

**GENETIC DIVERSITY IN THE WORLD'S OCEANS:
INVESTIGATING MARINE MAMMAL DIVERSITY USING BELUGA
WHALE POPULATION GENOMICS & PUBLICLY ARCHIVED DATA**

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ABSTRACT

Marine mammals are among the most remarkable animals on the planet, captivating human interest while playing key roles in marine ecosystems. They act as top predators, prey and environmental engineers, influencing nutrient cycling, habitat structure and ecosystem productivity. Despite their ecological significance, marine mammals face many challenges in the modern world and require targeted conservation efforts in the future if we want them to thrive in rapidly changing environment. Genetic diversity is a critical determinant of a population's ability to adapt to new conditions; however what drives genetic diversity in marine mammals on a global scale is not yet well understood. In this thesis, I uncovered large, global patterns in marine mammal genetic diversity distribution by taking advantage of publicly available data. I discovered that colder waters harbour genetically richer and interconnected populations than warm waters. Additionally, regions with higher marine mammal species richness tend to be inhabited by highly diverged populations with lower genetic diversity. In the following chapters, I narrowed my focus to a single species, *Delphinapterus leucas*, the beluga whales. Along the East-Canadian coast, I found six genetically distinct populations, each with their own distinct demographic history. After their divergence into separate genetic units around the end of the last ice age, most of these populations declined in their effective population sizes. Anthropogenic disturbances like commercial whaling have brought most of these populations down to levels far below their original sizes. In the final data chapter, I also discovered that the divergence of these populations has not been merely the result of neutral processes like genetic drift, but instead local adaptation, shaping the populations' genetic make-up to fit their local environment. Aside from a large number of genetic variations linked to increased ice coverage, I also found especially strong signals of local adaptation linked to the most southern population in the St. Lawrence estuary and its high productivity. The research in this thesis expands our

understanding of marine mammal biodiversity to a global level and addresses newly discovered genetic features of Canada's beluga populations which can help to inform conservation and management efforts in the future.

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DEDICATION

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GLOSSARY

Admixture	Interbreeding between individuals of genetically distinct populations
Allele	One of two or more alternative form of a gene at a given locus
Allelic richness	A measure of genetic variation within a population, measured as the number of alleles present, standardized for sample size
Coverage	The number of times a particular nucleotide position in a genome is read during DNA sequencing
Effective population size	The size of an idealized population that would experience the same rate of genetic drift as the observed population
F_{ST}	A measure of genetic differentiation among populations
Gene diversity	A measure of genetic variation within a population, measured as the probability that two alleles randomly drawn from a locus are different
Gene flow	The transfer of genetic material between conspecific populations, either through dispersal or interbreeding
Gene ontology	A standardized framework that links genes to functional groups
Genetic diversity	Variation of genetic material in a designated group like a population or species
Heterozygosity	See "Gene diversity"
Local adaptation	The process by which populations evolve traits that increase fitness specific to their local environment
Locus	A specific location within a genome
Population	A group of conspecific individuals which is genetically distinct from other conspecific groups

CHAPTER 1: INTRODUCTION

Some of the most awe-inspiring animals in the world can be found among the mammals living in our planet's oceans. The blue whale (*Balaenoptera musculus*) is the largest animal that has ever existed on earth (Ruud 1956). Dolphins have aspects of their intelligence rivaling those of many of our primate relatives (Marino et al. 2007; Reiss and Marino 2001). And whoever has seen a haulout of enormous walruses (*Odobenus rosmarus*) gathering on small islands will probably never forget the sight ("Haulout" 2022). Mammals can be found in the oceans all around the world (Pompa, Ehrlich, and Ceballos 2011). Wherever they live they attract the attention of humans around them. In our modern world of intercontinental travel, sites of whale or seal gatherings have become a massive attraction for tourism (Alteg 2019; Brenner, Mayer, and Stadler 2016; Dressler, Fikret, and Mathia 2001; Fujii et al. 2023), but even before the modern age, these animals have had great significance for the people and human cultures around them. Whales and walruses have been used by hunters for their oil and their lipid-rich meat (Gotfredsen, Appelt, and Hastrup 2018; Hoover et al. 2013; Kozlov and Zdor 2003; Tyrrell 2008), while the fur of seals was often considered a great resource for clothing for northern human populations (Schmidt et al. 2024).

