Exploration of grouping characteristics and spatial distribution of beluga whales (*Delphinapterus leucas*) in the Eastern Beaufort Sea

By

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The University of Manitoba campuses are located on original lands of Anishinaabeg, Cree, Oji-Cree, Dakota, and Dene peoples, and on the homeland of the Métis Nation.

This research was conducted in the Inuvialuit Settlement Region, land of the Inuvialuit peoples, as established by the Inuvialuit Final Agreement.

We respect the Treaties that were made on these territories, we acknowledge the harms and mistakes of the past, and we dedicate ourselves to move forward in partnership with Indigenous communities in a spirit of reconciliation and collaboration.

Abstract

Beluga whales (*Delphinapterus leucas*) are considered social whales, but like any other cetaceans, the study of social behaviour is challenging to conduct. Due to the wide distribution of the Eastern Beaufort Sea beluga whale population across its summering grounds, little is known about the large-scale grouping behaviour and spatial distribution of groups. The aim of this research is to explore the grouping characteristics and organization of beluga groups, as well as the habitat preference of different social groups in summer. First, we used aerial photographs captured in July 2019 to describe group size, age composition, inter-individual distance, and swimming direction of beluga groups. We compared characteristics between two key summer habitats: the extended offshore of the Beaufort Sea shelf and the inshore of the Mackenzie Estuary. Results showed that group size and inter-individual distance were similar in both habitats. The average distance in a group varied with age composition and the swimming direction varied between the offshore and inshore. Second, we used GPS locations of beluga sightings recorded by visual observers during aerial surveys conducted in July and August 2019. We investigated the distribution of three beluga social group types (individual belugas, groups of adults, and groups with calf) using hierarchical generalized additive models. The sea surface temperature, bathymetry, and slope described best the summer distribution. Areas of high preference were often associated with prey distribution, suggesting foraging as the main driver of habitat preference. We also hypothesized that body size energy requirements contributed to the variation between the group types. This study revealed for the first-time observations of grouping behaviour in the summer habitat of the Eastern Beaufort Sea beluga whales. Although the results do not reflect the extent and complexity of beluga social behaviour, this study now provides an information baseline for this beluga population. We also encourage multidisciplinary research as an opportunity to further collect data and explore other elements of beluga whale sociality.

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The research reported in Chapter 3 was conducted by Alexandra Mayette (conceptualization, methodology, visualization, writing). The methodology and manuscript have been reviewed by Marianne Marcoux (Fisheries and Oceans Canada, University of Manitoba), John Iacozza (University of Manitoba), Megan Ferguson (National Oceanic and Atmospheric Administration), and Lisa Loseto (Fisheries and Oceans Canada, University of Manitoba). Data curation of the August survey was done by Amelia Brower (University of Washington and National Oceanic and Atmospheric Administration). The manuscript is in preparation for submission.

Chapter 1. General Introduction

1.1 Background

Evolution of group-living animals

Across taxonomic groups, animals are observed living in different patterns of aggregations, with widely varying social structures and organizations (Wilson, 2000; Rubenstein and Abbot, 2017). Animal sociality evolves in response to selective pressures when they provide a fitness advantage in life-history events such as mating, feeding, parental care, and predation (Acevedo-Gutiérrez, 2018). Living in groups is, however, a trade-off between benefits (e.g., increased access to food and mating opportunities, reduced risk of predation and calf mortality) and costs (e.g., increased resource and mating competition, greater visibility to predators, exposure to diseases and parasites) (Connor et al., 1998; Mann et al., 2000; Silk, 2007; McHugh, 2019). As sociality shapes evolutionary patterns, ecology, and biology of a species or population, the study of animal grouping behaviour has become increasingly relevant to understanding the full range of social strategies and how they vary among or within species (Whitehead, 1997; Kutsukake, 2009; Ward and Webster, 2016, McHugh, 2019).

Methods to study sociality in marine mammals

Long-term studies of terrestrial animal socialities, particularly primates, but also marsupials (kangaroos, wallabies), ungulates (elephants, bovids), and carnivores (wolves, lions), have led to a better understanding of concepts and hypotheses on social behaviour (Mann, 2000; Smith et al., 2017). Knowledge on behavioural ecology of marine mammals, such as cetaceans, is lagging behind that of terrestrial animals due to research challenges arising from environmental characteristics: access to habitat, underwater behaviour, difficulty in handling or marking, etc (Connor et al., 1998; Whitehead et al., 2000). Cetacean spatial scales can extend over thousands of kilometres and temporal scales over several decades (Whitehead et al., 2000). Arctic species are even more difficult to observe because of their remote distribution and fieldwork conditions (sea-ice cover, access to areas, weather, costs, etc.) Under these circumstances, inference has become particularly prevalent in this field of study (Whitehead et al., 2000). Any type of data available,

even from strandings and by-catch, has been used to try to characterize the social structure of species (Whitehead et al., 2000).

Today, many tools and methods have been developed to obtain a more detailed and accurate representation of social behaviour, structure, and organization of marine species, with their own advantages. Some techniques focus on one individual or one group for a long period of time (e.g., telemetry, focal follow), while others cover several individuals or groups over a short period (e.g., surveys, scan sampling) (Mann, 2000). Information on specific behaviours can be collected (e.g., diving, movement, vocalizations) and individual identification (e.g., photographic identification, genetics) can help describe conspecific associations and networks (Whitehead et al., 2000; Whitehead and Van Parijs, 2010). After data collection, social structures are analyzed depending on the approach (ecological or psychological), the unit of organization observed (community or individual), and the level (interaction, relationship, or structure) (Scott, 1956; Hinde, 1976; Whitehead, 1997).

Group size, composition, and cohesion

Describing group size, composition, and degree of cohesiveness is part of the early steps and is key when investigating social behaviour (Aureli et al., 2008; Reiczigel et al., 2008; Gowans, 2019). The definition of "group" must be established prior to data sampling and is usually based on the animals spatial and temporal proximity (usually a specific body length) as well as participation in a coordinated activity (Mann, 2000; Whitehead, 2008). Looking at group size can help determine the basic social unit, which then facilitates the quantification of interactions and associations within a group, necessary to build more complex social networks (Whitehead and Van Parijs, 2010). Group size can also provide insight into the distribution and possible range of aggregations (Reiczigel et al., 2008). Group composition and inter-individual distance can be used to reveal patterns of group cohesion. Indeed, the spatial organization can determine threshold distances of attraction versus repulsion to other individuals or groups, as well as optimal distances to benefit from group protection and facilitate information transmission, without being hindered in movements (Aureli et al., 2012; Ward and Webster, 2016).

Species distribution and habitat modelling

Other elements of ecology related to the benefits and costs of grouping are relevant to explore, such as conspecific interactions, foraging, mortality risk, mating, ontogeny, habitat selection, and energetics (Ward and Webster, 2016; Bräger and Bräger, 2019). Understanding the relationship between an animal distribution or movement with its environment can be a complex task, but achievable with species distribution and habitat models. Habitat selection analyses are a highly simplified process that captures the selection and use of habitat, within an available habitat (Northrup et al., 2022). Many types of models can be used to address different objectives, but they usually require occurrence or movement data from one or many animals, as well as discrete or continuous environmental covariates relevant to the habitat (McCabe et al., 2021; Northrup et al., 2022). The data is fit to a modelling algorithm (e.g., generalized linear model, resource selection functions, MaxEnt, etc.), evaluated, validated, and then the results can be mapped (Elith and Leathwick, 2009; Northrup et al., 2022). When exploring population sociality, habitat models can be used to assess the distribution and/or resource selection of different social group types (e.g., Lindsay et al. 2016; Pace et al. 2018). Although they have inherent uncertainties and limitations, models can help establish conservation and resource management strategies (Robinson et al., 2017).

Sociality of odontocetes

Odontocetes, or toothed whales, are frequently studied for their social behaviour, as most have complex and rich social lives (Connor et al., 1998). Sociality of odontocetes can be described in two types: matrilineal or fission-fusion (Vaughn-Hirshorn, 2019). Killer whales (*Orcinus orca*) are one of the best examples of matrilineal societies, where pods are formed of matriarchal hierarchical social structures, stable for decades (Bigg et al., 1990; Baird and Whitehead, 2000; Parsons et al., 2009). Similarly, sperm whales (*Physeter macrocephalus*) maintain strong bonds between units of females and calves, even when associated with other units (Best, 1979; Lyrholm et al., 1999; Konrad et al., 2018). On the other hand, fission-fusion socialities are dynamic associations of individuals, which vary in group size, composition, and cohesion over time (Aureli et al., 2008). Dolphin populations are good examples of fission-fusion societies, with aggregations of up to hundreds of individuals (Shane et al., 1986; Bearzi et al., 1997; Gygax, 2002; Karczmarski et al., 2005; Stockin et al., 2009; Lunardi and Ferreira, 2014; Gerrodette et al., 2019).

Beluga whales

Beluga whales (*Delphinapterus leucas*) are distinctive odontocetes, with white skin and melon head, and members of the Monodontidae family along with the narwhal (*Monodon monoceros*) (O'Corry-Crowe, 2018). In Canada, eight designatable units (i.e., populations) are recognized by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), named after their summering habitat (COSEWIC, 2016). Distributed across the circumpolar Arctic and in some sub-Arctic regions, belugas are well adapted to cold environments (Reeves et al., 2014). Studies on different beluga populations have shown the influence of many environmental conditions on habitat use, such as bathymetric features, sea surface temperature, distance to shore, tides, currents, and sea ice (Loseto et al., 2006; Goetz et al., 2007; Hauser et al., 2017; Hornby et al., 2017; Ouellet et al., 2021).

Beluga whales exhibit sexual size dimorphism, i.e., males are larger than females (Heide-Jørgensen and Teilmann, 1994; Stewart, 1994), which result in variation in the diet and diving capacity (Martin and Smith, 1999; Marcoux et al., 2012; Choy et al., 2020). However, belugas do not have other obvious morphological sexual differences, which poses a challenge when identifying whales in the wild. Size and colour are generally the physical characteristics used to visually estimate the age of a beluga (Smith et al., 1994; Michaud, 2014; McGuire et al., 2020). Indeed, other than size growth, newborns have dark grey skin that lightens as they grow, turning completely white by the time they become subadults (Sergeant, 1973).

Females lactate for a period of 20 to 24 months, resulting in calves closely following their mother for two to three migrations cycles (Brodie, 1971; Sergeant, 1973; Colbeck et al., 2013; Matthews and Ferguson, 2015). The nursing period is thought to also facilitate cultural migratory learning for calves (Brodie, 1969; O'Corry-Crowe et al., 2018). During this period, calves spend time in proximity to kin and non-kin (Krasnova et al., 2006; Krasnova et al., 2009; Colbeck et al., 2013; O'Corry-Crowe et al., 2020). Allomaternal behaviour has been observed, where non-mother cares for the calf (Krasnova et al., 2009; Aubin et al., 2021). This gregarious behaviour suggests that belugas have complex social interactions.

Belugas forms groups, sometimes large herds, and use an extensive range of vocalizations associated with distinct behaviours (Sjare and Smith, 1986a; Sjare and Smith, 1986b; Belikov and Bel'kovich, 2003; Panova et al., 2012; O'Corry-Crowe, 2018; Vergara and Mikus, 2019; O'Corry-

Crowe et al., 2020). As with any other cetaceans, research on social behaviour of wild belugas is difficult to conduct, especially for Arctic populations. Captive belugas in human care have facilitated the observations of interactive behaviours in small groups, leading to synergistic efforts to understand beluga behaviour in both settings (see review by Hill et al. 2021). Still, studies on wild beluga populations have been able to identify common patterns of group composition. Females are generally observed in groups with calf and juveniles, not necessarily excluding males (Colbeck et al., 2013; Krasnova et al., 2014; McGuire et al., 2020; O'Corry-Crowe et al., 2020). As juveniles become more independent, they swim further away from the maternal group (Halteman and Ryan, 2019; McGuire et al., 2020). Younger males can form their own group with other belugas of their size (Smith et al., 1994; Andrianov et al., 2009; Suydam, 2009; Colbeck et al., 2013; Michaud, 2014; McGuire et al., 2020; O'Corry-Crowe et al., 2020). Beluga observed alone are most likely large, older males (Krasnova et al., 2006; Colbeck et al., 2013; O'Corry-Crowe et al., 2020). Group size and composition remain overall flexible and dynamic within a population, where groups can join and leave other groups, suggesting that beluga whales are in a fission-fusion type of sociality (Bel'kovich and Sh'ekotov, 1993; Krasnova et al., 2012; Alekseeva et al., 2013; Michaud, 2014; O'Corry-Crowe et al., 2020).

Eastern Beaufort Sea beluga population

The Eastern Beaufort Sea (EBS) beluga population is one of the eight Canadian beluga populations and one of the most abundant (COSEWIC, 2016). Abundance assessments have estimated the population at ~32 500 whales and COSEWIC has assigned it a status of "not at risk" (COSEWIC, 2004; Muto et al., 2021). EBS belugas migrate from the Bering Sea in spring following the ice retreat, to their summering range in the Beaufort Sea and surrounding areas (Richard et al., 2001; Hornby et al., 2016). From mid to late July, belugas show high fidelity to the bays in the Mackenzie Estuary, forming large aggregations (~2 000 whales) (Harwood et al., 1996; Harwood et al., 2014). It is suggested that the contrasting environmental conditions of the estuary (i.e., warm, shallow waters and freshwater input) compared to the offshore attract belugas for calving and moulting (St. Aubin et al., 1990; Scharffenberg et al., 2019). Telemetry studies have also shown offshore movements in the Amundsen Gulf, M'Clure Strait, and Viscount Melville Sound throughout the summer (Richard et al., 2001; Storrie et al., 2022). EBS belugas feed primarily on Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*), which are considered one of the main drivers

of their summer distribution (Loseto et al., 2009; Hauser et al., 2017; Hornby et al., 2017; Choy et al., 2020).

Inuvialuit and beluga research

Every summer, communities of the Inuvialuit Settlement Region (ISR) in Northwest Territories, Canada, hunt *qilalugaq* (belugas) from the EBS stock, as a traditional and cultural subsistence harvest (Harwood and Smith, 2002; Usher, 2002). While the delta communities of Aklavik, Inuvik, and Tuktoyaktuk hunt in the shallow, turbid bays of the Mackenzie Estuary, the other three communities, Paulatuk, Sachs Harbour and Ulukhaktok, harvest more opportunistically offshore (Harwood et al., 2015). Paulatuk is the community that harvest the most outside of the Mackenzie Delta, mainly in the clear waters of Darnley Bay (Harwood et al., 2015). Interest in protecting EBS belugas and the rights of Inuvialuit hunters has led to conservation and sustainable harvest regulations, as well as collaborative monitoring and research programs between federal institutions and Inuvialuit organizations (Loseto et al., 2018b; Breton-Honeyman et al., 2021). Traditional and ecological knowledge (TEK) about EBS belugas has previously been gathered from local knowledge holders and experts (Byers and Robert, 1995; Inuuvik Community Corporation et al., 2006; Hartwig, 2009; KAVIK-AXYS Inc, 2012). Those reports document information on beluga distribution, seasonal migrations, physical characteristics, and some behavioural activity in harvesting sites or areas of high ecological significance. More recently, projects involving Inuvialuit and scientists have co-produced knowledge on beluga health and climate change impacts (Loseto et al., 2018a; Loseto et al., 2018b; Ostertag et al., 2018; Waugh et al., 2018), but both sides still acknowledge the need to obtain more information on beluga behaviour and to improve meaningful involvement of community members in scientific research (e.g., FJMC Research Priorities Summary 2020-2021). Bridging Western science and TEK is increasingly recognized as a significant tool in research, conservation, and management (Huntington, 2000; Thornton and Scheer, 2012), but also as an approach to decolonize scientific research and value Indigenous ways of knowing (Held, 2019).

1.2 Thesis Structure and Objectives

This research aims to improve knowledge on the grouping behaviour of the Eastern Beaufort Sea beluga whale population in summer. Elements of sociality are explored with data collected during aerial surveys conducted in 2019. Following the general introduction on sociality and methods for studying social behaviour in marine mammals (Chapter 1), this thesis addresses two specific objectives. Using aerial photographs captured during the survey, the first objective is to compare group characteristics and spatial organization of beluga whales in two key summer habitats, the Beaufort Sea offshore shelf and the shallow waters of the Mackenzie Estuary (Chapter 2). The second objective is to investigate the habitat preference of three types of beluga social groups in the extended offshore areas of the Beaufort Sea, in July and August (Chapter 3). The concluding chapter summarises the objectives, discusses the contributions of this research, and highlights potential future work (Chapter 4).

We were not able to go back to the communities in the Inuvialuit Settlement Region to engage with knowledge holders and share insights on social behaviour as planned due to COVID-19 travel restrictions in the Canadian Arctic. However, there was still an opportunity throughout this thesis to acknowledge Indigenous knowledge, discuss the importance of Inuit inclusion in Arctic research, and recommend potential avenues for integrative projects on beluga social behaviour.

1.3 Literature Cited

Acevedo-Gutiérrez, A. (2018). Group Behavior. In B. Würsig, J. G. M. Thewissen and K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (pp. 428-435). Academic Press.

Alekseeva, Y. I., Panova, E. M. and Bel'kovich, V. M. (2013). Behavioral and Acoustical Characteristics of the Reproductive Gathering of Beluga Whales (*Delphinapterus leucas*) in the Vicinity of Myagostrov, Golyi Sosnovets, and Roganka Islands (Onega Bay, the White Sea). *Biology Bulletin, 40*(3), 307-317. doi:10.1134/S1062359013030023

Andrianov, V. V., Bel'kovich, V. M. and Lukin, L. R. (2009). White Whale (*Delphinapterus leucas*) Distribution in Onega Bay of the White Sea in the Summer. *Oceanology, 49*(1), 73-82. doi:10.1134/S0001437009010093

Aubin, J. A., Michaud, R. and Vander Wal, E. (2021). Prospective evolutionary drivers of allocare in wild belugas. *Behaviour, 158*(8-9), 727-756. doi:https://doi.org/10.1163/1568539X-bja10094

Aureli, F., Schaffner, C. M., Asensio, N. and Lusseau, D. (2012). What is a subgroup? How socioecological factors influence interindividual distance. *Behavioral Ecology, 23*(6), 1308-1315. doi:https://doi.org/10.1093/beheco/ars122

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, Simon K., Call, J., Chapman, Colin A., Connor, R., Di Fiore, A., Dunbar, Robin I. M., Henzi, S. P., Holekamp, K., Korstjens, Amanda H., Layton, R., Lee, P., Lehmann, J., Manson, Joseph H., Ramos-Fernandez, G., Stier, Karen B. and van Schaik, Carel P. (2008). Fission-Fusion Dynamics: New Research Frameworks. *Current Anthropology, 49*(4), 627-654. doi:10.1086/586708

Baird, R. W. and Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology, 78*(12), 2096-2105. doi:10.1139/z00-155

Bearzi, G., Notarbartolo-DI-Sciara, G. and Politi, E. (1997). Social Ecology of Bottlenose Dolphins in the Kvarnerić (Northern Adriatic Sea). *Marine Mammal Science, 13*(4), 650-668. doi:10.1111/j.1748-7692.1997.tb00089.x

Bel'kovich, V. M. and Sh'ekotov, M. N. (1993). *The Belukha Whale: Natural Behavior and Bioacoustics.* Woods Hole, MA: Woods Hole Oceanographic Institution.

Belikov, R. and Bel'kovich, V. M. (2003). Underwater vocalization of the Beluga Whales (*Delphinaterus leucas*) in a reproductive gathering in various behavioural situations. *Oceanology, 43*(1), 112-120.

Best, P. B. (1979). Social Organization in Sperm Whales, *Physeter macrocephalus*. In H. E. Winn and B. L. Olla (Eds.), *Behavior of Marine Animals* (pp. 227-289). New York: Plenum Press.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B. and Balacomb, K. C. (1990). *Social organization and genealogy of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State*. Rep. Int. Whaling Comm. Spec. Issue 12.

Bräger, S. and Bräger, Z. (2019). Movement Patterns of Odontocetes Through Space and Time. In B. Würsig (Eds.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 117-144). Cham, Switzerland: Springer International Publishing.

Breton-Honeyman, K., Huntington, H. P., Basterfield, M., Campbell, K., Dicker, J., Gray, T., Jakobsen, A. E. R., Jean-Gagnon, F., Lee, D., Laing, R., Loseto, L., McCarney, P., Noksana Jr, J., Palliser, T., Ruben, L., Tartak, C., Townley, J. and Zdor, E. (2021). Beluga whale stewardship and collaborative research practices among Indigenous peoples in the Arctic. *Polar Research, 40*(S1), doi:10.33265/polar.v40.5522

Brodie, P. F. (1969). Duration of Lactation in Cetacea: An Indicator of Required Learning? *The American Midland Naturalist, 82*(1), 312-314. doi:10.2307/2423849

Brodie, P. F. (1971). A Reconsideration of Aspects of Growth, Reproduction, and Behavior of the White Whale (*Delphinapterus leucas*), with Reference to the Cumberland Sound, Baffin Island, Population. *Journal of the Fisheries Research Board of Canada, 28*(9), 1309-1318. doi:10.1139/f71-198

Byers, T. and Robert, L. W. (1995). *Harpoons and Ulus: Collective wisdom and traditions of Inuvialuit regarding the beluga ("qilalugaq") in the Mackenzie River estuary*. 89 p.

Choy, E. S., Giraldo, C., Rosenberg, B., Roth, J. D., Ehrman, A. D., Majewski, A., Swanson, H., Power, M., Reist, J. D. and Loseto, L. L. (2020). Variation in the diet of beluga whales in response to changes in prey availability: insights on changes in the Beaufort Sea ecosystem. *Marine Ecology Progress Series, 647*, 195-210. doi:https://doi.org/10.3354/meps13413

Colbeck, G. J., Duchesne, P., Postma, L. D., Lesage, V., Hammill, M. O. and Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society B: Biological Sciences, 280*(1752), 20122552. doi:10.1098/rspb.2012.2552

Connor, R. C., Mann, J., Tyack, P. L. and Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology & Evolution, 13*(6), 228-232. doi:https://doi.org/10.1016/S0169-5347(98)01326-3

COSEWIC (2004). *COSEWIC assessment and update status report on the beluga whale Delphinapterus leucas in Canada*. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 70 p.

COSEWIC (2016). *Designatable Units for Beluga Whales (Delphinapterus leucas) in Canada*. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 73 p.

Elith, J. and Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics, 40*(1), 677-697. doi:10.1146/annurev.ecolsys.110308.120159

Gerrodette, T., Perryman, W. L. and Oedekoven, C. S. (2019). Accuracy and precision of dolphin group size estimates. *Marine Mammal Science, 35*(1), 22-39. doi:10.1111/mms.12506

Goetz, K. T., Rugh, D. J., Read, A. J. and Hobbs, R. C. (2007). Habitat use in a marine ecosystem: beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Marine Ecology Progress Series, 330*, 247-256. doi:10.3354/meps330247

Gowans, S. (2019). Grouping Behaviors of Dolphins and Other Toothed Whales. In B. Würsig (Eds.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 3-24). Cham, Switzerland: Springer International Publishing.

Gygax, L. (2002). Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns. *Behavioral Ecology, 13*(5), 583-590. doi:10.1093/beheco/13.5.583

Halteman, D. M. and Ryan, W. L. (2019). The Effect of Group Composition on the Social Behaviors of Beluga Whales (*Delphinapterus leucas*) in an Artificial Environment. *Aquatic Mammals, 45*(3), 303-310. doi:10.1578/AM.45.3.2019.303

Hartwig, L. (2009). *Mapping Traditional Knowledge Related to the Identification of Ecologically and Biologically Significant Areas in the Beaufort Sea*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2895: iii+25p.

Harwood, L. A., Iacozza, J., Auld, J. C., Norton, P. and Loseto, L. (2014). Belugas in the Mackenzie River estuary, NT, Canada: Habitat use and hot spots in the Tarium Niryutait Marine Protected Area. *Ocean & Coastal Management, 100*, 128-138. doi:10.1016/j.ocecoaman.2014.08.004

Harwood, L. A., Innes, S., Norton, P. and Kingsley, M. C. S. (1996). Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea and west Amundsen Gulf during late July 1992. *Canadian Journal of Fisheries and Aquatic Sciences, 53*, 2262-2273. doi:https://doi.org/10.1139/f96-180

Harwood, L. A., Kingsley, M. C. S. and Pokiak, F. (2015). *Monitoring beluga harvests in the Mackenzie Delta and near Paulatuk, NT, Canada: harvest efficiency and trend, size and sex of landed whales, and reproduction, 1970-2009*. Can. Manuscr. Rep. Fish. Aquat. Sci. 3059: vi + 32 p.

Harwood, L. A. and Smith, T. G. (2002). Whales of the Inuvialuit Settlement Region in Canada's Western Arctic: An Overview and Outlook. *Arctic, 55*(supp 1), 77-93. doi:https://doi.org/10.14430/arctic736

Hauser, D. D. W., Laidre, K. L., Stern, H. L., Moore, S. E., Suydam, R. S. and Richard, P. R. (2017). Habitat selection by two beluga whale populations in the Chukchi and Beaufort seas. *PLoS ONE, 12*(2), e0172755. doi:10.1371/journal.pone.0172755

Heide-Jørgensen, M. P. and Teilmann, J. (1994). Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. *Meddelelser om Grønland Bioscience, 39*, 195-212.

Held, M. B. E. (2019). Decolonizing Research Paradigms in the Context of Settler Colonialism: An Unsettling, Mutual, and Collaborative Effort. *International Journal of Qualitative Methods, 18*, 1609406918821574. doi:10.1177/1609406918821574

Hill, H. M. M., Yeater, D. B. and Noonan, M. (2021). Synergy between behavioural research on beluga whales (*Delphinapterus leucas*) conducted in zoological and wild settings. *Polar Research, 40*(S1), doi:10.33265/polar.v40.5508

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man, 11*(1), 1-17. doi:10.2307/2800384

Hornby, C. A., Hoover, C., Iacozza, J., Barber, D. G. and Loseto, L. L. (2016). Spring conditions and habitat use of beluga whales (*Delphinapterus leucas*) during arrival to the Mackenzie River Estuary. *Polar Biology, 39*(12), 2319-2334. doi:10.1007/s00300-016-1899-9

Hornby, C. A., Iacozza, J., Hoover, C., Barber, D. G. and Loseto, L. L. (2017). Beluga whale *Delphinapterus leucas* late summer habitat use and support for foraging areas in the Canadian Beaufort Sea. *Marine Ecology Progress Series, 574*, 243-257. doi:10.3354/meps12178

Huntington, H. P. (2000). Using Traditional Ecological Knowledge in Science: Methods and Applications. *Ecological Applications, 10*(5), 1270-1274. doi:https://doi.org/10.1890/1051-0761(2000)010[1270:UTEKIS]2.0.CO;2

Inuuvik Community Corporation, Tuktuuyaqtuuq Community Corporation and Akłarvik Community Corporation (2006). *Inuvialuit Settlement Region Traditional Knowledge Report*. 200 p.

Karczmarski, L., Würsig, B., Gailey, G., Larson, K. W. and Vanderlip, C. (2005). Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. *Behavioral Ecology, 16*(4), 675-685. doi:10.1093/beheco/ari028

KAVIK-AXYS Inc (2012). *Traditional and Local Knowledge Workshop for the Paulatuk Area of Interest*. 46 p.

Konrad, C. M., Gero, S., Frasier, T. and Whitehead, H. (2018). Kinship influences sperm whale social organization within, but generally not among, social units. *Royal Society Open Science, 5*(8), 180914. doi:10.1098/rsos.180914

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. (2006). Mother-Infant Spatial Relations in Wild Beluga (*Delphinapterus leucas*) during Postnatal Development under Natural Conditions. *Biology Bulletin, 33*(1), 53-58. doi:10.1134/s1062359006010079

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. (2009). Formation of Behavior in the White Sea Beluga Calf, *Delphinapterus leucas*, during Early Postnatal Ontogenesis. *Russian Journal of Marine Biology, 35*(1), 53-59. doi:10.1134/s1063074009010088

Krasnova, V. V., Chernetsky, A. D., Kirillova, O. I. and Bel'kovich, V. M. (2012). The Dynamics of the Abundance, Age, and Sex Structure of the Solovetsky Reproductive Gathering of the Beluga Whale *Delphinapterus leucas* (Onega Bay, White Sea). *Russian Journal of Marine Biology, 38*(3), 218-225. doi:https://doi.org/10.1134/S1063074012030078

Krasnova, V. V., Chernetskya, A. D., Zheludkovab, A. I. and Bel'kovicha, V. M. (2014). Parental Behavior of the Beluga Whale (*Delphinapterus leucas*) in Natural Environment. *Biology Bulletin, 41*(4), 349-356. doi: https://doi.org/10.1134/S1062359014040062

Kutsukake, N. (2009). Complexity, dynamics and diversity of sociality in group-living mammals. *Ecological Research, 24*(3), 521-531. doi:10.1007/s11284-008-0563-4

Lindsay, R. E., Constantine, R., Robbins, J., Mattila, D. K., Tagarino, A. and Dennis, T. E. (2016). Characterising essential breeding habitat for whales informs the development of large-scale Marine Protected Areas in the South Pacific. *Marine Ecology Progress Series, 548*, 263-275. doi: https://doi.org/10.3354/meps11663

Loseto, L., Lam, J. and Iacozza, J. (2018a). Beluga Summit: knowledge sharing of the eastern Beaufort Sea beluga whale. *Arctic Science, 4*(3), i-iv. doi:10.1139/as-2018-0011

Loseto, L. L., Hoover, C., Ostertag, S., Whalen, D., Pearce, T., Paulic, J., Iacozza, J. and MacPhee, S. (2018b). Beluga whales (*Delphinapterus leucas*), environmental change and marine protected areas in the Western Canadian Arctic. *Estuarine, Coastal and Shelf Science, 212*, 128-137. doi:10.1016/j.ecss.2018.05.026

Loseto, L. L., Richard, P., Stern, G. A., Orr, J. and Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology, 84*(12), 1743-1751. doi:10.1139/z06-160

Loseto, L. L., Stern, G. A., Connelly, T. L., Deibel, D., Gemmill, B., Prokopowicz, A., Fortier, L. and Ferguson, S. H. (2009). Summer diet of beluga whales inferred by fatty acid analysis of the eastern Beaufort Sea food web. *Journal of Experimental Marine Biology and Ecology, 374*(1), 12-18. doi:https://doi.org/10.1016/j.jembe.2009.03.015

Lunardi, D. G. and Ferreira, R. G. (2014). Fission-fusion dynamics of Guiana dolphin (*Sotalia guianensis*) groups at Pipa Bay, Rio Grande do Norte, Brazil. *Marine Mammal Science*, *30*(4), 1401-1416. doi:https://doi.org/10.1111/mms.12121

Lyrholm, T., Leimar, O., Johanneson, B. and Gyllensten, U. (1999). Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1417), 347-354. doi:10.1098/rspb.1999.0644

Mann, J. (2000). Unraveling the Dynamics of Social Life: Long-term Studies and Observational Methods. In J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead (Eds.), *Cetaceans Societies: Field Studies of Dolphins and Whales* (pp. 45-64). Chicago: University of Chicago Press.

Mann, J., Connor, R. C., Tyack, P. L. and Whitehead, H. (2000). *Cetacean Societies: Field Studies of Dolphins and Whales.* Chicago: University of Chicago Press.

