group type comparisons the critical p-value was 0.0083).

4.4 Results

Distribution

Our aerial surveys sighted 4,502 beluga whales over nine days (500 per day ± 300 SD) in 2014 and 2017, with a mean kernel density of 2.68 km^{-2} (±11.37 SD) in 2014 and 7.04 km^{-2} (±37.49 SD) in 2017. The distribution of whales these years was densest within the central area of Clearwater Fjord (Figure 4.5), but was contracted to the north and northeast portion of Clearwater Fjord in 2017 compared to 2014 (Figure 4.6). The spatial distribution patterns of juvenile whales (subadults, yearlings, neonates, and juveniles of an unknown age) was similar to that of all whales, with a similar contraction in range between years, but a mean kernel density of 0.25 km^{-2} (±1.14 SD) in 2014 and 0.82 km^{-2} (±4.92 SD) in 2017 (Figure 4.6). The distribution of neonates indicates that there may be important calving areas for the population in the northeast portion of Clearwater Fjord, with a mean kernel density of whales from 0.03 (±0.16 SD) to 0.16 (±1.20 SD) (Figure 4.6).

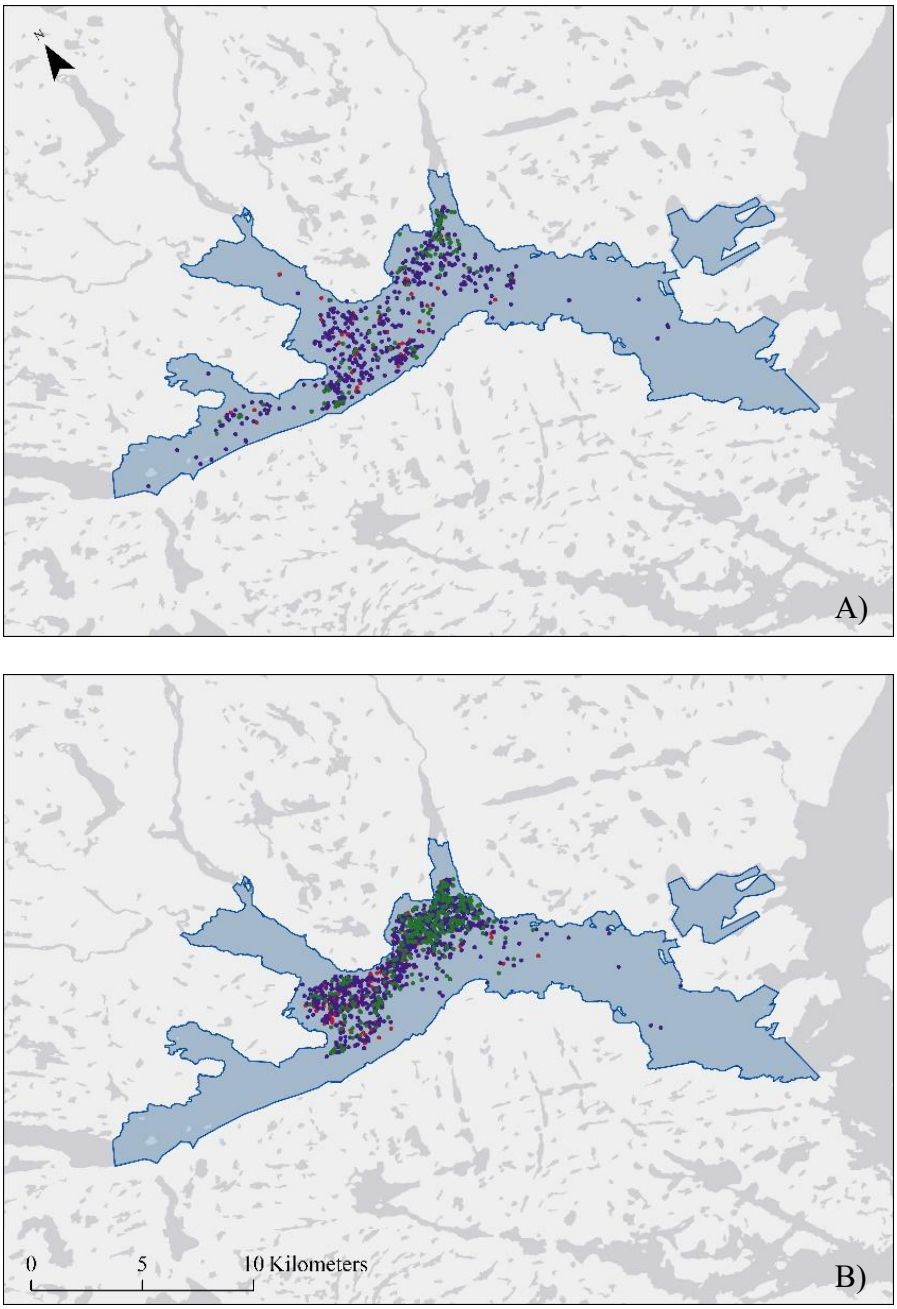


Figure 4.5: The distribution of beluga whales in Clearwater Fjord, Cumberland Sound showing adults (purple), whales of an unknown age (red), and juveniles (green) from aerial surveys in 2014 (A) and 2017 (B).

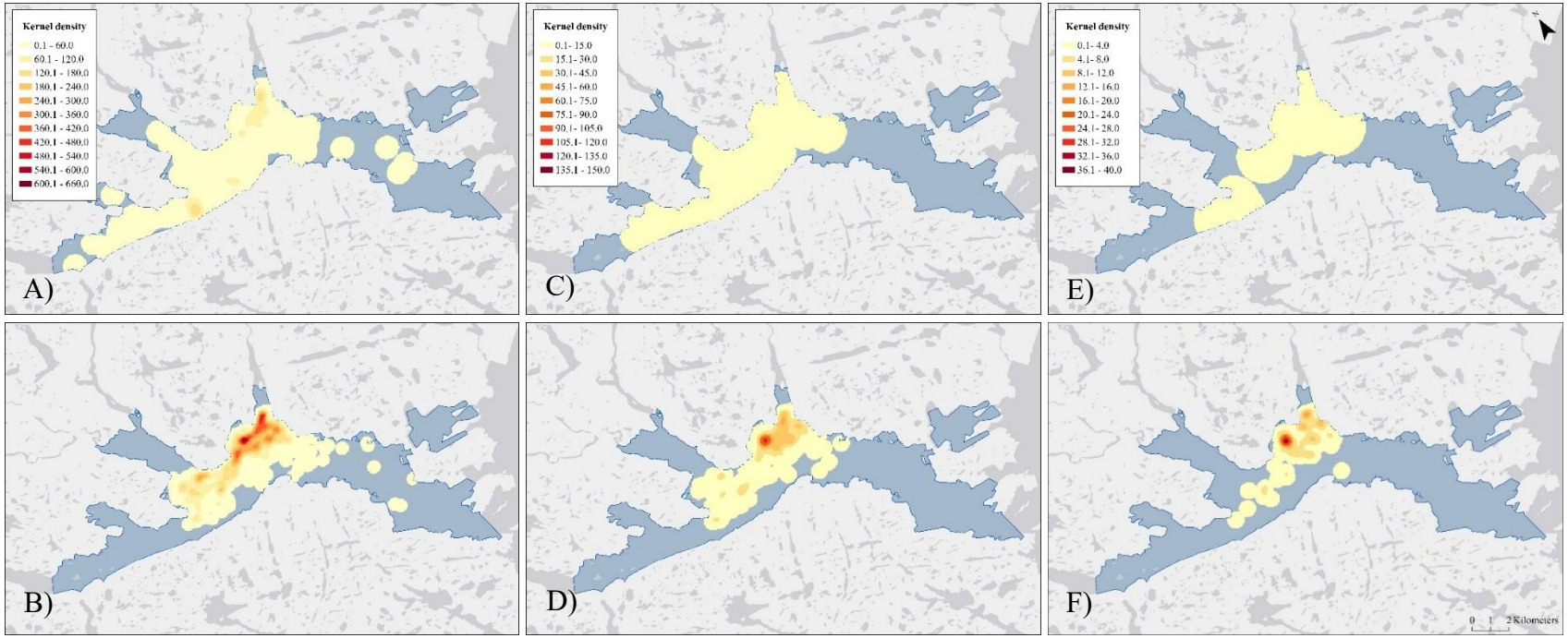


Figure 4.6: Kernel density (whales per square km) of beluga whales in Clearwater Fjord, Cumberland Sound based on sightings during the 2014 (top) and 2017 (bottom) aerial surveys. The 2014 surveys were conducted on August 3, 4, 10, and 11, and the 2017 surveys were conducted on July 29 and August 4, 7, 8, and 12. Shown are the density of all whales in 2014 (A) and 2017 (B), juvenile beluga whales (subadults, yearlings, neonates, and juveniles of unknown age) in 2014 (C) and 2017 (D), and neonate beluga whales in 2014 (E) and 2017 (F) aerial surveys. Note a different scale is used for each age class.

We identified 562 beluga whales over four days in the drone surveys (140 per day ± 45 SD) in 2017, 2018, and 2019. The distribution of neonates from the drone surveys was more concentrated in the north-central area of the fjord, but the analysis of their distribution using this method was limited given the lack of complete photographic coverage of Clearwater Fjord (Figure 4.2).

Age classes

In the aerial surveys, the age class distributions shifted significantly from 2014 to 2017 (Fisher's exact test, $p < 0.001$, Table 4.2; Figure 4.7). More detailed pairwise comparisons of each age class between the two years showed that the proportion of adults decreased ($p < 0.001$) from the 2014 to 2017 aerial surveys, while the unknown age class increased ($p < 0.001$), with no change in the proportions of neonates ($p = 0.132$), subadults ($p = 0.454$), yearlings ($p = 0.105$) or unknown juveniles ($p = 0.889$). We found no significant differences in drone survey age class distributions from 2017 to 2018 ($p = 0.859$) and from 2018 to 2019 (both days included, $p = 0.690$), or between the two drone surveys in 2019 ($p = 0.419$, Table 4.2). In 2017, when both aerial and drone surveys were conducted, the overall proportion of age classes observed by the two methods differed ($p = 0.001$). In the drone surveys we found lower proportions of unknown individuals ($p < 0.001$) (Table 4.2; Figure 4.7), with no significant difference between adults ($p = 0.003$), subadults ($p = 0.285$), yearlings ($p = 0.571$), neonates ($p = 0.244$), or unknown juveniles ($p = 0.238$). For the second test to determine if the surveys still differed after the exclusion of the unknown age classes, we found no significant differences between the two methods ($p = 0.566$).