However, marine mammals influence their environment in more ways than just serving human interests. Marine mammals are often part of complex food webs. For example, seals have a top-down predator role on fish in their habitat (Kappa et al. 2026), while themselves serving as primary prey for polar bears (*Ursus maritimus*) who rely heavily on their blubber to build up their own fat that sustains them through the ice free months of the year (Stirling and Archibald 1977). Recent decades have also shed more and more light on the role of marine mammals as environmental engineers. From sea otters (*Enhydra lutris*) maintaining kelp forests (Estes and Palmisano 1974) to manatees (*Trichechus* spp.) altering the structure of seagrass ecosystems (Marsh, O'Shea, and Reynolds 2011), marine mammals

play a crucial role in shaping the marine ecosystem. We also learned more about how whales contribute in essential ways to the marine nutrient cycle, helping to enrich the oceanic ecosystem on the water surfaces, as well as in the deep. Their excrements help bring nutrients from the deep oceans up to the surface, a process called "whale pump" (Roman and McCarthy 2010). This helps with fertilize the water surface, increasing plankton growth which then further stimulates the growth of fish populations. In the other direction, whale carcasses also help provide nutrients to the ocean floor when they sink, a process called "whale falls" (Smith et al. 2015). It is undeniable that, wherever these animals find their habitat, they contribute significantly to the sustainability of their ecosystem.

Unfortunately, like most wildlife, marine mammals have been struggling in the modern world. Anthropogenic climate change is rapidly changing their environment (Avila, Kaschner, and Dormann 2018; Kovacs et al. 2011). It happens to such a drastic extent that natural response mechanisms, like adapting to new conditions, often are not sufficient to counteract the detrimental impact these environmental changes have on marine mammal populations. The world's oceans are very susceptible to the specific alterations our planet is currently undergoing. Oceans are a potent carbon sinks (DeVries 2022; Heinze et al. 2015), meaning the increased concentrations of carbon dioxide, as well as large parts of the excess heat from our atmosphere are being absorbed into the oceans. This has many consequences, like acidification or deoxygenation of the waters which undermines the specific environmental conditions marine species have adapted to (Cheung, Wei, and Levin 2022; Steckbauer, Klein, and Duarte 2020). Combining this with direct ways humans put pressure on marine wildlife communities, like commercial fishing or chemical pollutants being dumped into the oceans (Maxwell et al. 2013), results in cascading destructive forces on these environments. Many of these effects are felt by marine mammals indirectly; for instance, depletion of their prey communities through overfishing (Gundi 2016; Rupil et al. 2022), oceanic acidification and deoxygenation (Cheung et al. 2022; Steckbauer et al. 2020). Other

examples hit marine mammals even more directly. For example commercial whaling and seal hunting over the last two centuries have destroyed many previously large populations (Koss et al. 2023; O’Corry-Crowe et al. 1997), and while today there is effort put into the protection and management of these animals, there are still many places where human hunting is being conducted beyond the level of sustainability (Environmental Investigation Agency 2018; Liu, Chengzhi, and Chen 2025), while in other places populations have already been extirpated or brought so close to extinction that recovery is an uphill battle (Estes et al. 2006; Watt et al. 2021). That said the way anthropogenic pressures affect marine mammal populations can be very heterogenous. For example, warmer, shorter winters with less sea ice may have a negative effect on many marine species like walruses (Jay, Fischbach, and Kochnev 2012; Udevitz et al. 2017) or polar bears (Bromaghin et al. 2015; de la Guardia et al. 2013); however they are welcomed by species like orcas (*Orcinus orca*) who's prey species (i.e. beluga whales) have adapted to seek shelter from hunting predators under sea ice (Kimber et al. 2025). Less sea ice means easier hunts for orcas, which is why in the recent past we have seen them expanding their habitat range (Higdon and Ferguson 2009). It is very apparent: Our planet is changing and the success of marine mammal species in the future will depend on how well they can adjust.