Marcoux, M., McMeans, B. C., Fisk, A. T. and Ferguson, S. H. (2012). Composition and temporal variation in the diet of beluga whales, derived from stable isotopes. *Marine Ecology Progress Series, 471*, 283-291. doi: https://doi.org/10.3354/meps10029

Martin, A. R. and Smith, T. G. (1999). Strategy and capability of wild belugas, *Delphinapterus leucas*, during deep, benthic diving. *Canadian Journal of Zoology, 77*(11), 1783-1793. doi:10.1139/z99-129

Matthews, C. J. D. and Ferguson, S. H. (2015). Weaning age variation in beluga whales (*Delphinapterus leucas*). *Journal of Mammalogy, 96*(2), 425-437. doi:10.1093/jmammal/gyv046

McCabe, J. D., Clare, J. D., Miller, T. A., Katzner, T. E., Cooper, J., Somershoe, S., Hanni, D., Kelly, C. A., Sargent, R., Soehren, E. C., Threadgill, C., Maddox, M., Stober, J., Martell, M., Salo, T., Berry, A., Lanzone, M. J., Braham, M. A. and McClure, C. J. W. (2021). Resource selection functions based on hierarchical generalized additive models provide new insights into individual animal variation and species distributions. *Ecography*, doi:https://doi.org/10.1111/ecog.06058

McGuire, T. L., Himes Boor, G. K., McClung, J. R., Stephens, A. D., Garner, C., Shelden, K. E. W. and Wright, B. (2020). Distribution and habitat use by endangered Cook Inlet beluga whales: Patterns observed during a photo-identification study, 2005–2017. *Aquatic Conservation: Marine and Freshwater Ecosystems, 30*, 2402-2427. doi:10.1002/aqc.3378

McHugh, K. (2019). Odontocete Social Strategies and Tactics Along and Inshore. In B. Würsig (Eds.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 165-182). Cham, Switzerland: Springer International Publishing.

Michaud, R. (2014). *St. Lawrence Estuary beluga (Delphinapterus leucas) population parameters based on photo-identification surveys, 1989-2012*. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/130.

Muto, M. M., Helker, V. T., Delean, B. J., Young, N. C., Freed, J. C., Angliss, R. P., Friday, N. A., Boveng, P. L., Breiwick, J. M., Brost, B. M., Cameron, M. F., Clapham, P. J., Crance, J. L., Dahle, S. P., Dahlheim, M. E., Fadely, B. S., Ferguson, M. C., W., F. L., Goetz, K. T., Hobbs R. C., Ivashchenko Y. V., Kennedy, A. S., London, J. M., Mizroch, S. A., Ream, R. R., Richmond, E. L., Shelden, K. E. W., Sweeney, K. L., Towell, R, Wade, G. P. R., Waite, J. M., Zerbini, A. N (2021). *Alaska marine mammal stock assessments, 2020.* U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-421. 398 p.

Northrup, J. M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M. P., Leclerc, M., Prokopenko, C. M. and Gerber, B. D. (2022). Conceptual and methodological advances in

habitat-selection modeling: guidelines for ecology and evolution. *Ecological Applications, 32*(1), e02470. doi:https://doi.org/10.1002/eap.2470

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K. and Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLoS ONE, 13*(3), e0194201. doi:https://doi.org/10.1371/journal.pone.0194201

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T. G., Lydersen, C., Kovacs, K. M., Orr, J., Harwood, L., Litovka, D. and Ferrer, T. (2020). Group structure and kinship in beluga whale societies. *Scientific Reports, 10*, 11462. doi:10.1038/s41598-020-67314-w

O'Corry-Crowe, G. M. (2018). Beluga Whale: *Delphinapterus leucas*. In B. Würsig, J. G. M. Thewissen and K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals (Third Edition)* (pp. 93-96). Academic Press.

Ostertag, S. K., Loseto, L. L., Snow, K., Lam, J., Hynes, K. and Gillman, D. V. (2018). "That's how we know they're healthy": the inclusion of traditional ecological knowledge in beluga health monitoring in the Inuvialuit Settlement Region. *Arctic Science, 4*, 292-320. doi:10.1139/as-2017-0050

Ouellet, J. F., Michaud, R., Moisan, M. and Lesage, V. (2021). Estimating the proportion of a beluga population using specific areas from connectivity patterns and abundance indices. *Ecosphere, 12*(6), e03560. doi:10.1002/ecs2.3560

Pace, D. S., Arcangeli, A., Mussi, B., Vivaldi, C., Ledon, C., Lagorio, S., Giacomini, G., Pavan, G. and Ardizzone, G. (2018). Habitat suitability modeling in different sperm whale social groups. *The Journal of Wildlife Management, 82*(5), 1062-1073. doi:https://doi.org/10.1002/jwmg.21453

Panova, E. M., Belikov, R. A., Agafonov, A. V. and Bel'Kovich, V. M. (2012). The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). *Oceanology, 52*(1), 79-87. doi:10.1134/s000143701201016x

Parsons, K. M., Balcomb, K. C., Ford, J. K. B. and Durban, J. W. (2009). The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Animal Behaviour, 77*(4), 963-971. doi:https://doi.org/10.1016/j.anbehav.2009.01.018

Reeves, R. R., Ewins, P. J., Agbayani, S., Heide-Jørgensen, M. P., Kovacs, K. M., Lydersen, C., Suydam, R., Elliott, W., Polet, G., van Dijk, Y. and Blijleven, R. (2014). Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. *Marine Policy, 44*, 375-389. doi:https://doi.org/10.1016/j.marpol.2013.10.005

Reiczigel, J., Lang, Z., Rózsa, L. and Tóthmérész, B. (2008). Measures of sociality: two different views of group size. *Animal Behaviour, 75*(2), 715-721. doi:10.1016/j.anbehav.2007.05.020

Richard, P. R., Martin, A. R. and Orr, J. R. (2001). Summer and Autumn Movements of Belugas of the Eastern Beaufort Sea Stock. *Arctic, 54*(3), 223-236. doi:https://doi.org/10.14430/arctic783

Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E. and Lundquist, C. J. (2017). A Systematic Review of Marine-Based Species Distribution Models (SDMs) with Recommendations for Best Practice. *Frontiers in Marine Science, 4*(421), doi:10.3389/fmars.2017.00421

Rubenstein, D. R. and Abbot, P. (2017). The Evolution of Social Evolution. In D. R. Rubenstein and P. Abbot (Eds.), *Comparative Social Evolution* (pp. 1-18). Cambridge Univsersity Press.

Scharffenberg, K., Whalen, D., Marcoux, M., Iacozza, J., Davoren, G. and Loseto, L. (2019). Environmental drivers of beluga whale *Delphinapterus leucas* habitat use in the Mackenzie Estuary, Northwest Territories, Canada. *Marine Ecology Progress Series, 626*, 209-226. doi:https://doi.org/10.3354/meps13011

Scott, J. P. (1956). The Analysis of Social Organization in Animals. *Ecology, 37*(2), 213-221. doi:10.2307/1933133

Sergeant, D. E. (1973). Biology of White Whales (*Delphinapterus leucas*) in Western Hudson Bay. *Journal of the Fisheries Research Board of Canada, 30*(8), 1065-1090. doi:10.1139/f73-178

Shane, S. H., Wells, R. S. and Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science, 2*(1), 34-63. doi:10.1111/j.1748-7692.1986.tb00026.x

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*, 539-559. doi:10.1098/rstb.2006.1994

Sjare, B. L. and Smith, T. G. (1986a). The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. *Canadian Journal of Zoology, 64*(12), 2824-2831. doi:10.1139/z86-406

Sjare, B. L. and Smith, T. G. (1986b). The vocal repertoire of white whales, *Delphinapterus leucas*, summering in Cunningham Inlet, Northwest Territories. *Canadian Journal of Zoology, 64*(2), 407-415. doi:10.1139/z86-063

Smith, J. E., Lacey, E. A. and Hayes, L. D. (2017). Sociality in Non-Primate Mammals. In (Eds.), *Comparative Social Evolution* (pp. 284-319). Cambridge University Press.

Smith, T. G., Hammil, M. O. and Martin, A. R. (1994). Herd composition and behaviour of white whales (*Delphinapterus leucas*) in two Canadian arctic estuaries. *Meddelelser om Grønland Bioscience, 39*, 175-184.

St. Aubin, D. J., Smith, T. G. and Geraci, J. R. (1990). Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. *Canadian Journal of Zoology*, 68(2), 359-367. doi:10.1139/z90-051

Stewart, R. E. A. (1994). Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. *Meddelelser om Grønland Bioscience, 39*, 217-225.

Stockin, K. A., Binedell, V., Wiseman, N., Brunton, D. H. and Orams, M. B. (2009). Behavior of free-ranging common dolphins (*Delphinus sp.*) in the Hauraki Gulf, New Zealand. *Marine Mammal Science, 25*(2), 283-301. doi:10.1111/j.1748-7692.2008.00262.x

Storrie, L., Hussey, N. E., MacPhee, S. A., O'Corry-Crowe, G., Iacozza, J., Barber, D. G., Nunes, A. and Loseto, L. L. (2022). Year-Round Dive Characteristics of Male Beluga Whales

From the Eastern Beaufort Sea Population Indicate Seasonal Shifts in Foraging Strategies. *Frontiers in Marine Science, 8*, 715412. doi:10.3389/fmars.2021.715412

Suydam, R. S. (2009). *Age, growth, reproduction, and movements of beluga whales (Delphinapterus leucas) from the eastern Chukchi Sea*. [Doctoral thesis, University of Washington].

Thornton, T. F. and Scheer, A. M. (2012). Collaborative Engagement of Local and Traditional Knowledge and Science in Marine Environments: A Review. *Ecology and Society, 17*(3), doi:10.5751/ES-04714-170308

Usher, P. J. (2002). Inuvialuit Use of the Beaufort Sea and its Resources, 1960–2000. *Arctic, 55*(supp 1), 18-28. doi:https://doi.org/10.14430/arctic732

Vaughn-Hirshorn, R. (2019). Social Ecology of Feeding in an Open Ocean. In B. Würsig (Eds.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 51-73). Cham, Switzerland: Springer International Publishing.

Vergara, V. and Mikus, M.-A. (2019). Contact call diversity in natural beluga entrapments in an Arctic estuary: Preliminary evidence of vocal signatures in wild belugas. *Marine Mammal Science*, *35*(2), 434-465. doi:10.1111/mms.12538

Ward, A. and Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals.* Cham, Switzerland: Springer International Publishing.

Waugh, D., Pearce, T., Ostertag, S. K., Pokiak, V., Collings, P. and Loseto, L. L. (2018). Inuvialuit traditional ecological knowledge of beluga whale (*Delphinapterus leucas*) under changing climatic conditions in Tuktoyaktuk, NT. *Arctic Science, 4*(3), 242-258. doi:10.1139/as-2017-0034

Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour, 53*, 1053-1067. doi:https://doi.org/10.1006/anbe.1996.0358

Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis.* Chicago: University of Chicago Press.

Whitehead, H., Christal, J. and Tyack, P. L. (2000). Studying Cetacean Social Structure in Space and Time: Innovative Techniques. In J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead (Eds.), *Cetaceans Societies: Field Studies of Dolphins and Whales* (pp. 65-90). Chicago: University of Chicago Press.

Whitehead, H. and Van Parijs, S. (2010). Studying marine mammal social systems. In I. L. Boyd, W. D. Bowen and S. J. Iverson (Eds.), *Marine Mammal Ecology and Conservation: A Handbook of Techniques* (pp. 263-282). Oxford: Oxford University Press.

Wilson, E. O. (2000). *Sociobiology: The New Synthesis.* Cambridge: Belknap Press of Harvard Univsersity Press.

Chapter 2. Group Characteristics and Spatial Organization of the Eastern Beaufort Sea Beluga Whale (*Delphinapterus leucas*) Population Using Aerial Photographs

2.1 Abstract

While it is known that beluga whales (*Delphinapterus leucas* (Pallas, 1776)) are social animals, sociality within populations remains complex and poorly understood. Using aerial photographs taken in mid-July and early August 2019, we examined group characteristics and spatial organization of the Eastern Beaufort Sea beluga population in two distinct summering areas: (1) the continental shelf and offshore region of the southeast Beaufort Sea, and (2) the inshore of the Mackenzie Estuary. Observations revealed that the average group size was similar in both environments. A piecewise regression analysis showed that belugas were found to be most frequently within 24.6 m of another beluga in the offshore, and within 22.0 m in the inshore. The average inter-individual distance of groups composed of subadults and/or adults was greater than that of groups including younger whales in both environments. Also, the swimming direction of individuals in a group differed less in the offshore than in the inshore. We suggest that habitat shapes the types of activity conducted and that spatial cohesion within groups persists across environmental conditions but changes with age composition. By identifying elements of social structure and important areas for Eastern Beaufort Sea belugas, our results highlight the value of habitat conservation.

2.2 Introduction

Group living occurs when the benefits of life events, such as reproduction, foraging, parental care, and protection from predators, outweigh the costs of social aggregation (e.g., higher exposure to predators, food competition, risk of disease transmission) (Krause and Ruxton, 2002; Silk, 2007). Investigating group size is an early step in exploring social behaviour of animals, providing insight into the possible extent of aggregation and can reveal the optimal group size, which represents the

best trade-off between benefits and costs of social grouping in a given environment (Giraldeau, 1988; Ward and Webster, 2016). Other measures like the inter-individual distance (IID) provide information on the spatial arrangement within a group that would favour protection, communication, and cultural transmission, without hindering movement (Warburton and Lazarus, 1991; Ward and Webster, 2016) and can be used to identify subgroups and threshold distances of attraction versus repulsion to another individual or group (Aureli et al., 2012).

Most cetaceans are social animals and understanding such sociality is challenging compared to terrestrial animals (e.g., hard to access environment, underwater behaviour, large home range, lifespan of several decades, etc.) (Connor et al., 1998; Mann et al., 2000). The sociality of studied odontocete species varies from small and highly stable units of kin to temporary aggregations of thousands of individuals (Mann et al., 2000; Würsig, 2019). One distinct odontocete of the Arctic and sub-Arctic regions is the beluga whale, *Delphinapterus leucas* (Pallas, 1776) (O'Corry-Crowe, 2018). Studies conducted on small groups of captive belugas in aquarium settings have recorded interactive social behaviours (Recchia, 1994; Hill and Campbell, 2014; Hill et al., 2016; Halteman and Ryan, 2019). Research on wild beluga populations has also reported a variety of observations, such as herding and group dynamic (Smith et al., 1994; Krasnova et al., 2012; Anderson et al., 2017), high acoustic activity and contact calls (Panova et al., 2012; Vergara and Mikus, 2019), and allomaternal care (Aubin et al., 2021), which suggests rich and complex social lives (O'Corry-Crowe et al., 2020). However, similar to other cetaceans, much is still unknown about the social organization of beluga whales in their natural habitat.

The Eastern Beaufort Sea (EBS) beluga whale population is one of the largest beluga populations in Canada, estimated at approximately 32 500 whales (Harwood and Norton, 1996; Muto et al., 2021). Each year, EBS belugas migrate to the Beaufort Sea, following the retreat of sea ice in the spring (Asselin et al., 2011; Hornby et al., 2014) and spend the summer travelling between the Mackenzie Estuary, Amundsen Gulf and M'Clure Strait (Richard et al., 2001; Storrie et al., 2022). From early to late July, EBS belugas show high fidelity to the Mackenzie Estuary (Brown Gladden et al., 1997; Harwood et al., 2014), where large aggregations of nearly 2 000 whales have been recorded (Harwood and Norton, 1996). In contrast to the offshore, the Mackenzie Estuary contains many shallow and warm bays, that receive large inputs of freshwater, especially in the spring (Carmack et al., 2004). The freshwater environment of the Mackenzie Estuary triggers moulting,

i.e., shedding caused by the growth and replacement of the epidermis, and provides thermal advantage for calving (St. Aubin et al., 1990; Scharffenberg et al., 2019). It is also during the summer that Inuvialuit, Inuit of the western Canadian Arctic, engage in a subsistence harvest of beluga whales in the Mackenzie Estuary, as well as opportunistic hunts in coastal areas outside of the Mackenzie Estuary (Usher, 2002; Waugh et al., 2018).

Using aerial photos from a large-scale survey conducted by Fisheries and Oceans Canada in 2019, this study aims to describe the group characteristics and spatial organization of the EBS belugas in two key summer habitats, the open water of the Beaufort Sea shelf and extensive offshore areas (offshore), and the shallow waters of the Mackenzie Estuary (inshore). Previous tagging studies have demonstrated sexual segregation in the summer distribution of EBS belugas, with males selecting deep offshore areas for energy-rich food, while females with calves select open water habitat near the coast for protection and moulting (Loseto et al., 2006; Hauser et al., 2017), suggesting that habitat preference differs according to social factors such as sex and age. Based on our current knowledge of cost and benefits of grouping, are there differences in the characteristics of groups found in different habitats?

2.3 Methods

Research approach

This study is part of a larger research program focused on Arctic marine ecosystem health using beluga whale health, diet, and movement ecology in the Beaufort Sea (Breton-Honeyman et al., 2021). Within this region and co-management context, government researchers and Inuvialuit routinely work together to identify research priorities and to design and conduct studies (e.g. (Loseto et al., 2018a; Loseto et al., 2018b; Ostertag et al., 2018). Prior to conducting the aerial survey, all six communities in the Inuvialuit Settlement Region were visited in 2018 and in-person consultations were held with co-management boards and community members (local Hunters and Trappers Committees (HTC)) to develop the research questions and co-design the aerial survey. After confirming local support, study protocols were approved by the Inuvialuit Game Council and the Fisheries Joint Management Committee in 2019.

Initially, this project intended to bring the aerial survey photos back to knowledge holders in the community of Paulatuk, located on Darnley Bay on the coast of the Beaufort Sea (69.35°N; 124.07°W), with the goal to improve interpretation of the aerial photograph data (Table S2.1, Figure S2.1). As Inuvialuit from Paulatuk harvest beluga whales in clear water, residents in this area possess substantial knowledge of beluga group characteristics and social organization which would help contextualize our analysis. Unfortunately, due to COVID-19 travel restrictions, we were not able to proceed with formal data co-interpretation workshops, however, we were able to meet with the Paulatuk HTC remotely to share and discuss the findings of our quantitative analysis. During this meeting, HTC members shared insightful perspectives and proposed using small drones to investigate beluga movement and social behaviour further. This community-led project, which evolved partially from this discussion with the HTC, is now underway and being shaped by the research priorities and interests of the community.

Study area

From mid-July to early August 2019, Fisheries and Oceans Canada conducted an aerial survey to update the abundance estimate for the EBS beluga population. Two major strata were covered: the offshore region, including the southeast Beaufort Sea, Amundsen Gulf, and Prince of Wales Strait (Longitude = -141°W to -115°W; Latitude = 69°N to 73°N) (Figure 2.1A), and the inshore region of the Mackenzie Delta including Shallow Bay, Mackenzie Bay, and Kugmallit Bay (Longitude = -137.72°W to -133.05°W; Latitude = 68.90°N to 69.61°N) (Figure 2.1B). The offshore eastern Beaufort Sea consists of a continental shelf that extends 50 to 150 km north of the coast, before a deep drop into the Canadian Basin at the ~80 m isobath (Hill et al., 1991; Carmack et al., 2004). The estuary is a highly turbid mixing zone, located at the mouth of the Mackenzie River with a depth of less than 20 m (Macdonald and Yu, 2006).
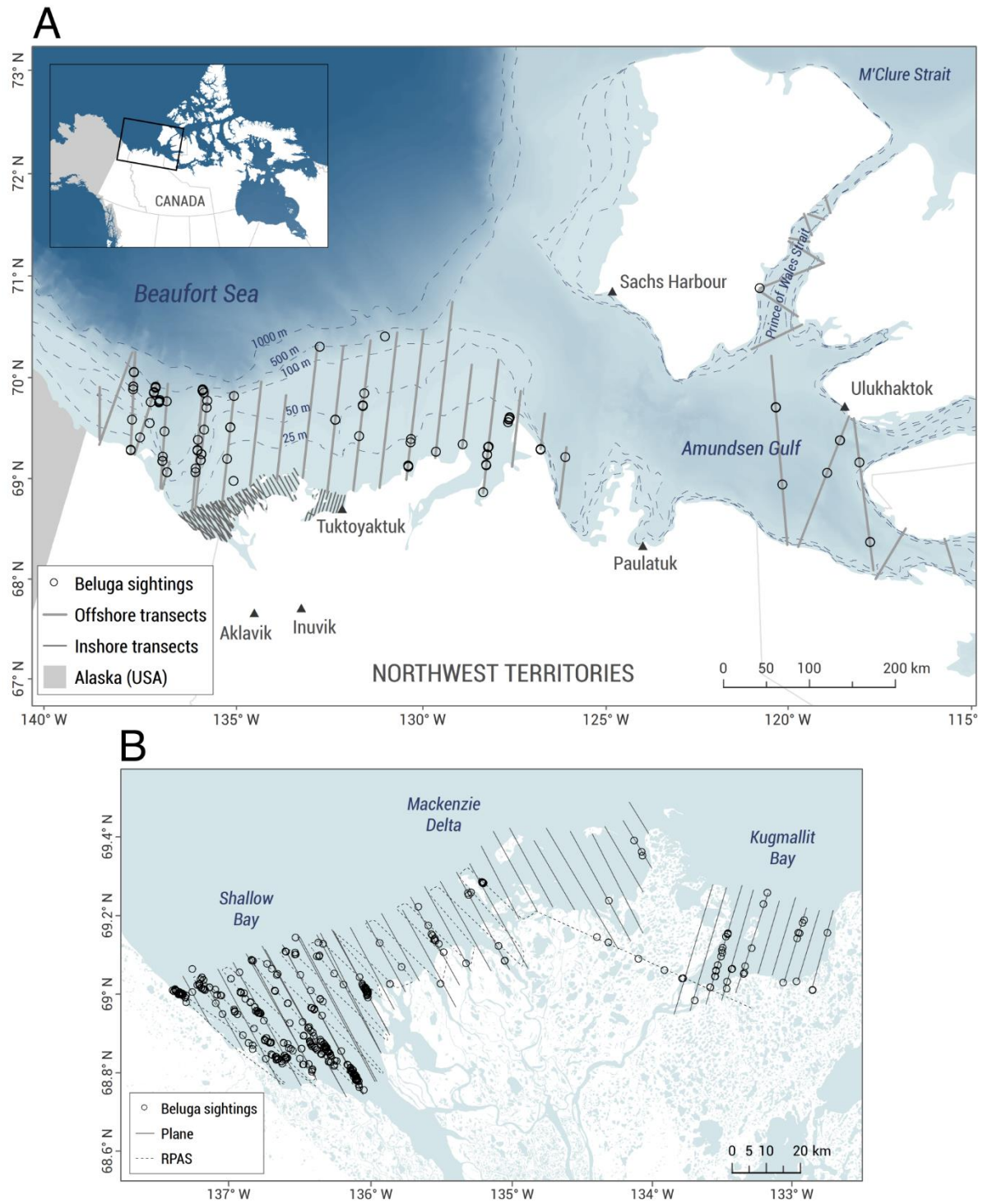
Figure 2.1 Sightings of individual beluga whales captured on photo during the 2019 Eastern Beaufort Sea beluga aerial survey. A) Offshore transect lines surveyed by plane. B) Enlarged area of the inshore transect lines surveyed by plane and by the remotely piloted aircraft system (RPAS).

Aerial survey and photo collection

The aerial survey was designed based on the last population abundance assessment in 1992, recent beluga tagging projects in the Canadian Beaufort Sea, and consultation with Inuvialuit representatives (Harwood and Norton, 1996; Storrie et al., 2022). Different survey protocols were applied between offshore and inshore areas based on the primary objective of assessing population abundance (e.g., Watt et al. 2021). Two Twin Otter aircraft were used and equipped with an optical glass-covered camera hatch at the rear underbelly of the plane. Position, altitude, speed, and heading of the aircraft were logged every second with a Bad Elf GPS Pro+ unit (Bad Elf, West Hartford, Connecticut, USA). For the offshore transects, aircraft were flown at a target altitude of 1 000 ft. (305 m) and a target speed of 100-110 knots (185-204 km/h). Flights were only flown in ideal conditions i.e., no rain, no risk of icing, ceilings of 1 000 ft or higher, no fog over the water and Beaufort Sea State of less than 3 (Environment and Climate Change Canada, 2017).

Each aircraft was equipped with two Nikon D850 cameras, one with a 25 mm lens (shooting RAW) and the other with a 50 mm lens (shooting JPEG), as a backup. Cameras were mounted in the covered camera hatch at the rear of the plane, facing straight down, with the longest side perpendicular to the track line. Photographic survey coverage for the offshore transects was approximately 127 604 m^2/photograph (437 m x 292 m) for the 25 mm lens. Cameras were connected to a laptop computer and remotely controlled by the Nikon Camera Control Pro 2 software to adjust settings such as shutter speed, aperture, and capture interval, throughout the flight. On offshore transects, photos were taken at a continuous interval of 3 sec to achieve a ~20% overlap for the offshore strata. Every photograph was geotagged via Bluetooth GPS receiver uplink (Bald Elf GSP Pro+ linked to Unleashed D200+ Bluetooth Module (Foolography, Berlin, Germany)).

The inshore stratum was surveyed by the Twin Otter aircraft at a target altitude of 2 000 ft (610 m) and a target speed of 100-110 knots (185-204 km/h) as well as by a remotely piloted aircraft system (RPAS), called the SeaHunter based out of the University of Fairbanks, Alaska (https://acuasi.alaska.edu/systems/seahunter). The RPAS surveyed Shallow Bay and Mackenzie Delta with the same camera system as the plane (i.e., Nikon D850 with a 25 mm lens). Photos of the inshore transects were captured at a continuous interval of 7 sec, with a photographic survey coverage for the inshore transects of approximately 510 125 m^2/photograph (875 m x 583 m).

Imagery analysis

Aerial photos were georeferenced and imported in ArcMap version 10.6.1 (ESRI, 2019). All photos with whales were detected manually. Some photos with beluga were taken in transition between transects and were kept in the analysis to increase the sample size. Next, a body length vector was created from the middle of the tail to the forehead and the geographic coordinates of the start, middle, and end of the vector were extracted for each whale. The vectors were not used for precise measurements of the body length since they were not standardized with the altitude and principal axes (roll, pitch, and yaw) of the plane. Duplicate whales in overlapping photo areas were identified but removed from the analysis.

Based on the 10 metres chain rule previously used with belugas and narwhals (*Monodon monoceros*) (Cosens and Dueck, 1991; Mann et al., 2000; Lemieux Lefebvre et al., 2018), a "group" was defined as individuals that are within one to two body lengths (limit of 10 m) from at least one individual in the group. The age of individuals was classified based on the size and position relative to the closest individual, and the skin colour (Caron and Smith, 1990; Krasnova et al., 2006; Michaud, 2014; Charry et al., 2018; Lemieux Lefebvre et al., 2018) (Table 2.1, Figure 2.2). Two different group types were identified: groups including at least one young whale (newborn, calf, or young juvenile) and groups composed of subadults and/or adults only. Unfortunately, the resolution of the photos did not make it possible to distinguish more precise classes, however, we considered subadults to behave more like adults than like young whales (Aubin et al., 2021). Whales that were either too deep underwater to properly detect or had partially visible bodies, were identified as unknown.

Table 2.1 Characteristics used for the age classification of beluga whales (*Delphinapterus leucas*) captured in aerial photographs.

Age	Body size	Position relative to adult	Colour
Newborn, calf and young juvenile	0.9 – 3 m (1/3 to 2/3 of adult size)	Close to adult, positioned at side, tail, above, ahead, below, or behind	Dark grey, light grey
Subadult and adult	3 – 4.5 m (>2/3 of adult size)	Usually keep a more apparent distance to other belugas	Light grey, white

Figure 2.2 Examples of aerial photographs from the 2019 Eastern Beaufort Sea beluga aerial survey. Photos have been enlarged and cropped to focus on the beluga groups. A) Group of four adult belugas offshore, B) Adult-young pair offshore, C) Group of six belugas offshore including five subadults/adults and one young, and D) Group of six subadults/adults inshore

Data processing

The spatial analyses for the swimming angle and the IID were achieved using the package "geosphere" (Hijmans et al., 2019) in R version 3.6.3 (R Core Team, 2020). The swimming direction was obtained by calculating the bearing from the North (0°) from the start and end coordinates of the body length vector. A matrix of IID was calculated using the geodesic distance between the middle coordinates of each beluga whale in a two-dimension aerial plan. Assuming the flying height was constant, the aerial photographic coverage was 437 m wide at sea, so only distances of 437 m or less were considered. The empirical cumulative distribution function was computed from the density function of the histogram of all distances (44 bins of 10 m) and a

piecewise regression model was performed with the R package "segmented" (Muggeo, 2020), to find the breakpoint value of two segments, following equation (1):

$$(1) \quad y_i = \begin{cases} \beta_0 + \beta_1 x_i + e_i, & \text{for } x_i \leq \alpha \\ \beta_0 + \beta_1 x_i + \beta_2 (x_i - \alpha) + e_i, & \text{for } x_i > \alpha \end{cases}$$

where y is the cumulative density, x is the distance between individuals, α is the breakpoint between the two segments, and e is the error (Toms and Lesperance, 2003). In this case, the breakpoint would detect a discontinuity in the frequency of inter-individual distances (a weak slope of the cumulative density indicates a low frequency of distance values, while a sharp slope indicates a high frequency). The value of the breakpoint thus identifies the threshold between the most and least common distances to other whales. A two-sided Mann-Whitney test was performed to compare the distributions of the distances between offshore and inshore.

The circular mean (μ), which indicate the average direction (angle), and the mean resultant length (ρ), which is a measure of spread, were both calculated for groups of three and more belugas using the package "circular" (Agostinelli and Lund, 2017).

2.4 Results

The photographs taken on the transects covered a total offshore area of 1 673 km^2 and a total inshore area of 2 096 km^2 (Table 2.2). The survey was completed in seven days and a total of 64 625 photos (55 411 offshore and 9 214 inshore) were taken, including additional photos taken in transition between transects. From these, a total of 716 belugas were identified.

Table 2.2 Details of the 2019 aerial survey strata flown by the Twin Otter aircraft and the remotely piloted aircraft system (RPAS), including strata flown, number of transects, distance flown (km) and total areas covered by photographs (km^2).

Strata	Number of transects	Orientation	Distance flown (km)	Area covered by camera (km^2)
Twin Otter				
Beaufort Sea offshore	22	N-S	3 144	1 231
Amundsen Gulf	5	N-S	674	294
Prince of Wales Strait	8	W-E	338	148
Shallow Bay	10	NW-SE	642	571
Mackenzie Delta	19	NW-SE	522	468
Kugmallit Bay	10	N-S	291	260
RPAS				
Shallow Bay	12	NW-SE	537	320
Mackenzie Delta	11	NW-SE	359	477
Total	97		6 507	3 769

Offshore area

A total of 203 whales (166 adults; 34 young; 3 unknown) were identified in the offshore area. A total of 45 groups were identified ($n = 104$ whales), representing 51.2% of the whales offshore, and ranging from one to eight individuals (Table 2.3). The average composition of groups was 71.4% subadults or adults, 28.3% young (newborn, calf, or juveniles) and 0.3% unknown. The average group size was 1.41 ($\pm$ 0.90) belugas, and the average IID within a group was 4.34 ($\pm$ 3.44) m. The average IID for groups that include at least one young whale was 2.88 ($\pm$ 3.10) m and 6.54 ($\pm$ 2.70) m for groups composed of subadults and/or adults only. The piecewise regression of the empirical cumulative density function ($n = 385$) computed a breaking point value of 24.6 m (SE: 0.5 m; $R^2 = 0.991$) (Figure 2.3). The slope before the knot was 1.46e-02 (SE: 3.70e-04) and

1.72e-03 (SE: 1.63e-05) after the knot. The average swimming direction was compared between groups. The mean resultant length (ρ) is a measure of spread with a value between 0 and 1, where 0 indicates a large spread between angles and 1 indicates the same value of angles (Cremers and Klugkist, 2018). For groups of three or more belugas based on the 10 m distance limit ($n = 4$), the ρ were all 0.99 (Table S2.2).

Inshore area

For the inshore area, a total of 513 whales were identified by photographs (377 adults; 60 young; 76 unknowns). Using the 10 m chain rule, we obtained 63 groups ($n = 164$ whales), which represented 32.0% of the total whales inshore (Table 2.3). Groups were composed on average of 63.5% subadults or adults, 26.2% young and 10.3% unknown. The resolution of the inshore photos and the turbidity of water (i.e., brown colour) made it harder to distinguish the age if belugas were partially submerged, which explains the larger proportion of unknowns compared to the offshore. Because of their smaller size and darker skin, the number of young whales could have been underestimated. Group size ranged from one to six individuals with a mean of 1.25 (± 0.68). The average IID within a group was 4.78 (± 3.05) m, 3.47 (± 2.53) m for groups including at least one young whale, and 6.13 (± 2.99) m for groups of subadults and/or adults. The piecewise regression breakpoint of the empirical cumulative density function ($n = 1\,070$) was calculated at 22.0 m (SE: 0.4 m; $R^2 = 0.997$) (Figure 2.3). The slope of the first segment was 9.43e-03 (SE: 2.10e-04) and the second slope was 1.88e-03 (SE: 4.30e-06). The Mann-Whitney test showed that the two distributions of distances (offshore and inshore) were significantly different ($W = 247653$; $p > 0.001$). For groups of more than two belugas based on the 10 m distance limit ($n = 24$), the mean resultant length ρ ranges from 0.33 to 0.99 (Table S2.2).