Table 4.2: Group membership of a subsample of identified whales in Cumberland Sound, Nunavut during a photographic identificaiton program using drones. The group number is listed with the date and time the group was captured in drone photographs, as well as presence (x) and absence (blank) of 13 identified whales showing both short-term (day and week) and multi-year associations between some group members.

Group #	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
Date	18 Aug 17	18 Aug 17	11 Aug 18	11 Aug 18	14 Aug 19	14 Aug 19	14 Aug 19	14 Aug 19	22 Aug 19	22 Aug 19
Start time	12:40	18:43	14:30	15:47	8:24	8:48	8:51	10:13	8:51	10:14
End time	12:43	18:43	14:31	15:47	8:24	8:49	8:55	10:15	8:52	10:15
Whale 1		×	×	×	×		×	×		
Whale 2	×		×				×			×
Whale 3	×						×			×
Whale 4	×									×
Whale 5		×		×						
Whale 6		×		×	×			×		
Whale 7			×	×						
Whale 8										
Whale 9						×	×			
Whale 10					×	×	×	×		
Whale 11						×			×	
Whale 12					×		×			
Whale 13						×			×	

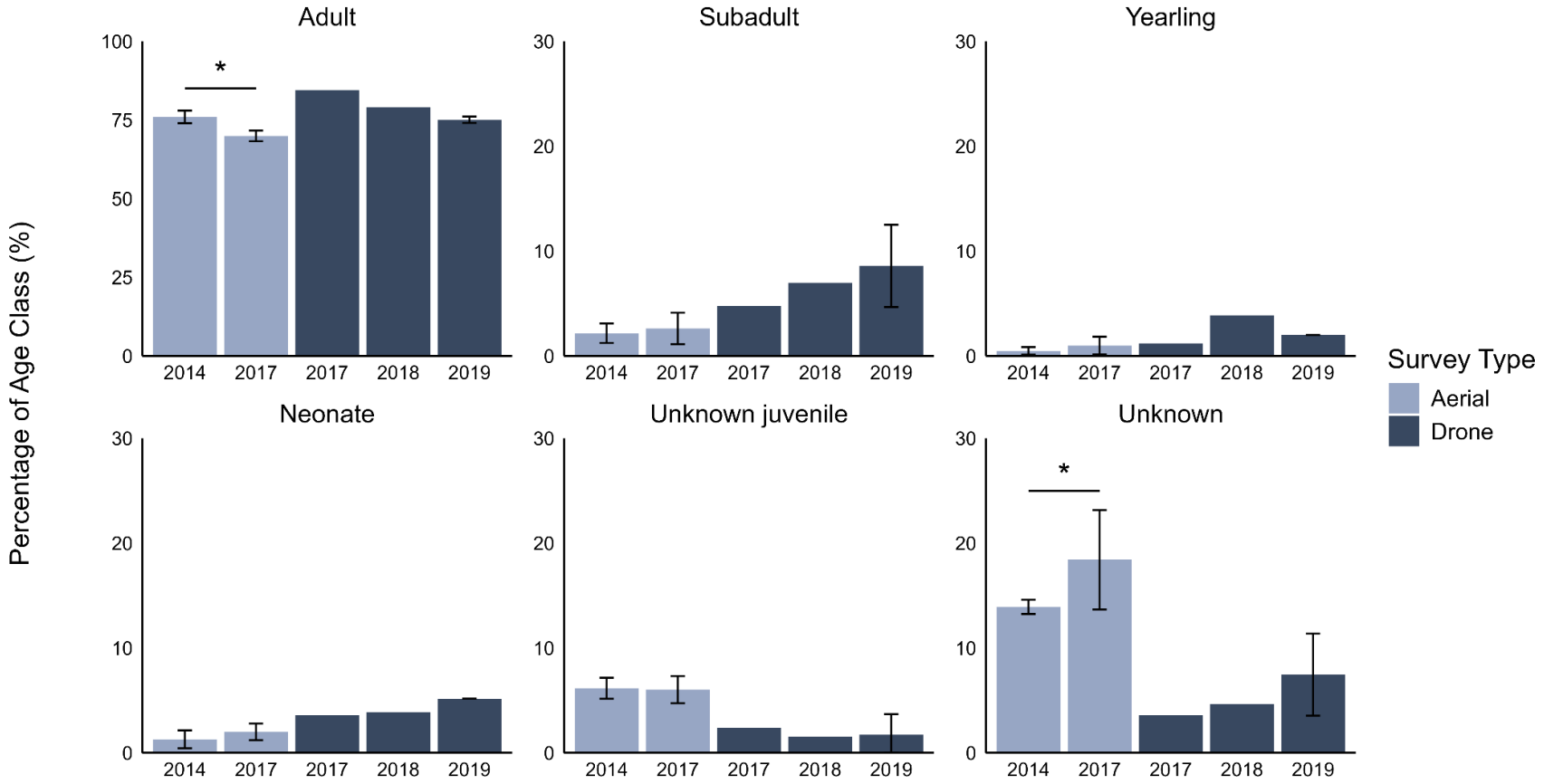


Figure 4.7: Percentage (%) of beluga whales assigned to one of the following age classes based on size and color: adult, subadult, yearling, neonate, unknown juvenile, and unknown age. Classifications were made from aerial surveys with 4-5 survey days per year (2014 and 2017) and drone surveys with 1-2 survey days per year (2017-2019). Error bars denote 95% confidence intervals in years where there was more than one survey. Note that the y-axis scale for the adult age class differs from the rest. Significance is denoted * (Fisher's exact test, $p < 0.05$).

Social organization

The number of groups observed in the aerial surveys ranged from 55–363 depending on the survey day, while the drone survey observations ranged from 23–53 groups (Table 4.1). The distribution of group types significantly differed between aerial and drone surveys with all years combined (Fisher's exact test, $p < 0.001$), but not when only 2017 drone and 2017 aerial were compared ($p = 0.433$). The proportion of groups with only one whale ranged from 23–75% for aerial surveys and 20–43% for drone surveys, and the most common group type observed in both aerial and drone surveys across all years was a single adult group with no juveniles present. For aerial surveys, single adult groups made up a total of 985 groups, accounting for 46.6% of all groups. In drone surveys, single adult groups made up 38 groups, or 24.7% of all groups (Figure 4.8), significantly less than the aerial surveys ($p < 0.001$). Mixed groups, consisting of more than one adult and at least one juvenile, were the second most common group type, comprising 430 groups (20.4%) of aerial survey groups and 55 groups (35.7%) of drone survey groups ($p < 0.001$). There was no significant difference between aerial and drone surveys for groups containing multiple adults, which accounted for 511 groups (24.5%) in aerial surveys and 43 groups (26.9%) in drone surveys ($p = 0.506$). One adult with juvenile(s) and groups with juveniles only accounted for 162 groups (7.7%) of aerial surveys and 24 groups (15.6%) of drone surveys ($p = 0.003$). Neonates were found in 4–19% of the total groups depending on the year and survey type, with 81 groups in aerial surveys and 44 groups in drone surveys. Additionally, neonates, yearlings, subadults, and unknown juveniles were found in 16–53% of all groups.