One of the strongest factors determining how well a population can adapt to new environmental conditions is their genetic diversity (Kardos et al. 2021; O’Brien et al. 2025). The higher the variety of genes and genetic composition is in any given group of reproducing individuals, the more likely it is that at least some of the offspring will meet the requirements of the changing conditions in which they grow up. This is why the field of population genetics has become more and more essential for conservation and management of endangered wildlife (Fenster et al. 2018; Hohenlohe, Funk, and Rajora 2021). Keeping merely the numbers of individuals high in a population will not do a lot of good if the population is so genetically homogenous and inbred that there is no flexibility to respond if the environment

suddenly undergoes drastic changes. Population genetics provides the tools to understand wildlife populations in this light. Measures like allelic richness or gene diversity, the degree of genetic divergence between populations or measures quantifying genetic drift, like effective population size, all shed light on a species' evolutionary potential (Kardos et al. 2021). These metrics help identify inbreeding or fragmentation in populations, processes that can slowly erode the resilience of a population towards rapid environmental changes. It is essential to understand marine mammal species in that light, given their often long generation times and complex social structures (Brakes and Dall 2016; Orgeret et al. 2022). Genetic data can reveal hidden vulnerabilities that might otherwise go undetected.

Across marine mammals as a whole, genetic diversity is not evenly distributed throughout the world's oceans (Yuan et al. 2021). However, while we have a variety of studies that investigate wildlife diversity on land (Schmidt 2022; Schmidt, Dray, and Garroway 2022) or amongst fishes (Karachaliou et al. 2025), the underlying mechanisms that shape this distribution in marine mammals is not well understood. This is why the first part of this work synthesizes broad-scale data on marine mammal genetic diversity and links it to key environmental drivers like chlorophyll concentration, sea surface temperature, salinity, human impact and regional species richness. By comparing patterns across many species and populations, it becomes possible to identify both common trends and unique exceptions, providing a framework for understanding why some populations display high evolutionary potential while others may be at greater risk. This synthesis establishes a broader evolutionary and ecological context, which can support better future understanding of individual species; which is the focus of the remaining part of this work: *Delphinapterus leucas*, the beluga whale.

The beluga whale is one of the marine mammal species that is of particular interest in our goal of better understanding population genetics in marine mammals. It is an exceptionally fitting example species for marine mammals, meeting most criteria that make marine

mammals stand out as a group amongst other wildlife. Belugas are very long lived animals (Lowry, Hobbs, and O’Corry-Crowe 2018) and therefore more susceptible to detrimental effects of a fast changing environment. Most populations can be found in Arctic or near-Arctic waters (O’Corry-Crowe 2009), a region that is undergoing even more rapid changes resulting from climate change than most other places on earth (Rantanen et al. 2022). They have a complex relationship with sea ice; migrating during the winter to escape the freezing over of the estuaries they inhabit during the summer, but also using pack ice to escape from orca predation (Breed et al. 2017; Ferguson, Kingsley, and Higdon 2012). They live in complex social configurations and are known to have fairly defined population structure (O’Corry-Crowe et al. 2020). They have also experienced a lot of direct pressure imposed by humans through commercial hunting (Harwood, Kingsley, and Smith 2014; Mitchell and Reeves 1981; Reeves and Mitchell 1984; Rugh, Shelden, and Hobbs 2010; Tinker et al. 2024; Watt et al. 2021). The way all of this has shaped the evolutionary history of Canada's belugas and the forces shaping their current diversity are still not fully understood. The different distinct populations along the Canadian coast need to be better understood in terms of their genetic structure and their current status if we want our targeted management and conservation to be fruitful. Some of these populations are still large and so far seem to withstand any negative effect of the anthropogenic influences around them (COSEWIC 2020). Meanwhile, other populations have declined rapidly over the last centuries (sometimes as a by-product of activities like commercial whaling, sometimes by targeted extirpation of a population to reduce competition with local fisheries (Reeves and Mitchell 1984)). It is still unclear how much local environmental variation has driven population-specific adaptations or whether most of their genetic resilience stems from broader shared evolutionary processes.

To address these questions, the remaining chapters of this work will focus in detail on Canadian beluga populations. I examine their population structure, demographic history and effective population sizes, providing a clear outline of how these groups are connected, how

their numbers have changed through time and where potential genetic vulnerabilities may lie. Understanding these patterns is essential for interpreting the species' capacity to respond to rapidly shifting Arctic conditions. Additionally, I explore whether any regions of the beluga genome carries signs of local adaptation to the diverse environmental conditions these whales encounter across Canada's waters. By tying genomic patterns into ecological context, this work aims to shed light on whether different populations are adapting to their local habitats and what this might mean for their future persistence as environmental changes continue to accelerate.