Table 2.3 Characteristics of groups measured from aerial photographs in the offshore area (including Beaufort Sea, Amundsen Gulf and Prince of Wales Strait strata) and the inshore area (including Mackenzie Delta, Shallow Bay and Kugmallit Bay strata). Characteristics were measured with a 10 m distance limit chain rule to define groups.

Group metrics	Habitat	
	Offshore	Inshore
Number of groups of more than one whale	45 ($n = 104$)	63 ($n = 164$)
Percentage of whales observed in groups	51.2%	32.0%
Range of group size	1 - 8	1 - 6
Mean of group size ($\pm$ SD)	1.41 ($\pm$ 0.90)	1.25 ($\pm$ 0.68)
Median of group size	1	1
Adult-young pairs (confirmed)	28	41
Mean group size with young ($\pm$ SD)	2.44 ($\pm$ 1.48)	2.50 ($\pm$ 0.98)
Average proportion of age class in a group ($\pm$ SD)		
Adult	0.714 ($\pm$ 0.242)	0.635 ($\pm$ 0.293)
Young	0.283 ($\pm$ 0.243)	0.262 ($\pm$ 0.277)
Unknown	0.003 ($\pm$ 0.186)	0.103 ($\pm$ 0.253)
Average inter-individual distance in a group ($\pm$ SD)		
All individuals of a group	4.34 ($\pm$ 3.44) m	4.78 ($\pm$ 3.05) m
Groups including young	2.88 ($\pm$ 3.10) m	3.47 ($\pm$ 2.53) m
Groups of subadults/adults only	6.54 ($\pm$ 2.70) m	6.13 ($\pm$ 2.99) m
Piecewise regression breakpoint ($\pm$ SE)	24.6 ($\pm$ 0.5) m	22.0 ($\pm$ 0.4) m
Range of mean resultant from group swimming direction	0.99 – 0.99	0.33 – 0.99
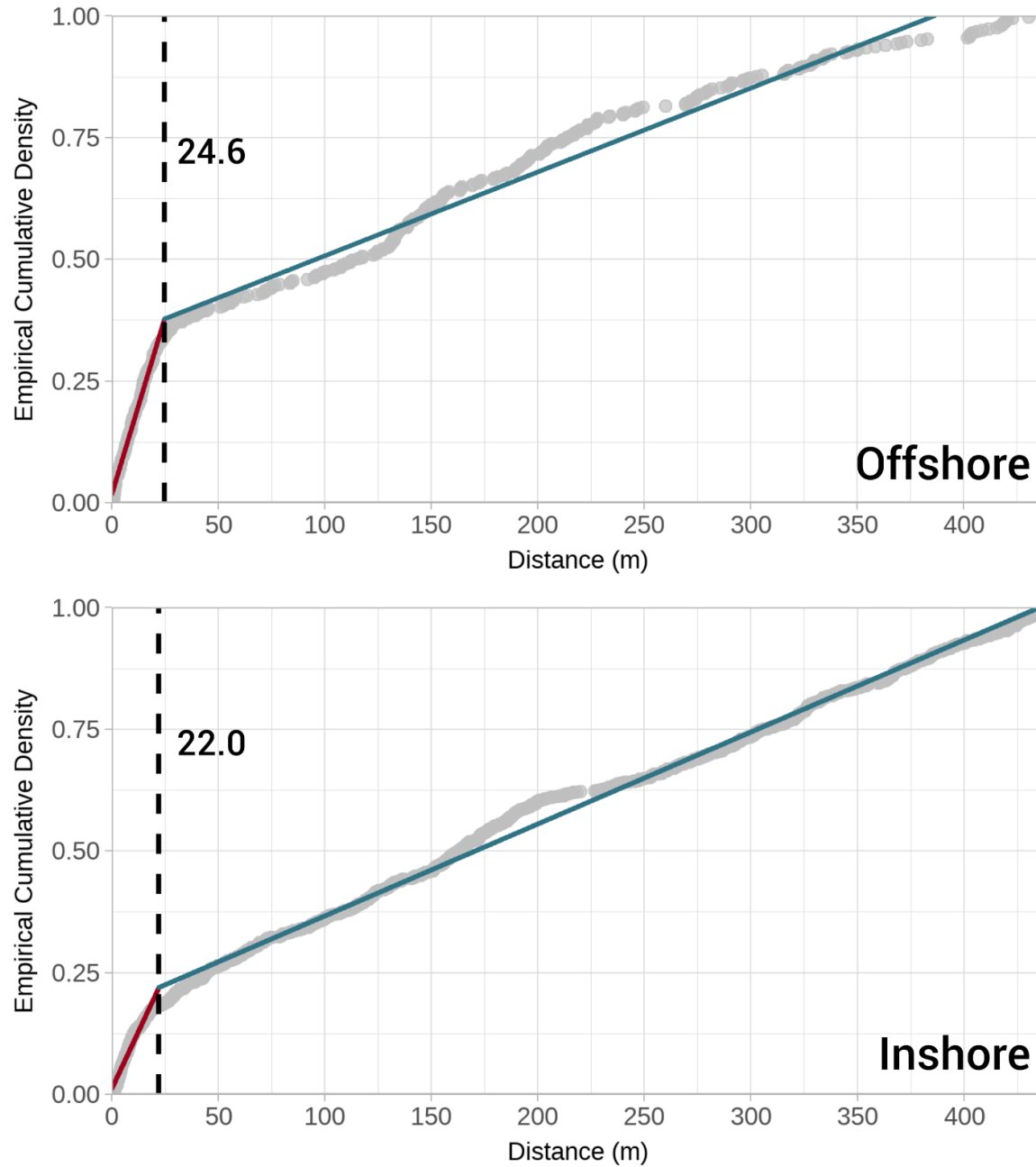
Figure 2.3 Piecewise regressions of the cumulative density of inter-individual distances offshore ($R^2 =$ 0.991) and inshore ($R^2 = 0.997$). The breakpoint (dashed line) was identified at 24.6 m offshore and at 22.0 m inshore. The slope before the knot was 1.46e-02 (red) and 1.72e-03 after the knot (blue) offshore. The slope before the knot was 9.43e-03 (red) and 1.88e-03 (blue) after inshore.

2.5 Discussion

The results of this study showed that group sizes were similar between the offshore strata (i.e., Beaufort Sea, Amundsen Gulf, and Prince of Wales Strait) and inshore strata (i.e., Mackenzie Delta, Shallow Bay, and Kugmallit Bay). Spatial organization of whales within a group, as expressed by the measure of IID was also similar in both environments but differed with group composition. The variance in swimming direction was different in the two environments.

Group size and range

Based on the common 10 metres chain rule for defining groups, analysis of photographs showed that belugas in the offshore area were more often alone or in small groups (eight whales or less). The distribution of group size followed the general rule observed in many group-living animals, where small groups are more frequent and large groups are rare (Reiczigel et al., 2008; Ward and Webster, 2016). Our results from aerial photos are not so different from those obtained by visual observers during the survey: average group size of 1.36 ($\pm$ 0.83) and maximum group size of seven whales (Fisheries and Oceans Canada, *unpublished data*). When compared to the results of other Canadian aerial surveys conducted in the same area of the southeastern Beaufort Sea, the average group size in 2019 is smaller than in previous years (Table 2.4). However, the 1985 and 1992 surveys also had small average group sizes (Harwood et al., 1996; Harwood and Kingsley, 2013). It should be noted that these previous surveys had similar protocols and were conducted at similar time periods in late July or August, however, they defined groups as belugas within five body lengths (Harwood et al., 1996; Harwood and Kingsley, 2013).

Table 2.4 Comparison of the average size (± SD) and range of beluga (*Delphinapterus leucas*) groups from previous offshore Canadian aerial surveys in the Beaufort Sea (1982[a], 1984-1985[a], 1992[b] and 2007-09[a]) with the 2019 results of the aerial survey in the Beaufort Sea from aerial photo analysis and visual observers.

	1982	1984	1985	1992	2007	2008	2009	2019 Photos	2019 Observer
Average group size (± SD)	2.6 (± 3.3)	2.2 (± 1.9)	1.7 (± 1.4)	1.65 (± 1.43)	3.4 (± 3.0)	2.2 (± 4.6)	3.4 (± 3.2)	1.40 (± 0.90)	1.36 (± 0.83)
Range	1 - 15	1 - 10	1 - 6	1 - 12	1 - 13	1 - 60	1 - 18	1 - 8	1 - 7

[a] data reported in Harwood and Kingsley (2013)
[b] data reported in Harwood et al. (1996)

For the inshore area, the results also showed that whales were alone or in small groups. The average group size, 1.23, was similar to that of the offshore, and there were no sightings of groups of more than six whales. However, it is possible that the number of belugas detected in the photos was underestimated due to the resolution of the photos taken at 2 000 ft, combined with the high turbidity of water in the estuary, making it challenging to see whales that were partially submerged. Aggregations of beluga whales in the estuary in late July are well known and this hotspot has led to the establishment of marine protected areas in the region as part of conservation efforts (Harwood et al., 2014). It is also not uncommon for Inuvialuit hunters to harvest whales from groups of 6-10 whales (Ostertag et al., 2019). According to Inuvialuit traditional ecological knowledge recorded in the Delta communities (Inuvik, Aklavik and Tuktoyaktuk, see Figure 2.1), harvesters highlight the importance of the estuary for social activity and calving (Byers and Robert, 1995; Waugh et al., 2018), which should correlate with gregarious behaviour (Krasnova et al., 2009; Smith et al., 2016). Although these behaviours were not evident during the 2019 aerial survey, other factors may have influenced beluga group size during the sampling period other than photograph resolution or water turbidity.

Another explanation for the small group size observed in the inshore area could be related to the weather. Indeed, scientists and Inuvialuit have noticed that the Beaufort Sea is experiencing

increased storm activity in the last few years, including the summer of 2019 (Waugh et al., 2018; Lim et al., 2020; Scharffenberg et al., 2020). Belugas tend to leave the Mackenzie Estuary during storms to seek refuge offshore and can take up to five days to return (Scharffenberg et al., 2020). Storm events can be defined as winds exceeding 37 km/h for six consecutive hours (Solomon et al., 1994). During the night of 20-21 July, strong winds of up to 68 and 57 km/h have been recorded at Shingle Point (68.95°N; 137.22°W) and Tuktoyaktuk (69.43°N; 133.02°W) weather stations respectively (Environment and Climate Change Canada, 2020), two days prior to the inshore survey (23 July). Winds of speed exceeding 37 km/h were also recorded on 25, 27 and 31 July (Environment and Climate Change Canada, 2020), only a few days before the area was surveyed again (28 July and 2 August). High winds have been previously correlated with an increase in wave height and decrease in beluga detections from passive acoustic monitoring (Scharffenberg et al., 2019). The conditions in the estuary could have caused belugas to temporarily leave the estuary and disperse in the offshore at the time the photos were taken.

Inter-individual distance

To our knowledge, the analysis of IID with a piecewise regression from aerial photographs has not been done before for a cetacean population. Similar to our study, Aureli et al. (2012) used a piecewise regression to find thresholds in the IID and to identify subgroups in primates. Although no other studies have used this method with cetaceans to investigate IID, other ecological studies have used piecewise regression as a robust method to detect changes or discontinuity in a response variable in marine animals (Toms and Lesperance 2003, e.g., sea turtles: Lamont and Houser 2014, otters: Thometz et al. 2014, polar bears: Atwood et al. 2016). The piecewise regression showed that in the offshore of the Beaufort Sea, belugas were more frequently found within 24.6 m of another whale, while in the inshore area of the Mackenzie Estuary, whales were found within 22.0 m. Our findings show that social cohesion, as assessed here by the IID, is constant across habitats but rather change with group composition.

The breakpoints in both habitats suggest that individuals in a group remain within a certain swimming distance of each other and that this spatial organization persists despite habitat change. These results contradict previous suggestions that different behaviours are associated with environmental features (Loseto et al., 2006; Hauser et al., 2017) that would have caused variation in the IID (Ward and Webster, 2016). As an example, variation in spatial cohesion via distance

between hamadryas baboons (*Papio hamadryas*) was observed when food availability changed and when predators were heard (Schreier and Swedell, 2012). Similarly, groups of Japanese macaques (*Macaca fuscata*) also adjusted their spatial organization in response to activities, seasons, and food distribution, although the distances were extremely large in summer, leading larger groups to split into subgroups (Sugiura et al., 2011). In Guiana dolphins (*Sotalia guianensis*), groups were closer together when resting, travelling, and socializing (≤ 2 m), and further apart when foraging and milling (2 – 20 m), sometimes leading to group fission (Lunardi and Ferreira, 2014). Aureli et al. (2012) used the breakpoint of the piecewise regression from IID of spider monkeys (*Ateles geoffroyi*) to define this threshold distance caused by attraction for subgroup formation. Attraction can play a role in structuring and maintaining subgroups through social cohesion which may vary with environment, behaviour, group size, etc. (Warburton and Lazarus, 1991; Aureli et al., 2012; Ward and Webster, 2016). The distance of ~20-25 m revealed in both environments of this study, may reflect the ideal spacing between beluga subgroups, favourable for communication, information transmission, and protection, while not hindering movement (Ward and Webster, 2016). This spatial integrity is maintained across a range of environmental conditions, possibly driven by social factors influencing cohesion (e.g., kinship, group size, sex ratio). A similar pattern was observed in coyotes (*Canis latrans*), where the social cohesion, described by distance within the pack, did not vary with seasons or prey availability, implying that the level of sociality was stable despite changes in their biological needs and environment (Gifford et al., 2017). Although examples of terrestrial animal societies are relevant, the marine environment is different from the terrestrial environment and many factors need to be considered when investigating IID (e.g., 3D space, visibility, sound propagation, food distribution). Nevertheless, it is possible that social cohesion is a stronger driver of social behaviour than expected in beluga sociality of the EBS population in the summer.

We found that group composition influenced spatial organization. In both environments, measurements of the average IID within a group revealed that individuals within subadult and/or adult-only groups swam at greater distances from each other than individuals within groups with young ones. The influence of group composition on distances between individuals has been documented in other species, like in patas monkeys (*Erythrocebus patas*) and gelada baboons (*Theropithecus gelada*), where female-female pairs stayed closer than male-male pairs (Kummer, 1974). In various species of dolphins, groups including calves or juveniles were swimming closer

together than groups of adults only (Scott and Perryman, 1991; Lunardi and Ferreira, 2014). Proximity between wolves (*Canis lupus signatus*) in a pack was also used to examine social cohesion and was influenced by the strength of the social bond between individuals (Soriano et al., 2021). Although the resolution of the photos did not always allow for accurate characterization of age class or sex, our results are in line with those of studies on other species. We know that calves are more likely to swim alongside a female in their early years (Krasnova et al., 2006; Krasnova et al., 2009) and that the distance between mother and calf increases as the calf matures and becomes more independent (Halteman and Ryan, 2019; McGuire et al., 2020). Independence could cause groups of adult whales to swim at greater distances from each other (Lunardi and Ferreira, 2014). On the other hand, individuals in groups including calves could swim closer together to ensure better protection, parental and allomaternal care, as well as cultural learning (Krasnova et al., 2006; Krasnova et al., 2009; O'Corry-Crowe et al., 2018; Aubin et al., 2021).

The results from the piecewise regression analysis showed that groups of belugas tend to stay within 24 and 22 m of another beluga, in the offshore and inshore environments respectively. Therefore, using four to five body lengths (~15-25 m) as a way to define beluga groups during observations or aerial surveys (Harwood et al., 1996; Harwood and Kingsley, 2013; O'Corry-Crowe et al., 2020) is more in line with our findings than using one to two body-lengths (~5-10 m) (Cosens and Dueck, 1991; Lemieux Lefebvre et al., 2018). Further research on inter-individual distance, particularly including movement, speed, large group size, and sex of the whales, is needed to better understand the social factors that drive the spatial organization and social cohesion of beluga whale groups.

Swimming direction

The variation in swimming direction between individuals in a group supports the idea that spatial organization is different in the two environments. In the offshore area, groups showed little variation in bearing compared to groups in the inshore area. However, this spatial organization could simply reflect the type of behaviour conducted in different environments, while maintaining similar group patterns (i.e., group size, composition, and distance between individuals). Lemieux Lefebvre et al. (2018) found that directional movements of belugas in the St. Lawrence Estuary were more associated with pelagic diving and travel while milling movements were associated with benthic diving, parental care, and socialization. Knowledge holders of Indigenous beluga

hunting communities around the Bering and Chukotka Seas also link similar swimming directions with travelling and different directions with feeding (Huntington et al., 1999; Mymrin et al., 1999). Recent examinations of the EBS beluga diet found Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*), mostly found on the Beaufort Sea shelf and in the Amundsen Gulf, to be the preferred prey species (Majewski et al., 2016; Majewski et al., 2017; Choy et al., 2020). In contrast, the environmental conditions of the Mackenzie Estuary further support the use of the estuary for moulting and thermal advantage (Scharffenberg et al., 2019). This supports the idea that the inshore is more conducive for social activity and the offshore is more favourable for travel and deep foraging dives.

Sociality of beluga whales

Our results regarding group size and distances within groups seem to be consistent with a fission-fusion sociality, where groups join and leave other groups in a dynamic framework (Whitehead and Van Parijs, 2010). O'Corry-Crowe et al. (2020) recently provided genetic evidence of this framework which had been witnessed during a number of field studies of belugas (Bel'kovich and Sh'ekotov, 1993; Krasnova et al., 2012; Alekseeva et al., 2013; McGuire et al., 2014; Michaud, 2014). Based on this concept, EBS belugas could remain in more small stable groups across summering grounds and then temporarily merge with other groups to form larger aggregations in particular areas, like the Mackenzie Estuary and other harvesting areas (KAVIK-AXYS Inc, 2012; Harwood et al., 2015). Considering the variety of their social behaviours and the use of their extensive vocalizations, belugas could maintain complex societies without having to be in large groups or in close proximity to other whales, creating dynamic societies over time and space (O'Corry-Crowe, 2018).

Study limitations and research opportunities

Studying remote marine mammals is challenging and it can often be difficult to collect data across multiple years. Although costly, aerial surveys are currently still the most useful method to assess beluga populations and cover large areas, such as the Beaufort Sea shelf and hundreds of kilometres off the coastline. Aerial photographs capture a snapshot of whales moving in a three-dimensional environment and distributed over a large range. Belugas, especially young ones, could have been missed by being underwater at the time the plane was flying over and transects over turbid water could have led to undetected belugas or misclassification of the age. We acknowledge

that this study presents results that are only based on one season, and therefore we are unable to extrapolate population trends or draw conclusions beyond our year of data. However, this is an opportunity to compare results with different methods (drone footage, boat or platform observations, etc.) or time periods. Our discussion also highlighted the value of considering and recognizing different perspectives beyond western science. We believe that local and/or Indigenous knowledge should be more commonplace in social behaviour studies, as these bodies of knowledge provide information on baselines and changing conditions that can help identify more effective conservation strategies (Thornton and Scheer, 2012). Bringing together these two forms of knowledge, rooted in observations from different temporal and spatial scales, can be complementary in producing a broader picture of beluga social behaviour (Duerden and Kuhn, 1998; Houde, 2007; Alexander et al., 2019). Although we included general traditional ecological knowledge observations here, the local expertise on beluga whales and the environment could be further considered through interviews and consultation, to situate the photos within a broader context of time and space and to help interpret group characteristics and spatial organization. The analysis of aerial photographs in this paper is one part of a multifaceted effort, and further research, particularly that which bridges or co-produces knowledge is needed to understand the complex social life of beluga whales.

Conclusion

This study used aerial photographs to describe group characteristics and spatial organization of EBS beluga groups in two summer habitats, the Beaufort Sea and surroundings (offshore) and the Mackenzie estuary (inshore). We found that group patterns did not differ in both environments and that the offshore is likely to be used more for travelling and foraging behaviours whereas the inshore is more conducive to socializing and milling behaviours. We conclude that environmental properties can shape beluga activities and behaviours (described here by swimming direction), but group patterns (described by group size and IID) are maintained and change mainly with group composition. Based on our IID results, we recommend using 15-25 meters (four to five body lengths) when describing beluga group composition.

The relevance of behavioural research for conservation is increasingly recognized (Berger-Tal et al., 2016; Weiss et al., 2021). Despite the limitation of aerial photos, the use of proxy measures such as group composition and IID still allows us to explore different elements of social behaviour.

As our results have shown, the study of group behaviour can help to identify elements that define social structures and areas of social importance to belugas and point to the conservation value of the habitat. Thus, by integrating elements of social life with beluga biology and ecology, we are in a better position to study the impacts of anthropogenic threats (e.g., habitat loss, pollution, shipping activities, climate change, etc.) and to develop applied conservation and management guidelines (Whitehead, 1997; Berger-Tal et al., 2016; Brakes et al., 2021).

2.6 Literature Cited

Agostinelli, C. and Lund, U. (2017). R package circular: Circular Statistics (version 0.4-93).

Alekseeva, Y. I., Panova, E. M. and Bel'kovich, V. M. (2013). Behavioral and Acoustical Characteristics of the Reproductive Gathering of Beluga Whales (*Delphinapterus leucas*) in the Vicinity of Myagostrov, Golyi Sosnovets, and Roganka Islands (Onega Bay, the White Sea). *Biology Bulletin*, *40*(3), 307-317. doi:10.1134/S1062359013030023

Alexander, S. M., Provencher, J. F., Henri, D. A., Taylor, J. J., Lloren, J. I., Nanayakkara, L., Johnson, J. T. and Cooke, S. J. (2019). Bridging Indigenous and science-based knowledge in coastal and marine research, monitoring, and management in Canada. *Environmental Evidence*, *8*(1), 36. doi:10.1186/s13750-019-0181-3

Anderson, P. A., Poe, R. B., Thompson, L. A., Weber, N. and A.Romano, T. (2017). Behavioral responses of beluga whales (*Delphinapterus leucas*) to environmental variation in an Arctic estuary. *Behavioral Processes*, *145*, 48-59.

Asselin, N. C., Barber, D. G., Stirling, I., Ferguson, S. H. and Richard, P. R. (2011). Beluga (*Delphinapterus leucas*) habitat selection in the eastern Beaufort Sea in spring, 1975–1979. *Polar Biology*, *34*(12), 1973-1988. doi:10.1007/s00300-011-0990-5

Atwood, T. C., Peacock, E., McKinney, M. A., Lillie, K., Wilson, R., Douglas, D. C., Miller, S. and Terletzky, P. (2016). Rapid Environmental Change Drives Increased Land Use by an Arctic Marine Predator. *PLoS ONE*, *11*(6), e0155932. doi:10.1371/journal.pone.0155932

Aubin, J. A., Michaud, R. and Vander Wal, E. (2021). Prospective evolutionary drivers of allocare in wild belugas. *Behaviour*, *158*(8-9), 727-756. doi:https://doi.org/10.1163/1568539X-bja10094

Aureli, F., Schaffner, C. M., Asensio, N. and Lusseau, D. (2012). What is a subgroup? How socioecological factors influence interindividual distance. *Behavioral Ecology*, *23*(6), 1308-1315. doi:https://doi.org/10.1093/beheco/ars122

Bel'kovich, V. M. and Sh'ekotov, M. N. (1993). *The Belukha Whale: Natural Behavior and Bioacoustics*. Woods Hole, MA: Woods Hole Oceanographic Institution.

Berger-Tal, O., Blumstein, D. T., Carroll, S., Fisher, R. N., Mesnick, S. L., Owen, M. A., Saltz, D., Claire, C. C. S. and Swaisgood, R. R. (2016). A systematic survey of the integration of animal behavior into conservation. *Conservation Biology*, *30*(4), 744-753. doi:10.1111/cobi.12654

Brakes, P., Carroll, E. L., Dall, S. R. X., Keith, S. A., McGregor, P. K., Mesnick, S. L., Noad, M. J., Rendell, L., Robbins, M. M., Rutz, C., Thornton, A., Whiten, A., Whiting, M. J., Aplin, L. M., Bearhop, S., Ciucci, P., Fishlock, V., Ford, J. K. B., Notarbartolo di Sciara, G. Simmonds, M. P., Spina, F., Wade, P. R., Whitehead, H., Williams, J. and Garland, E. C. (2021). A deepening understanding of animal culture suggests lessons for conservation. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1949), 20202718. doi:10.1098/rspb.2020.2718

Breton-Honeyman, K., Huntington, H. P., Basterfield, M., Campbell, K., Dicker, J., Gray, T., Jakobsen, A. E. R., Jean-Gagnon, F., Lee, D., Laing, R., Loseto, L., McCarney, P., Noksana Jr, J., Palliser, T., Ruben, L., Tartak, C., Townley, J. and Zdor, E. (2021). Beluga whale stewardship and collaborative research practices among Indigenous peoples in the Arctic. *Polar Research*, *40*(S1), doi:10.33265/polar.v40.5522

Brown Gladden, J. G., Ferguson, M. M. and Clayton, J. W. (1997). Matriarchal genetic population structure of North American beluga whales *Delphinapterus leucas* (Cetacea: Monodontidae). *Molecular Ecology*, *6*(11), 1033-1046. doi:10.1046/j.1365-294X.1997.00275.x

Byers, T. and Robert, L. W. (1995). *Harpoons and Ulus: Collective wisdom and traditions of Inuvialuit regarding the beluga ("qilalugaq") in the Mackenzie River estuary.* 89 p.

Carmack, E. C., Macdonald, R. W. and Jasper, S. (2004). Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. *Marine Ecology Progress Series*, *277*, 37-50. doi:10.3354/meps277037

Caron, L. M. J. and Smith, T. G. (1990). Philopatry and site tenacity of belugas, Delphinapterus leucas, hunted by the Inuit at the Nastapoka estuary, eastern Hudson Bay. In T. G. Smith, D. J. S. Aubin and J. R. Geraci (Eds.), *Advances in research on the beluga whale, Delphinapterus leucas* (pp. 69-79). Canadian Bulletin of Fisheries and Aquatic Sciences 224.

Charry, B., Marcoux, M. and Humphries, M. M. (2018). Aerial photographic identification of narwhal (*Monodon monoceros*) newborns and their spatial proximity to the nearest adult female. *Arctic Science*, *4*(4), 513-524. doi:10.1139/as-2017-0051

Choy, E. S., Giraldo, C., Rosenberg, B., Roth, J. D., Ehrman, A. D., Majewski, A., Swanson, H., Power, M., Reist, J. D. and Loseto, L. L. (2020). Variation in the diet of beluga whales in response to changes in prey availability: insights on changes in the Beaufort Sea ecosystem. *Marine Ecology Progress Series*, *647*, 195-210. doi:https://doi.org/10.3354/meps13413

Connor, R. C., Mann, J., Tyack, P. L. and Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology & Evolution*, *13*(6), 228-232. doi:https://doi.org/10.1016/S0169-5347(98)01326-3

Cosens, S. E. and Dueck, L. P. (1991). Group size and activity patterns of belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) during spring migration in Lancaster Sound. *Canadian Journal of Zoology*, *69*, 1630-1635. doi:https://doi.org/10.1139/z91-227

Cremers, J. and Klugkist, I. (2018). One Direction? A Tutorial for Circular Data Analysis Using R With Examples in Cognitive Psychology. *Frontiers in Psychology*, 9, doi:10.3389/fpsyg.2018.02040

Duerden, F. and Kuhn, R. G. (1998). Scale, context, and application of traditional knowledge of the Canadian north. *Polar Record*, *34*(188), 31-38. doi:10.1017/S0032247400014959

Environment and Climate Change Canada (2020). Historical Data. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Environment and Climate Change Canada (May 28, 2021). Beaufort wind scale table. https://www.canada.ca/en/environment-climate-change/services/general-marine-weather-information/understanding-forecasts/beaufort-wind-scale-table.html

ESRI (Environmental Systems Research Institute) (2019). ArcGIS Pro version 10.6.1.

Gifford, S. J., Gese, E. M. and Parmenter, R. R. (2017). Space use and social ecology of coyotes (*Canis latrans*) in a high-elevation ecosystem: relative stability in a changing environment. *Journal of Ethology*, *35*(1), 37-49. doi:10.1007/s10164-016-0488-2

Giraldeau, L.-A. (1988). The Stable Group and the Determinant of Foraging Group Size. In C. N. Slobodchikoff (Eds.), *The Ecology of Social Behavior* (pp. 33-53). Academic Press.

Halteman, D. M. and Ryan, W. L. (2019). The Effect of Group Composition on the Social Behaviors of Beluga Whales (*Delphinapterus leucas*) in an Artificial Environment. *Aquatic Mammals*, *45*(3), 303-310. doi:10.1578/AM.45.3.2019.303

Harwood, L. A., Iacozza, J., Auld, J. C., Norton, P. and Loseto, L. (2014). Belugas in the Mackenzie River estuary, NT, Canada: Habitat use and hot spots in the Tarium Niryutait Marine Protected Area. *Ocean & Coastal Management*, *100*, 128-138. doi:10.1016/j.ocecoaman.2014.08.004

Harwood, L. A., Innes, S., Norton, P. and Kingsley, M. C. S. (1996). Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea and west Amundsen Gulf during late July 1992. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 2262-2273. doi:https://doi.org/10.1139/f96-180

Harwood, L. A. and Kingsley, M. C. S. (2013). Trends in the Offshore Distribution and Relative Abundance of Beaufort Sea Belugas, 1982-85 vs 2007-09. *Arctic*, *66*(3), 247-256. doi:http://www.jstor.org/stable/23594627

Harwood, L. A., Kingsley, M. C. S. and Pokiak, F. (2015*). Monitoring beluga harvests in the Mackenzie Delta and near Paulatuk, NT, Canada: harvest efficiency and trend, size and sex of landed whales, and reproduction, 1970-2009.* Can. Manuscr. Rep. Fish. Aquat. Sci. 3059: vi + 32 p.

Harwood, L. A. and Norton, P. (1996). *Aerial survey data from the southeast Beaufort Sea, Mackenzie River estuary and West Amundsen Gulf, July 1992.* Can. Data Rep. Fish. Aquat. Sci. 965: iv + 25 p.

Hauser, D. D. W., Laidre, K. L., Stern, H. L., Moore, S. E., Suydam, R. S. and Richard, P. R. (2017). Habitat selection by two beluga whale populations in the Chukchi and Beaufort seas. *PLoS ONE*, *12*(2), e0172755. doi:10.1371/journal.pone.0172755

Hijmans, R. J., Williams, E. and Vennes, C. (2019). R package geosphere: Spherical Trigonometry (version 1.5-10).

Hill, H. M., Alvarez, C. J., Dietrich, S. and Lacy, K. (2016). Preliminary Findings in Beluga (*Delphinapterus leucas*) Tactile Interactions. *Aquatic Mammals*, *42*(3), 277-291. doi:http://dx.doi.org/10.1578/AM.42.3.2016.277

Hill, H. M. and Campbell, C. (2014). The frequency and nature of allocare by a group of belugas (*Delphinapterus leucas*) in human care. *International Journal of Comparative Psychology*, *27*(4), 501-514. doi:https://escholarship.org/uc/item/4pr8386p

Hill, P. R., Blasco, S. M., Harper, J. R. and Fissel, D. B. (1991). Sedimentation on the Canadian Beaufort Shelf. *Continental Shelf Research*, *11*(8), 821-842. doi:https://doi.org/10.1016/0278-4343(91)90081-G

Hornby, C., Hoover, C., Joynt, A., Torontow, V., Hynes, K. and Loseto, L. (2014). *Arrival of Beluga (Delphinapterus leucas) to the Mackenzie Estuary in Relation to Sea Ice: Report on Spring 2011-2013 aerial surveys.* Can. Data Rep. Fish. Aquat. Sci. 1251: vii + 25 p.