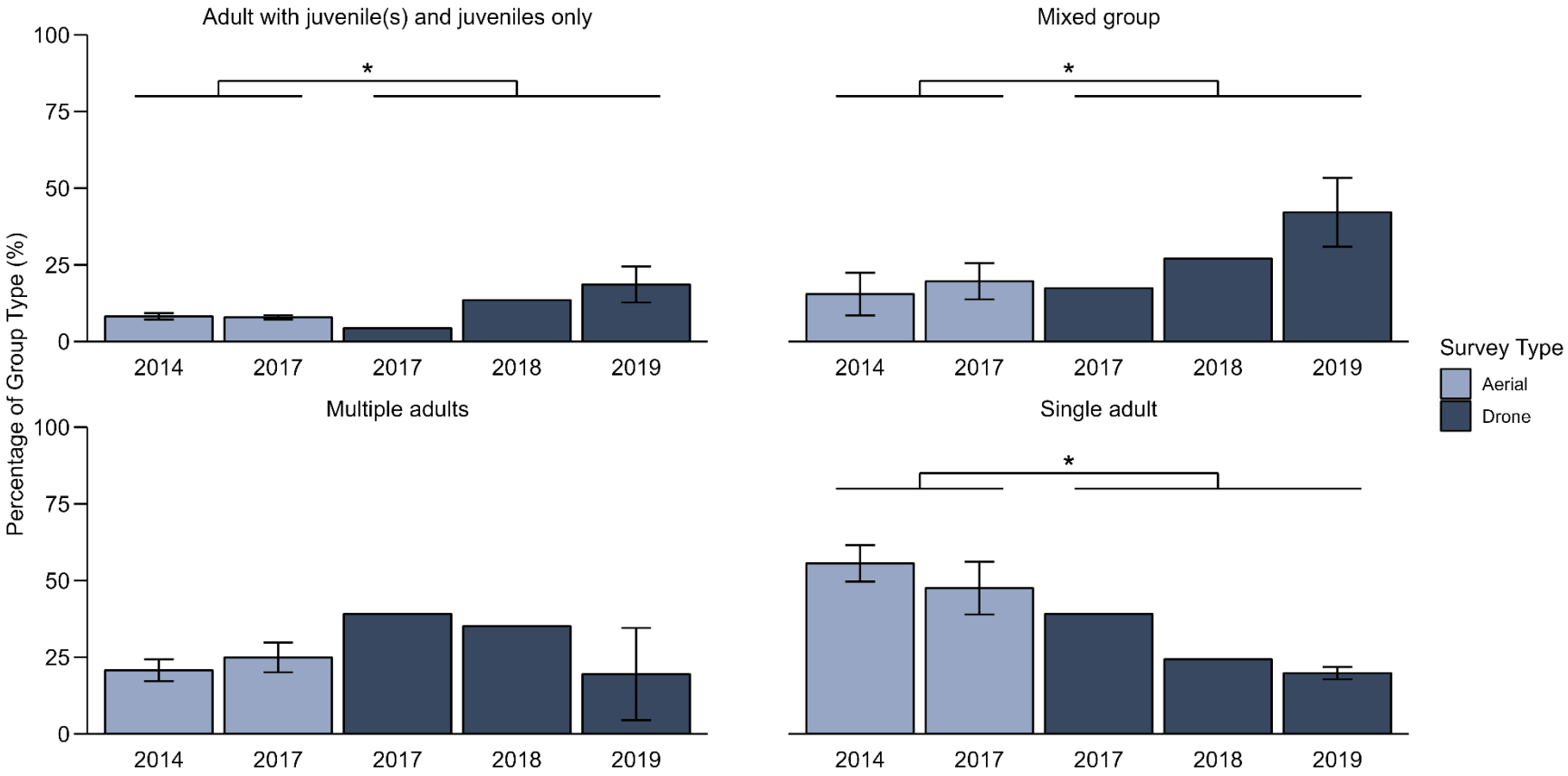


Figure 4.8: Percentage of group types observed in Cumberland Sound in aerial (2014 and 2017) and drone (2017-2019) surveys. Groups were classified as one adult with juvenile(s) and juveniles only (one adult with one or more juveniles or a group with juveniles only), mixed group (at least two adults and at least one juvenile), multiple adults, and single adult.

Associations between whales

The photo-ID catalog that was created using drone photographs resulted in several recaptures of whales within the same day, week, and over several years (Ryan et al. 2022). From 2017–2019, 93 individuals were identified, of which 24 were reidentified over more than one year (Ryan et al., 2022). Three whales that were identified in 2017 by unique scars and markings on their bodies were resighted together during the drone survey in 2018, and two of the three whales were resighted together approximately two hours later on the same day in 2018. A group of 13 identified whales had mixed group memberships spanning three years, with some whales together in the same group in multiple encounters within a day (e.g., Whale 10 and Whale 12), on both survey days in 2019, which occurred eight days apart (e.g., Whale 2 and Whale 3), or over several consecutive years (e.g., Whale 1 and Whale 6) (Table 4.2; Figure 4.2). There were 15 groups in which multiple individuals were resighted together, and 13 of these groups were composed of only adult and unknown aged whales. The two mixed groups occurred in 2017 and 2018; the mixed group in 2017 comprised 13 adults, three subadults, one neonate, and one unknown juvenile and in 2018 the group comprised 13 adults and one subadult. Of these identified whales, only one was resighted in another mixed group out of the 12 different groupings observed.

4.5 Discussion

This study provided the first detailed description of important demographic characteristics for the endangered Cumberland Sound beluga whale population. By using both aerial and drone survey methods, we were able to obtain a more complete social and demographic understanding of the population including the summer distribution, age structure, and social organization. Each method has advantages, such as the larger sample size obtained with the aerial survey and more complete coverage (i.e., less biased in space), and the high-resolution imagery from the drone photography that allowed recognition of many individual whales. Because of the finer-scale details available from the drone photographs, we were able to examine associations between individual whales over time. Given the population's COSEWIC status as 'endangered' (COSEWIC 2020), as well as its importance in the ecosystem and to the community of

Pangnirtung, it is important to incorporate multiple methods and collect both broader scope and high-resolution data to understand important life-history and social characteristics, which may help with recovery planning.

In summer, a large portion of this beluga whale population resides in the north, Clearwater Fjord, and this area may be the only calving ground for the population, as indicated by IQ, aerial surveys, and telemetry data, (Kilabuk, 1998; Richard & Stewart, 2009). IQ also identified the northeast and southwest portion of Clearwater Fjord as the most important areas for calving (Kilabuk, 1998), which is consistent with the distribution of neonates we found during the aerial surveys. Drone photography showed a lack of neonates in the eastern portion of the fjord, while they were concentrated in the north-central area; this trend may be because sampling in the east was lower due to relatively few whales sighted from the vessel and with the drone in that area. The time of day and recent weather events may also have influenced visibility and whale distribution, potentially affecting the surveys. Clearwater Fjord has noticeable changes in water clarity throughout the day as a freshwater plume causes glacial silt to enter the fjord, making the northwest portion extremely turbid. The movements of beluga whales in Clearwater Fjord, as estimated from satellite imagery (Belanger et al., 2023) and acoustic recordings (Booy et al., 2021), do not seem influenced by the plume, tide or time of day; however, our ability to detect whales with both methods was reduced because visibility was limited to the whales at the surface. Thus, surveys conducted during these freshwater plumes may have resulted in incorrect estimations of group size, membership, and total whales present for both methods, especially the aerial surveys where only a brief glimpse of groups was possible, or during the drone surveys when negative survey bias of these areas may have occurred because whale presence appeared to be low.

The two methods produced similar age structures, but the proportion of almost all juvenile age classes identified (with the exception of yearlings) was higher from drone photographs than from the aerial surveys, likely because the enhanced resolution and the ability to view groups for longer periods of time allowed for more accurate determination of age class and size. Conversely, the proportions of juveniles of an unknown age class and whales that could not be

classified into a specific age group were lower in the drone surveys than in the aerial surveys. The St. Lawrence Estuary age class estimations, based on photographic aerial surveys and mortalities, and the White Sea estimations, based on visual observations and video recordings (Krasnova et al., 2012; Mosnier et al., 2015), suggest that methodological differences can yield slightly varied proportions but are generally consistent enough for comparative analysis. Overall, the proportion of juveniles estimated from both methods in our study is lower than values reported in other populations (Burns & Seaman, 1986; Krasnova et al., 2012; McGuire et al., 2020; Mosnier et al., 2015). Juveniles made up 33–42% of the population in St. Lawrence Estuary (Mosnier et al., 2015) and 40–55% in the White Sea (Krasnova et al., 2012), which is considerably higher than the 10–11% from aerial surveys and 13–18% from drone surveys observed in Cumberland Sound. These differences may indicate lower reproductive rates or lower survivorship of calves and older juveniles in Cumberland Sound, possibly due to harvest or other factors, and warrant further exploration. Lower reproductive rates in this population could also have contributed to their lack of recovery after overharvesting during the commercial whaling period.

The observed neonate proportion in our study (2-5%, varying by year and survey method) was notably low compared to the 2–12% typically found in other populations, with geographic and temporal variation commonly reported and differences resulting from varied methods of collecting these data (Burns & Seaman, 1986; Hobbs et al., 2016; Koski et al., 2002; McGuire et al., 2020; Michaud, 2014; Mosnier et al., 2015). The lowest proportion of neonates recorded is in Cook Inlet, Alaska, which is also an endangered population that similarly has not recovered to its historic levels after commercial hunting reduced its population size. Neonates made up on average 2% of the Cook Inlet population, but there was variability between years, with neonates making up to 12% of the population in August one year (Hobbs et al., 2016; McGuire et al., 2020). Neonates comprised 6–7.5% of whales in the St. Lawrence Estuary population, which is also endangered (Mosnier et al., 2015). Cyclical variation in birth rates has also been observed in this population, with cycles lasting 2 to 3 years, and a 5-year period of low birth rates. However, the 2-year calving cycle did not indicate reproductive success, as it coincided with high neonate mortality and a declining proportion of juvenile whales (Michaud, 2014; Mosnier et al., 2015).

Beluga whale populations that are not endangered or threatened, unlike Cumberland Sound and the previous examples, tend to have higher proportions of neonates (Burns & Seaman, 1986; Koski et al., 2002; Sergeant, 1973). In populations that are considered stable and healthy, such as western Hudson Bay and the High Arctic - Baffin Bay population, neonates were estimated at 11% (Sergeant, 1973) and 12% (Koski et al., 2002) of the population, respectively (Hobbs et al., 2020). In the three abundant beluga whale populations in northern Alaska, neonates made up 9.5% of the population as estimated from hunted whales (Burns & Seaman, 1986). These hunts consisted of driving whales into shallow water and harvesting as many as possible, and this method was biased towards older, larger whales since they resulted in the highest yield; this would have resulted in an underestimation of neonates in the population. However, whales in this study were aged under the assumption that two growth layer groups (GLGs) are formed in the teeth per year as opposed to one GLG per year, which is the accepted standard now, and thus the value of 9.5% neonates may be an overestimation since it likely included yearlings as well (Burns & Seaman, 1986; Lockyer et al., 2007; Waugh et al., 2018).

Integrating IQ, which indicates that calving primarily occurs from July to early August, our drone surveys conducted in mid-August (August 11 to August 22) should have been timed to estimate the majority of calves born that year (Kilabuk, 1998); however, the aerial surveys occurred from July 29 to August 12, which may have underestimated the number of calves because the calving season was still underway, and this difference could account for the discrepancy between our neonate estimates from aerial surveys (2%) and drones (4–5%). Neonates may also be underestimated in our population if the calving season occurs late or occurs over a longer period into fall. In Cook Inlet, the calving season occurs from July to October (McGuire et al., 2020), while in other populations in Alaska, West Greenland, and western Hudson Bay, calving season begins as early as March–April and ends in May–July (Beck et al., 1994; Burns & Seaman, 1986; Sergeant, 1973). Further investigation into the calving season in Cumberland Sound could either provide confidence in our current methods or indicate a shift to later aerial survey dates is needed. Neonates may also have been missed in the aerial survey photos because of the combination of lower resolution photographs and neonates preferential positioning under their mother, at her fluke, or in other obscured positions more than

would be seen in other age classes (Krasnova et al., 2006, 2009). The possibility that neonates were missed because we surveyed too early or because they were below their mothers, however, would not account for the low number of subadults relative to the proportion of neonates in this population and relative to other populations, as discussed below.