With this work we are trying to bridge the gap between large-scale patterns of genetic diversity in marine mammals and the fine-scale, population-specific processes that shape the evolutionary potential of a single species. By combining global perspectives with detailed genomic analyses of Canadian beluga populations, this study aims to identify vulnerabilities and adaptive capacities that determine a population's resilience to rapid environmental changes. We seek to uncover how historical demographic shifts, current population structure and local environmental pressures interact to influence genetic variation, drift, divergence and potential for local adaptation. Our results are relevant for understanding the evolutionary biology of belugas, but also have broader implications for marine mammal conservation in a changing Arctic. By pinpointing populations at risk, highlighting genetic features that might support resilience and revealing the environmental conditions that most strongly shape adaptation, it provides a framework for forward-thinking, science based stewardship of the biodiversity of one the most fascinating and wondrous fauna in the world.

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CHAPTER 2: INVESTIGATING THE GLOBAL GENETIC DIVERSITY DISTRIBUTION IN MARINE MAMMALS

Running head: Global diversity distribution in marine mammals

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Abstract

Understanding the environmental and anthropogenic drivers shaping global patterns of genetic diversity in marine mammals is essential for predicting how these animals will respond to rapid environmental changes. Although species-level diversity patterns in marine mammals are increasingly well documented, the question of whether there are general environmental correlates of population-level genetic diversity that apply across species is poorly understood. We compiled a global dataset of microsatellite-based estimates of genetic diversity, allelic richness and population-specific F_{ST} for marine mammals and assessed how these metrics relate to natural environmental gradients, human impacts and species richness. Across species, both gene diversity and allelic richness declined with increasing sea surface temperature, while population-specific F_{ST} increased, indicating greater genetic differentiation in warmer waters. In contrast, chlorophyll concentration and salinity variability showed no consistent relationships with genetic metrics. Measures of human influences on the environment were not strong predictors of genetic diversity either. This is likely because their effects are linked to broader environmental conditions and may not reflect the specific disturbances most relevant to population genetic processes. Species richness was negatively correlated with within-population genetic diversity and positively correlated with population differentiation, suggesting that environments capable of supporting diverse marine mammal communities may do so through ecological specialization and smaller population sizes. Together, our findings identify temperature and species diversity as primary correlates of genetic diversity patterns in marine mammals and highlight the importance of integrating genetic data into biodiversity management and conservation planning.

Introduction

Biodiversity is under threat due to global climate change and the extraction and use of natural resources (Bellard et al. 2012; Habibullah et al. 2022; Wudu et al. 2023). Although substantial research advances have been made in recent years (Karachaliou et al. 2025; Schmidt et al. 2020; Vachon, Whitehead, and Frasier 2018), patterns of biodiversity at the genetic level remain poorly understood for most taxa (Paz-Vinas et al. 2025). This makes understanding how species and ecosystems might respond to environmental change challenging. Genetic diversity underlies the capacity for populations to adaptively respond to environmental change, which underpins population persistence in changing environments (Kardos et al. 2021) and ultimately ecosystem resilience (O'Brien et al. 2025). Here, we investigate natural and human-associated correlates of genetic diversity in marine mammal populations worldwide and explore whether patterns of genetic diversity are correlated with biodiversity patterns in species richness.

Marine mammals are key taxa in marine ecosystems, as predators (Bowen 1997; Kiszka, Heithaus, and Wirsing 2015), ecosystem engineers (Briand 2025; Roman and McCarthy 2010) and indicators of ocean health (Bossart 2011; Plön et al. 2024). However, many species have experienced substantial historical declines and continue to face pressure from climate change, pollution, and the adverse effects of increased human activity in the oceans (Avila, Kaschner, and Dormann 2018; Kovacs et al. 2011). Understanding global patterns of genetic diversity in marine mammals is therefore essential for anticipating their capacity to adapt to rapid environmental change and for informing effective conservation and management strategies.