Houde, N. (2007). The Six Faces of Traditional Ecological Knowledge: Challenges and Opportunities for Canadian Co-Management Arrangements. *Ecology and Society*, *12*(2), 34. doi:http://www.ecologyandsociety.org/vol12/iss2/art34/

Huntington, H. P., Communities of Buckland, Elim, Koyuk, Point Lay and and Shaktoolik (1999). Traditional Knowledge of the Ecology of Beluga Whales (*Delphinapterus leucas*) in the Eastern Chukchi and Northern Bering Seas, Alaska. *Arctic*, *52*(1), 49-61. doi:https://doi.org/10.14430/arctic909

KAVIK-AXYS Inc (2012). *Traditional and Local Knowledge Workshop for the Paulatuk Area of Interest.*

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. (2006). Mother-Infant Spatial Relations in Wild Beluga (*Delphinapterus leucas*) during Postnatal Development under Natural Conditions. *Biology Bulletin*, *33*(1), 53-58. doi:10.1134/s1062359006010079

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. (2009). Formation of Behavior in the White Sea Beluga Calf, *Delphinapterus leucas*, during Early Postnatal Ontogenesis. Russian *Journal of Marine Biology*, *35*(1), 53-59. doi:10.1134/s1063074009010088

Krasnova, V. V., Chernetsky, A. D., Kirillova, O. I. and Bel'kovich, V. M. (2012). The Dynamics of the Abundance, Age, and Sex Structure of the Solovetsky Reproductive Gathering of the Beluga Whale *Delphinapterus leucas* (Onega Bay, White Sea). *Russian Journal of Marine Biology*, *38*(3), 218-225. doi:https://doi.org/10.1134/S1063074012030078

Krause, J. and Ruxton, G. (2002). *Living in Groups*. Oxford: Oxford University Press.

Kummer, H. (1974). Distribution of Interindividual Distances in Patas Monkeys and Gelada Baboons. *Folia Primatol*, *21*, 153-160. doi:10.1159/000155598

Lamont, M. M. and Houser, C. (2014). Spatial distribution of loggerhead turtle (*Caretta caretta*) emergences along a highly dynamic beach in the northern Gulf of Mexico. Journal of *Experimental Marine Biology and Ecology*, *453*, 98-107. doi:https://doi.org/10.1016/j.jembe.2013.11.006

Lemieux Lefebvre, S., Lesage, V., Michaud, R. and Humphries, M. M. (2018). Classifying and combining herd surface activities and individual dive profiles to identify summer behaviours of beluga (*Delphinapterus leucas*) from the St. Lawrence Estuary, Canada. *Canadian Journal of Zoology*, *96*(5), 393-410. doi:10.1139/cjz-2017-0015

Lim, M., Whalen, D., J. Mann, P., Fraser, P., Berry, H. B., Irish, C., Cockney, K. and Woodward, J. (2020). Effective Monitoring of Permafrost Coast Erosion: Wide-scale Storm Impacts on Outer Islands in the Mackenzie Delta Area. *Frontiers in Earth Science*, *8*, 561322. doi:10.3389/feart.2020.561322

Loseto, L., Lam, J. and Iacozza, J. (2018a). Beluga Summit: knowledge sharing of the eastern Beaufort Sea beluga whale. *Arctic Science*, *4*(3), i-iv. doi:10.1139/as-2018-0011

Loseto, L. L., Hoover, C., Ostertag, S., Whalen, D., Pearce, T., Paulic, J., Iacozza, J. and MacPhee, S. (2018b). Beluga whales (*Delphinapterus leucas*), environmental change and marine protected areas in the Western Canadian Arctic. *Estuarine, Coastal and Shelf Science*, *212*, 128-137. doi:10.1016/j.ecss.2018.05.026

Loseto, L. L., Richard, P., Stern, G. A., Orr, J. and Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology*, *84*(12), 1743-1751. doi:10.1139/z06-160

Lunardi, D. G. and Ferreira, R. G. (2014). Fission-fusion dynamics of Guiana dolphin (*Sotalia guianensis*) groups at Pipa Bay, Rio Grande do Norte, Brazil. *Marine Mammal Science*, *30*(4), 1401-1416. doi:https://doi.org/10.1111/mms.12121

Macdonald, R. W. and Yu, Y. (2006). The Mackenzie Estuary of the Arctic Ocean. In P. J. Wangersky (Eds.), *Estuaries* (pp. 91-120). Berlin: Springer Berlin Heidelberg.

Majewski, A. R., Atchison, S., MacPhee, S., Eert, J., Niemi, A., Michel, C. and Reist, J. D. (2017). Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. *Deep Sea Research Part I: Oceanographic Research Papers*, *121*, 169-182. doi:https://doi.org/10.1016/j.dsr.2017.01.009

Majewski, A. R., Suchy, K. D., Atchison, S. P., Henry, J., MacPhee, S. A., Walkusz, W., Eert, J., Dempsey, M., Niemi, A., de Montety, L., Geoffroy, M., Giraldo, C., Michel, C., Archambault, P., Williams, W. J., Fortier, L. and Reist, J. D. (2016). *Uniqueness of Fishes and Habitat Utilization in Oil & Gas Lease Blocks Relative to Non-Lease Areas in the Canadian Beaufort Sea*. Environmental Studies Revolving Funds Report Series, No. XXX, Ottawa. Xi + 90 p.

Mann, J., Connor, R. C., Tyack, P. L. and Whitehead, H. (2000). *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: University of Chicago Press.

McGuire, T., Stephens, A. and Bisson, L. (2014). *Photo-identification of Cook Inlet Beluga Whales in the Waters of the Kenai Peninsula Borough, Alaska. Final Report of Field Activities and Belugas Identified 2011–2013*. Report prepared by LGL Alaska Research Associates, Inc., Anchorage, Alaska, for the Kenai Peninsula Borough. 92 p. + Appendices.

McGuire, T. L., Himes Boor, G. K., McClung, J. R., Stephens, A. D., Garner, C., Shelden, K. E. W. and Wright, B. (2020). Distribution and habitat use by endangered Cook Inlet beluga whales: Patterns observed during a photo-identification study, 2005–2017. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*, 2402-2427. doi:10.1002/aqc.3378

Michaud, R. (2014). *St. Lawrence Estuary beluga (Delphinapterus leucas) population parameters based on photo-identification surveys, 1989-2012*. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/130.

Muggeo, V. M. R. (2020). R package segmented: Regression Models with Break-Points/Change-Points Estimation (version 1.2-0).

Muto, M. M., Helker, V. T., Delean, B. J., Young, N. C., Freed, J. C., Angliss, R. P., Friday, N. A., Boveng, P. L., Breiwick, J. M., Brost, B. M., Cameron, M. F., Clapham, P. J., Crance, J. L., Dahle, S. P., Dahlheim, M. E., Fadely, B. S., Ferguson, M. C., W., F. L., Goetz, K. T., Hobbs R. C., Ivashchenko Y. V., Kennedy, A. S., London, J. M., Mizroch, S. A., Ream, R. R., Richmond, E. L., Shelden, K. E. W., Sweeney, K. L., Towell, R, Wade, G. P. R., Waite, J. M., Zerbini, A. N (2021). *Alaska marine mammal stock assessments, 2020.* U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-421. 398 p.

Mymrin, N. I., The Communities of Novoe Chaplino, S., Uelen and Yanrakinnot and Huntington, H. P. (1999). Traditional Knowledge of the Ecology of Beluga Whales (*Delphinapterus leucas*) in the Northern Bering Sea, Chukotka, Russia. *Arctic*, *52*(1), 62-70. doi:www.jstor.org/stable/40512181

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K. and Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLoS ONE*, *13*(3), e0194201. doi:https://doi.org/10.1371/journal.pone.0194201

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T. G., Lydersen, C., Kovacs, K. M., Orr, J., Harwood, L., Litovka, D. and Ferrer, T. (2020). Group structure and kinship in beluga whale societies. *Scientific Reports*, *10*, 11462. doi:10.1038/s41598-020-67314-w

O'Corry-Crowe, G. M. (2018). Beluga Whale: Delphinapterus leucas. In B. Würsig, J. G. M. Thewissen and K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (Third Edition) (pp. 93-96). Academic Press.

Ostertag, S., Green, B., Ruben, D., Hynes, K., Swainson, D. and Loseto, L. (2019). *Recorded Observations of Beluga Whales (Delphinapterus leucas) Made by Inuvialuit Harvesters in the Inuvialuit Settlement Region, NT, in 2014 and 2015*. Can. Tech. Rep. Fish. Aquat. Sci. 3338: vi+18 p.

Ostertag, S. K., Loseto, L. L., Snow, K., Lam, J., Hynes, K. and Gillman, D. V. (2018). "That's how we know they're healthy": the inclusion of traditional ecological knowledge in beluga health monitoring in the Inuvialuit Settlement Region. *Arctic Science*, *4*, 292-320. doi:10.1139/as-2017-0050

Panova, E. M., Belikov, R. A., Agafonov, A. V. and Bel'Kovich, V. M. (2012). The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). *Oceanology*, *52*(1), 79-87. doi:10.1134/s000143701201016x

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/

Recchia, C. A. (1994). Social Behaviour of Captive Belugas, *Delphinapterus leucas*. [Doctoral dissertation, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution].

Reiczigel, J., Lang, Z., Rózsa, L. and Tóthmérész, B. (2008). Measures of sociality: two different views of group size. *Animal Behaviour*, *75*(2), 715-721. doi:10.1016/j.anbehav.2007.05.020

Richard, P. R., Martin, A. R. and Orr, J. R. (2001). Summer and Autumn Movements of Belugas of the Eastern Beaufort Sea Stock. *Arctic*, *54*(3), 223-236. doi:https://doi.org/10.14430/arctic783

Scharffenberg, K., Whalen, D., Marcoux, M., Iacozza, J., Davoren, G. and Loseto, L. (2019). Environmental drivers of beluga whale *Delphinapterus leucas* habitat use in the Mackenzie Estuary, Northwest Territories, Canada. *Marine Ecology Progress Series*, *626*, 209-226. doi:https://doi.org/10.3354/meps13011

Scharffenberg, K. C., Whalen, D., MacPhee, S. A., Marcoux, M., Iacozza, J., Davoren, G. and Loseto, L. L. (2020). Oceanographic, ecological, and socio-economic impacts of an unusual summer storm in the Mackenzie Estuary. *Arctic Science*, *6*(2), 62-76. doi:10.1139/as-2018-0029

Schreier, A. L. and Swedell, L. (2012). Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *American Journal of Physical Anthropology*, *148*(4), 580-588. doi:https://doi.org/10.1002/ajpa.22076

Scott, M. D. and Perryman, W. L. (1991). Using aerial photogrammetry to study dolphin school structure. In K. Pryor and K. S. Norris (Eds.), *Dolphin Societies: Discoveries and Puzzles* (pp. 227-241). Berkeley: University of California Press.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 539-559. doi:10.1098/rstb.2006.1994

Smith, H., Frère, C., Kobryn, H. and Bejder, L. (2016). Dolphin sociality, distribution and calving as important behavioural patterns informing management. *Animal Conservation*, *19*(5), 462-471. doi:https://doi.org/10.1111/acv.12263

Smith, T. G., Hammil, M. O. and Martin, A. R. (1994). Herd composition and behaviour of white whales (*Delphinapterus leucas*) in two Canadian arctic estuaries. *Meddelelser om Grønland Bioscience*, *39*, 175-184.

Solomon, S. M., Forbes, D. L. and Kierstead, B. (1994). *Coastal impacts of climate change: Beaufort Sea erosion study*. Geological Survey of Canada 2890.

Soriano, A. I., Vinyoles, D. and Maté, C. (2021). Inter-individual Distance in Different Captive Packs of Iberian Wolf (*Canis lupus signatus*): Management Applications. *Journal of Applied Animal Welfare Science*, *24*(1), 72-82. doi:10.1080/10888705.2020.1790366

St. Aubin, D. J., Smith, T. G. and Geraci, J. R. (1990). Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. *Canadian Journal of Zoology*, *68*(2), 359-367. doi:10.1139/z90-051

Storrie, L., Hussey, N. E., MacPhee, S. A., O'Corry-Crowe, G., Iacozza, J., Barber, D. G., Nunes, A. and Loseto, L. L. (2022). Year-Round Dive Characteristics of Male Beluga Whales From the Eastern Beaufort Sea Population Indicate Seasonal Shifts in Foraging Strategies. *Frontiers in Marine Science*, *8*, 715412. doi:10.3389/fmars.2021.715412

Sugiura, H., Shimooka, Y. and Tsuji, Y. (2011). Variation in Spatial Cohesiveness in a Group of Japanese Macaques (*Macaca fuscata*). *International Journal of Primatology*, *32*(6), 1348-1366. doi:10.1007/s10764-011-9533-8

Thometz, N. M., Tinker, M. T., Staedler, M. M., Mayer, K. A. and Williams, T. M. (2014). Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends. *Journal of Experimental Biology*, *217*(12), 2053-2061. doi:10.1242/jeb.099739

Thornton, T. F. and Scheer, A. M. (2012). Collaborative Engagement of Local and Traditional Knowledge and Science in Marine Environments: A Review. *Ecology and Society*, *17*(3), doi:10.5751/ES-04714-170308

Toms, J. D. and Lesperance, M. L. (2003). Piecewise Regression: A Tool for Identifying Ecological Thresholds. *Ecology*, *84*(8), 2034-2041. doi:https://www.jstor.org/stable/3450028

Usher, P. J. (2002). Inuvialuit Use of the Beaufort Sea and its Resources, 1960–2000. *Arctic*, *55*(supp 1), 18-28. doi:https://doi.org/10.14430/arctic732

Vergara, V. and Mikus, M.-A. (2019). Contact call diversity in natural beluga entrapments in an Arctic estuary: Preliminary evidence of vocal signatures in wild belugas. *Marine Mammal Science*, *35*(2), 434-465. doi:10.1111/mms.12538

Warburton, K. and Lazarus, J. (1991). Tendency-Distance Models of Social Cohesion in Animal Groups. *Journal of Theoretical Biology*, *150*(4), 473-488.

Ward, A. and Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals*. Cham, Switzerland: Springer International Publishing.

Watt, C. A., Marcoux, M., Ferguson, S. H., Hammill, M. O. and Matthews, C. J. D. (2021). Population dynamics of the threatened Cumberland Sound beluga (*Delphinapterus leucas*) population. *Arctic Science*, *0*(0), 1-22. doi:10.1139/as-2019-0030

Waugh, D., Pearce, T., Ostertag, S. K., Pokiak, V., Collings, P. and Loseto, L. L. (2018). Inuvialuit traditional ecological knowledge of beluga whale (*Delphinapterus leucas*) under changing climatic conditions in Tuktoyaktuk, NT. *Arctic Science*, *4*(3), 242-258. doi:10.1139/as-2017-0034

Weiss, M. N., Ellis, S. and Croft, D. P. (2021). Diversity and Consequences of Social Network Structure in Toothed Whales. *Frontiers in Marine Science*, *8*(921), doi:10.3389/fmars.2021.688842

Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour*, *53*, 1053-1067. doi:https://doi.org/10.1006/anbe.1996.0358

Whitehead, H. and Van Parijs, S. (2010). Studying marine mammal social systems. In I. L. Boyd, W. D. Bowen and S. J. Iverson (Eds.), *Marine Mammal Ecology and Conservation: A Handbook of Techniques* (pp. 263-282). Oxford: Oxford University Press.

Würsig, B. (2019). *Ethology and Behavioral Ecology of Odontocetes*. Switzerland: Springer.

2.7 Supplementary Materials

Table S2.1 Timeline of steps and communications undertaken for the co-interpretation project with the community of Paulatuk

Date	Communication
November 5, 2019	Letter of proposal for the photo co-interpretation project sent to Paulatuk Hunter and Trappers Committee (PHTC).
December 2-5, 2019	Poster presentation on the project proposal at ArcticNet Scientific Meeting in Halifax (NS).
January 2020	Aerial survey and project presented in the AN MPA annual report.
January 21, 2020	Presentation to the annual Fisheries Joint Management Committee (FJMC) meeting in Winnipeg (MB).
February 22 to March 10, 2020	Inuvialuit Settlement Region community tour.
February 28, 2020	Drop-in day in Paulatuk.
March 2020	Implementation of COVID-19 lockdown and travel restrictions.
March 16, 2020	New letter of support to PHTC with a review of the community tour.
April 5, 2020	Letter to the AN MPA representative for PHTC.
May 8, 2020	Letter to PHTC.
October 5, 2020	Letter to PHTC.
November 2, 2020	Letter to PHTC.
November 17, 2020	Thesis committee meeting about re-designing the project objectives.
December 10, 2020	Presentation to ArcticNet (virtual) on the aerial photo analysis. Discussion in break out room with members of the PHTC about the community interest in looking at behaviour. Mention of using drones in the summer.
December 18, 2020	Thesis committee meeting about re-designing the project objectives.
January 4, 2021	Letter of support received from PHTC for co-interpretation project and proposition of including drone footage.
January 20, 2021	Full-day meeting with PHTC (virtual). Presentation of the results on the aerial photo analysis and discussion on the potential use of drones to observe social behaviour.

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December 22, 2020

Alexandra Mayette, MSc Student, Centre for Earth Observation Science (CEOS), Arctic Science Partnership
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Email: mayettea@myumanitoba.ca
Phone: 819-319-8296

Re: Proposed Co-Interpretation Project about Beluga Whales Groups

We are very happy to announce that the Paulatuk HTC are in support of this project and to learn more of its characteristics. To better understand the Beluga in general it can help us make better decisions for future programs and how we may be able to protect this important species that we heavily rely on. We are excited to further discuss the Beluga and its behaviour with you in the near future.

We, as a community in partnership with science can benefit from this short project and would like to go ahead. We would also like to add using a drone in the AN MPA and the Darnley Bay to further observe our Beluga, we see many multi-purposes using this method, we can discuss further as the programs and project proposals go forward.

We also will be glad to select a local to assist in this Co-Interpretation project who will be of great asset to this project.

We look forward to working with you in the future.

Should you require anything further, please do not hesitate to contact us.

Sincerely,

DIGITALLY SIGNED

Diane Ruben

Raymond Ruben, *President*

cc. Dr. Lisa Loseto, Arctic Aquatic Research Division, DFO Winnipeg, MB

Figure S2.1 Letter of support from the Paulatuk Hunters and Trappers Committee.

Table S2.2 Mean angle of swimming direction and mean resultant length of each beluga group (group size > 2) in the offshore of the Beaufort Sea and inshore of the Mackenzie Estuary, using 10 m as the distance limit to define groups.

		Offshore	
Group ID (n = 4)	**Group size (10 m)**	**Mean angle (μ)**	**Mean resultant length (ρ)**
BE_66	3	329 °	0.9993
BE_07	4	251°	0.9998
BE_84	7	291°	0.9947
BE_97	8	342°	0.9993

		Inshore	
Group ID (n = 24)			
iBE_35	3	254°	0.9990
iBE_64	3	78°	0.9922
iBE_71	3	89°	0.8727
iBE_74	3	158°	0.9875
iBE_81	3	58°	0.9994
iBE_89	3	18°	0.9434
iBE_119	3	315°	0.6921
iBE_122	3	308°	0.8755
iBE_123	3	216 °	0.9998
iBE_145	3	201°	0.9939
iBE_172	3	278°	0.9982
iBE_173	3	177°	0.3333
iBE_210	3	275°	0.9970
iBE_212	3	331°	0.8094
iBE_236	3	142°	0.9985
iBE_29	3	106°	0.9986
iBE_80	4	83°	0.9820
iBE_127	4	256°	0.9856
iBE_149	4	196°	0.9981
iBE_201	4	97°	0.9505
iBE_55	5	67°	0.6805
iBE_66	5	74°	0.9987
iBE_213	5	135°	0.3089
iBE_171	6	198°	0.9270

Chapter 3. Summer Distribution and Habitat Preference of Beluga Whale Social Groups in the Eastern Beaufort Sea

3.1 Abstract

Habitat influences the distribution and behaviour of animals and when individual needs vary within a population, the different environmental conditions can lead to habitat segregation. The Eastern Beaufort Sea beluga (*Delphinapterus leucas*) population forms groups of various compositions and has a particularly extensive summering ground, covering multiple habitat types. The aim of this study is to compare the summer habitat preference of three beluga social group types: individual belugas, groups of adults, and groups with calf. Presence data was collected during two aerial surveys in July and August 2019. For both months, we used hierarchical generalized additive models to analyze the group type distribution with four environmental covariates: sea surface temperature, bathymetry, slope, and distance to the coastline. Models including sea surface temperature and bathymetric features best explained the distribution of belugas. Individual belugas had higher preferences for deeper and colder areas. In July, groups of adults preferred the continental shelf compared to groups with calf who preferred the continental slope. Groups of adults and groups with calf were mostly found in the Amundsen Gulf in August. The distribution of belugas often corresponded to that of their main prey, Arctic cod, suggesting that foraging opportunities and size-related energy requirements explain the habitat use.

3.2 Introduction

Forming groups has many benefits for animals, such as better protection from predators, access to food, cooperation, and communication (Krause and Ruxton, 2002; Silk, 2007). When distinct group types are formed from a specific composition of individuals (e.g., based on sex, age, or kinship) within a population, it refers to *social segregation* (Conradt, 2005; Ward and Webster, 2016). If group types differ in their spatial distribution and thus in their use of the habitat, it is described as *habitat segregation* (Conradt, 2005). Hypotheses have been put forward to explain

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why individuals or groups within a population select different habitats (Ruckstuhl and Neuhaus, 2000; Conradt, 2005; Michaud, 2005). For example, the foraging selection hypothesis implies that individuals with higher energy requirements (e.g., lactating females, growing individuals, metabolic costs related to body size) select habitats with available high-quality food (e.g., Breed et al., 2006; Staniland and Robinson, 2008). Predation risk is another hypothesis where more vulnerable animals choose a habitat that offers better protection even if the food is of lower quality, or conversely, where less vulnerable animals choose a habitat with a higher risk of predation but better food quality (e.g., Grignolio et al., 2007; Hay et al., 2008).

Social and habitat segregation is observed in many animal species (Ruckstuhl and Neuhaus, 2002; Wolf et al., 2005; Wearmouth and Sims, 2008; Kock et al., 2013; Cleasby et al., 2015), including in marine mammals (Michaud, 2005). Sperm whales (*Physeter macrocephalus*) are a great example of social segregation where distinct groups are observed: groups of females with calves and juveniles, groups of all males of similar size, and single large males (Best, 1979; Whitehead, 2003; Whitehead, 2018). The distribution of each group class varies, sometimes creating extreme latitudinal segregation (Rice, 1989; Lyrholm et al., 1999; Mizroch and Rice, 2013). Humpback whales (*Megaptera novaeangliae*) exhibit habitat segregation, where females and groups with calf tend to stay in shallow areas closer to shore for better protection against predators, aggressive males, or turbulent oceanic conditions, while groups of adults select deeper and further off coast areas (Smultea, 1994; Guidino et al., 2014; Lindsay et al., 2016). In bowhead whales (*Balaena mysticetus*), as whales increase in body size, they select deeper waters (Koski and Miller, 2009).

Beluga whales (*Delphinapterus leucas*) are social whales that aggregate into various group types. Groups typically range from 2 to 20 whales and the age composition can be described as mother-calf dyads, juveniles only, adults only, or mixed-age group (O'Corry-Crowe et al., 2009; Krasnova et al., 2012; McGuire et al., 2020; O'Corry-Crowe et al., 2020). Large seasonal aggregations can also reach up to hundreds of belugas (Harwood and Norton, 1996; Krasnova et al., 2012). Many environmental conditions have been found to influence habitat use in different beluga populations, such as bathymetric features, sea surface temperature, distance to shore, tides, currents, and sea ice measures, but have rarely been assessed taking into account different social groups (Loseto et al., 2006; Goetz et al., 2007; Hauser et al., 2017; Hornby et al., 2017; Ouellet et al., 2021).

The Eastern Beaufort Sea (EBS) beluga whale population migrates seasonally to the Beaufort Sea and has an extensive range of habitat types within its summering grounds, including the open-water continental shelf, the shallow estuary, and the heavy ice concentrated Arctic Archipelago (Richard et al., 2001; Harwood et al., 2014a; Storrie et al., 2022). Sexual and habitat segregation has been observed from tagged belugas, where females select open water habitats close to shore, while males select sea ice concentrated areas further from the mainland (Richard et al., 2001; Loseto et al., 2006; Hauser et al., 2017). It is hypothesized that male and female belugas select different habitats based on foraging opportunities or predation risk (Loseto et al., 2006; Hauser et al., 2017). If foraging and protection from predators affect grouping behaviour, then habitat use could differ between different types of beluga groups.

The objective of this study is to model the habitat preference of EBS belugas in their summering grounds in July and August, accounting for the variability between social groups. In this study, following Beyer et al. (2010) definition, we refer to *habitat preference* as the habitat use relative to a sample of available environment described from statistical methods. Based on literature on habitat use and segregation in cetacean populations, we expect to see a difference in the habitat use between individuals and groups, and between groups of different age compositions. Groups of belugas, especially including young whales, would prefer environments closer to shore and in warmer waters to reduce predation risk. Solitary belugas would prefer habitat in deeper and colder waters to access higher quality food. Understanding the divergences in habitat use of distinct group types and their relationship to the environment can provide useful information for population management, conservation, and assessment of climate change impacts (Robinson et al., 2017).

3.3 Methods

Area of study

Two aerial surveys were conducted in 2019 in the southeastern Beaufort Sea, primarily covering the Beaufort Sea shelf and Amundsen Gulf, but with additional transect lines in Prince of Wales Strait and west of Banks Island (Longitude = 115-140°W; Latitude = 68-73°N). The southeastern Beaufort Sea consists of a continental shelf that extends 50 to 150 km north of the Mackenzie Delta, with the Mackenzie Canyon to the west and the Amundsen Gulf to the east (Hill et al., 1991;

Carmack et al., 2004) (Figure 3.1). Around the isobaths 60 – 100 m, the slope changes rapidly (2-6°) leading to the deep Canadian Basin (> 1 000 m) (Weber, 1989; Williams and Carmack, 2008; Osborne and Forest, 2016).
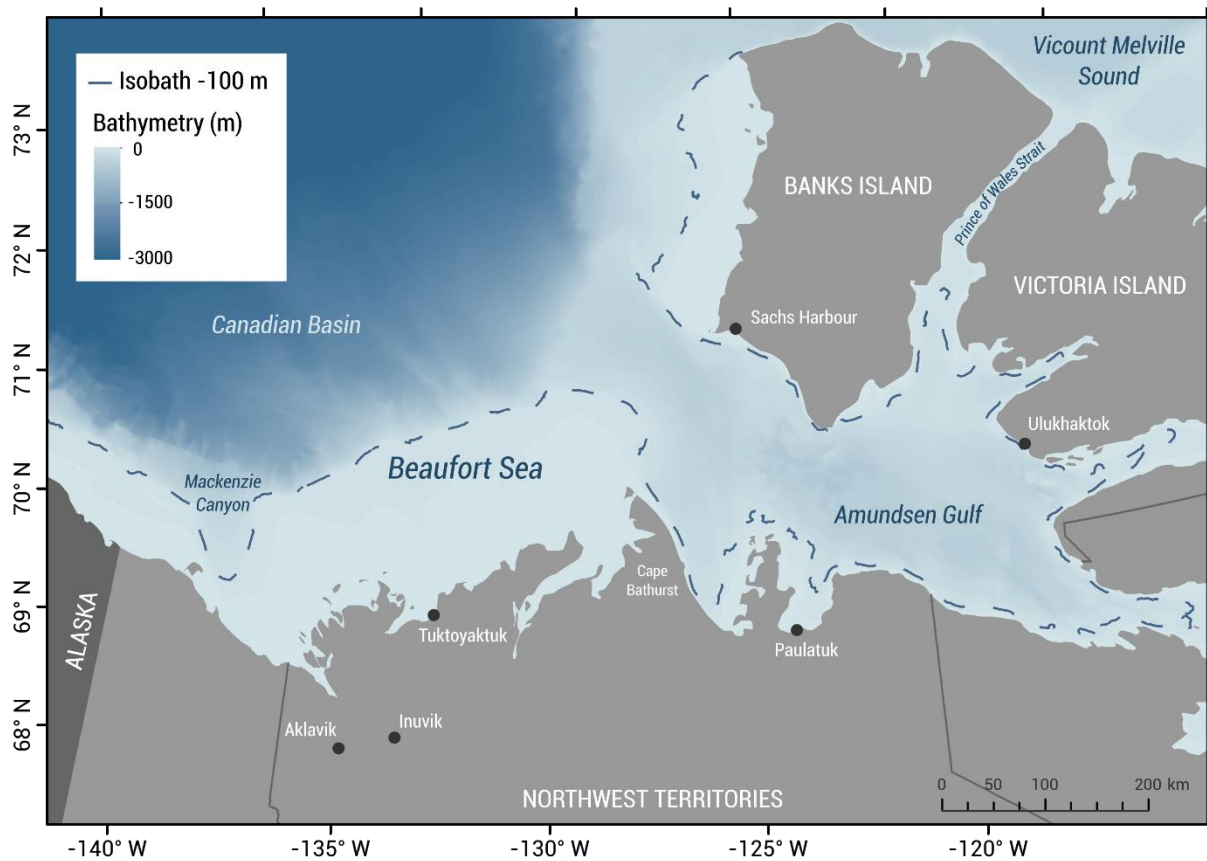
Figure 3.1 Study area of the Beaufort Sea, western Canadian Arctic, with main locations.

Aerial surveys

<u>July survey</u>

The first aerial survey was conducted by Fisheries and Oceans Canada (DFO) from 21 July to 2 August 2019 (Figure 3.2). The survey was designed based on previous Canadian aerial surveys, recent tagging data, and consultation with Inuvialuit communities (Harwood and Norton, 1996; Hauser et al., 2014; Storrie et al., 2022). Two De Havilland Twin Otter aircraft (Kenn-Borek Air,

Ltd., Calgary, Canada) were used to fly the survey. Each aircraft was equipped with four bubble windows. Position, altitude, speed and heading of the aircraft were logged every second with a Global Positioning System unit (Bad Elf GPS Pro+, from Bad Elf, West Hartford, Connecticut, USA). Flights were only flown in ideal conditions i.e., no rain, no risk of icing, ceilings of 305 m (1 000 ft) or higher, no fog over the water and Beaufort Sea State equal or less than 3 (Environment and Climate Change Canada, 2017). Aircraft were flown at a target altitude of 305 m (1 000 ft) and a target speed of 185-204 km/h (100-110 knots). Given these conditions and the time available for the survey, the transect lines were surveyed in a discontinuous manner, depending on the weather conditions on the day of the flight.

The survey was flown with a line-transect method and a double platform approach (Buckland, 2001). The aircraft follow a series of straight lines and observers are looking down through bubble windows (Buckland, 2001). The two primary observers were at the front of the aircraft while the secondary observers were at the rear. Black curtains were hung up behind the front observer seats to visually isolate the observers from one another and ensure independent sightings. Bose A20 aviation headsets (Bose Corporation, Framingham, Massachusetts, USA) were also used to acoustically isolate the observers while on the transect. Observers used Geometers V2 from Pi Technology (Pi Technology, Seltjarnarnes, Iceland http://geometer.pitemp.com/). This USB device measures the declination angle of visible targets more accurately than clinometers, while simultaneously recording GPS locations, time, and other measurements. Each observer had a geometer connected via USB to a Microsoft Surface Pro tablet, running the geometer Pi Attitude software (Hansen et al., 2020). Each tablet was also connected via Bluetooth to the observer's headset (used to record voice) and the GPS Bad Elf+ to geo-reference each sighting. One sighting was defined as either a single beluga or a group of belugas (whales within 1-2 body lengths of each other) visible at the surface. When the sighting was abeam of the aircraft, the geometer recorded the location of the single whale or the middle of the group.