Examining trends in the proportions of neonates in one year and yearlings in the following year can provide an estimation for calf survival. In 2017, neonates made up 4% of the population as estimated using the drone method, while in 2018 the proportion of yearlings was 4%. This consistency indicates that between these years, survival of neonates may have been high, or we under-estimated neonates in 2017. In 2018, neonates made up 4% of the population, but the following year (2019) yearlings only accounted for 2% of the population. The natural survival rate for neonates is estimated at approximately 80–93% in other populations (Beland et al., 1988; Burns & Seaman, 1986; Himes Boor et al., 2023; Watt et al., 2020), so this decline should be monitored as the photo-ID program continues. Yearlings made up an estimated 1% of the population in aerial surveys in 2014 and 2017, and the 2017 drone survey. Yearling abundance may be low due to reduced survival from a number of factors, including poor condition of the mother or incidental mortality from the harvest. Alternatively, the proportion of yearlings may be underestimated because they are typically the darkest-colored age group and may be missed if below the surface. However, the drone focal follows involved photographing every member of the group when possible, so it should be less likely to miss yearlings. As the photo-ID program continues we will continue to monitor the proportion of neonates in one year and yearlings in the next, to determine if survival for this age group is lower than in other populations. Yearlings being weaned may experience increased mortality risk, as they become less dependent and less cared for by their mothers (Matthews & Ferguson, 2015).

The higher resolution of drone imagery likely contributes to more accurate identification and categorization of age classes compared to aerial surveys (Álvarez-González et al., 2023). However, the absence of a significant difference in age classifications between the 2017 drone and aerial surveys, when excluding unknown age classes, suggests that the likelihood of observing these age classes does not significantly differ between aerial and drone surveys. The

implications of these results are that there is no bias toward any particular age class being designated as “unknown” in the aerial survey, just a higher rate of unknown classifications across all ages. The stability in age class distributions observed in drone surveys over consecutive years suggests a potential methodological advantage in monitoring population trends with less variability introduced by the uncertainty of the aerial survey method (Álvarez-González et al., 2023). Consistent counts of age classes between 2014 and 2017 aerial surveys, apart from adults which declined and unknown ages which increased, suggests that the measures of juvenile age classes may be consistent over time. Several factors could have led to more unknown classifications in 2017, such as more days of poor water quality, which could have resulted in the counts of adults being impacted more than other age classes (proportionate with their frequency being higher than other age classes) (Watt et al., 2020).

The proportion of subadults in the Cumberland Sound population (2-8%) is lower than we would expect given the proportion of neonates and yearlings, since these classes would age up and remain within the “subadult” category for several years; it is also lower than we would expect given the proportions in other populations, where 20–30% is commonly reported (Burns & Seaman, 1986; Koski et al., 2002; Krasnova et al., 2012; Mosnier et al., 2015). It is unknown what precise age range our “subadult” classification represents, given the variation in how whales progress from gray to white and natural variation in growth rates. Size and color do not always correspond to sexual maturity; some light gray individuals have been identified as sexually mature based on their association with calves, and white whales can be sexually immature based on examinations of their reproductive tracts (Brodie, 1971; Heide-Jørgensen & Lockyer, 2001; McGuire et al., 2020; Sergeant, 1973; Shelden et al., 2020). The aerial surveys covered a larger portion of the population and likely included many single adult whales that the drone surveys may have missed. The enhanced resolution of drone imagery, conversely, likely aids in the distinction between subadults and adults.

Subadult survivorship may be low due to the harvest; alternatively, because most whales in this age group are likely weaned and can travel independently from their mother (Matthews & Ferguson, 2015), they may be using different areas of Cumberland Sound that we did not cover

with our photographic surveys. During one of two 2014 visual surveys where observers counted whales in the northern section of Cumberland Sound, a large number of whales were seen outside of Clearwater Fjord; 78 whales were seen primarily in Kangilo Fjord, just southwest of Clearwater Fjord (Marcoux et al., 2016). The whales seen on the survey transect generated an estimated 987 whales after considering the survey area covered and adjusting for whales beneath the surface (Marcoux et al., 2016). There is no indication of separate habitats for subadults, either from IQ or from past methods such as movement data, but whales have been sighted in aerial surveys and satellite imagery outside of Clearwater Fjord; most notably, there have been sightings in Kangilo and Kangerk Fjords, but these sightings are usually of small groups that are widely dispersed and with no consistent distribution patterns (Belanger et al., 2023; Watt et al., 2020). The presence of other suitable habitats could be explored further during future aerial surveys when observers count whales outside Clearwater Fjord.

Group composition was relatively similar across years, with adult whales only (single or multiple) making up the highest proportion of group type followed by mixed groups of at least two adults and one juvenile, except in the 2019 survey when more mixed groups were observed than any other group type. In Cook Inlet, neonates were in at least 30% of the groups (McGuire et al., 2020), while in Cumberland Sound neonates were found in 14–19% of groups from the drone photographs. The lower proportion of groups with neonates in our population may either indicate a lower birth rate, lower neonate survival in some years, or that more mother/neonate pairs associate together in the same group in Cumberland Sound. Beluga whale calves nurse for 1–3 years and may remain associated with their mothers for several years after this time (Matthews & Ferguson, 2015; McGuire et al., 2020). Groups with one adult (the presumed mother) and multiple calves of different ages were rare but occurred in 2-6% of the groups from 2017–2019. The percentage of groups with one adult whale and two juveniles would be higher for the Cumberland Sound population if we counted instances where this type of grouping occurred within larger groups, but our classification considered that a mixed group. Though no significant difference was found between the 2017 drone and aerial group type data, the statistical difference between group types with all years combined may be a result of the resolution or sampling size of each method, and warrants further investigation. The drone

surveys likely resulted in more accurate group composition observations, given whales below the surface in one photograph would usually surface later during the focal follow, while the aerial survey would have captured a larger portion of the population. The two methods combined provide a more complete picture of the social groupings in Cumberland Sound.

Beluga whales are highly social whales most often found in groups of 2–10, and for the larger populations, can even form communities of aggregated whales in the thousands (O'Corry-Crowe, 2009; O'Corry-Crowe et al., 2020). The proportion of groups comprised of a single whale we identified was higher for the aerial surveys than the drone surveys. For this metric, we would expect the aerial surveys to be more accurate since they cover a larger proportion of the summer aggregation area, include more groups (greater sample size), and are not subject to bias associated with distribution or influence of the research vessel. The aerial survey would not be biased towards large groups but could have missed whales below the surface, inflating the number of small groups or single whales. On the other hand, drone surveys followed groups for longer and therefore would account for most, if not all, whales below the surface. Because the drone surveys involved opportunistic sightings of whales from the boat or from the drone, these surveys were likely biased towards larger groups that would have been easier to see. The average group size was larger for the drone surveys than the aerial surveys, which supports a possible bias towards larger groups in the drone surveys or may be an indication of our greater ability to collect the whole group size when collecting drone footage rather than static aerial survey images.

In our study, 25% of all drone survey groups and 47% of all aerial survey groups comprised only one whale. These values are within normal ranges reported in other studies but can be hard to compare because sometimes different metrics are used to define a group such as all whales visible at the surface, or whales within one to two body lengths. In aerial surveys using live counts in Bristol Bay, Alaska, single whales made up 29% of all groups (Citta et al., 2019). In the Beaufort Sea, Alaska, single whales made up 48.8% of groups offshore and 68% of groups inshore but because this study used separation of one to two body lengths to define groups, we would expect these numbers to be significantly higher than our study (Mayette et al., 2022).

It is possible that group size in Cumberland Sound differs from other populations. The distribution of their prey may be smaller and patchier than in other populations, requiring individuals to target different areas (Benoit-Bird et al., 2013). The small size of the population may also be a factor. Whales may be spread farther apart within a social group than would occur in populations that have a larger abundance within a limited area (Schradin et al., 2020). Alternatively, the lower proportion of juveniles may lead to fewer mixed groups and fewer single adults with juveniles, resulting in more older, solitary adult whales that no longer depend on groups to gain knowledge (Rendell et al., 2019). Males may also break off from all-male social groups to increase their chances of successful mating if females are limited due to population size, which could result in a higher occurrence of single whales (Emlen et al., 1977); though beluga whales typically mate from March to June (Burns & Seaman, 1986; Heide-Jørgensen & Teilmann, 1994; Robeck et al., 2005), the remnants of breaking up social groups may last into the summer. The number of solitary whales may also be a product of the harvest; beluga whales typically gather in nearshore areas during killer whale attacks, as these locations are inaccessible to killer whales without the risk of stranding (Westdal et al., 2016). However, during harvesting activities, beluga whales may have adopted different survival strategies, since larger groups are more visible, and nearshore areas offer no protection from hunters (Laursen et al., 2016). Altered grouping patterns in response to harvesting would also align with the timing of our surveys, as the harvest occurs in July and August, during our study period (DFO, 2022).

Within endangered populations, some of the most important predictors of extinction risk of marine mammals are low birth rate, small social group size, and small geographic range (Davidson et al., 2012). The Cumberland Sound beluga whale population may be especially at risk given the small range they inhabit compared to other marine mammals and even other beluga whale populations, and the seeming contraction in their range between the two aerial surveys. The range contraction could be a result of a number of different factors, such as changes in prey availability or distribution, habitat degradation, or predation pressure (Higdon & Ferguson 2009; Kelley et al., 2012; Marcoux et al., 2012; Rugh et al. 2010; Watt et al., 2016). The contraction in their distribution may also indicate a reduced population size, as the range of a species tends to shrink when abundance decreases (Brown, 1984). The contraction in range has

been observed in the Cook Inlet beluga whale population as well, where even with hunting, industrial development, and other anthropogenic threats, the population contracted to areas of high human impact rather than to other areas of their range or emigrating out of Cook Inlet entirely (Rugh et al., 2010). Neither the Cook Inlet nor St. Lawrence beluga whale populations, both of which were reduced after overharvesting and do not undergo large migrations to breed with other populations, have recovered after the cessation of hunting (Hammill et al., 2007; Mahoney & Shelden, 2000; Michaud, 2014; Mosnier et al., 2015).