Global patterns of species richness in marine mammals tend to vary with latitude and are correlated with temperature, habitat productivity, and habitat heterogeneity (Kaschner et al. 2011; Tittensor et al. 2010). Marine mammal species richness tends to peak in the temperate zones and decline toward the tropics and poles (Kaschner et al. 2011; Snelgrove et al. 2016).

The extent to which there are generalizable predictors of genetic diversity across populations within a species range, and whether species richness and genetic diversity are correlated, has not been explored in marine mammals.

Following patterns of genetic diversity in terrestrial mammals (Schmidt, Dray, and Garroway 2022), we predicted that biogeographic patterns of neutral nuclear genetic diversity across marine mammal populations should reflect the size of local populations and the consequent strength of genetic drift. Population size should, in part, be linked to environmental capacities for supporting populations and species. Smaller populations are likely to occur in regions with limited resources because such areas cannot support large numbers of individuals. We also expect population sizes to be relatively small and therefore experience stronger genetic drift in heterogeneous environments. In these instances, we expect that heterogeneous environments will tend to foster local adaptation associated with specialization on local resources (Vellend 2005; Worm and Tittensor 2018). Resource specialization should divide populations into smaller groups. At the same time, we expect heterogeneous environments to support more diverse communities and thus have higher levels of species richness (Schmidt, Dray, and Garroway 2022).

We explored correlations among a series of natural and human-related environmental predictors of genetic composition of local populations. Specifically, we were interested in exploring chlorophyll concentration, sea surface temperature, salinity range, distance to human population center, cumulative human activity impact and species richness.

Chlorophyll concentration reflects phytoplankton biomass and is often used as an indicator of surface net primary productivity in marine ecosystems (Aruga and Monsi 1963; van de Poll et al. 2013). Higher chlorophyll levels are generally associated with regions that support abundant prey for marine mammals (O'Toole et al. 2015). Such regions should therefore be able to sustain larger or more stable populations, resulting in a positive correlation with genetic diversity.

Cold surface water tends to be productive due to thermal upwelling, a process by which cold ocean water is mixed with nutrient-rich, deeper water into the surface layers. Upwelling facilitates higher productivity, not only through elevated chlorophyll concentrations (Riebesell et al. 2009; Sarmiento et al. 2004) but also from communities of high-lipid, energy-rich prey species. This provides more efficient foraging opportunities for large marine predators (Behrenfeld et al. 2006; Field et al. 1998; Venegas, Rivas, and Trembl 2025), which are abundant amongst marine mammals. Therefore, regions with low surface temperatures resulting in upwelling should also be able to support larger populations that experience less drift than populations in warmer waters (Behrenfeld et al. 2006; Field et al. 1998; Venegas et al. 2025). Additionally, glacial dynamics have likely shaped genetic patterns in cold-water regions through repeated cycles of population fragmentation and mixing. During glacial periods, advancing glaciers forced many marine mammal populations into separate glacial refugia, where prolonged isolation increased genetic divergence among populations. When the ice retreats, these isolated groups would expand into newly available habitats and come back into contact with one another. Such secondary contact events could increase within-population genetic diversity in cold waters by introducing alleles from previously distinct populations. Divergence between populations would remain high because only parts of the range experience admixture. This pattern has been documented in several marine mammal species, such as harbour seals and walrus, where populations in refugia admixed postglacially (Ruiz-Puerta et al. 2023; Westlake and O’Corry-Crowe 2002). Elevated productivity due to upwelling and admixture of glacial refugia populations are not mutually exclusive and would both result in cold-water regions harboring elevated genetic diversity and divergence across populations.

We expected salinity variability to be correlated with population sizes and thus genetic diversity across marine mammal species' ranges through its influence on prey distribution and habitat structure. Changes in salinity influence zooplankton community composition and their

reproduction and growth, which can affect the abundance and spatial clustering of forage fish and other prey (Hall and Lewandowska 2022). Marine predators often respond to such variability in their environment by shifting foraging patterns, which can influence gene flow and population density (Speakman et al. 2021). Such salinity-driven habitat heterogeneity could reduce population sizes in areas where prey becomes more spatially or temporarily patchy, reducing genetic diversity. Therefore, we predicted that regions with high salinity variability would be negatively correlated with genetic diversity and positively correlated with genetic divergence in marine mammals, reflecting environmental instability and niche fragmentation.