<u>August survey</u>

The second aerial survey was conducted in August by the National Oceanic and Atmospheric Administration (NOAA) and the Bureau of Ocean Energy Management (BOEM) from 8 August to 27 August 2019 over the entire Beaufort Sea shelf and the Amundsen Gulf. Only effort and sightings within the longitude of the Canadian area of the Beaufort Sea and Amundsen Gulf

(118°W-141°W) were used in this analysis (Figure 3.2). One Turbo Commander (Clearwater Air, Inc., Anchorage, Alaska, USA) aircraft and one De Havilland Twin Otter (Kenn-Borek Air, Ltd.) aircraft were used for the survey, each equipped with bubble windows. Transects were flown in ideal conditions i.e., good visibility, cloud ceiling of more than 335 m (1 100 ft), Beaufort Sea State of less than 5. Aircraft were flown at a target speed of 213 km/h (115 knots) and target altitude of 396 m (1 300 ft) but could fly as low as 305 m (1 000 ft) to avoid low ceilings.

The survey was conducted using a line-transect method and a single platform approach, i.e., only primary observers. Sightings of belugas were recorded with a specialized software developed for the Aerial Surveys of Arctic Marine Mammals (ASAMM) project. A single beluga or a group of belugas (whales within 5 body lengths of each other) visible at the surface was counted as one sighting. Details of the aerial survey conducted by NOAA and BOEM can be found in Clarke et al. (2020).
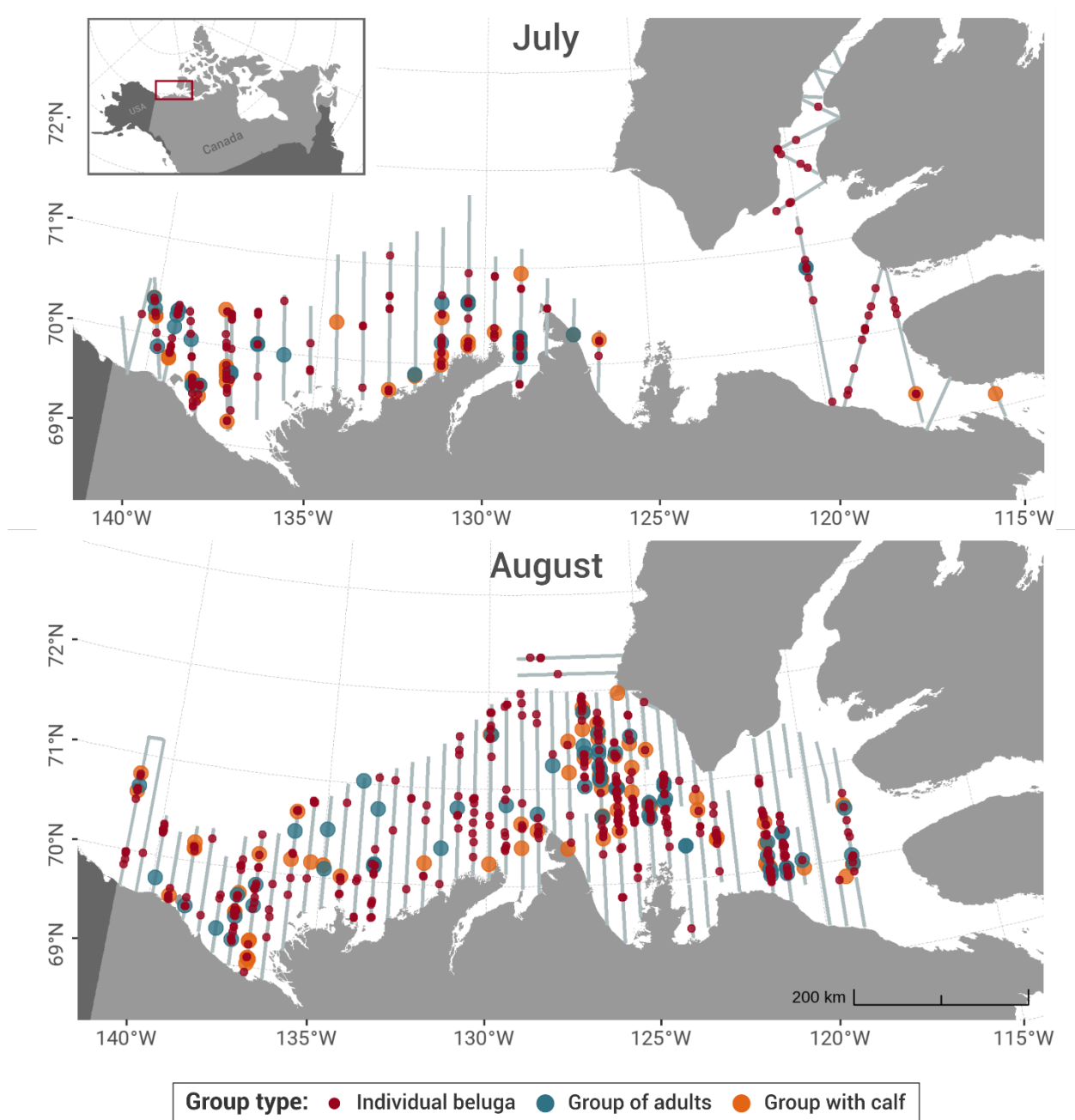
Figure 3.2 Maps of the transects flown during the two aerial surveys conducted in the southeastern Beaufort Sea in 2019. Above: July survey conducted by DFO (Canada), from 21 July to 2 August 2019. Below: August survey conducted by NOAA and BOEM (USA), from 8 to 27 August 2019. Points represent sightings of beluga whale, and the colours and sizes represent the three different group types of belugas.

Observation data

For both surveys, group size was estimated by observers on the plane. In August only, for very large groups, the aircraft would divert from the transect and circle back around the group for a brief period to get a better estimate of the group size. Young beluga (i.e., newborn, calf, or juvenile) were identified in a general category of "calf" and were identified based on the relative size compared to a close adult and skin colour, as newborn belugas have dark grey skin that gradually turns white as they grow. Data from the July survey was standardized according to the time of the audio recordings between the primary and secondary observers and duplicated whale sightings were identified and removed based on the time of the sighting (maximum 5-sec difference), swimming direction, latitude and longitude, and group size. Data from the August survey was processed and provided by NOAA.

All analyses were conducted using R version 4.1.2. (R Core Team, Vienna, Austria). Geospatial data were transformed into an equidistant conic projection for analysis. Transect lines were separated into 8 km segments (a trade-off between the satellite image grid cell resolution and the number of absences generated), merging the last two segments if the final segment was less than 8 km long. A 1 km buffer with a flat end on each side of the transect was computed, as well as the centroid of each buffered segment. For each of those segments, we indicated the presence (1) or absence (0) of the following three social group types:

a) **Individual beluga:** single white whale, most likely subadult or adult,
b) **Group of adults:** group of belugas composed only of white whales, most likely subadults or adults,
c) **Group with calf:** group of belugas that includes at least one whale identified as a calf.

Environmental covariates

Sea surface temperature

The sea surface temperature (SST) data layers were acquired by the remote sensing sensor MODIS onboard the Aqua satellite and available on NASA's OceanColor Web (https://oceancolor.gsfc.nasa.gov/). SST (11 μ daytime) level-3 data were downloaded for 8-day periods from 20 July to 28 August 2019, with a 4 km cell resolution (0.0417° x 0.0417°).

Bathymetry

The bathymetric (BATHY) grid was retrieved from the General Bathymetric Chart of the Oceans (GEBCO) 2020 (https://www.gebco.net/). The grid resolution was resampled from 0.00417° x 0.00417° to 0.0417° x 0.0417° so that the cell size matched the cell size of the sea surface temperature grid.

Slope

Bathymetric slope (SLOPE) was calculated as the degree of change in bathymetry using GEBCO raster data set. Eight neighbours were used to calculate the slope with the function "raster::terrain" (Hijmans et al., 2021).

Distance to shore

The shortest distance to the coastline (DIST) was measured with the function "geosphere::dist2Line" (Hijmans et al., 2019). For each centroid of the buffered segment, the shortest geodesic distance to the polygon shapefile representing land boundaries was computed (Administrative boundaries in Canada – CanVec 1M, Open Government Licence Canada).

The SST, bathymetry, and slope values were extracted at the centroid of each buffered effort segment from the raster layers with the function "raster::extract" (Hijmans et al., 2021) using the "simple" method, i.e. returning the cell value where the point falls. If the extraction returned a null value, the "bilinear" method was used to extract a value interpolated from the values of the four nearest cells. If after extracting from both methods segments still had at least one null covariate value, they were excluded from the analysis. SST was the only dynamic variable and was extracted from the 8-day layer encompassing the day each segment was flown.

Correlation

Including presence and absence observations, each covariate was scaled and centred around its mean and standard deviation. After scaling, environmental variables were tested for multicollinearity. Because the variables were not normally distributed, Spearman's rank-order correlation coefficient, r_S, was computed as a non-parametric measure with the function "GGally::ggcorr" (Schloerke et al., 2021). If two covariates were highly correlated, only one of the two were considered in one model, except for the model including all four covariates. The

value at which a correlation coefficient is considered high may vary according to the purpose of a study (Asuero et al., 2006). In this case, given the model design and study area, variables were considered highly correlated if the coefficient value reached +/- 0.68 (Taylor, 1990).

Models

Following Pedersen et al. (2019) and McCabe et al. (2021), we used a hierarchical generalized additive model (HGAM) based on a resource selection function design. HGAMs are flexible non-linear models that allow variation between groups in the shape of the response function (Pedersen et al., 2019). Due to the differences in survey protocol and effort, we fit independent models for each month (i.e., July was modelled separately from August) with a binomial function and complementary log-log link using the "mgcv" package (Wood, 2021). In addition to the four environmental covariates, beluga group types were included as a 3-level factor variable. We fit models that account for a global smoother with a shared penalty, with restricted maximum likelihood (REML). This type of model allows each group level to have its own functional response, while being penalized (shared penalty) if it deviates too far from the global functional response that accounts for the shared information between all groups (global smoother) (Pedersen et al., 2019). Details of the model parameters can be found in the Supplementary Materials. We tested models with univariate smooths and bivariate smooths that allowed interactions. For univariate smooths models, all four covariates were tested individually and together in one model.

The best model was determined by a combination of the lowest REML, deviance explained, Akaike Information Criterion (AIC), and p-value of each term. The fitted values from the best model for each month were mapped on a hexagonal grid of the study area. The predicted values used the average SST of the two 8-day periods with survey effort in July (20 July to 4 August 2019) and the three 8-day periods for August (5 to 28 August 2019) extracted from the raster layers at each point. The environmental variables used for prediction were scaled by the respective mean and standard deviation from the data used to build the models.

3.4 Results

A total of 277 belugas were observed during the July survey and 426 during the August survey with available environmental data (Table 3.1). In July, 210 individual belugas were sighted which represented 93 transect segments with a presence. For groups of adults and groups with calf, we observed 37 and 30 respective groups, which are 31 and 20 segments with presence. In August, 315 observations of individual belugas were used, representing 162 presences on the transect segments. Additionally, 54 groups of adults and 57 groups with calf were sighted, for a total of 44 and 45 segments with presence. The difference between the total number of transect segments and the presence represents the number of absences used in the model. The correlation test showed a high positive correlation (+ 0.7) between bathymetry and slope (Figure 3.3). The other variables were weakly or moderately correlated. For both months, all group types had the same correlation matrix using presence and absence data. Considering the collinearity and to compute ecologically significant models, we only tested the models with either bathymetry or slope.

Table 3.1 Summary, by beluga group type and month, of the number observed, and the number of transect segments with group type present and absent, during periods with available environmental data. These are the sample sizes used to build the hierarchical GAMs.

Group type	July			August		
	Beluga observed	Number of segments with presence	Number of segments with absence	Beluga observed	Number of segments with presence	Number of segments with absence
Individuals	210	93	296	315	162	664
Groups of adults	37	31	358	54	44	782
Groups with calf	30	20	369	57	45	781
Total	**277**	**389**		**426**	**826**	
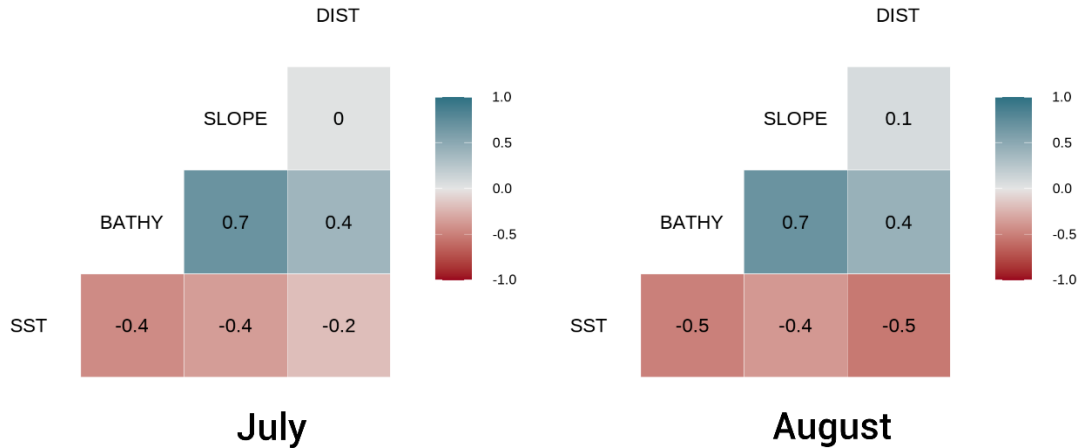
Figure 3.3 Spearman correlation matrix with coefficients between the four environmental variables for July and August.

Population functional response

The best model for July included the interaction between sea surface temperature and slope (REML = 441.83) (Table 3.2). The next best model included the interaction between SST and bathymetry (REML = 443.35). For August, the best model included the interaction between SST and bathymetry (REML = 709.71) (Table 3.3). The second-best model for August included bathymetry only (REML = 731.94). The model including SST and slope did not perform as well for August (REML = 783.79) as for July. Each model showed a global response for the observed population, i.e., a similar functional response to the covariate (Pedersen et al., 2019). In the July model, preference for sea surface temperature peaked around 7-10°C for all group types (Figure 3.4). In August, all beluga groups showed a high preference for areas with a temperature around 2-4 °C and bathymetry of 300-500 m (Figure 3.4). All groups also had a low preference for shallow waters (< 250 m) (Figure 3.4). Details on each variable effect curve can be found in the supplementary material (Figure S3.3, Figure S3.4, Figure S3.5).

Group type response

We also examined the group-level response for each type of social group for each month and the relative preference for specific environmental conditions (Figure 3.4). In July, the slope measured from the change in the degree of the bathymetry was the variable that generated the most variation

between group types. Individual adults and groups with calf had a higher preference for high slope (> 2°), while groups of adults preferred areas of low slope (< 1°). Individual belugas were found mostly at the continental slope, in waters of 8-10°C. In comparison to the other group types, individuals had higher preferences for colder waters (< 2°C). Groups of adults used habitat on the continental shelf with temperatures between 8-10°C. They were more likely to be in colder waters than groups with calf, but not more than individuals. Groups with at least one calf also had a higher preference for high slope, similar to individuals. Of all group types, they had the lowest preference for cold waters on the continental shelf.

In August, individual responses were less pronounced. Individual belugas had high preferences for very deep and cold waters (> 1 500 m, 1-2°C), which, considering the survey coverage, is associated with the continental slope and the start of Canadian Basin (see Figure S3.1). As mentioned above, individual adults were also found in areas around 500 m where temperature was a little warmer (2-4°C), but preference was lower than the two other groups. Groups of adults showed a high preference for the two same habitats as well but had a higher preference for the 500 m bathymetry. Groups with calf had a higher preference for the area around 500 m and SST of 2-4 °C. Except for one sighting (Figure 3.5), they were not found in the Canadian Basin, past the continental slope.

We also investigated results from the second-best model for July, since it included the same significant covariates as the August best model (SST and bathymetry) (see Figure S3.4, Figure S3.6, Figure S3.7). A similar global response with a high preference for SST of 8-10°C combined with a depth of < 200 m in all group types is observed. For individual adults and groups with calf, the model also showed a high preference for a bathymetry of 400-600 m with temperatures around 4-7°C.

Table 3.2 Model performance for July, sorted by ascending restricted maximum likelihood (REML) score. Covariates included in each model are indicated by the smoothing terms. The Akaike Information Criterion (AIC) for each model and the effective degree of freedom (EDF) with the p-value for each term are included.

Smoothing terms	R^2	Deviance explained (%)	REML	AIC	EDF	p-value
s(SST, SLOPE)	0.0869	13.1	441.83	898.7	8.8	**6.77e-6***
s(SST, SLOPE, GRP.TYPE)					3.4	**<2e-16***
s(SST, BATHY)	0.0836	12.9	443.35	900.1	7.4	**0.00031***
s(SST, BATHY, GRP.TYPE)					4.3	**<2e-16***
s(SST, DIST)	0.0895	14.2	444.53	901.3	12.3	0.167
s(SST, DIST, GRP.TYPE)					4.7	**<2e-16***
s(SLOPE, DIST)	0.0852	12.6	445.52	900.4	6.6	**0.004***
s(SLOPE, DIST, GRP.TYPE)					4.9	**<2e-16***
s(SST)	0.0883	13.3	451.26	893.2	4.0	**6.41e-5***
s(SST, GRP.TYPE)					1.9	**<2e-16***
s(BATHY)					1.0	**0.04***
s(BATHY, GRP.TYPE)					0.4	0.26
s(SLOPE)					1.0	0.48
s(SLOPE, GRP.TYPE)					0.9	0.15
s(DIST)					2.0	0.084
s(DIST, GRP.TYPE)					0.001	0.36
s(SST)	0.0709	10.9	454.63	903.0	2.9	**0.0017***
s(SST, GRP.TYPE)					2.4	**<2e-16***
s(DIST)	0.0629	9.76	460.69	915.2	2.8	0.089
s(DIST, GRP.TYPE)					3.1	**<2e-16***
s(BATHY)	0.0684	9.92	462.64	916.9	3.4	0.12
s(BATHY, GRP.TYPE)					3.9	**<2e-16***
s(SLOPE)	0.0628	8.87	464.45	921.9	1.0	0.99
s(SLOPE, GRP.TYPE)					4.2	**<2e-16***

Table 3.3 Model performance for August, sorted by ascending restricted maximum likelihood (REML) score. Covariates included in each model are indicated by the smoothing terms. The Akaike Information Criterion (AIC) for each model and the effective degree of freedom (EDF) with the p-value for each term are included.

Smoothing terms	R²	Deviance explained (%)	REML	AIC	EDF	p-value
s(SST, BATHY)	0.173	23.1	709.71	1419.2	20.1	**<2e-16***
s(SST, BATHY, GRP.TYPE)					3.8	**<2e-16***
s(SST)	0.174	22.6	721.48	1425.9	4.3	**0.007***
s(SST, GRP.TYPE)					1.0	**0.15**
s(BATHY)					6.0	**<2e-16***
s(BATHY, GRP.TYPE)					1.3	**0.01***
s(SLOPE)					3.5	0.11
s(SLOPE, GRP.TYPE)					1.1	0.10
s(DIST)					1.0	0.14
s(DIST, GRP.TYPE)					2.8	**0.0007***
s(BATHY)	0.145	19.3	731.94	1449.2	5.3	**<2e-16***
s(BATHY, GRP.TYPE)					3.5	**<2e-16***
s(SLOPE, DIST)	0.112	16.2	778.45	1548.8	13.5	**<2e-16***
s(SLOPE, DIST, GRP.TYPE)					13.8	**<2e-16***
s(SST, DIST)	0.0980	15.2	782.98	1563.0	21.8	**<2e-16***
s(SST, DIST, GRP.TYPE)					3.3	**<2e-16***
s(SST, SLOPE)	0.0949	14.1	783.79	1571.3	15.9	**<2e-16***
s(SST, SLOPE, GRP.TYPE)					4.3	**<2e-16***
s(SLOPE)	0.079	11.9	798.40	1580.8	5.7	**<2e-16***
s(SLOPE, GRP.TYPE)					3.6	**<2e-16***
s(DIST)	0.0673	10.8	803.64	1597.1	4.0	**4.46e-6***
s(DIST, GRP.TYPE)					3.2	**<2e-16***
s(SST)	0.0625	10.5	810.50	1608.6	5.9	**0.0009***
s(SST, GRP.TYPE)					4.0	**<2e-16***
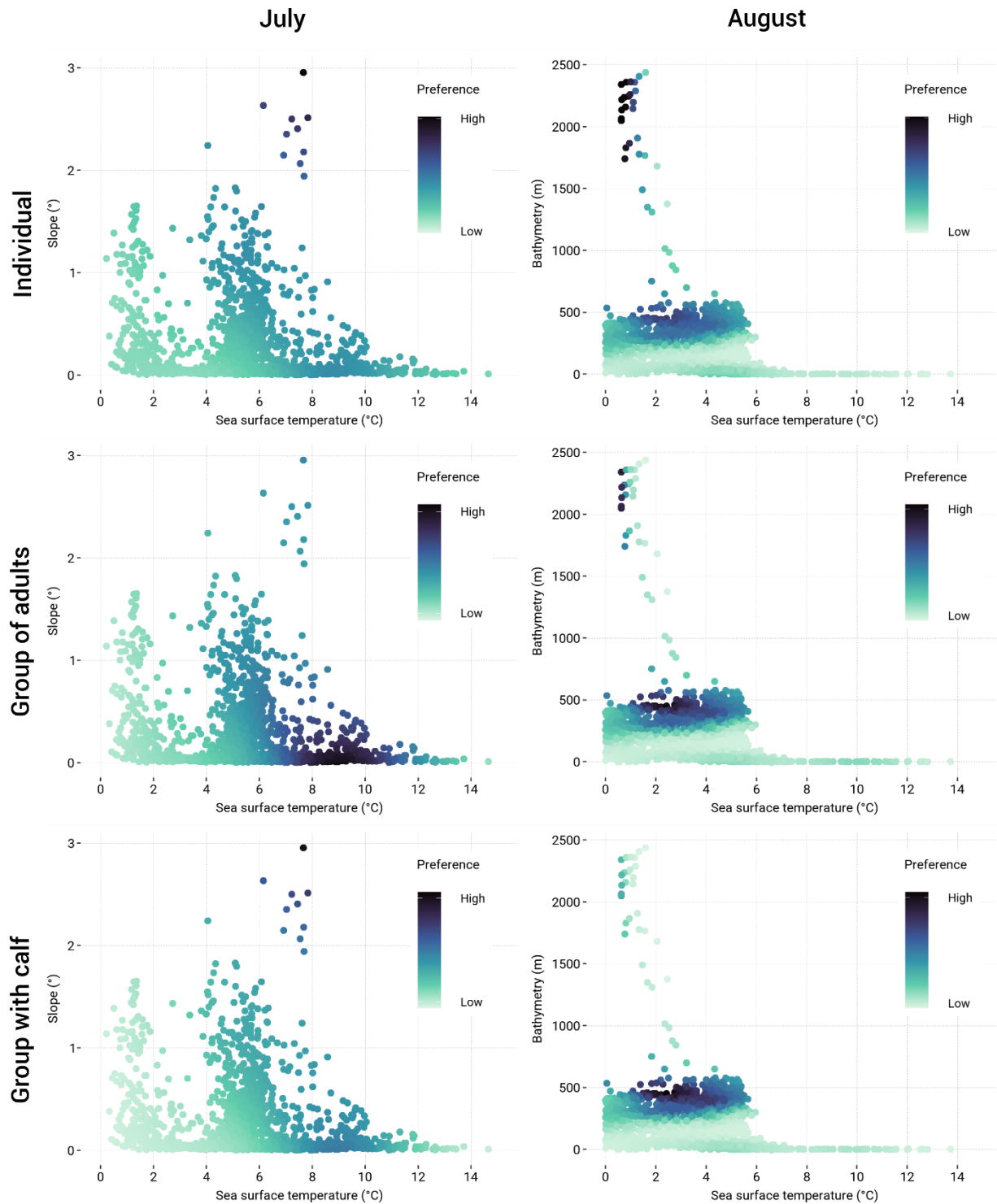
Figure 3.4 Relative preference of beluga group types for environmental covariates included in the best model for each month. Left: Response from the July model with sea surface temperature and slope. Right: Response from the August model with sea surface temperature and bathymetry. Note the different covariates on the y-axis between months.
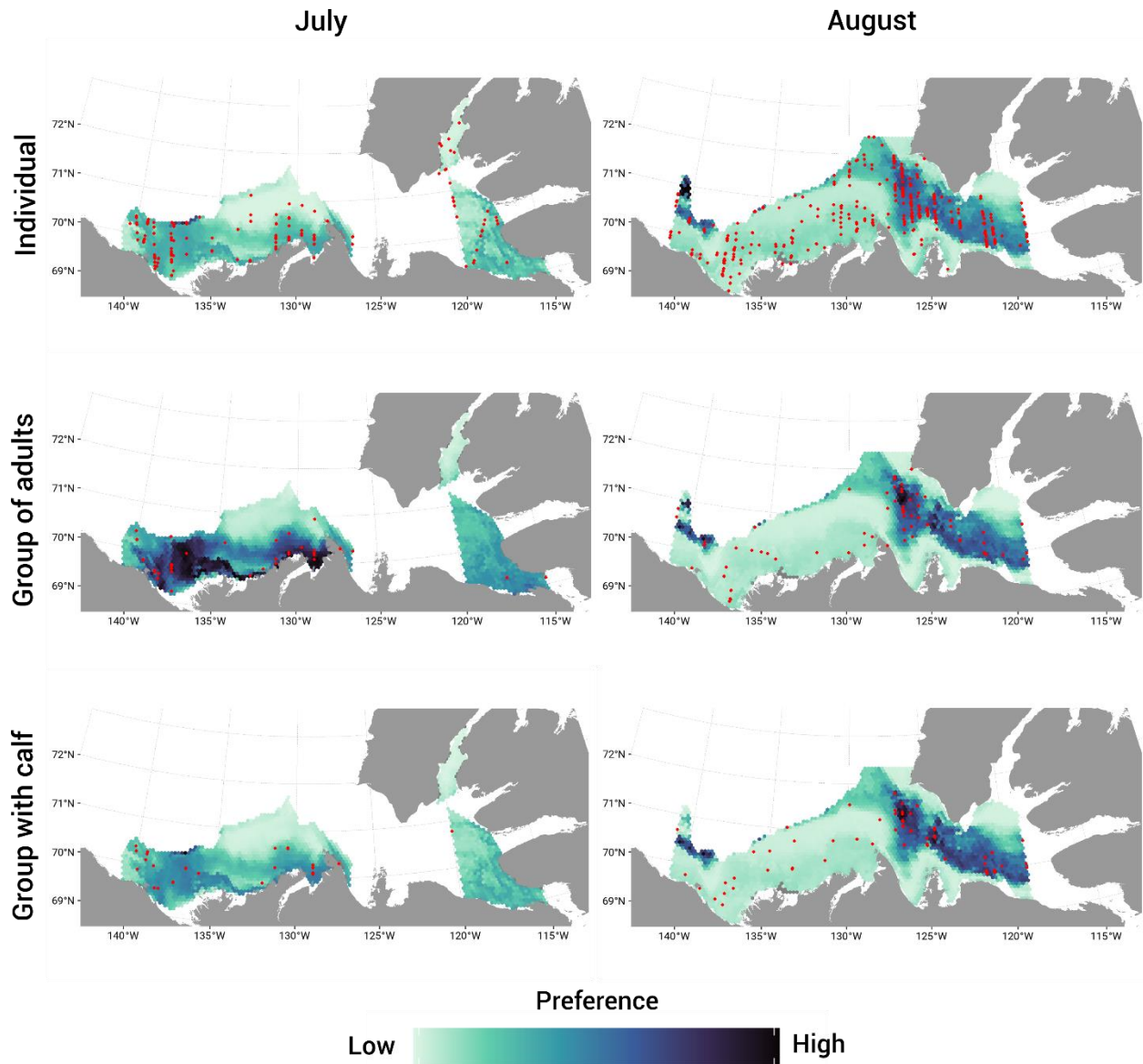
Figure 3.5 Maps of the relative preference of belugas by group type based on the best model for each month. The red points represent the locations of belugas observed during the survey.

3.5 Discussion

This study showed differences in the habitat preference of three different social group types of belugas in the Beaufort Sea for July and August 2019. The results reveal that for both months, the main environmental predictors of the models were sea surface temperature and slope or

bathymetry, which were highly positively correlated. Comparison of habitat preference between the two months should be practised with caution as the survey methods (e.g., group definition, flight height) and areas covered were different (especially the Amundsen Gulf). Because the survey effort was not continuous in July, differences in the study coverage affect the available environment sample on which the habitat preference is based and prevent direct comparison of the two models (Beyer et al., 2010). There are however shared patterns in the habitat use, presented in this discussion.

Grouping patterns

To interpret habitat use of the different group types, we need to understand the composition of these groups. In this study, observations were classified into three group types: individual belugas, groups of adults only, and groups with at least one calf. Specific age or sex of the individuals cannot be confirmed with the survey methods but based on observations of beluga groups in other populations, we can infer possible compositions of these group types. For instance, individual belugas are most likely to be large adult males. Male belugas tend to leave mixed age groups with females once they become independent and remain solitary or associate with other males (Krasnova et al., 2006; Colbeck et al., 2013; O'Corry-Crowe et al., 2018; O'Corry-Crowe et al., 2020). The groups composed of adults included white adults and/or subadults whales and were indeed probably formed by younger males (Smith et al., 1994; Suydam, 2009; Colbeck et al., 2013; Michaud, 2014). Groupings of males of similar size are observed in many beluga populations, exhibiting behaviours such as coordinated movement, socializing, rubbing, and aggression (Andrianov et al., 2009; Colbeck et al., 2013; McGuire et al., 2020; O'Corry-Crowe et al., 2020). The last group type, groups with calf, included mother-calf dyad or groups of mixed-age whales. If calves are present in a group, it generally includes females but does not necessarily exclude males (Colbeck et al., 2013; Krasnova et al., 2014; McGuire et al., 2020; O'Corry-Crowe et al., 2020). Interactions between mixed-age belugas can lead to allocare of calves by other adults or juveniles (Krasnova et al., 2009; Krasnova et al., 2014; Aubin et al., 2021). The nursing period of beluga calves is considered an important social learning phase from kin or non-kin (Krasnova et al., 2009; Colbeck et al., 2013; O'Corry-Crowe et al., 2020). These three social types of associations are formed because of the benefits gained from that particular group size and composition, and can lead to different behaviours (Lemieux Lefebvre et al., 2018).

Habitat preference in July

Within the July surveyed area, sightings of belugas were mostly occurring west of the Beaufort Sea shelf and off the Tuktoyaktuk Peninsula (Figure S3.2). The sea surface temperature and slope are explaining the best the distribution of group types. First, the preferred temperature in July 2019 ranged around 7-10°C, which is similar to the most selected temperature range of 6-10°C in habitat models of EBS belugas in August 2007 and 2008 (Hornby et al., 2017). This range of temperature corresponds mainly to the Beaufort Shelf and the Amundsen Gulf when the survey was conducted (Figure S3.1). The sea surface temperatures were much colder (< 2°C) at the northern limit of the survey lines, northeast of the Beaufort Sea and in the Prince of Wales Strait (Figure S3.1). Presence of belugas matches those warmer temperatures, except for the Amundsen Gulf, and absences are associated with low preference of colder water temperatures (Figure 3.5). The model also showed individual belugas having a higher preference for colder temperatures compared to the two other group types. This explains the distribution of single adults in Prince of Wales Strait, the only group type observed in that area in July. Belugas travel through Prince of Wales Strait to reach Viscount Melville Sound and M'Clure Strait (Richard et al., 2001). This area of the Arctic Archipelagos is heavily ice-concentrated and to date, only male belugas have been tracked in this area (Richard et al., 2001; Loseto et al., 2006; Hauser et al., 2017; Storrie et al., 2022).

The second covariate was the bathymetric slope. Individuals and groups with calf preferred the areas with higher slope, whereas groups of adults only preferred low slope or the continental shelf. Within the July survey limits, a high slope is associated with the edge of the Canadian Basin (Figure S3.1). A steep slope or abrupt change in bathymetry, enhances the formation of upwelling, such as at the Beaufort Sea shelf-break (Williams and Carmack, 2008; Kirillov et al., 2016). Upwellings bring nutrient-rich water upward in the water column and increase local primary production (Pickart et al., 2013). Slope has been demonstrated to influence EBS beluga distribution, in areas such as the Barrow Canyon (western Beaufort Sea) and along the Beaufort slope margin (Asselin et al., 2011; Hauser, 2016; Hauser et al., 2017). Bathymetry can also be considered as an influential variable in belugas distribution in July, as it was included in the second-best model, and was positively correlated with the slope. Two areas had relatively high preference depending on the group type: areas of < 200 m and SST between 8-10°C, and areas 400-600 m deep with water temperature between 4-7°C (see Supplementary Material). The

preference for depth of 400-600 m is similar to the preferred depth in August (see next section), representing the continental slope area and the Amundsen Gulf (Figure S3.6, Figure S3.7).