The method of removal may affect the resilience of a population as well (Wade et al., 2012). The only example of a beluga whale population increasing in size is in Bristol Bay, where there was no history of overexploitation, and no drive or net hunting techniques (Lowry et al., 2008; Wade et al., 2012). Cumberland Sound has a history of both hunting techniques, as well as hunting with harpoons and rifles (Stewart, 2018). Between 1860 and 1966, the region was overexploited; records show that 14,079 whales were commercially hunted and an additional 2,765 were taken in subsistence harvests during this period (Stewart, 2018). Although commercial hunts ceased after 1966, subsistence hunting continued, resulting in the capture of 2,487 whales from 1967 to 2016, with annual takes ranging from 15 to 178 whales (Stewart, 2018). Since 2016, a quota for subsistence harvesting has been set at 41 whales. Additional whales are also removed from the system when they are struck and lost, and the prevalence of scarred whales in the population suggests that a number of whales are struck and survive as well (Ryan et al., 2022). It is unknown how many whales are struck and not harvested, but the current harvest is unsustainable (Watt et al. 2021).

From the photo-ID catalog, we found several instances of multi-year associations between individual whales. Long-term associations outside the mother/calf pairing or beyond the period of lactation may develop in odontocetes because of the enhanced benefits of group-living such as increased predator defense or foraging efficiency, but also because of information exchange, the transmission of social knowledge, and learning through culture (Brakes, 2019; Brent et al., 2015; Kappeler et al., 2013; Wade et al., 2012). In some odontocete species, these associations involve transmissions of culture and knowledge from specific key individuals in the group; if these

individuals are removed, the entire group may experience a loss of knowledge about foraging opportunities or dangers, or social networks may fracture (Brakes, 2019; Brent et al., 2015; Busson et al., 2019; Lusseau & Newman, 2004; O'Corry-Crowe et al., 2020; Wade et al., 2012; Williams & Lusseau, 2006). The cohesion of these associations and social groups, and the complexity of their social systems, may make odontocetes less resilient to hunting than mysticete species (Wade et al., 2012).

The several instances of multi-year associations we found between individuals suggest that random mixing of individuals is unlikely and that there is some stability in the social structure of at least part of the population over time. Beluga whales likely have complex social systems that could either consist of stable social units or fission-fusion, where groups are formed based on different behavioral contexts (Michaud, 2005; O'Corry-Crowe et al., 2020). Many of the associations found between whales were between adults in groups without known juveniles present. Likely because most juveniles could not be identified to the individual level, we did not find evidence of multi-year associations between an adult and juvenile whale. Although we do not have genetic samples of the individuals sighted together in Cumberland Sound, several have been resighted over multiple years together without calves accompanying them or any other members in the group, suggesting these observations may be of all-male groupings. There may be genetic associations among these males, as has been found in other populations, or they may be multi-year associations between non-kin (O'Corry-Crowe et al., 2020). The lack of resightings of identified whales together with calves or in groups consistently including calves suggests that matrilineal kin groups are less likely. If matrilineal kin groups were common, we would expect to see more calves in the groups of reidentified whales. In St. Lawrence, males seem to form long-term alliances while female whales have looser connections (Michaud, 2005). Since whales with no markings, or markings that were not unique or likely to be permanent, were not included in these analyses, there are likely many more associations than what we have reported here. With the continuation of the photo-ID catalog, these associations will continue to be monitored with the possible addition of more data, such as genetic sampling or extended videos to monitor behavior.

Arctic odontocetes may rely even more on key individuals for the transmission of cultural knowledge than their temperate counterparts due to the high amount of environmental variability in the Arctic, primarily due to dynamic ice cover, harsh weather conditions, and complete darkness for part of the year (Blix, 2016). The extent to which the importance of key individuals may apply to beluga whales is unknown but should be explored further, particularly in Cumberland Sound where the whales exhibit significantly higher physiological stress levels (Kucheravy et al., 2022), and the removal of whales through the harvest may have unintended and deleterious impacts if key individuals are lost. Removals of even a small percentage of a population each year can lead to the overexploitation of odontocetes, which in turn can reduce birth rates, so the current removal rates of the Cumberland Sound population may be increasing its risk of extinction (Wade et al., 2012). In addition, when culture, behavior, and social factors like social learning are important in a population, a healthy population size can be imperative to avoid compounding effects of hunting such as losing cultural diversity (Wade et al., 2012; Whitehead, 2010).

4.6 Conclusion

Employing both aerial and drone surveys provided a more comprehensive and detailed view of the Cumberland Sound beluga whale population than could have been achieved using either method alone. The proportion of juveniles, particularly subadults, is markedly lower in Cumberland Sound than in other populations, which may suggest low survivorship of juvenile whales (Burns & Seaman, 1986; Koski et al. 2002; Krasnova et al., 2012; Mosnier et al., 2015). The low proportion of these young age classes, as well as the potential causes of mortality, warrant further exploration. As the photo-ID program progresses, integrating age proportions estimated from drone surveys could enhance the accuracy of aerial survey estimates, particularly when both methodologies are synchronized temporally and spatially. The continuation of the photo-ID program will also allow for the monitoring of long-term associations between individual whales and more insight into the social structure of whales in this population and beluga whales in general, which remains relatively poorly understood. Developing a long-term photo-ID catalog of known individuals will facilitate precise survival rate estimates specific to

the Cumberland Sound population, providing essential data for accurately projecting future population dynamics and tailoring effective conservation strategies. Understanding the demographic structure and social dynamics through photographic identification and analysis of age class proportions, particularly juveniles, is vital. This knowledge can be used by management bodies to make more informed decisions concerning this population and aid in its long-term viability.

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Chapter 5 - Photographic evidence of tagging impacts for two beluga whales from the Cumberland Sound and western Hudson Bay populations

5.1 Abstract

Beluga whale (*Delphinapterus leucas* (Pallas, 1776)) movements, habitat use, and diving behaviour have been studied using satellite-linked transmitters for decades. The inaccessibility of Arctic and subarctic habitats makes these instruments especially valuable for beluga whale research. The long-term effects that tags and tag attachments have on beluga whales, however, are not well known because resightings occur relatively infrequently. Here, we describe two beluga whales photographed during photographic monitoring programs of two populations: western Hudson Bay and Cumberland Sound. The beluga whale photographed in western Hudson Bay had scars consistent with the tag pins migrating out, which is thought to occur when the tag is pulled posteriorly due to drag. The beluga whale photographed in Cumberland Sound had all three tag pins still in place 11–21 years after they were inserted. Both whales appeared to be in good body condition with no evidence of infection, and the beluga whale from Cumberland Sound was accompanied by a 1-year-old calf. Resightings of previously tagged whales are infrequent for the western Hudson Bay population and have never been documented in Cumberland Sound. However, through long-term photographic monitoring programs, additional sightings may provide more information regarding the method of tag loss and the long-term effects of tagging on whale health and productivity.

5.2 Introduction

Deployments of satellite-linked transmitters (hereafter referred to as “tagging”) are a common and effective way to monitor movements and dive behaviour of cetacean species over long periods of time and in areas that are largely inaccessible to researchers (Andrews et al. 2019; International Whaling Commission 2020). Satellite telemetry devices have been especially useful in monitoring Arctic cetaceans that remain in the Arctic and subarctic year-round, where weather, darkness, logistics, and sea ice conditions can limit research (Quakenbush et al. 2010; Hauser et al. 2017; Mallory et al. 2018). One such Arctic resident species is the beluga

whale (*Delphinapterus leucas* (Pallas, 1776)). Tagging programs have proven to be largely successful for gathering information about beluga whale migrations (Sergeant and Brodie 1969; Hauser et al. 2017), habitat use (Loseto et al. 2006), and dive behaviour (Goetz et al. 2012; Watt et al. 2016). Reported resightings or recaptures of previously tagged beluga whales occur relatively infrequently; however, these events can provide useful information about individuals post-tagging. Such information includes the condition of the tag attachment site, survival, the method of tag loss, reproductive status, information about movement after tag loss, and further insight into the delineation between beluga whale populations as the movements of tagged whales between populations (or lack thereof) can be tracked (Sergeant and Brodie 1969; Orr et al. 1998; McGuire et al. 2021).

The first resightings of western Hudson Bay, Canada tagged beluga whales occurred in 1967–1968 of whales that had been tagged with harpoon tags; the harpoon tags were created using tags that had originally been designed for fish tagging programs, which were attached to applicators set on simple hand harpoons, and inserted approximately 5 cm into the skin (Sergeant and Brodie 1969). Two whales were harvested 5–7 weeks after harpoon tags were deployed and one whale was resighted approximately one year after tagging. In all three cases, the tags were still embedded in the skin. The resighting of the live whale occurred during a stranding event and allowed for inspection of the attachment site, which was completely healed with minimal scarring (Sergeant and Brodie 1969).

Beginning in the 1980s, satellite tags were used more frequently to monitor marine mammal species. The method of attaching satellite tags using pins is more intrusive than the harpoon tag and typically involves net capture of the whale and inserting two or three polyethylene pins (8 mm diameter) approximately 8–12 cm below the dorsal ridge of the physically restrained whale (Fig. 1) (Orr et al. 1998, 2001). Holes for the pins are made with a sharp trocar for a clean cut through the skin and blubber to minimize trauma. A beluga whale tagging program in the Canadian High Arctic in the 1990s resulted in the first confirmed recaptures of beluga whales with tag attachment scars, followed by the harvest of an eastern Chukchi Sea whale with tag attachment scars in 1999 (Orr et al. 1998; Suydam et al. 2005). One whale from the Canadian

High Arctic tagging program was recaptured approximately 10 months after tagging and had three 15 mm deep V-shaped notches in the dorsal ridge, with a slight gray indentation between the original location of the three pins and the V-shaped notches; no infection was apparent (Orr et al. 1998). The gray coloration of the skin has been observed in other studies and is thought to be associated with new growth or healing in beluga whales (Geraci and Bruce-Allen 1987; Orr et al. 1998). Two whales with suspected tag scars were harvested 12 months after tagging in the High Arctic and eastern Chukchi Sea. The scars were similar but with only two V-shaped notches in the dorsal ridge because two pins had been used to attach them, and there was no sign of infection (Orr et al. 1998; Suydam et al. 2005).

Resightings of beluga whales with tags or evidence of tags can provide information about effects on health, such as body condition and reproductive success (McGuire et al. 2021). Understanding the cause of tag loss is also critical because tag loss or the migration of tag attachments out of the body can be a significant contributor to satellite signal termination, and the longevity of tags is directly impacted by both infection and the movement of the implanted pins within the tissue (Geraci and Smith 1990; Orr et al. 1998). Because tagging is an invasive method, it is important to evaluate the quality of the data (e.g., how long the tags remain attached and transmit data) relative to the impact on the animals. Here, we describe recent resightings of two beluga whales from the eastern Canadian Arctic (western Hudson Bay, Manitoba, and Cumberland Sound, Nunavut) that had been tagged with satellite transmitters and opportunistically resighted during photographic monitoring studies. These are the first documented resightings of whales that had been tagged with modern satellite-linked instruments in their respective populations.

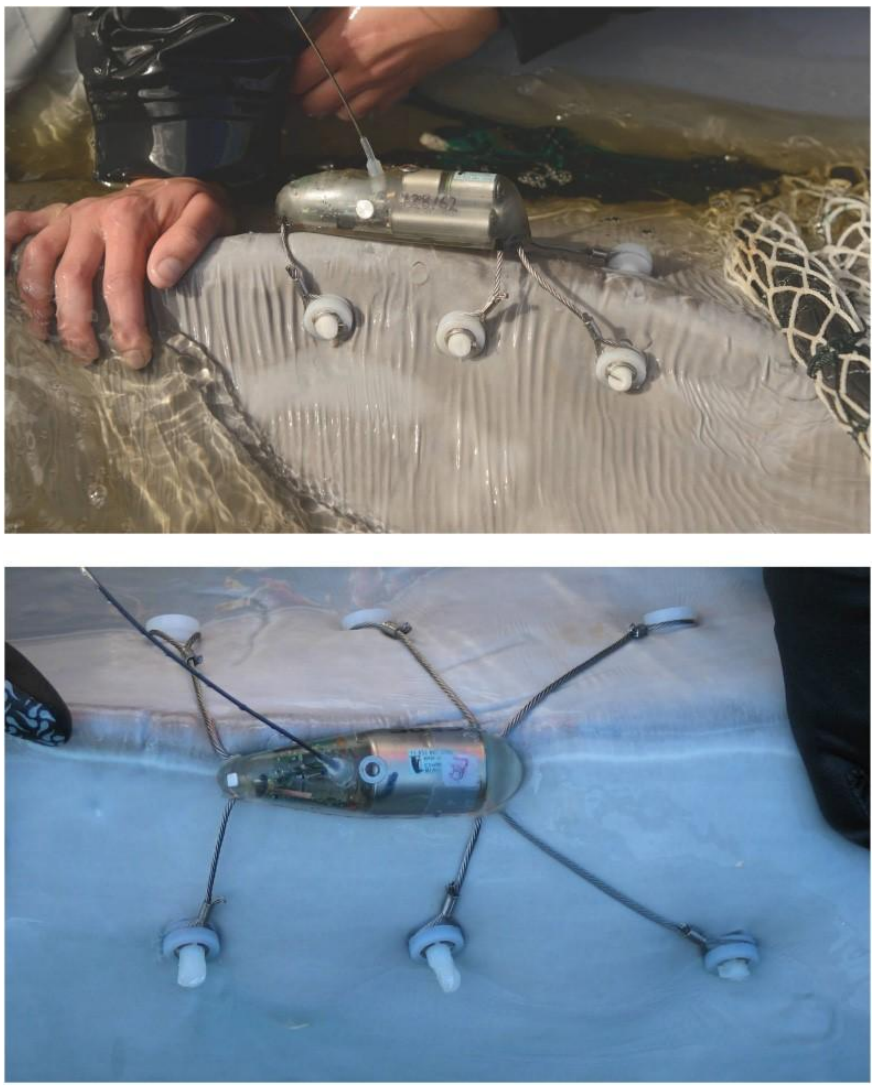


Figure 5.1: Examples of satellite-linked transmitter attachments on beluga whales (anterior on right) in Churchill, western Hudson Bay, 2008 (top) and Cumberland Sound, Nunavut, 2008 (bottom). Photo credit: Fisheries and Oceans Canada.

5.3 Methods

Photographic monitoring programs for beluga whales have been conducted in the western Hudson Bay (WHB) and Cumberland Sound (CS) populations since 2016 and 2017, respectively, to identify individuals and document behaviour, social associations, body condition, and habitat use. Photographic monitoring of the WHB population has occurred in the area around the Churchill River using an Axis F41 underwater camera (Axis Communications AB, Sweden)

annually as part of the Beluga Bits project (https://www.zooniverse.org/projects/stephenresearch/beluga-bits). Photographs of the tagged whale were collected under Animal Use Protocol permit number FWI-ACC-2019-17. The livestream camera footage is part of a project hosted by Explore.org to engage viewers about subarctic ecosystems, and the Beluga Bits project uses stills from the footage to identify whales and various social and life history parameters.

Photographs of the CS beluga whale population were taken using a Phantom 3 or 4 drone (DJI, China). Photographs of the CS tagged whale were collected under Animal Use Protocol permit number FWI-ACC-2019-10 following procedures to minimize the disturbance on the whales, including flying at an altitude that would not elicit an adverse reaction and turning the boat engine off when possible. The photo-identification surveys were conducted over 1–4 days in a small area within CS, Clearwater Fjord, where beluga whales are known to congregate during the summer (Richard and Stewart 2009). The drone was flown by an experienced drone pilot at 10–30 m directly above the whales. The photo-identification program uses scarring on the dorsal sections of the whales to identify individuals over several years, and 93 individuals with unique scars or markings have been identified from 2017 to 2019 (Ryan et al. 2022). Resightings of whales will ultimately be used to estimate the abundance of the endangered population using mark–recapture models.

5.4 Results

Beluga whales with satellite tag scars and tag remnants were sighted in two Canadian beluga whale populations. A whale with scars fitting the pattern of those from three attachment pins of a satellite tag (Fig. 2) was photographed in the Churchill River in WHB on 7 August 2019. The scarring at the tag site indicated that the three tag attachment pins migrated out of the dorsal ridge due to hydrodynamic forces from drag that was created by the tag package during swimming. The scars included light gray skin leading from where the pins were initially inserted to V-shaped notches in the dorsal ridge. The attachment sites were healed with no sign of infection. When photographed, this whale was classified as an adult based on size and coloration and was in good body condition judging by the presence of rails, which are ridges of blubber

stores that can develop longitudinally on the ventral surface of beluga whales (Werth and Ford 2012; Rouse et al. 2017).



Figure 5.2: Satellite tag pin scars on a beluga whale observed in the Churchill River, western Hudson Bay on 7 August 2019. Underwater photographs were taken during the Churchill photographic monitoring program in Churchill River area, which was initiated in 2016. Photo credits: Beluga Bits/Explore.org.

The second whale, photographed in Cumberland Sound on 14 August 2019, had all three tag attachment pins intact (Fig. 3). This whale belongs to the endangered CS beluga whale population (DFO 2019; COSEWIC 2020). The satellite tag detached from the pins, but the pins were still in the dorsal ridge. Given the dates of the tagging programs, the pins from this tag remained in the whale for at least 11 years and for as many as 21 years at the time it was photographed. This beluga whale was a presumed female accompanied by a 1-year-old calf and appeared to be in good body condition with no obvious infection at the pin sites. The calf also appeared to be in good condition.



Figure 5.3: Satellite tag attachment pins in an adult beluga whale accompanied by a calf in Cumberland Sound, Nunavut on 14 August 2019. Photographs were taken during the Cumberland Sound photographic monitoring program in Clearwater Fjord, which was initiated in 2017 (Ryan et al. 2022). Photo credit: Fisheries and Oceans Canada.

5.5 Discussion

The effects of satellite tagging on beluga whales are poorly understood. It is important to document body condition, productivity, and survival when possible after tagging programs to identify long-term impacts and evaluate what is learned relative to what the potential effects may be. Analysis of tag attachment sites can provide valuable information that can be used to improve tag attachment methods, making them more effective and less harmful. The sightings of these two beluga whales with tag pins and pin scars provide additional insights into the effects of satellite tags, especially given the limited number of resightings in these and many other beluga whale populations. While these resightings only provide information about these two whales and not the healing or survival of other tagged individuals in either population, both whales appeared to be in good health with no sign of infection at the tagging site and with evidence of successful

reproduction in one whale, though notably the two methods of tag release were markedly different.

The WHB whale had most likely been tagged during one of three tagging programs concentrated in estuaries along the coast of southern and western Hudson Bay, where whales congregate during the summer: the Nelson ($n = 13$; 2002–2005), Seal ($n = 6$; 2012), and Churchill Rivers ($n = 8$; 2015) (Fig. 4) (Westdal et al. 2016; Matthews et al. 2017; Smith et al. 2017). The WHB population is the largest beluga whale population worldwide, numbering over 50 000 whales (Matthews et al. 2017) and ranges several hundred to thousands of kilometers between summering grounds on the west and southern coast of WHB and winter habitat in the Hudson Strait (see Hobbs et al. 2020). Assuming this whale summered in the same general geographic region every year as has been reported for other populations (Colbeck et al. 2013; O'Corry-Crowe et al. 2018), it could have been tagged in the same general location where it was photographed in the Churchill River in 2015, tagged 90 km to the north at the Seal River in 2012, or 250 km to the south at the Nelson River in 2002–2005 (Fig. 4). However, it is possible that the WHB whale could have been a whale tagged in other areas of Hudson Bay (eastern Hudson Bay or James Bay) and without a photographic identification catalog or genetic confirmation, we have no means to be sure of the individual identity of previously tagged whales.