Habitat preference in August

Considering the coverage of this survey, belugas in August were mostly observed in the Amundsen Gulf (Figure S3.2). The best model included sea surface temperature and bathymetry as explanatory covariates of the beluga distribution in August. The preferred range of SST was lower than in July, although the overall average water temperature in August was colder than the average in July (Figure S3.1). Belugas selected colder water temperature range (2-6°C) in August when warmer temperatures were less available (Hornby et al., 2017). Individual adults in August also had a higher relative preference to colder temperatures (< 2°C) compared to the other two group types as observed in July as well.

In August, the seafloor bathymetry seemed to be the main variable differentiating group types. All three groups showed a preference for depth of 300-500 m, but single adults had a higher preference for areas in deep waters ($> 1\ 500$ m). Within the limits of the August survey, the Amundsen Gulf and the edge of the Canadian Basin (northwest Beaufort Sea) had the combination of the two preferred conditions (300-500 m, 2-4 °C) (Figure 3.5). The deepest and coldest areas were the small section above the Canadian Basin. From other aerial survey-based habitat models, depths of 200-500 m were also more selected by EBS belugas from aerial surveys in June (Asselin et al., 2011), but differed from the preferred depth range (0-50 m) of belugas observed in August of other years (Hornby et al., 2017). This distribution is more comparable to habitat use observed in August from tagged belugas in various years. Females were observed using the Amundsen Gulf in higher proportion to males, who were using deeper areas such as Viscount Melville Sound and the Canadian Basin (Richard et al., 2001; Hauser et al., 2014; Hauser et al., 2017).

Foraging selection hypothesis

Foraging opportunities appear to be the primary driver for the distribution of Eastern Beaufort Sea belugas in the summer of 2019. Arctic cod (*Boreogadus saida*) is one of the most abundant fish in the Beaufort Sea and the main prey of EBS belugas (Loseto et al., 2009; Rand and Logerwell, 2010; Choy et al., 2020). Depth is a key explanatory variable of fish assemblage in the Beaufort Sea, and Arctic cod has been primarily found at depth of 350-500 m (Majewski et al., 2016;

Majewski et al., 2017). This matches the preferred depth of 300-600 m for all beluga group types in July (second model) and August. The size of Arctic cod also varies with bathymetry due to their prey availability in the water column. Majewski et al. (2016) found that smaller Arctic cod fed on small *Calanus* preys in shallow waters (< 200 m) while larger cod fed on large *Themisto* preys in deeper waters (> 200 m), particularly in the upper slope zone. In the Amundsen Gulf, aggregations of Arctic cod were detected at depths of about 200 m in December, associated with sea ice cover, but then migrated to greater depths in the following months, up to 500-600 m in May (Geoffroy et al., 2011).

In past studies of EBS belugas habitat use, bathymetric features (distance to coast, depth, slope) were among the main predictors of the July and August distribution, supporting foraging opportunities (Hauser et al., 2017; Hornby et al., 2017). However, these studies did not examine the effect of group composition on the distribution. Beluga whales exhibit size dimorphism and size-related energy requirements can be reflected in differences in diet between size and sex (Loseto et al., 2008; Marcoux et al., 2012; Choy et al., 2020). Investigation of the dive behaviour in beluga males has demonstrated deep benthic and pelagic dives at the continental slope (Storrie et al., 2022). These types of dives can be highly energy-intensive (longer post-dive surface intervals) but are most likely compensated by the abundance and/or superior quality of food (Storrie et al., 2022). This observation aligned with the distribution of single adult males in deeper areas and preferring the continental slope. Males can prey on higher-quality fish by accessing deeper and further areas compared to the two other group types. Sex differences in foraging behaviour are observed in other animals, especially ungulates (Du Toit, 2005). For instance, elephant males have more energy to devote to foraging than females, who are limited by reproductive and social needs (Shannon et al., 2006).

In July, groups with calf had preference for the continental slope. Females with calves could be looking for high-quality food as well, as females are lactating for at about 2 years (Matthews and Ferguson, 2015). Many female mammals have shown to increase foraging activity or food quality to compensate for lactation (e.g., bats (Barclay, 1989), squirrels (Michener, 1998), monkeys (McCabe and Fedigan, 2007; Dias et al., 2011; Ruivo et al., 2017), zebras (Neuhaus and Ruckstuhl, 2002), goats (Hamel and Côté, 2009)). If in a mixed-age group, mothers can also benefit from the presence of other group members to care for her calf while she feeds (Krasnova et al., 2014).

Groups of adults had a large range of habitat preferences between July and August, from the continental shelf to the Amundsen Gulf, and to deeper and colder zones. These groups were composed of subadults and/or adults, but the lack of more precise size or age discrimination within groups could have the effect of hiding more specific patterns of habitat preference. As mentioned above, size and age can cause different energetic requirements for an individual and, depending on the age composition of the group, different foraging behaviours could emerge. Diet varies with beluga size, as larger beluga feed on bigger, more fatty fish and further offshore compared to smaller belugas (Loseto et al., 2009; Marcoux et al., 2012; Choy et al., 2017; Choy et al., 2020). In previous studies in the EBS, habitat use of beluga males also depended on their size, sometimes comparable to that of females with calves or sometimes to that of mixed-age groups (Loseto et al., 2006). There may be more spatial segregation by size within groups of adults, but we cannot conclude specific patterns of habitat use by this group type with the classification used in this study.

Predation risk hypothesis

The predation risk is unlikely to explain the divergence of distribution between individual belugas, groups of adults, and groups with calf. As observed in other species (Heithaus and Dill, 2002; Mumma et al., 2017; Iranzo et al., 2018), we would have expected the more vulnerable groups to avoid areas with high predation risk. The main predators of belugas are killer whales (*Orcinus orca*), polar bears (*Ursus maritimus*), and humans (O'Corry-Crowe, 2018). Although a strong increase in killer whale presence is observed in the eastern Canadian Arctic (Ferguson et al., 2010), no evidence indicates an increase of the predator presence in the western Canadian Arctic and the Beaufort Sea (Higdon and Ferguson, 2009; Higdon et al., 2013). Killer whales were not detected by recent acoustic surveys of marine mammals either (Pyć et al., 2016). On the other hand, belugas are still present in polar bears diet in the Beaufort Sea (Boucher et al., 2019; Florko et al., 2020). The proportion is however low compared to seals and beluga consumption is usually higher in spring than in summer, correlated with heavy sea ice conditions, as polar bears rely on sea ice and possibly ice entrapment events to hunt beluga (McKinney et al., 2017; Florko et al., 2020; Florko et al., 2021). The aerial surveys were not conducted in areas with high sea ice concentrations, due to the difficulty for observers to detect whales through the ice. Thus, we cannot infer a predation effect on belugas in proximity to sea ice or cover within the surveyed area. The results of the

models in this current study do not show specific patterns of avoiding areas to minimize predation risk, especially by groups with calf. Without drawing any definite conclusions, it seems that the risk of predation is relatively low for the EBS beluga population during the summer, and therefore would not be a main driver of the group types distribution.

Social segregation and beluga sociality

The results of this study revealed variations and similarities in the habitat preference of the three social groups for July and August. Individual beluga showed distinct use of deeper and colder waters. Groups of adults and groups with calf had similar habitat preferences, especially in August, but groups with calf also showed similarities with individuals in July. Those responses are possibly explained by Arctic cod main areas of distribution. Our results hint at habitat preferences based on foraging and size-related energy requirements, which could create a social segregation based on energetics as a by-product (Conradt, 2005). Energy requirements change with group size, sex, and age, which were not taken into account in this study and more explicit patterns of segregation could have been masked within our general group classification. For instance, within groups of adults, different groups could segregate depending on whether they are composed of young subadult males or large older males. Or, groups with calf could select different habitats if it is a mother-calf dyad or a large mixed-age group. Even more complex, there are indications that beluga populations follow a fission-fusion sociality framework, where groups join or separate, and group composition can change seasonally (Smith and Martin, 1994; Whitehead and Van Parijs, 2010; Michaud, 2014; O'Corry-Crowe et al., 2020). The timings and causes of joining or leaving other groups are not fully understood and probably relate to the benefits or costs of aggregating. Group foraging behaviour has multiple dimensions, where peers benefit from cooperation in access to food, allocare of young ones, and social learning, but also risk resource competition (Whitehead, 1996; Benoit-Bird and Au, 2009; Daura-Jorge et al., 2012; Vaughn-Hirshorn, 2019). More detail on group composition, including sex and age, and group behaviour would improve our understanding of foraging strategies and differences in habitat use of EBS belugas.

Limitations and future opportunities

Modelling habitat use is a powerful tool but also entails limitations. Aerial surveys have the advantage of covering extremely large areas and give an overview of distribution within an extensive home range. However, the survey effort can influence the sample of available habitat

and sightings of belugas during surveys are a snapshot in space and time of a highly mobile animal in a dynamic three-dimensional environment. A different sampled available area or scale can change the estimated coefficients of habitat preference (Beyer et al., 2010; Paton and Matthiopoulos, 2016). Additionally, the occurrence of animals in a habitat does not necessarily mean selection and a single sighting does not represent the proportion of time spent in one area (Beyer et al., 2010). Both surveys were flown only in perfect conditions (i.e., small waves, no celling, no heavy sea ice concentration, etc.) and whale detections and correct age identification are conditional on the expertise of the observers in the aircraft. Calves could have been hidden under larger belugas or individual whales could have been part of a group that was diving at the time.

Yet, the collaboration between different institutions has allowed us to work with more information and explore different months in the summer, over different environmental conditions. This study used two different datasets collected independently but revealed similar patterns in distribution and significant environmental conditions for the EBS beluga population. Habitat selection is dynamic, especially in the marine environment and distribution and resource selection of one population can change between years (Asselin et al., 2011; Hornby et al., 2017). Beluga societies are also dynamic and group composition can change within a season (Smith et al., 1994; Krasnova et al., 2012; McGuire et al., 2020). Further research is still needed to collect more data and to understand the complexity in habitat use in Beaufort Sea belugas, but accessible and shared data can improve research as well as support conservation and management challenges (Reichman et al., 2011). Complementary investigations on the social group composition including sex, age, and group size and on spatial distribution including movement behaviour, such as diving and swimming behaviours are necessary to better grasp the context (e.g., Nolet et al., 1993; Bjørge et al., 1995; Revelles et al., 2007; Beyer et al., 2010).

Consultations with different knowledge holders can also provide unique perspectives on behaviour and habitat use. In the Arctic, many Indigenous communities have a long history of harvesting beluga whales which is reflected in traditional and local ecological knowledge or TEK (Breton-Honeyman et al., 2016a; Breton-Honeyman et al., 2021). TEK observations of group behaviour, associations, and use of the environment have been recorded in Alaska, Russia, and Canada (Kilabuk, 1998; Huntington et al., 1999; Mymrin et al., 1999; Huntington, 2000; Lewis et al., 2009;

Breton-Honeyman et al., 2016b; Waugh et al., 2018). Integration of both western science and local expertise in habitat modelling is possible (e.g., Polfus et al. 2014) and can reveal important patterns for assessment of climate change impacts and implementation of wildlife conservation and management policies (Robinson et al., 2017; Skroblin et al., 2021). Decline of body conditions and change in diet in fish and marine mammals have already been detected in the Beaufort Sea ecosystem (Harwood et al., 2014b; Harwood et al., 2015; Choy et al., 2020). If the distribution of beluga social groups is mainly influenced by foraging and that beluga's primary prey is vulnerable to climate changes, understanding habitat use is necessary to assess impacts on the Eastern Beaufort Sea beluga population and the communities that depend on it.

3.6 Literature Cited

Andrianov, V. V., Bel'kovich, V. M. and Lukin, L. R. (2009). White Whale (*Delphinapterus leucas*) Distribution in Onega Bay of the White Sea in the Summer. *Oceanology, 49*(1), 73-82. doi:10.1134/S0001437009010093

Asselin, N. C., Barber, D. G., Stirling, I., Ferguson, S. H. and Richard, P. R. (2011). Beluga (*Delphinapterus leucas*) habitat selection in the eastern Beaufort Sea in spring, 1975–1979. *Polar Biology, 34*(12), 1973-1988. doi:10.1007/s00300-011-0990-5

Asuero, A. G., Sayago, A. and González, A. G. (2006). The Correlation Coefficient: An Overview. *Critical Reviews in Analytical Chemistry, 36*(1), 41-59. doi:10.1080/10408340500526766

Aubin, J. A., Michaud, R. and Vander Wal, E. (2021). Prospective evolutionary drivers of allocare in wild belugas. *Behaviour, 158*(8-9), 727-756. doi:https://doi.org/10.1163/1568539X-bja10094

Barclay, R. M. R. (1989). The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. *Behavioral Ecology and Sociobiology, 24*(1), 31-37. doi:10.1007/BF00300115

Benoit-Bird, K. J. and Au, W. W. L. (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *The Journal of the Acoustical Society of America, 125*(1), 125-137. doi:10.1121/1.2967480

Best, P. B. (1979). Social Organization in Sperm Whales, *Physeter macrocephalus*. In H. E. Winn and B. L. Olla (Eds.), *Behavior of Marine Animals* (pp. 227-289). New York: Plenum Press.

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M. and Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1550), 2245-2254. doi:10.1098/rstb.2010.0083

Bjørge, A., Thompson, D., Hammond, P., Fedak, M., Bryant, E., Aarefjord, H., Roen, R. and Olsen, M. (1995). Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. *Developments in Marine Biology*, 4, 211-223. doi:https://doi.org/10.1016/S0163-6995(06)80025-9

Boucher, N., Derocher, A. E. and Richardson, E. S. (2019). Variability in polar bear *Ursus maritimus* stable isotopes in relation to environmental change in the Canadian Beaufort Sea. *Marine Ecology Progress Series, 630*, 215-225. doi:https://doi.org/10.3354/meps13136

Breed, G. A., Bowen, W. D., McMillan, J. I. and Leonard, M. L. (2006). Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Royal Society B: Biological Sciences, 273*(1599), 2319-2326. doi:10.1098/rspb.2006.3581

Breton-Honeyman, K., Furgal, C. M. and Hammil, M. O. (2016a). Systematic Review and Critique of the Contributions of Traditional Ecological Knowledge of Beluga Whales in the Marine Mammal Literature. *Arctic, 69*(1), 37-46.

Breton-Honeyman, K., Hammill, M. O., Furgal, C. M. and Hickie, B. (2016b). Inuit Knowledge of beluga whale (*Delphinapterus leucas*) foraging ecology in Nunavik (Arctic Quebec), Canada. *Canadian Journal of Zoology, 94*(10), 713-726. doi:10.1139/cjz-2015-0259

Breton-Honeyman, K., Huntington, H. P., Basterfield, M., Campbell, K., Dicker, J., Gray, T., Jakobsen, A. E. R., Jean-Gagnon, F., Lee, D., Laing, R., Loseto, L., McCarney, P., Noksana Jr, J., Palliser, T., Ruben, L., Tartak, C., Townley, J. and Zdor, E. (2021). Beluga whale stewardship and collaborative research practices among Indigenous peoples in the Arctic. *Polar Research, 40*(S1), doi:10.33265/polar.v40.5522

Buckland, S. T. (2001). *Introduction to Distance Sampling: Estimating Abundance of Biological Populations.* Oxford: Oxford University Press.

Carmack, E. C., Macdonald, R. W. and Jasper, S. (2004). Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. *Marine Ecology Progress Series, 277*, 37-50. doi:10.3354/meps277037

Choy, E. S., Giraldo, C., Rosenberg, B., Roth, J. D., Ehrman, A. D., Majewski, A., Swanson, H., Power, M., Reist, J. D. and Loseto, L. L. (2020). Variation in the diet of beluga whales in

response to changes in prey availability: insights on changes in the Beaufort Sea ecosystem. *Marine Ecology Progress Series, 647*, 195-210. doi:https://doi.org/10.3354/meps13413

Choy, E. S., Rosenberg, B., Roth, J. D. and Loseto, L. L. (2017). Inter-annual variation in environmental factors affect the prey and body condition of beluga whales in the eastern Beaufort Sea. *Marine Ecology Progress Series, 579*, 213-225. doi:https://doi-org.uml.idm.oclc.org/10.3354/meps12256

Clarke, J. T., Brower, A. A., Ferguson, M. C., Willoughby, A. L. and Rotrock, A. D. (2020). *Distribution and Relative Abundance of Marine Mammals in the Eastern Chukchi Sea, Eastern and Western Beaufort Sea, and Amundsen Gulf, 2019.* Annual Report, OCS Study BOEM 2020-027.

Cleasby, I. R., Wakefield, E. D., Bodey, T. W., Davies, R. D., Patrick, S. C., Newton, J., Votier, S. C., Bearhop, S. and Hamer, K. C. (2015). Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series, 518*, 1-12. doi: 10.3354/meps11112

Colbeck, G. J., Duchesne, P., Postma, L. D., Lesage, V., Hammill, M. O. and Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society B: Biological Sciences, 280*(1752), 20122552. doi:10.1098/rspb.2012.2552

Conradt, L. (2005). Definitions, hypotheses, models and measures in the study of animal segregation. In K. Ruckstuhl and P. Neuhaus (Eds.), *Sexual Segregation in Vertebrates* (pp. 11-32). Cambridge: Cambridge University Press.

Daura-Jorge, F. G., Cantor, M., Ingram, S. N., Lusseau, D. and Simões-Lopes, P. C. (2012). The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biology Letters, 8*(5), 702-705. doi:10.1098/rsbl.2012.0174

Dias, P. A. D., Rangel-Negrín, A. and Canales-Espinosa, D. (2011). Effects of lactation on the time-budgets and foraging patterns of female black howlers (*Alouatta pigra*). *American Journal of Physical Anthropology, 145*(1), 137-146. doi:https://doi.org/10.1002/ajpa.21481

Du Toit, J. T. (2005). Sex differences in the foraging ecology of large mammalian herbivores. In K. Ruckstuhl and P. Neuhaus (Eds.), *Sexual Segregation in Vertebrates* (pp. 35-52). Cambridge: Cambridge University Press.

Environment and Climate Change Canada (May 28, 2021). *Beaufort wind scale table*. https://www.canada.ca/en/environment-climate-change/services/general-marine-weather-information/understanding-forecasts/beaufort-wind-scale-table.html

Ferguson, S. H., Higdon, J. W. and Chmelnitsky, E. G. (2010). The Rise of Killer Whales as a Major Arctic Predator. In S. H. Ferguson, L. L. Loseto and M. L. Mallory (Eds.), *A Little Less Arctic: Top Predators in the World's Largest Northern Inland Sea, Hudson Bay* (pp. 117-136). Dordrecht: Springer Netherlands.

Florko, K. R. N., Thiemann, G. W. and Bromaghin, J. F. (2020). Drivers and consequences of apex predator diet composition in the Canadian Beaufort Sea. *Oecologia, 194*(1), 51-63. doi:10.1007/s00442-020-04747-0

Florko, K. R. N., Thiemann, G. W., Bromaghin, J. F. and Richardson, E. S. (2021). Diet composition and body condition of polar bears (*Ursus maritimus*) in relation to sea ice habitat in the Canadian High Arctic. *Polar Biology, 44*(7), 1445-1456. doi:10.1007/s00300-021-02891-8

Geoffroy, M., Robert, D., Darnis, G. and Fortier, L. (2011). The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. *Polar Biology, 34*(12), 1959-1971. doi:10.1007/s00300-011-1019-9

Goetz, K. T., Rugh, D. J., Read, A. J. and Hobbs, R. C. (2007). Habitat use in a marine ecosystem: beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Marine Ecology Progress Series, 330*, 247-256. doi:10.3354/meps330247

Grignolio, S., Rossi, I., Bassano, B. and Apollonio, M. (2007). Predation Risk as a Factor Affecting Sexual Segregation in Alpine Ibex. *Journal of Mammalogy, 88*(6), 1488-1497. doi:10.1644/06-mamm-a-351r.1

Guidino, C., Llapapasca, M. A., Silva, S., Alcorta, B. and Pacheco, A. S. (2014). Patterns of Spatial and Temporal Distribution of Humpback Whales at the Southern Limit of the

Southeast Pacific Breeding Area. *PLoS ONE, 9*(11), e112627.
doi:10.1371/journal.pone.0112627

Hamel, S. and Côté, S. D. (2009). Foraging decisions in a capital breeder: trade-offs between
mass gain and lactation. *Oecologia, 161*(2), 421-432. doi:10.1007/s00442-009-1377-y

Hansen, R. G., Pike, D., Thorgilsson, B., Gunnlaugsson, T. and Lawson, J. (2020). The
Geometer: A New Device for Recording Angles in Visual Surveys. *NAMMCO Scientific
Publications, 11*, doi:https://doi.org/10.7557/3.5585

Harwood, L. A., Iacozza, J., Auld, J. C., Norton, P. and Loseto, L. (2014a). Belugas in the
Mackenzie River estuary, NT, Canada: Habitat use and hot spots in the Tarium Niryutait
Marine Protected Area. *Ocean & Coastal Management, 100*, 128-138.
doi:10.1016/j.ocecoaman.2014.08.004

Harwood, L. A., Kingsley, M. C. S. and Smith, T. G. (2014b). An Emerging Pattern of Declining
Growth Rates in Belugas of the Beaufort Sea: 1989 – 2008. *Arctic, 67*(4), 483-492.
doi:http://dx.doi.org/10.14430/arctic4423

Harwood, L. A. and Norton, P. (1996). *Aerial survey data from the southeast Beaufort Sea,
Mackenzie River estuary and West Amundsen Gulf, July 1992*. Can. Data Rep. Fish. Aquat.
Sci. 965: iv + 25 p.

Harwood, L. A., Smith, T. G., George, J. C., Sandstrom, S. J., Walkusz, W. and Divoky, G. J.
(2015). Change in the Beaufort Sea ecosystem: Diverging trends in body condition and/or
production in five marine vertebrate species. *Progress in Oceanography, 136*, 263-273.
doi:https://doi.org/10.1016/j.pocean.2015.05.003

Hauser, D. D. W. (2016). *Beluga whale distribution, migration, and behavior in a changing
Pacific Arctic*. [Doctoral dissertation, University of Washington].

Hauser, D. D. W., Laidre, K. L., Stern, H. L., Moore, S. E., Suydam, R. S. and Richard, P. R.
(2017). Habitat selection by two beluga whale populations in the Chukchi and Beaufort seas.
PLoS ONE, 12(2), e0172755. doi:10.1371/journal.pone.0172755

Hauser, D. D. W., Laidre, K. L., Suydam, R. S. and Richard, P. R. (2014). Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology, 37*, 1171–1183. doi:10.1007/s00300-014-1510-1

Hay, C. T., Cross, P. C. and Funston, P. J. (2008). Trade-offs of predation and foraging explain sexual segregation in African buffalo. *Journal of Animal Ecology, 77*(5), 850-858. doi:https://doi.org/10.1111/j.1365-2656.2008.01409.x

Heithaus, M. R. and Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, *83*(2), 480-491. doi: https://doi.org/10.1890/0012-9658(2002)083[0480:FAATSP]2.0.CO;2

Higdon, J. W., Byers, T., Brown, L. and Ferguson, S. H. (2013). Observations of killer whales (*Orcinus orca*) in the Canadian Beaufort Sea. *Polar Record, 49*(3), 307-314. doi:10.1017/S0032247412000356

Higdon, J. W. and Ferguson, S. H. (2009). Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. *Ecological Applications, 19*(5), 1365-1375. doi:https://doi.org/10.1890/07-1941.1

Hijmans, R. J., Etten, J. v., Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Hingee, K., Geosciences, I. f. M. A., Karney, C., Mattiuzzi, M., Mosher, S., Naimi, B., Nowosad, J., Pebesma, E., Perpinan Lamigueiro, O., Racine, E. B., Rowlingson, B., Shortridge, A., Venables, B. and Wueest, R. (2021). *R package raster: Geographic Data Analysis and Modeling (version 3.4-10).*

Hijmans, R. J., Williams, E. and Vennes, C. (2019). *R package geosphere: Spherical Trigonometry (version 1.5-10).*

Hill, P. R., Blasco, S. M., Harper, J. R. and Fissel, D. B. (1991). Sedimentation on the Canadian Beaufort Shelf. *Continental Shelf Research, 11*(8), 821-842. doi:https://doi.org/10.1016/0278-4343(91)90081-G

Hornby, C. A., Iacozza, J., Hoover, C., Barber, D. G. and Loseto, L. L. (2017). Beluga whale *Delphinapterus leucas* late summer habitat use and support for foraging areas in the Canadian Beaufort Sea. *Marine Ecology Progress Series, 574*, 243-257. doi:10.3354/meps12178

Huntington, H. P. (2000). Traditional Knowledge of the Ecology of Belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska *Marine Fisheries Review, 62*(3), 134-140.

Huntington, H. P., Communities of Buckland, Elim, Koyuk, Point Lay and and Shaktoolik (1999). Traditional Knowledge of the Ecology of Beluga Whales (*Delphinapterus leucas*) in the Eastern Chukchi and Northern Bering Seas, Alaska. *Arctic, 52*(1), 49-61. doi:https://doi.org/10.14430/arctic909

Iranzo, E. C., Wittmer, H. U., Traba, J., Acebes, P., Mata, C. and Malo, J. E. (2018) Predator occurrence and perceived predation risk determine grouping behavior in guanaco (*Lama guanicoe*). *Ethology*, *124*, 281-289. doi: https://doi.org/10.1111/eth.12727

Kilabuk, P. (1998). *A Study of Inuit Knowledge of the Southeast Baffin Beluga*.

Kirillov, S., Dmitrenko, I., Tremblay, B., Gratton, Y., Barber, D. and Rysgaard, S. (2016). Upwelling of Atlantic Water along the Canadian Beaufort Sea Continental Slope: Favorable Atmospheric Conditions and Seasonal and Interannual Variations. *Journal of Climate, 29*(12), 4509-4523. doi:10.1175/JCLI-D-15-0804.1

Kock, A., O'Riain, M. J., Mauff, K., Meÿer, M., Kotze, D. and Griffiths, C. (2013). Residency, Habitat Use and Sexual Segregation of White Sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS ONE, 8*(1), e55048. doi:10.1371/journal.pone.0055048

Koski, W. R. and Miller, G. W. (2009). Habitat Use by Different Size Classes of Bowhead Whales in the Central Beaufort Sea during Late Summer and Autumn. *Arctic, 82*(2), 137-150.

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. (2006). Mother-Infant Spatial Relations in Wild Beluga (*Delphinapterus leucas*) during Postnatal Development under Natural Conditions. *Biology Bulletin, 33*(1), 53-58. doi:10.1134/s1062359006010079

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. (2009). Formation of Behavior in the White Sea Beluga Calf, *Delphinapterus leucas*, during Early Postnatal Ontogenesis. *Russian Journal of Marine Biology, 35*(1), 53-59. doi:10.1134/s1063074009010088

Krasnova, V. V., Chernetsky, A. D., Kirillova, O. I. and Bel'kovich, V. M. (2012). The Dynamics of the Abundance, Age, and Sex Structure of the Solovetsky Reproductive Gathering of the Beluga Whale *Delphinapterus leucas* (Onega Bay, White Sea). *Russian Journal of Marine Biology, 38*(3), 218-225. doi:https://doi.org/10.1134/S1063074012030078

Krasnova, V. V., Chernetskya, A. D., Zheludkovab, A. I. and Bel'kovicha, V. M. (2014). Parental Behavior of the Beluga Whale (*Delphinapterus leucas*) in Natural Environment. *Biology Bulletin, 41*(4), 349-356.

Krause, J. and Ruxton, G. (2002). *Living in Groups.* Oxford: Oxford University Press.

Lemieux Lefebvre, S., Lesage, V., Michaud, R. and Humphries, M. M. (2018). Classifying and combining herd surface activities and individual dive profiles to identify summer behaviours of beluga (*Delphinapterus leucas*) from the St. Lawrence Estuary, Canada. *Canadian Journal of Zoology, 96*(5), 393-410. doi:10.1139/cjz-2017-0015

Lewis, A. E., Hammill, M. O., Power, M., Doidge, D. W. and Lesage, V. (2009). Movement and Aggregation of Eastern Hudson Bay Beluga Whales (*Delphinapterus leucas*): A Comparison of Patterns Found through Satellite Telemetry and Nunavik Traditional Ecological Knowledge. *Arctic, 62*(1), 13-24.

Lindsay, R. E., Constantine, R., Robbins, J., Mattila, D. K., Tagarino, A. and Dennis, T. E. (2016). Characterising essential breeding habitat for whales informs the development of large-scale Marine Protected Areas in the South Pacific. *Marine Ecology Progress Series, 548*, 263-275.

Loseto, L. L., Richard, P., Stern, G. A., Orr, J. and Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology, 84*(12), 1743-1751. doi:10.1139/z06-160

Loseto, L. L., Stern, G. A., Connelly, T. L., Deibel, D., Gemmill, B., Prokopowicz, A., Fortier, L. and Ferguson, S. H. (2009). Summer diet of beluga whales inferred by fatty acid analysis of the eastern Beaufort Sea food web. *Journal of Experimental Marine Biology and Ecology, 374*(1), 12-18. doi:https://doi.org/10.1016/j.jembe.2009.03.015

Loseto, L. L., Stern, G. A. and Ferguson, S. H. (2008). Size and Biomagnification: How Habitat Selection Explains Beluga Mercury Levels. *Environmental Science & Technology, 42*(11), 3982-3988. doi:10.1021/es7024388

Lyrholm, T., Leimar, O., Johanneson, B. and Gyllensten, U. (1999). Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1417), 347-354. doi:10.1098/rspb.1999.0644

Majewski, A. R., Atchison, S., MacPhee, S., Eert, J., Niemi, A., Michel, C. and Reist, J. D. (2017). Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. *Deep Sea Research Part I: Oceanographic Research Papers, 121*, 169-182. doi:https://doi.org/10.1016/j.dsr.2017.01.009

Majewski, A. R., Walkusz, W., Lynn, B. R., Atchison, S., Eert, J. and Reist, J. D. (2016). Distribution and diet of demersal Arctic Cod, *Boreogadus saida*, in relation to habitat characteristics in the Canadian Beaufort Sea. *Polar Biology, 39*, 1087-1098. doi:10.1007/s00300-015-1857-y

Marcoux, M., McMeans, B. C., Fisk, A. T. and Ferguson, S. H. (2012). Composition and temporal variation in the diet of beluga whales, derived from stable isotopes. *Marine Ecology Progress Series, 471*, 283-291. doi: https://doi.org/10.3354/meps10029

Matthews, C. J. D. and Ferguson, S. H. (2015). Weaning age variation in beluga whales (*Delphinapterus leucas*). *Journal of Mammalogy, 96*(2), 425-437. doi:10.1093/jmammal/gyv046

McCabe, G. M. and Fedigan, L. M. (2007). Effects of Reproductive Status on Energy Intake, Ingestion Rates, and Dietary Composition of Female Cebus capucinus at Santa Rosa, Costa Rica. *International Journal of Primatology, 28*(4), 837-851. doi:10.1007/s10764-007-9159-z

McGuire, T. L., Himes Boor, G. K., McClung, J. R., Stephens, A. D., Garner, C., Shelden, K. E. W. and Wright, B. (2020). Distribution and habitat use by endangered Cook Inlet beluga whales: Patterns observed during a photo-identification study, 2005–2017. *Aquatic Conservation: Marine and Freshwater Ecosystems, 30*, 2402-2427. doi:10.1002/aqc.3378

McKinney, M. A., Atwood, T. C., Iverson, S. J. and Peacock, E. (2017). Temporal complexity of southern Beaufort Sea polar bear diets during a period of increasing land use. *Ecosphere, 8*(1), e01633. doi:https://doi.org/10.1002/ecs2.1633

Michaud, R. (2005). Sociality and ecology of the odontocetes. In K. E. Ruckstuhl and P. Neuhaus (Eds.), *Sexual Segreagation in Vertebrates: Ecology of the Two Sexes* (pp. 303-326). Cambridge: Cambridge University Press.