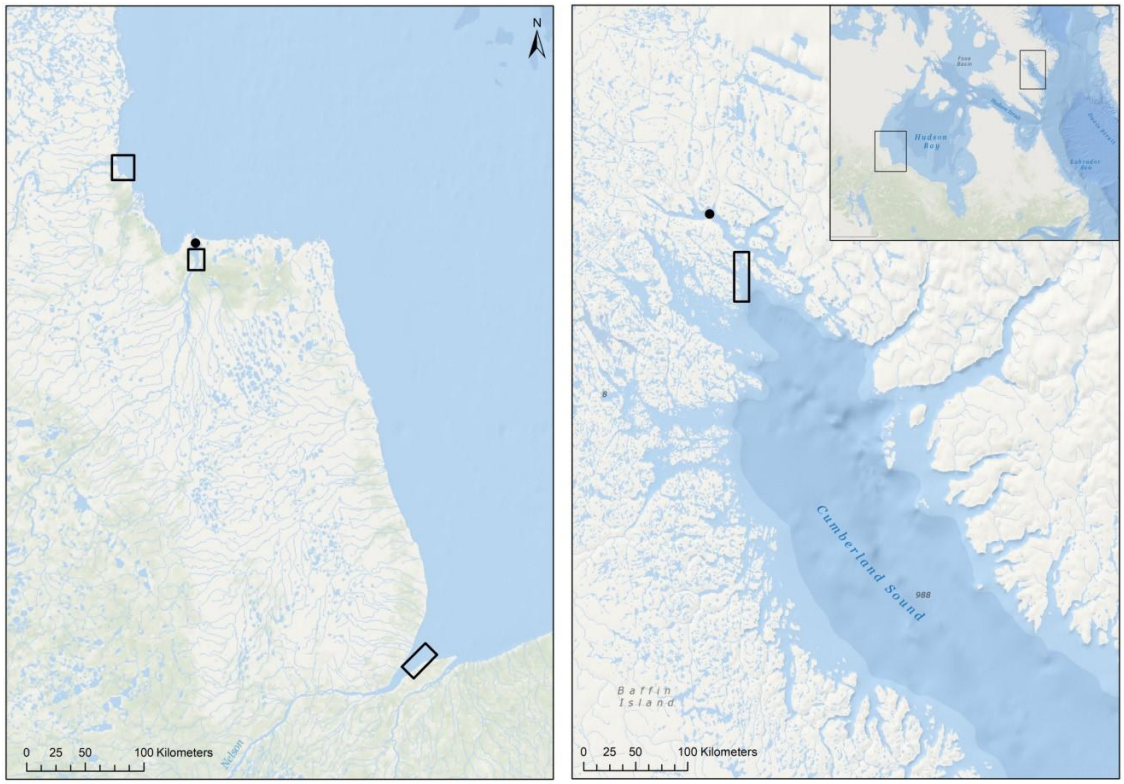


Figure 5.4: Locations of the beluga whale tagging sites (boxes) in western Hudson Bay in the Seal River (2012), Churchill River (2015), and Nelson River (2002–2005) and the tagging site in Cumberland Sound, Nunavut (1998–1999, 2006–2008). The locations of the whales photographed with tag pins and tag pin scars are denoted with circles in western Hudson Bay (7 August 2019) and in Cumberland Sound (14 August 2019). Map was generated using ArcGIS 10.7 (ESRI Inc., Redlands, CA, USA).

The CS population, conversely, is among few beluga whale populations that remain within a relatively small geographic area year-round, migrating from the north of Cumberland Sound to the southern extent of the Sound for winter (Richard and Stewart 2009). Whales in this population were tagged during 1998–1999 and 2006–2008 (Fig. 4) (Watt et al. 2016). The whale was located approximately 35 km from where it was tagged indicating long-term site fidelity of this individual (Fig. 4). This population has been depleted due to historic commercial hunting and subsistence harvesting that is currently above sustainable levels (DFO 2019). The population numbered approximately 1400 whales during the last aerial survey estimate in 2017 and has likely declined further since then (DFO 2019), and the population was listed as endangered in

2020 (COSEWIC 2020). The ongoing photo-identification program primarily involves using markings on the whales' dorsal surface, most of which are either from unknown causes or from scars from gunshot wounds that, once healed, remain relatively unchanged over time (Ryan et al. 2022).

Research on subcutaneous wound healing in captured beluga whales has demonstrated that beluga whales heal more slowly than other cetacean species (Geraci and Bruce-Allen 1987; Geraci and Smith 1990). In a study on healing after pin implantations, bleeding in beluga whales stopped after 24–48 h. However, in bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)), recovery from similar wounds took 30 min; this difference is likely due to the greater thickness of the epidermis in beluga whales (Geraci and Bruce-Allen 1987; Geraci and Smith 1990). Slow healing in beluga whales may leave them more susceptible to infection after tagging; wounds from satellite tags leave the whale at risk of infection because bacteria can be introduced in the opening of the wound where the tag was inserted (Geraci and Smith 1990; Weller 2008). Fungal diseases can also be introduced this way, as seen in a killer whale (*Orcinus orca* (Linnaeus, 1758)) after the attachment of a satellite tag (Huggins et al. 2020).

Tags can detach from the animal's body in a number of different ways; the tag attachments can migrate out of the body due to drag over time, or the pins can be pulled through their entry/exit holes after the cables that connect the tag to the pins have detached or frayed. The scars on the WHB whale, which consisted of lines from the original tag positions leading up to V-shaped notches where the tag and pins were pulled out through the dorsal ridge, are consistent with the tag attachments migrating out and also match the description of scarring from tagged beluga whales resighted in the late 1990s in the Canadian High Arctic (Orr et al. 1998), the eastern Chukchi Sea, Alaska (Suydam et al. 2005), and many whales in the Cook Inlet, Alaska population (McGuire and Stephens 2017).

Resightings of tagged beluga whales from the Cook Inlet population have occurred more frequently than in many others, due to the small population size (~270 whales) that remains year-round in Cook Inlet (Sheldon and Wade 2019) and a long-term photo-identification program that photographs hundreds of whales each year (McGuire et al. 2021). Out of 14 resighted tagged

whales in this population, 5 had infection at the tag site, visible in photographs, and 8 whales had sunken or concave dorsal ridges at the location where the tag would have rested (McGuire and Stephens 2016, 2017; McGuire et al. 2021). Many scars from Cook Inlet were similar to the WHB whale and consistent with the tag attachments migrating out, with a scar through the dorsal ridge creating a V-shape notch in the dorsal ridge (Orr et al. 1998; McGuire and Stephens 2017).

The resighting of embedded pins as in the CS whale has never been documented in beluga whales. In this case, the tag cables detached from the pins, consistent with tag loss, and the pins remained in place. Though there is no record of pins remaining in the skin in Cook Inlet whales, circle/hole-shaped scars have been documented at least two times in Cook Inlet, indicating tag loss; these whales had transmitted telemetry data for 125 and 238 days (McGuire and Stephens 2016). The shape of these scars indicates that the cable on one side of each pin released similarly to that in the CS whale, but the pins were then pulled out through the original holes. The presence of a calf with the CS whale indicates no serious long-term effects on its reproductive health. Resightings of tagged whales in small or endangered populations are especially significant because negative impacts of tags can disproportionately affect small populations, potentially with population-level effects (Weller 2008; International Whaling Commission 2020). Less invasive means of tagging (e.g., crossbow and harpoon style) can leave scars that are smaller and shallower and therefore likely less prone to infection (see Le Net 2018), but the duration of the tag is severely limited compared to the pin-attached tags.

Although the scars have healed in the WHB whale and there is no sign of infection in either whale at least 4 and 11 years after tagging, associated complications could still arise. The extensive photographic record in Cook Inlet has shown that after signs of recovery post-tagging, beluga whale health can still be impacted several years later (McGuire et al. 2021). After the scars had healed, the tag sites of some Cook Inlet whales still showed signs of infection and underwent other changes such as the roughening of the scar, changing of its edges and the surrounding skin, and the accumulation of debris in the scar site (McGuire et al. 2021). One whale that had been tagged in 2002 became infected in 2006; the tag site deteriorated and caused increasing concavity in the surrounding area, including the dorsal ridge itself, until its death in

2015. Its death was attributed to a lung infection that had led to a secondary infection at the tagging site (McGuire et al. 2021). In this and other populations, the cause of injury to many of the tagged whales remains poorly understood. It could be related to the tagging injuries themselves, infections being introduced at the tag site, or the stress of capture making them susceptible to other infections and poor body condition (McGuire et al. 2021).

Our sample size is limited and therefore there are limitations to what can be extrapolated to tagged whales in general. There was a notable lack of sightings of any other tagged whales although the sample sizes (27 and 20 in WHB and CS, respectively) of tagged whales was higher. In Churchill with its large population size (>50,000 whales), resightings would be less likely, but in Cumberland Sound (~1500 whales) we would expect to see more tagged whales (Matthews et al. 2017; DFO 2019). We also do not know what happened to the whales between the tagging events and sightings (4-17 years in Churchill and 11-21 years in Cumberland Sound), whether there was an infection that healed, or whether the Cumberland Sound had reproductive success before the calf it was sighted.

Resightings of previously tagged whales provide additional information after tagging and insight into the effects of tags themselves. The summer resightings of a WHB and a CS whale within 0–250 km and 35 km of their respective tagging locations, 4 and 11–21 years after their initial capture, suggest long-term site fidelity. Though infection was not observed, additional photographic monitoring of both populations to see whether infections appear several years after tagging, as has been documented in Cook Inlet (McGuire et al. 2021), or whether the tag sites remain unchanged, will provide information about the long-term effects of tagging and could help lead to improvements in the method of tag attachment. As with any method, the negative effects must be considered relative to information needs, especially in endangered populations such as Cumberland Sound. The ongoing photographic monitoring of both populations could yield additional information if these or other satellite-tagged whales are identified, including more detailed information about health, reproductive history, and site fidelity of previously tagged whales.