Michaud, R. (2014). *St. Lawrence Estuary beluga (Delphinapterus leucas) population parameters based on photo-identification surveys, 1989-2012*. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/130.

Michener, G. R. (1998). Sexual Differences in Reproductive Effort of Richardson's Ground Squirrels. *Journal of Mammalogy, 79*(1), 1-19. doi:10.2307/1382838

Mizroch, S. A. and Rice, D. W. (2013). Ocean nomads: Distribution and movements of sperm whales in the North Pacific shown by whaling data and discovery marks. *Marine Mammal Science, 29*(2), E136-E165. doi:https://doi.org/10.1111/j.1748-7692.2012.00601.x

Mumma, M. A., Gillingham, M. P., Johnson, C. J. and Parker, K. L. (2017). Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. *Ecology and Evolution*, *7*(23), 10266-10277. doi: https://doi.org/10.1002/ece3.3563

Mymrin, N. I., The Communities of Novoe Chaplino, S., Uelen and Yanrakinnot and Huntington, H. P. (1999). Traditional Knowledge of the Ecology of Beluga Whales (*Delphinapterus leucas*) in the Northern Bering Sea, Chukotka, Russia. *Arctic, 52*(1), 62-70. doi:www.jstor.org/stable/40512181

Neuhaus, P. and Ruckstuhl, K. E. (2002). The link between sexual dimorphism, activity budgets, and group cohesion: the case of the plains zebra (*Equus burchelli*). *Canadian Journal of Zoology, 80*(8), 1437-1441. doi:10.1139/Z02-126

Nolet, B. A., Dennis, E. H. W. and Kruuk, H. (1993). Diving of Otters (*Lutra lutra*) in a Marine Habitat: Use of Depths by a Single-Prey Loader. *Journal of Animal Ecology, 62*(1), 22-32. doi:10.2307/5479

O'Corry-Crowe, G., Lucey, W., Castellote, M. and Stafford, K. (2009). *Abundance, habitat use and behavior of beluga whales in Yakutat Bay, May 2008; as revealed by passive acoustic monitoring, visual observations and photo-ID*. Protected Resources Division Alaska Regional Office National Marine Fisheries Service National Oceanic and Atmospheric Administration Juneau Alaska.

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K. and Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLoS ONE, 13*(3), e0194201. doi:https://doi.org/10.1371/journal.pone.0194201

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T. G., Lydersen, C., Kovacs, K. M., Orr, J., Harwood, L., Litovka, D. and Ferrer, T. (2020). Group structure and kinship in beluga whale societies. *Scientific Reports, 10*, 11462. doi:10.1038/s41598-020-67314-w

O'Corry-Crowe, G. M. (2018). Beluga Whale: *Delphinapterus leucas*. In B. Würsig, J. G. M. Thewissen and K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals (Third Edition)* (pp. 93-96). Academic Press.

Osborne, P. D. and Forest, A. (2016). Sediment Dynamics from Coast to Slope – Southern Canadian Beaufort Sea. *Journal of Coastal Research, 75*(10075), 537-541. doi:10.2112/si75-108.1

Ouellet, J. F., Michaud, R., Moisan, M. and Lesage, V. (2021). Estimating the proportion of a beluga population using specific areas from connectivity patterns and abundance indices. *Ecosphere, 12*(6), e03560. doi:10.1002/ecs2.3560

Paton, R. S. and Matthiopoulos, J. (2016). Defining the scale of habitat availability for models of habitat selection. *Ecology, 97*(5), 1113-1122. doi:https://doi.org/10.1890/14-2241.1

Pedersen, E. J., Miller, D. L., Simpson, G. L. and Ross, N. (2019). Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ*, e6876. doi:https://doi.org/10.7717/peerj.6876

Pickart, R. S., Schulze, L. M., Moore, G. W. K., Charette, M. A., Arrigo, K. R., Dijken, G. and Danielson, S. L. (2013). Long-term trends of upwelling and impacts on primary productivity

in the Alaskan Beaufort Sea. *Deep-Sea Research Part I*, 79, 106-121. doi:http://dx.doi.org/10.1016/j.dsr.2013.05.003

Polfus, J. L., Heinemeyer, K., Hebblewhite, M. and Nation, T. R. T. F. (2014). Comparing traditional ecological knowledge and western science woodland caribou habitat models. *The Journal of Wildlife Management, 78*(1), 112-121. doi:https://doi.org/10.1002/jwmg.643

Pyć, C. D., Geoffroy, M. and Knudsen, F. R. (2016). An evaluation of active acoustic methods for detection of marine mammals in the Canadian Beaufort Sea. *Marine Mammal Science, 32*(1), 202-219. doi:https://doi.org/10.1111/mms.12250

Rand, K. M. and Logerwell, E. A. (2010). The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. *Polar Biology, 34*, 475-488.

Reichman, O. J., Jones, M. B. and Schildhauer, M. P. (2011). Challenges and Opportunities of Open Data in Ecology. *Science, 331*(6018), 703-705. doi:10.1126/science.1197962

Revelles, M., Cardona, L., Aguilar, A., San Félix, M. and Fernández, G. (2007). Habitat use by immature loggerhead sea turtles in the Algerian Basin (western Mediterranean): swimming behaviour, seasonality and dispersal pattern. *Marine Biology, 151*(4), 1501-1515. doi:10.1007/s00227-006-0602-z

Rice, D. W. (1989). Sperm whale *Physeter macrocephalus*. In S. H. Ridgway and R. J. Harrison (Eds.), *Handbook of marine mammals*, Cambridge: Academic Press.

Richard, P. R., Martin, A. R. and Orr, J. R. (2001). Summer and Autumn Movements of Belugas of the Eastern Beaufort Sea Stock. *Arctic, 54*(3), 223-236. doi:https://doi.org/10.14430/arctic783

Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E. and Lundquist, C. J. (2017). A Systematic Review of Marine-Based Species Distribution Models (SDMs) with Recommendations for Best Practice. *Frontiers in Marine Science, 4*(421), doi:10.3389/fmars.2017.00421

Ruckstuhl, K. E. and Neuhaus, P. (2000). Sexual Segregation in Ungulates: A New Approach. *Behaviour, 137*(3), 361-377. doi: http://www.jstor.org/stable/4535710

Ruckstuhl, K. E. and Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews, 77*(1), 77-96. doi:10.1017/S1464793101005814

Ruivo, L. V. P., Stone, A. I. and Fienup, M. (2017). Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (*Saimiri collinsi*) in an Amazonian rainforest. *American Journal of Primatology, 79*(6), e22657. doi:https://doi.org/10.1002/ajp.22657

Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg, A., Toomet, O., Crowley, J., Hofmann, H. and Wickham, H. (2021). *R package GGally: Extension to 'ggplot2' (version 2.1.2).*

Shannon, G., Page, B. R., DuVy, K. J. and Slotow, R. (2006). The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia, 150*, 344-354. doi:10.1007/s00442-006-0521-1

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*, 539-559. doi:10.1098/rstb.2006.1994

Skroblin, A., Carboon, T., Bidu, G., Chapman, N., Miller, M., Taylor, K., Taylor, W., Game, E. T. and Wintle, B. A. (2021). Including indigenous knowledge in species distribution modeling for increased ecological insights. *Conservation Biology, 35*(2), 587-597. doi:https://doi.org/10.1111/cobi.13373

Smith, T. G., Hammil, M. O. and Martin, A. R. (1994). Herd composition and behaviour of white whales (*Delphinapterus leucas*) in two Canadian arctic estuaries. *Meddelelser om Grønland Bioscience, 39*, 175-184.

Smith, T. G. and Martin, A. R. (1994). Distribution and Movements of Belugas, *Delphinapterus leucas*, in the Canadian High Arctic. *Canadian Journal of Fisheries and Aquatic Sciences, 51*, 1653-1663. doi:https://doi.org/10.1139/f94-166

Smultea, M. A. (1994). Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Canadian Journal of Zoology, 72*(5), 805-811. doi:10.1139/z94-109

Staniland, I. J. and Robinson, S. L. (2008). Segregation between the sexes: Antarctic fur seals, *Arctocephalus gazella*, foraging at South Georgia. *Animal Behaviour, 75*(4), 1581-1590. doi:https://doi.org/10.1016/j.anbehav.2007.10.012

Storrie, L., Hussey, N. E., MacPhee, S. A., O'Corry-Crowe, G., Iacozza, J., Barber, D. G., Nunes, A. and Loseto, L. L. (2022). Year-Round Dive Characteristics of Male Beluga Whales From the Eastern Beaufort Sea Population Indicate Seasonal Shifts in Foraging Strategies. *Frontiers in Marine Science, 8*, 715412. doi:10.3389/fmars.2021.715412

Suydam, R. S. (2009). *Age, growth, reproduction, and movements of beluga whales (Delphinapterus leucas) from the eastern Chukchi Sea*. [Doctoral thesis, University of Washington].

Taylor, R. (1990). Interpretation of the Correlation Coefficient: A Basic Review. *Journal of Diagnostic Medical Sonography, 6*(1), 35-39. doi:10.1177/875647939000600106

Vaughn-Hirshorn, R. (2019). Social Ecology of Feeding in an Open Ocean. In B. Würsig (Eds.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 51-73). Cham, Switzerland: Springer International Publishing.

Ward, A. and Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals.* Cham, Switzerland: Springer International Publishing.

Waugh, D., Pearce, T., Ostertag, S. K., Pokiak, V., Collings, P. and Loseto, L. L. (2018). Inuvialuit traditional ecological knowledge of beluga whale (*Delphinapterus leucas*) under changing climatic conditions in Tuktoyaktuk, NT. *Arctic Science, 4*(3), 242-258. doi:10.1139/as-2017-0034

Wearmouth, V. J. and Sims, D. W. (2008). Chapter 2 Sexual Segregation in Marine Fish, Reptiles, Birds and Mammals: Behaviour Patterns, Mechanisms and Conservation Implications. In (Eds.), *Advances in Marine Biology* (pp. 107-170). Cambridge: Academic Press.

Weber, J. R. (1989). Physiography and Bathymetry of the Arctic Ocean seafloor. In Y. Herman (Eds.), *The Arctic Seas: Climatology, Oceanography, Geology, and Biology* (pp. 797-828). Boston, MA: Springer US.

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology, 38*(4), 237-244. doi:10.1007/s002650050238

Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean.* Chicago: University of Chicago Press.

Whitehead, H. (2018). Sperm Whale: *Physeter macrocephalus*. In B. Würsig, J. G. M. Thewissen and K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals (Third Edition)* (pp. 919-925). Cambridge: Academic Press.

Whitehead, H. and Van Parijs, S. (2010). Studying marine mammal social systems. In I. L. Boyd, W. D. Bowen and S. J. Iverson (Eds.), *Marine Mammal Ecology and Conservation: A Handbook of Techniques* (pp. 263-282). Oxford: Oxford University Press.

Williams, W. J. and Carmack, E. C. (2008). Combined effect of wind-forcing and isobath divergence on upwelling at Cape Bathurst, Beaufort Sea. *Journal of Marine Research, 66*(5), 645-663. doi:https://doi.org/10.1357/002224008787536808

Wolf, J. B. W., Kauermann, G. and Trillmich, F. (2005). Males in the shade: habitat use and sexual segregation in the Galápagos sea lion (*Zalophus californianus wollebaeki*). *Behavioral Ecology and Sociobiology, 59*(2), 293-302. doi:10.1007/s00265-005-0042-7

Wood, S. N. (2021). *R package "mgcv": Mixed GAM Computation Vehicle with Automatic Smoothness Estimation (version 1.8-37).*

3.7 Supplementary Material

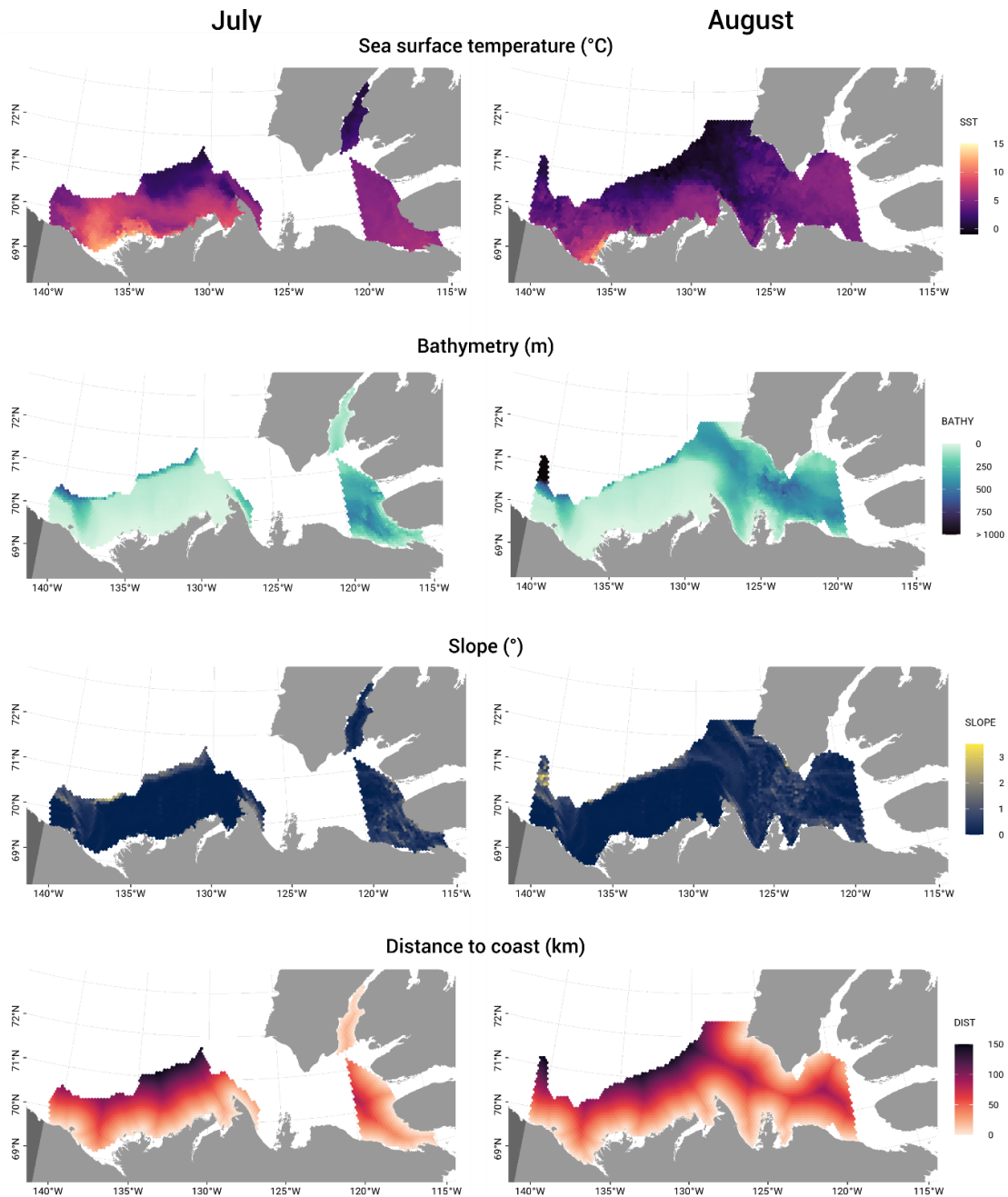*Environmental data of July and August 2019*

Figure S3.1 Environmental covariates used in the models. Left: Extent of the July survey. The sea surface temperature is the average temperature of the two 8-day periods of the survey (20 July to 4 August 2019). Right: Extent of the August survey. The sea surface temperature is the average temperature for the three 8-day periods of the survey (5 to 28 August 2019).

Projection details

Equidistant conic projection used: `"+proj=eqdc  +lat_1=69.42d  +lat_2=71.48d +lat_0=69.75d +lon_0=-129.2d +x_0=0 +y_0=0"`

Details of the models

Table S3.1 Hierarchical generalized additive model parameters used with "mgcv" package (Wood, 2021).

Argument	Explanation
`s()`, `te()`, `t2()`	Identify the terms to be smoothed. `s()` is used for one-dimensional term while `te()` is used for interaction between covariates (multi-dimensional) that are on different scales (Pedersen et al., 2019; McCabe et al., 2021)*. Pedersen et al. (2019) recommend `t2(full = TRUE)` for multi-dimensional global smoother with random effect that have a shared penalty (model GS in their paper which our model was based on).
`bs`	Three types of smoothers are used in this model (Wood, 2017; Pedersen et al., 2019). The factor-smoother interaction `fs` is a type of smoother that allow separate set of basis functions for each group but estimate one smoothing parameter for all of them together (Pedersen et al., 2019). The thin plate regression splines (TPRS or `tp`) type is used for general continuous covariates and penalize functions that are too wiggly. The random effects (`re`) type penalizes the functions that are too far from the average.
`k`	`k` is the maximum effective degree of freedom (EDF, which represent the complexity of a penalized smooth term) or maximum number of basis functions. Our choice of the value `k=10` is a trade-off between `k` being large enough to capture the variation in the response curve but not overfit (Pedersen et al., 2019; McCabe et al., 2021)*. For the random effect smoother, `k` is equal to the number of levels of the factor variable (Pedersen et al., 2019), so 3 in our case.
`m`	The argument `m` is a penalty order. `m=2` penalize on the squared derivative which means the more wiggly the functions are, the more penalized (models that overfit have large derivatives) (Pedersen et al., 2019). `m=1` is recommended on the group-level smoothers to reduce issues of collinearity (concurvity) between the global smoother and group-level smoother (Pedersen et al., 2019; McCabe et al., 2021)*.
`family`	We used `binomial` as our explanatory variable (BELUGA.P) is binary (absence – 0 or presence – 1) and to estimate the relative probability.
`link`	The complementary log-log or `cloglog` link is used when the number of 0s and 1s are unequal (Zuur et al., 2009).
`method`	The models were fit using the restricted maximum likelihood, `REML` smoothing parameter estimation. The use of REML is often preferred over the generalized cross-validation (GCV) (Wood, 2011; Wood, 2017). The score is the negative of the restricted log likelihood, and so the lower the value, the best (Woods, 2017).

*See McCabe et al. 2021 – Supplementary material

Equation 1 – univariate model

```
mod1 <- gam(y ~
     s(X1, bs = "tp", k = 10, m = 2) +
     s(X1, FACTOR, bs = "fs", k = 10, m = 2) +
     s(X2, bs = "tp", k = 10, m = 2) +
     s(X2, FACTOR, bs = "fs", k = 10, m = 2) + …,
     data = df, family = binomial(link = "cloglog"), method = "REML")
```

Global smoother for a covariate (function response of beluga)

```
s(X1, bs = "tp")
```

Smooth term for random effect with a shared penalty (penalty for being too far from the average of X1)

```
s(X1, FACOTR, bs = "fs")
```

Equation 2 – bivariate model

```
mod2 <- gam(y ~
     te(X1, X2, bs = "tp", k = 10, m = 2) +
     t2(X1, X2, FACTOR, bs = c("tp", "tp", "re"), k = c(10, 10, 3), m =
     2, full = TRUE),
     data = df, family = binomial(link = "cloglog"), method = "REML")
```

Global smoother for interaction between covariates

```
te(X1, X2, bs = "tp")
```

Smoother for group-level with shared penalty and interaction between covariates

```
t2(X1, X2, FACOTR, bs = c("tp", "tp", "re"), full = TRUE)
```

Models of longitude and latitude

July

Table S3.2 Performance for July spatial model, sorted from best restricted maximum likelihood (REML) score.

Smoothing terms	R^2	Deviance explained (%)	REML	AIC	EDF	p-value
s(LONG, LAT) + s(LONG, LAT, GRP.TYPE)	0.189	24.5	418.89		24.1 5.9	**<2e-16*** **<2e-16***
s(LONG) + s(LONG, GRP.TYPE) + s(LAT) + s(LAT, GRP.TYPE)	0.125	18.3	441.55		7.9 5.2 3.0 1.5	**<2e-16*** **<2e-16*** 0.07 **0.009***

August

Table S3.3 Performance for August spatial model, sorted from best restricted maximum likelihood (REML) score.

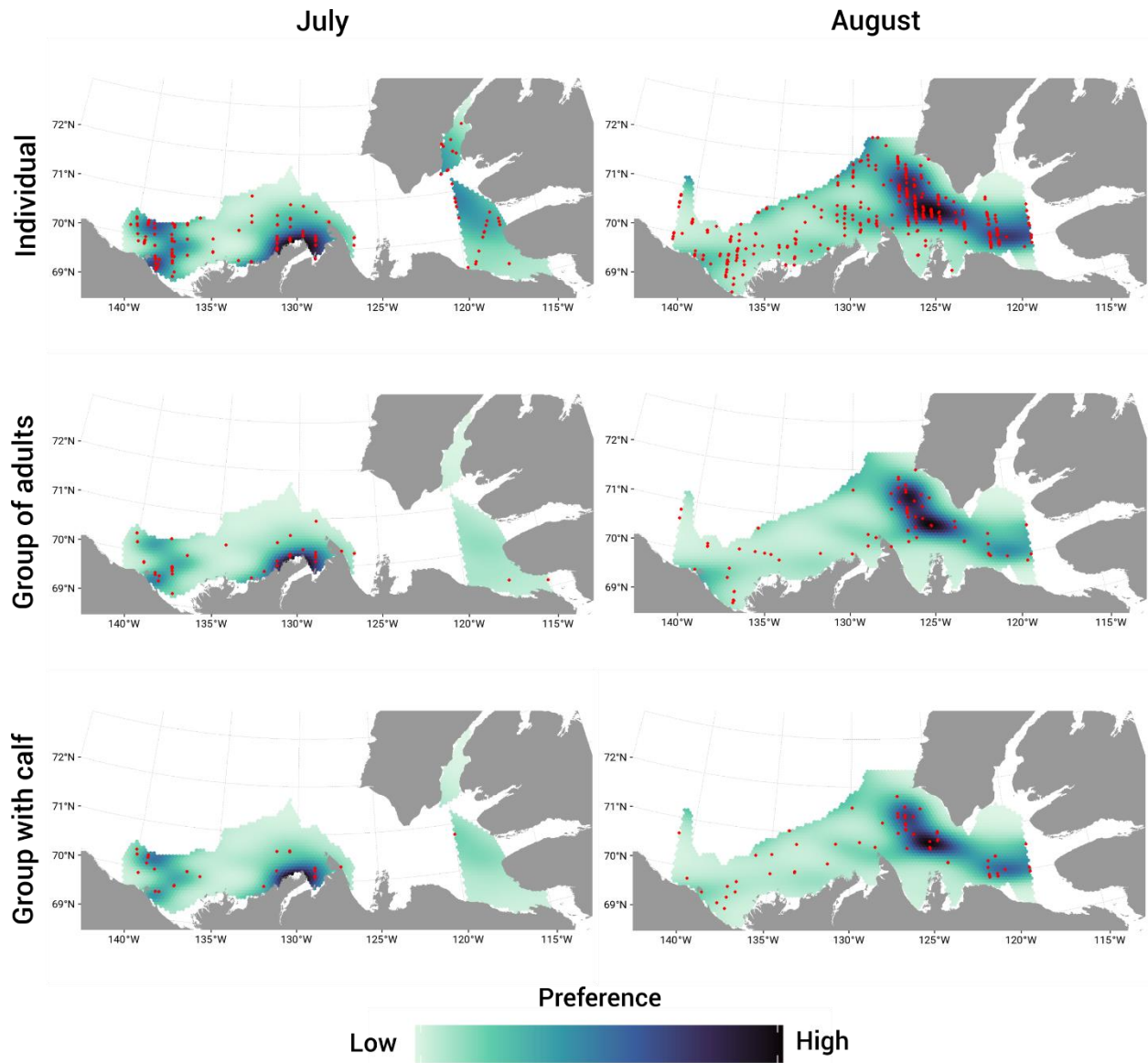| Smoothing terms	R^2	Deviance explained (%)	REML	AIC	EDF	p-value
s(LONG, LAT) + s(LONG, LAT, GRP.TYPE)	0.188	24.7	728.1		34.6 6.3	**<2e-16*** **<2e-16***
s(LONG) + s(LONG, GRP.TYPE) + s(LAT) + s(LAT, GRP.TYPE)	0.101	14.0	785.27		6.2 0.76 3.4 2.1	**<2e-16*** **0.0018*** **0.011*** **0.00012***

Figure S3.2 Map of the preference comparing July and August with the spatial models (longitude and latitude).
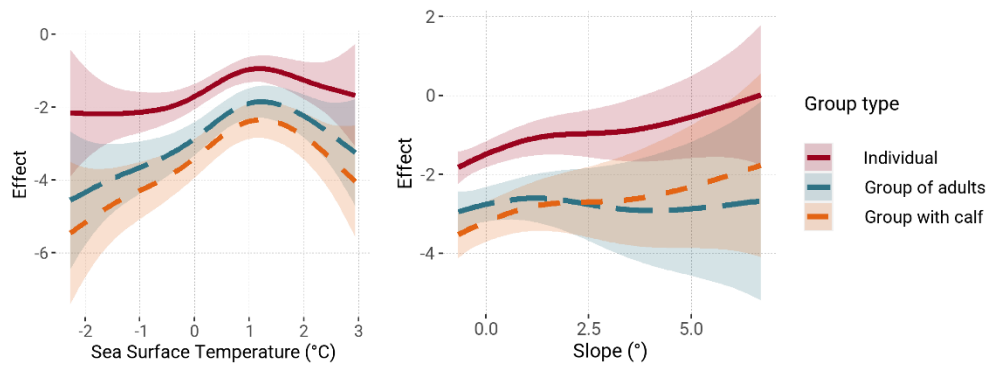
Model GS with environmental variables

<u>July</u>

Figure S3.3 Response curve of the best model for July with sea surface temperature and slope. Values are scaled and centred.
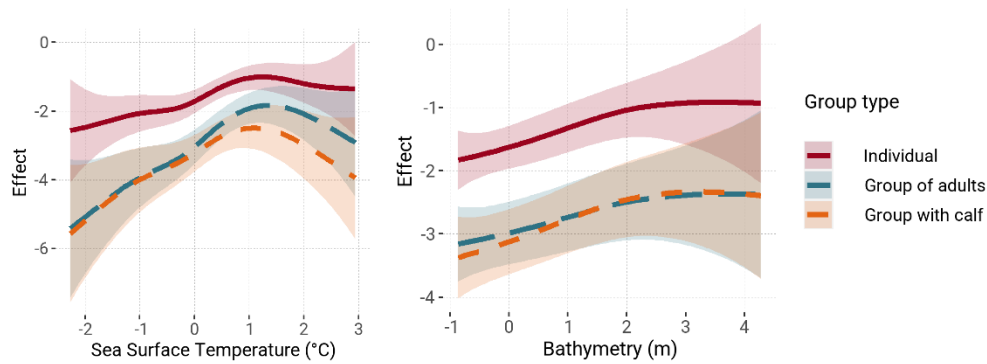

Figure S3.4 Response curve of the second best model for July with sea surface temperature and bathymetry. Values are scaled and centred.
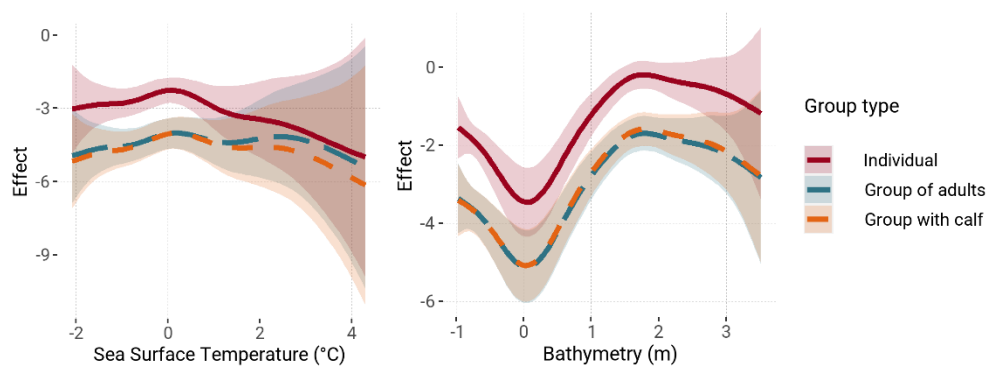
<u>August</u>

Figure S3.5 Response curve of the best model for August with sea surface temperature and bathymetry. Values are scaled and centred.