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Summary

Understanding the dynamics of endangered populations is crucial for developing effective conservation strategies, especially for populations facing environmental changes and anthropogenic disturbances (Abbitt et al. 2001; Blanck et al., 2007; Hernández-Yáñez et al. 2022; Murray et al. 2011; Ockinger et al., 2010). When species show no signs of recovery, it is necessary to explore aspects of their ecology that may indicate what is inhibiting their recovery (Hutchings et al. 2010; Lotze et al. 2017; Hutchings et al. 2015). Investigating key variables such as migration timing and drivers, prey preferences, reproductive rates, mortality rates, and population structure can provide valuable insight into the factors affecting population growth (Robinson et al. 2009; Cherry et al. 2013; Snell et al. 2022). Additionally, understanding the population-specific interactions between environmental changes, anthropogenic stressors, and the behavior and reactions associated with them is critical for predicting future population trends and designing targeted and effective conservation goals (Kiszka et al., 2015; Matley et al., 2015). Conservation initiatives may work for some populations but not others, so more detailed information about an endangered population will result in conservation efforts that are more effectively tailored to support recovery and long-term sustainability (Pimm et al., 2021).

This thesis explored various aspects of the ecology of the Cumberland Sound beluga whale population, using a combination of satellite telemetry, drone surveys, aerial surveys, and photographic identification to provide a comprehensive understanding of their demographic characteristics, social organization, migration patterns, and dive behavior. The research outlined here made a significant contribution to the field of marine mammal conservation by integrating these diverse methods and providing detailed insights into this species. The first chapter detailed various aspects of beluga whale ecology as a whole, relating information that is applicable to populations worldwide and detailing important interpopulation differences that should be noted for future research, including the reproductive and mortality rates of populations, habitat use, diet, and temporal trends and drivers of migration. This knowledge is necessary for understanding the subsequent chapters, which delved into more specific studies of the Cumberland Sound population.

The diet preferences and migration timing of beluga whales are diverse, as are the drivers of their migrations, their migration routes, and the distances they travel; the second chapter explored these aspects, many of which have demonstrated interpopulation variability (Bailleul et al., 2012; Boltunov and Belikov 2002; Goetz et al., 2012; Hauser et al., 2014, 2017, 2018; O'Corry-Crowe et al., 2016; Quakenbush et al. 2015). Satellite telemetry data from two distinct time periods (1998–1999 and 2006–2008) were used to examine the whales' movements, both location and depth. The migrations of the whales, which were predicted to depend on ice buildup within Cumberland Sound, significantly preceded any ice formation within Cumberland Sound. This finding varied from those in other populations that have found migration timing to vary by several weeks in response to changing dates of ice coverage, where the whales will remain in their summer habitat for as long as possible before migrating (Bailleul et al. 2012; O'Corry-Crowe et al., 2016; Hauser et al., 2017). The rigidity in the migration timing of the population could be detrimental, if for instance an anomalous ice event results in ice cover in their summer or autumn habitat. The distribution of their prey might also not be as uniform or reliable, which could result in reduced prey availability. We did not have sufficient data to explore the timing of their spring migration, but if that is as inflexible as the autumn migration, similar issues could arise if the ice remains longer in Cumberland Sound or their prey distribution is variable in spring.

The analysis of dive behavior showed more shallow dives in summer than autumn and winter, and more shallow dives in the second period (2006–2008) than the first (1998–1999), which supported the hypothesis that the whales' preferred prey had changed over time. The switch of prey was inferred from the shallower dives in the second time period, since capelin is typically found higher in the water column (Benoit et al. 2014; Falk-Petersen et al. 1986; Forster et al. 2020; Geoffroy et al. 2011; Jansen et al. 2021; McGowan et al. 2019). Capelin is also typically distributed farther south but expanded north into the ecosystem, likely associated with climate change enabling their expansion north, and they may have displaced Arctic cod as the preferred prey of Cumberland Sound beluga whales (Campana et al. 2020; Hobbs et al. 2020; Marcoux et al. 2012; Vacquié-Garcia et al. 2018; Watt et al. 2016). The long-term effects of this switch are hard to quantify but may impact the population since the abundance and distribution of capelin

can be variable, and they may potentially be lower in dietary quality (Choy et al., 2019, 2020; Marcoux et al., 2012; McKinney et al., 2012; Thiemann et al., 2008). Overall, this chapter provided insight into important aspects of Cumberland Sound beluga whale ecology and by examining these factors, the research shed light on how beluga whales navigate and utilize their habitat, which is essential for their conservation.

To monitor more detailed changes over time, drone photography was used to create a photographic identification catalog for the Cumberland Sound population. The study, conducted from 2017 to 2019, identified 93 unique individuals through drone photographs, which captured distinctive markings on the whales that were from unknown causes or from gunshots. This minimally invasive method allowed for the collection of high-resolution data without causing disturbance to the population, providing a reliable means of monitoring population demographics. The development of this catalog facilitates long-term tracking of individual whales, enhancing our understanding of their population dynamics. For example, long-term individual identification of the whales in this population will allow for the monitoring of reproductive and mortality rates of various age classes, which we know from Chapter 1 vary among populations, and opportunistic observations such as wound healing over time. The continuation of the catalog will also eventually allow for the use of mark-recapture abundance estimation that could supplement the aerial survey abundance estimates that have been used in the past. Accurate abundance estimation is vitally important for endangered populations.

Chapter 4 combined more detailed analysis of the drone survey data established in Chapter 3 with aerial survey data. The benefits and limitations of drones and aerial surveys were explored in this chapter, and the age structure, group structure, and social organization of the Cumberland Sound beluga whale population were explored and quantified. Aerial surveys conducted in 2014 and 2017 provided extensive coverage and suggested a potential contraction in the population's geographic range. These surveys were complemented by drone focal follows from 2017 to 2019. The study revealed a lower proportion of juveniles compared to other beluga whale populations, indicating possible problems with juvenile survival (Mosnier et al. 2015; Krasnova et al. 2012). Additionally, stable associations between individuals were documented across days and years,

suggesting the presence of persistent social groups, which is poorly understood and monitored in beluga whale populations. The combined use of aerial and drone surveys provided a comprehensive view of the population, demonstrating the benefit of using multiple research techniques to capture both broad-scale and fine-scale data. This integrated approach allowed for a more thorough understanding of how demographic factors and social behaviors influence population dynamics.

The fifth chapter investigated the long-term effects of satellite tagging on beluga whales. Two beluga whales, one from Western Hudson Bay and another from Cumberland Sound, were photographed with tag remnants and scars. The findings indicated that the whales exhibited no signs of infection and maintained good body condition, despite the presence of tag remnants for 10-21 years. This chapter underscored the importance of long-term monitoring to assess the implications of tagging and to refine tagging techniques for future research (Geraci & Smith 1990; Orr et al. 1998). The results highlighted the resilience of beluga whales to tagging but also stressed the potential long-term impacts, especially given some deleterious effects noted in other populations (McGuire et al. 2021). This chapter also demonstrated the continued benefits of drone use in capturing the Cumberland Sound whale with pins inserted although that whale was not visible to observers from the boat at the time of the survey.

Conclusions, contributions to knowledge, and future research directions

Overall, this thesis provided novel information about beluga whale ecology. The detailed insights gained from this research can inform targeted conservation strategies that address the specific needs and threats faced by beluga whales in Cumberland Sound, and may be applicable to other populations or species. Historical and ongoing overharvesting, both commercial and subsistence, significantly reduced the population and continues to impact its recovery. The current quota of 41 whales per year is unsustainable, as indicated by population models suggesting a continued decline under this quota (Watt et al. 2021). While overharvesting may be the primary threat that this population faces, the shift in preferred prey, contraction in overall range, and stability in migration timing are other factors that may impact the population. The rigidity in migration timing may expose the population to risks from anomalous ice events or mismatches with prey

availability, potentially affecting survival. Climate change and associated environmental changes, such as sea ice loss and shifts in prey distribution, pose additional threats to this beluga whale population. Further, the apparent shift in prey preference from Arctic cod to capelin over time may result, or possibly already has resulted, in inconsistent abundance and distribution of their prey or as yet unquantified energetic consequences.

Maintaining a long-term photographic identification catalog of known individuals will allow for the estimation of more accurate birth and mortality rates, providing essential data for accurately projecting future population dynamics and tailoring effective conservation strategies. A long-term photo-ID catalog will also allow for the calculation of mark-recapture abundance estimates, which is critical for an endangered population for which abundance is currently estimated every few years. Long-term monitoring of the population will also allow for the identification of healing over time in whales and possibly the continued monitoring of satellite-tagged whales. The high occurrence of scarring in the population may provide insights into the rate at which whales are struck during harvests. Gathering genetic data on groups during drone surveys could provide insight into the relationship between whales that show long-term associations, determining if these associations are due to relatedness among these individuals or not, which is a critical aspect of beluga social organization that remains poorly understood. A combination of the photographic identification program and biopsy sampling of individuals captured in the drone photography would provide many of these suggested insights.

The aerial and drone surveys indicated a lower proportion of juveniles compared to other beluga whale populations, suggesting potential challenges in juvenile survival. Low juvenile survival could be contributing to stagnant or decreasing population sizes. These findings suggest that the population may be experiencing demographic challenges, possibly related to hunting pressure or environmental stressors, which could have long-term implications. A potential contraction in the population's geographic range could also limit access to critical habitats needed for foraging, calving, and protection from predators. Annual drone surveys in Clearwater Fjord would be ideal for monitoring, so there is consistency over time and because the population is concentrated in this area. The continuation of staggered aerial surveys would also allow for the continued

comparison between drone and aerial survey results and a more comprehensive view of the population. The integrated approach used in this thesis demonstrated the importance of employing multiple research methods to gather data that can inform conservation strategies.

Future research efforts should explore long-term environmental trends and how the population responds to them. It is important to consider potential environmental stressors, such as shifts in sea ice cover, temperature fluctuations, and changes in prey availability, in future conservation planning. Future research should focus specifically on collecting data to help quantify relationships between environmental variables and demographic parameters. In addition, tracking the presence of predators, such as killer whales, and their impact on the Cumberland Sound beluga population could provide insight into mortality rates and inform management decisions (Ferguson et al. 2010; Lefort et al. 2020). Increased killer whale presence may be influencing beluga distribution, movement patterns, and mortality rates. Understanding the extent of predation risk and its potential effects on beluga habitat selection will help refine conservation strategies. The insights gained from the research outlined in this thesis and suggested future directions can inform targeted conservation initiatives that address the specific needs and threats faced by beluga whales in Cumberland Sound, with possible applications to other populations and species.

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