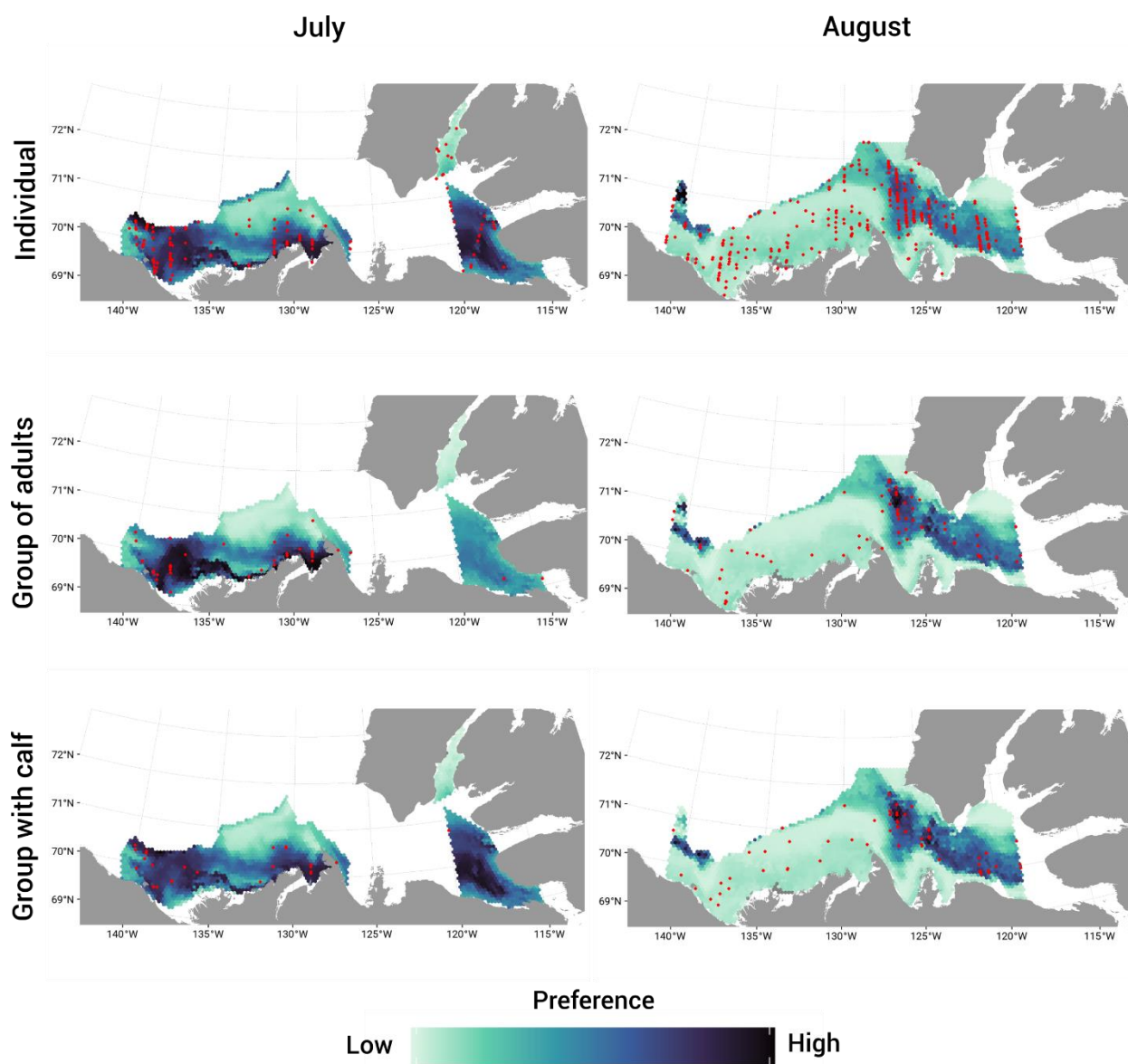**Figure S3.6** Map of the preference comparing July and August with the models of sea surface temperature and bathymetry
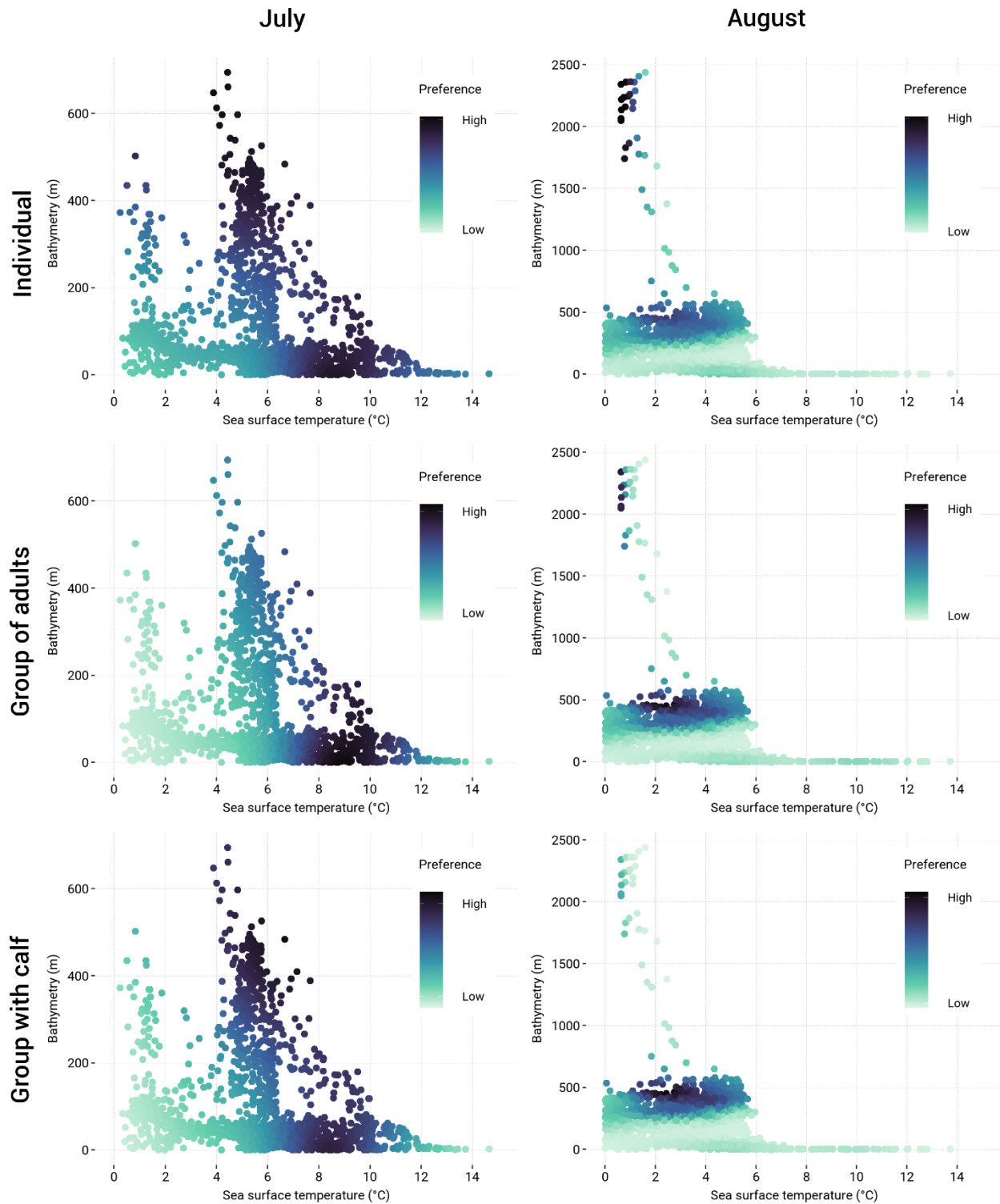
Figure S3.7 Comparison of the relative preference of beluga group types for the models including sea surface temperature and bathymetry. Left: Response from the July model. Right: Response from the August model. Note that the range of the y axis for the bathymetry differs between months.

Literature Cited

McCabe, J. D., Clare, J. D., Miller, T. A., Katzner, T. E., Cooper, J., Somershoe, S., Hanni, D., Kelly, C. A., Sargent, R., Soehren, E. C., Threadgill, C., Maddox, M., Stober, J., Martell, M., Salo, T., Berry, A., Lanzone, M. J., Braham, M. A. & McClure, C. J. W. (2021). Resource selection functions based on hierarchical generalized additive models provide new insights into individual animal variation and species distributions. *Ecography*, doi: https://doi.org/10.1111/ecog.06058

Pedersen, E. J., Miller, D. L., Simpson, G. L. & Ross, N. (2019). Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ*, e6876. doi: https://doi.org/10.7717/peerj.6876

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*, *73*,3-36. doi: https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wood, S. N. (2017) *Generalized Additive Models: An Introduction with R.* (2e ed.). Boca Raton, FL: CRC Press.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009) GLM and GAM for Absence–Presence and Proportional Data. In (Eds.), *Mixed effects models and extensions in ecology with R* (pp. 245-259). New York: Springer New York.

Chapter 4. Conclusion

4.1 Contribution, Limitations, and Research Opportunities

Summary

Sociality is an important part of the evolution, ecology, and biology of species (Whitehead, 1997; Kutsukake, 2009; Ward and Webster, 2016). It influences foraging, predation, parental care, communications, culture, and many other aspects of life history (Acevedo-Gutiérrez, 2018). Despite new technologies that allow access to various types of data, research on social behaviour remains challenging, and even more so for Arctic marine mammals (Whitehead et al., 2000). Therefore, any type of data available is an opportunity to observe elements of sociality (Whitehead et al., 2000). For the Eastern Beaufort Sea (EBS) beluga whale (*Delphinapterus leucas*) population, scientific studies have previously described group size and range from surveys and sexual segregation (Harwood et al., 1996; Loseto et al., 2006; Harwood and Kingsley, 2013; Hauser et al., 2017), but no study has only focused on group behaviour. This is partly due to the extensive range of EBS belugas in the summer (Richard et al., 2001; Storrie et al., 2022), which makes it difficult to observe groups at anything other than a small, local, and nearshore scale. For this study, we took the opportunity of analyzing data collected during a large scale aerial survey in late July 2019. A visual and photographic survey covered most of the Beaufort Sea shelf, as well as parts of the Amundsen Gulf and Prince of Wales Strait. A photographic survey only was also conducted in the Mackenzie Delta. The last time the EBS belugas were surveyed with similar coverage was in 1992 (Harwood et al., 1996) and new updated information is needed to understand the social context of this population.

First, we used aerial photographs to describe group characteristics and spatial organization of belugas and compared the Beaufort Sea shelf and the Mackenzie Estuary. Contrasting environmental conditions define these two habitats: the Beaufort Sea is a broad, open-water continental shelf (offshore) while the Mackenzie Estuary contains many shallow bays, with turbid and warm water (inshore). Using photogrammetry techniques and piecewise regressions, we compared group metrics in the two habitats, expecting to see differences. We observed that some characteristics remain constant across the environments, including the group size and inter-individual distances. In both offshore and inshore, belugas were alone or in small groups and stay

within a distance of 24.6 m offshore and 22.0 m inshore. The average distance between whales in a group was smaller if the group included a young whale. Swimming direction was more coordinated offshore than inshore. We suggested that the type of activity conducted can change across habitats, but social cohesion persists.

Second, we used the locations of occurrence data from the visual survey to investigate the distribution of different beluga social group types across the extended offshore area of the Beaufort Sea shelf and the Amundsen Gulf. We collaborated with the National Oceanic and Atmospheric Administration (NOAA) and the Bureau of Ocean Energy Management (BOEM) to use additional data for the month of August 2019. Habitat preference of individual belugas, groups of adults only, and groups with calf in July and August 2019 were analyzed using hierarchical generalized additive models. Results showed that sea surface temperature, bathymetry, and slope were explaining best the distribution. Individual belugas were found at the continental slope in July and in the Amundsen Gulf and deeper surroundings in August. They usually had higher preferences for deeper and colder waters compared to the other two group types. Groups of adults were located on the continental shelf in July and in the Amundsen Gulf in August. Groups with calf preferred the high slope in July and stayed in the Amundsen Gulf in August. We suggested that foraging opportunities best explain the habitat preference of EBS belugas in the summer. We also suggested that the observed variation in the distribution of the social group types is possibly associated with size-related energy requirements and with the quality and distribution of prey in the habitat.

Limitations

This research explored the social organization and distribution of EBS belugas at a large scale for the first time. Aerial surveys are a great method to cover extensive areas, capture photographs, and take GPS locations of multiple individuals or groups (Mann, 2000). However, this sampling method limits the interpretation of social behaviour, as it only gives an overview of one instant moment for each individual or group. Beluga whales, like other cetaceans, are mobile animals, moving constantly in a three-dimensional environment. Only whales that were not fully submerged are detected, which restricts photogrammetric measurements and location data to visible animals, in one position, despite their movement and behaviour being dynamic. The EBS beluga population have an especially large summer range and are distributed across various types of habitats and dynamic environmental conditions (e.g., water temperature, sea ice concentration, prey

distribution, etc.) (Galley et al., 2008; Hauser et al., 2014; Majewski et al., 2016; Hauser et al., 2017). Water turbidity in the estuary was also a major limitation in the accurate detection of beluga groups, as mentioned in Chapter 2. Although we support, in both chapters, beluga sociality following a fission-fusion pattern, a lot of the group dynamics (i.e., interactions, associations, activity budget, etc.) were not captured with static photographs or a single GPS position along one transect line. Thus, data collected with only the aerial survey is probably not enough to describe the full extent of beluga behaviour (Mann, 2000).

Presence data collected by visual observers onboard the aircraft also limits the interpretation of habitat preference. The habitat preference model is based only on the available habitat sample examined (in this case, the transect lines). Considering the EBS beluga summering range from other studies (Richard et al., 2001; Hauser et al., 2014), our model represented only a portion of the actual accessible habitat. Using a different available area or scale (smaller or larger) could modify the estimates of the habitat preference coefficients (Beyer et al., 2010; Paton and Matthiopoulos, 2016). Furthermore, the presence or absence of group types within the buffered segments depends on the identification of the observers and does not take into account belugas that are underwater at the time the aircraft is flying over the transect. The model is therefore based on pseudo-absences, and not on true absences. The detection of an animal in a habitat can also be misinterpreted as selected resources, which is why combining movement data with presence data increases the accuracy of a habitat model (Beyer et al., 2010). As mentioned in Chapter 3, due to the different survey efforts between July and August, our results are not fully comparable. Aerial surveys in the Arctic are costly and the survey effort is generally dependent on weather conditions, which do not guarantee complete coverage of the pre-established survey plan. The lack of information on the presence of belugas, especially in July in the Amundsen Gulf, prevents us from detecting seasonal movements or areas of high interest (Becker et al., 2014; Gilles et al., 2016).

Contribution to knowledge and future opportunities

Still, this research is relevant as it is the first to investigate elements of beluga sociality in the Beaufort Sea. For the first time, we used piecewise regression analyses to measure thresholds in the frequency of inter-individual distance on beluga groups and hierarchical generalize additive models to describe habitat preference of social group types. Although the results do not capture

the full range and dynamics of beluga social behaviour, it now creates a baseline of information for future work conducted in the area.

For instance, the description of group characteristics and analyses of social structures can be further explored with other sampling methods (boat observation, drone, acoustic, telemetry, genetics, etc.), and at other scales. Using multi-disciplinary methods to collect observations would give a larger picture of the social behaviour of this beluga population. Individual identification and focal follow methods allow for more detailed information about identity, encounters, and behaviour (Whitehead and Van Parijs, 2010). Additionally, the emergence of new technology such as unmanned aerial systems or vehicles (UAS/UAV), provides a new and more efficient way to collect behavioural data, with longer observational capacity and minimal disturbance (Torres et al., 2018). UASs have been particularly effective with cetaceans, exposing unique social behaviour and interactions (e.g., Hartman et al., 2020; Orbach et al., 2020; Ramos et al., 2021).

Furthermore, there is now a vast choice of algorithms for habitat selection analyses or species distribution models (e.g., resource selection functions (RSF), generalized linear or additive model (GLM, GAM), maximum entropy (MaxEnt), ecological niche factor analysis (ENFA), random forest (RF), etc.) Some studies have even tested multiple algorithms with the same dataset to find the best performing one (Hoffman et al., 2010; Derville et al., 2018; Robinson et al., 2021). Long-term studies are also better at capturing and describing more general patterns of population behaviours (McHugh, 2019). All these models require occurrence data, but observations of Arctic marine mammals are difficult to obtain, which is why data sharing and accessibility should be a more common practice, thus providing more support for conservation and management decisions (Reichman et al., 2011). Collaboration between institutions has enabled this project to expand the data on beluga sightings in the Beaufort Sea in summer and helped detect patterns that would not have been apparent with the July data only. With new or complementary data from the same months over different years, distribution models of the EBS beluga population can be more accurate.

Knowledge bridging and co-production

Indigenous communities in the circumpolar Arctic have previously contributed to the understanding of aspects of beluga whale biology, documented in peer-reviewed papers or grey literature (see review by Breton-Honeyman et al. 2016). With similar intentions, our initial plan

was to bring the aerial photographs to the community of Paulatuk and exchange insights on various elements of beluga sociality but was disrupted by the COVID-19 pandemic. Although we tried to include recorded observations of traditional ecological knowledge, little has been collected on the subject in our study area. We believe, however, that beluga social behaviour is a topic of interest to Inuvialuit and that this study can serve as a starting tool to engage conversation with knowledge holders in future co-production projects in the Inuvialuit Settlement Region. Methodical procedures exist to analyze social systems mathematically (Whitehead, 1997), but animal behaviour varies in time and space, shaped by genetic, ecological, and social factors (Kappeler et al., 2013). Indigenous People have a more holistic understanding of nature and may use different indicators of sociality (Berkes and Berkes, 2009). We believe the Inuvialuit perspective would highlight observations and information on social behaviour that haven't been captured in scientific studies in the Beaufort Sea yet. Collaborative research would help provide a broader picture on beluga sociality, as well as benefit research on other beluga populations, as elements of sociality are common across populations (O'Corry-Crowe et al., 2018; O'Corry-Crowe et al., 2020).

Epistemological differences between western science and Indigenous knowledge can lead to a reluctance to engage in synergistic research (Mistry and Berardi, 2016). However, frameworks exist to support the coexistence and complementary of multiple knowledge systems in research (Reid et al., 2021). Bridging western science and traditional local or ecological knowledge is a practice increasingly recognized, contributing to research, conservation, and species management (Thornton and Scheer, 2012). Furthermore, the inclusion of Indigenous insight and participation in scientific research processes is part of the efforts to decolonize western science and advocate for Indigenous equity and self-determination (Mistry and Berardi, 2016; Held, 2019).

Conclusion

Sociality is complex but plays a major role in population viability and adaptation to changes (Brakes et al., 2021). We are beginning to recognize and study the depth of social behaviour, such as culture in cetaceans, and the importance of further integrating this knowledge into conservation policy plans (Rendell and Whitehead, 2001; Brakes et al., 2021). As the marine environment is subject to increased anthropogenic impacts, including the Beaufort Sea (Wood et al., 2013; Sydeman et al., 2015; IPCC, 2019), studies on social behaviour will continue to be needed to

understand adaptative mechanisms, assess impacts on individual fitness and population dynamics, as well as establish effective biodiversity and species conservation and management plans.

4.2 Literature Cited

Acevedo-Gutiérrez, A. (2018). Group Behavior. In B. Würsig, J. G. M. Thewissen and K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (pp. 428-435). Cambridge: Academic Press.

Becker, E. A., Forney, K. A., Foley, D. G., Smith, R. C., Moore, T. J. and Barlow, J. (2014). Predicting seasonal density patterns of California cetaceans based on habitat models. *Endangered Species Research, 23*(1), 1-22.

Berkes, F. and Berkes, M. K. (2009). Ecological complexity, fuzzy logic, and holism in indigenous knowledge. *Futures, 41*(1), 6-12. doi:https://doi.org/10.1016/j.futures.2008.07.003

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M. and Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1550), 2245-2254. doi:10.1098/rstb.2010.0083

Brakes, P., Carroll, E. L., Dall, S. R. X., Keith, S. A., McGregor, P. K., Mesnick, S. L., Noad, M. J., Rendell, L., Robbins, M. M., Rutz, C., Thornton, A., Whiten, A., Whiting, M. J., Aplin, L. M., Bearhop, S., Ciucci, P., Fishlock, V., Ford, J. K. B., Notarbartolo di Sciara, G. Simmonds, M. P., Spina, F., Wade, P. R., Whitehead, H., Williams, J. and Garland, E. C. (2021). A deepening understanding of animal culture suggests lessons for conservation. *Proceedings of the Royal Society B: Biological Sciences, 288*(1949), 20202718. doi:10.1098/rspb.2020.2718

Breton-Honeyman, K., Furgal, C. M. and Hammil, M. O. (2016). Systematic Review and Critique of the Contributions of Traditional Ecological Knowledge of Beluga Whales in the Marine Mammal Literature. *Arctic, 69*(1), 37-46.

Derville, S., Torres, L. G., Iovan, C. and Garrigue, C. (2018). Finding the right fit: Comparative cetacean distribution models using multiple data sources and statistical approaches. *Diversity and Distributions, 24*(11), 1657-1673. doi:https://doi.org/10.1111/ddi.12782

Galley, R. J., Key, E., Barber, D. G., Hwang, B. J. and Ehn, J. K. (2008). Spatial and temporal variability of sea ice in the southern Beaufort Sea and Amundsen Gulf: 1980–2004. *Journal of Geophysical Research: Oceans, 113*(C5), doi:https://doi.org/10.1029/2007JC004553

Gilles, A., Viquerat, S., Becker, E. A., Forney, K. A., Geelhoed, S. C. V., Haelters, J., Nabe-Nielsen, J., Scheidat, M., Siebert, U., Sveegaard, S., van Beest, F. M., van Bemmelen, R. and Aarts, G. (2016). Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. *Ecosphere, 7*(6), e01367. doi:https://doi.org/10.1002/ecs2.1367

Hartman, K., van der Harst, P. and Vilela, R. (2020). Continuous Focal Group Follows Operated by a Drone Enable Analysis of the Relation Between Sociality and Position in a Group of Male Risso's Dolphins (*Grampus griseus*). *Frontiers in Marine Science, 7*, doi:10.3389/fmars.2020.00283

Harwood, L. A., Innes, S., Norton, P. and Kingsley, M. C. S. (1996). Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea and west Amundsen Gulf during late July 1992. *Canadian Journal of Fisheries and Aquatic Sciences, 53*, 2262-2273. doi:https://doi.org/10.1139/f96-180

Harwood, L. A. and Kingsley, M. C. S. (2013). Trends in the Offshore Distribution and Relative Abundance of Beaufort Sea Belugas, 1982-85 vs 2007-09. *Arctic, 66*(3), 247-256. doi:http://www.jstor.org/stable/23594627

Hauser, D. D. W., Laidre, K. L., Stern, H. L., Moore, S. E., Suydam, R. S. and Richard, P. R. (2017). Habitat selection by two beluga whale populations in the Chukchi and Beaufort seas. *PLoS ONE, 12*(2), e0172755. doi:10.1371/journal.pone.0172755

Hauser, D. D. W., Laidre, K. L., Suydam, R. S. and Richard, P. R. (2014). Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology, 37*, 1171–1183. doi:10.1007/s00300-014-1510-1

Held, M. B. E. (2019). Decolonizing Research Paradigms in the Context of Settler Colonialism: An Unsettling, Mutual, and Collaborative Effort. *International Journal of Qualitative Methods, 18*, 1609406918821574. doi:10.1177/1609406918821574

Hoffman, J. D., Aguilar-Amuchastegui, N. and Tyre, A. J. (2010). Use of simulated data from a process-based habitat model to evaluate methods for predicting species occurrence. *Ecography*, *33*, 656-666. doi:10.1 1 1 l/j.l600-0587.2009.05495.x

IPCC (2019). Technical Summary. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, E. P. P. Zhai, K. Mintenbeck, M. Tignor, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama and N. M. Weyer (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* (pp. 34).

Kappeler, P. M., Barrett, L., Blumstein, D. T. and Clutton-Brock, T. H. (2013). Constraints and flexibility in mammalian social behaviour: introduction and synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1618), 20120337. doi:10.1098/rstb.2012.0337

Kutsukake, N. (2009). Complexity, dynamics and diversity of sociality in group-living mammals. *Ecological Research, 24*(3), 521-531. doi:10.1007/s11284-008-0563-4

Loseto, L. L., Richard, P., Stern, G. A., Orr, J. and Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology, 84*(12), 1743-1751. doi:10.1139/z06-160

Majewski, A. R., Walkusz, W., Lynn, B. R., Atchison, S., Eert, J. and Reist, J. D. (2016). Distribution and diet of demersal Arctic Cod, *Boreogadus saida*, in relation to habitat characteristics in the Canadian Beaufort Sea. *Polar Biology, 39*, 1087-1098. doi:10.1007/s00300-015-1857-y

Mann, J. (2000). Unraveling the Dynamics of Social Life: Long-term Studies and Observational Methods. In J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead (Eds.), *Cetaceans Societies: Field Studies of Dolphins and Whales* (pp. 45-64). Chicago: University of Chicago Press.

McHugh, K. (2019). Odontocete Social Strategies and Tactics Along and Inshore. In B. Würsig (Eds.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 165-182). Cham, Switzerland: Springer International Publishing.

Mistry, J. and Berardi, A. (2016). Bridging indigenous and scientific knowledge. *Science, 352*(6291), 1274-1275. doi:10.1126/science.aaf1160

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K. and Mahoney, B. (2018). Migratory culture,

population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLoS ONE, 13*(3), e0194201. doi:https://doi.org/10.1371/journal.pone.0194201

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T. G., Lydersen, C., Kovacs, K. M., Orr, J., Harwood, L., Litovka, D. and Ferrer, T. (2020). Group structure and kinship in beluga whale societies. *Scientific Reports, 10*, 11462. doi:10.1038/s41598-020-67314-w

Orbach, D. N., Eaton, J., Fiori, L., Piwetz, S., Weir, J. S., Würsig, M. and Würsig, B. (2020). Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle. *Marine Mammal Science, 36*(4), 1097-1110. doi:https://doi.org/10.1111/mms.12695

Paton, R. S. and Matthiopoulos, J. (2016). Defining the scale of habitat availability for models of habitat selection. *Ecology, 97*(5), 1113-1122. doi:https://doi.org/10.1890/14-2241.1

Ramos, E. A., Kiszka, J. J., Pouey-Santalou, V., Ramírez Barragán, R., García Chávez, A. J. and Audley, K. (2021). Food sharing in rough-toothed dolphins off southwestern Mexico. *Marine Mammal Science, 37*(1), 352-360. doi:https://doi.org/10.1111/mms.12727

Reichman, O. J., Jones, M. B. and Schildhauer, M. P. (2011). Challenges and Opportunities of Open Data in Ecology. *Science, 331*(6018), 703-705. doi:10.1126/science.1197962

Reid, A. J., Eckert, L. E., Lane, J.-F., Young, N., Hinch, S. G., Darimont, C. T., Cooke, S. J., Ban, N. C. and Marshall, A. (2021). "Two-Eyed Seeing": An Indigenous framework to transform fisheries research and management. *Fish and Fisheries, 22*(2), 243-261. doi:https://doi.org/10.1111/faf.12516

Rendell, L. and Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences, 24*, 309-382. doi:https://doi.org/10.1016/B978-0-12-373553-9.00068-7

Richard, P. R., Martin, A. R. and Orr, J. R. (2001). Summer and Autumn Movements of Belugas of the Eastern Beaufort Sea Stock. *Arctic, 54*(3), 223-236. doi:https://doi.org/10.14430/arctic783

Robinson, C. L. K., Proudfoot, B., Rooper, C. N. and Bertram, D. F. (2021). Comparison of spatial distribution models to predict subtidal burying habitat of the forage fish *Ammodytes*

personatus in the Strait of Georgia, British Columbia, Canada. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(10), 2855-2869. doi:https://doi.org/10.1002/aqc.3593

Storrie, L., Hussey, N. E., MacPhee, S. A., O'Corry-Crowe, G., Iacozza, J., Barber, D. G., Nunes, A. and Loseto, L. L. (2022). Year-Round Dive Characteristics of Male Beluga Whales From the Eastern Beaufort Sea Population Indicate Seasonal Shifts in Foraging Strategies. *Frontiers in Marine Science, 8*, 715412. doi:10.3389/fmars.2021.715412

Sydeman, W. J., Poloczanska, E., Reed, T. E. and Thompson, S. A. (2015). Climate change and marine vertebrates. *Science, 350*(6262), 772-777. doi:10.1126/science.aac9874

Thornton, T. F. and Scheer, A. M. (2012). Collaborative Engagement of Local and Traditional Knowledge and Science in Marine Environments: A Review. *Ecology and Society, 17*(3), doi:10.5751/ES-04714-170308

Torres, L. G., Nieukirk, S. L., Lemos, L. and Chandler, T. E. (2018). Drone Up! Quantifying Whale Behavior From a New Perspective Improves Observational Capacity. *Frontiers in Marine Science, 5*(319), doi:10.3389/fmars.2018.00319

Ward, A. and Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals.* Cham, Switzerland: Springer International Publishing.

Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour, 53*, 1053-1067. doi:https://doi.org/10.1006/anbe.1996.0358

Whitehead, H., Christal, J. and Tyack, P. L. (2000). Studying Cetacean Social Structure in Space and Time: Innovative Techniques. In J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead (Eds.), *Cetaceans Societies: Field Studies of Dolphins and Whales* (pp. 65-90). Chicago: University of Chicago Press.

Whitehead, H. and Van Parijs, S. (2010). Studying marine mammal social systems. In I. L. Boyd, W. D. Bowen and S. J. Iverson (Eds.), *Marine Mammal Ecology and Conservation: A Handbook of Techniques* (pp. 263-282). Oxford: Oxford University Press.

Wood, K. R., Overland, J. E., Salo, S. A., Bond, N. A., Williams, W. J. and Dong, X. (2013). Is there a ''new normal'' climate in the Beaufort Sea? *Polar Research, 32*(0), doi:10.3402/polar.v32i0.19552

Appendix

Graphical abstract for the Canadian Journal of Zoology
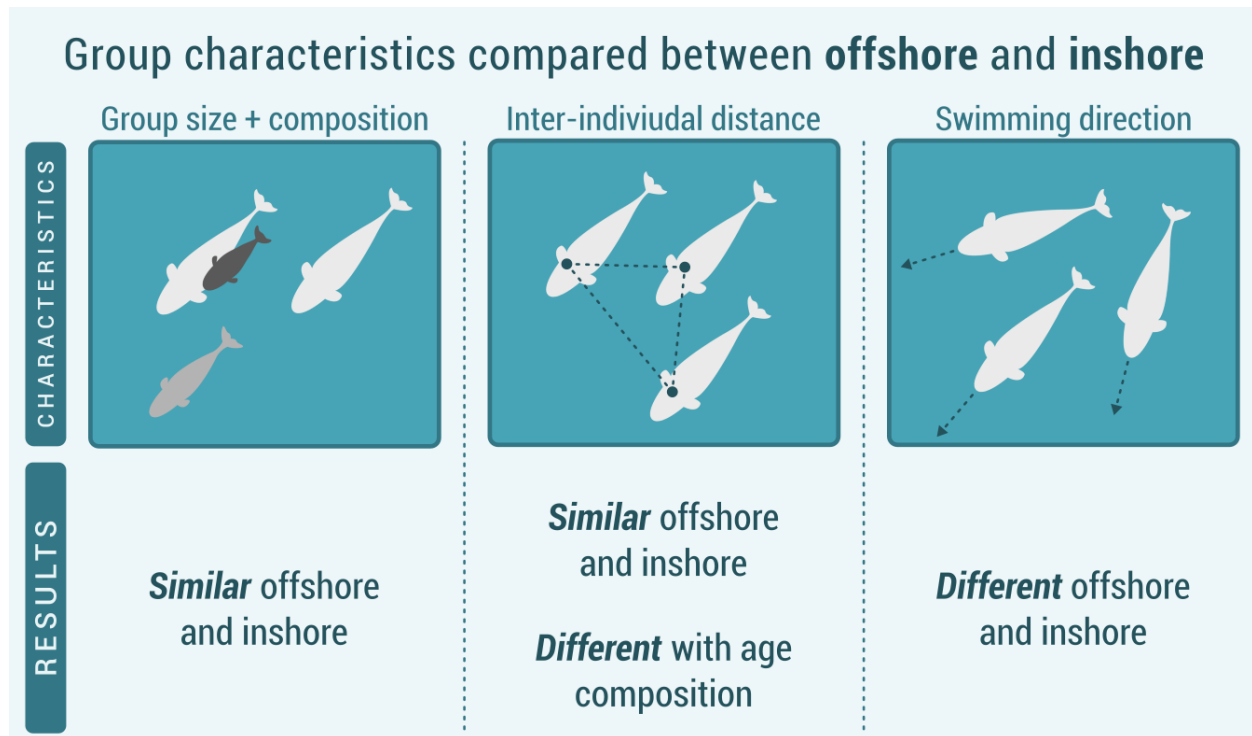
(Created by Alexandra Mayette)

USING PHOTOS TO EXPLORE GROUP CHARACTERISTICS

ALEXANDRA MAYETTE - MSc

Social behaviour is an important aspect of beluga life history, but is very challenging to study. To help understand how belugas are organized into groups, I used photos taken from planes during the 2019 aerial survey. I looked at groups and identified the group size and approximate age of each beluga, the distance between whales and the swimming direction. I also compared the group characteristics between the transects lines that were flown in the **offshore** area (including Beaufort Sea shelf, Amundsen Gulf, and Prince of Wales Strait) and **inshore** area (including Mackenzie Delta, Shallow Bay and Kugmallit Bay).

We found that:
- The average number of belugas in a group was similar offshore and inshore.
- The distance between beluga in a group was similar offshore and inshore.
- Belugas in a group including young whales were closer together than groups of adult-only.
- Groups were swimming in one direction offshore, while inshore, belugas would swim in more different directions.

Groups offshore ———————————————— Group inshore ————————

(Created by Alexandra Mayette)

# HABITAT PREFERENCE OF DIFFERENT SOCIAL GROUPS

ALEXANDRA MAYETTE - MSc

Depending on their age and sex, belugas have different needs, whether for food, protection, or learning. This can lead beluga to group together and use different habitat types to meet these needs. I use beluga sightings from the 2019 aerial survey conducted in July by DFO and another survey conducted in August 2019 by NOAA (Alaska, US). With these two datasets, I'm looking to see if three different types of social groups are using the same habitat or if they need different environmental conditions.

3 group types:
- Individual belugas
- Groups of adult only
- Groups with calf

August 2019

Dark blue means high preference

Groups with calf observed on the survey
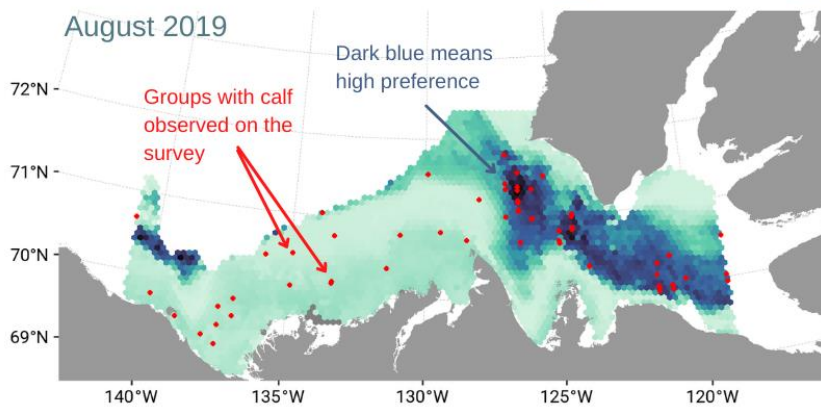
For example, this is a map of the August observations of groups of belugas with at least one calf. You can see these groups are found away from the coast, in areas where the depth is about 500 m, especially the Amundsen Gulf.

(Created by Alexandra Mayette)