The effects of human activities on the genetic composition of wild populations can be idiosyncratic (Miles et al. 2019; Schmidt et al. 2020; Schmidt and Garroway 2021), but there is evidence that a population's proximity to humans is consistently associated with reduced genetic diversity for terrestrial mammals (Schmidt et al. 2020) and marine fishes (Karachaliou et al. 2025). Few coastal regions remain unaffected by the environmental footprint of human activity (Williams et al. 2022). Proximity to human activity can be estimated by a sample site's distance to the closest provincial capital, which we expect to be associated with shipping activity, pollution, development and direct hunting. Marine mammal populations near coastal human population centers may have reduced genetic diversity due to the negative effects of human settlements on habitat quality and, therefore, a locality's capacity to support large populations (e.g., Karachaliou et al. 2025). We also used an estimate of cumulative human impacts developed by Halpern et al. (2015) to capture overall human influence on the environment. This index is a global composite measure of cumulative human effects on environments that summarizes 19 metrics of human-caused marine stressors on 20 categories of marine ecosystems. Disturbance measures used the effects of settlements, climate change, and fishing pressure, among numerous other threats to the marine environment. We expected

that all metrics of human disturbance would reduce population sizes, thus increasing genetic drift and reducing genetic diversity.

Finally, we expected species richness and genetic diversity within species ranges to be inversely correlated. Heterogeneous environments should foster local adaptation, thereby reducing gene flow and increasing population differentiation. At the same time, heterogeneous populations and environments also tend to support diverse communities of species and thus high levels of species richness. This pattern has been demonstrated in terrestrial mammals (Schmidt, Dray, and Garroway 2022).

By building a global dataset of genetic diversity estimates with key environmental factors, both natural and human-associated, we aim to identify the general environmental predictors of genetic diversity across species ranges and test for links between genetic diversity and species richness. Linking genetic diversity to environmental and anthropogenic drivers can improve our understanding of how marine mammal communities may respond to ongoing environmental change and help maintain biodiversity across multiple ecological scales.

Methods

For our study, we chose two measures of genetic diversity, gene diversity and allelic richness (El Mousadik and Petit 1996; Nei 1973), and a measure of population differentiation (population-specific F_{ST} ; (Weir and Goudet 2017)). Gene diversity reflects the evenness and diversity of alleles in a sample. Allelic richness is a count of alleles present in a sample of individuals corrected for sample size. Population-specific F_{ST} is an estimate of the degree a population has diverged from other conspecific populations (Weir and Goudet 2017).

We systematically compiled our dataset from archived microsatellite data for marine mammal populations worldwide. Following previous work on large-scale genetic diversity patterns (Karachaliou et al. 2025; Chloe Schmidt 2022), we searched the IUCN Red List (<https://www.iucnredlist.org/>) using the advanced filter for mammals and marine regions to compile a list of marine mammal species names and then used this list and the keywords "microsatellite" and "microsat*" to search for archived microsatellite data using the DataONE R package (Jones, Slaughter, and Nahf 2017). DataONE is a platform that enables searches and data access across major ecological and environmental data repositories. We chose neutral microsatellite markers because they are the most common marker type in data archives, and they estimate genome-wide diversity effectively (Mittell, Nakagawa, and Hadfield 2015) and microsatellite datasets remain the most common and widely spatially sampled nuclear genetic marker type archived in data repositories (Leigh et al. 2021). For all sampling sites, we used coordinates included in archived data when available or georeferenced maps of sample locations provided in the publication using QGIS (QGIS Development Team 2021). Data not clearly assigned to a geographic location, and sites with fewer than 5 individuals were excluded. We excluded polar bear (*Ursus maritimus*) samples from the main analysis, amounting to 18 sampling sites and 2,748 individuals. Polar bears were omitted because they have only recently evolved a fully marine lifestyle. They diverged from grizzly bears (*Ursus arctos*) only a short time ago. While estimates can vary, most genetic evidence support a time of divergence less than one million years ago, with the most accepted estimate placing it around 400,000 years ago (Liu et al. 2014; Shafer 2023). Meanwhile, all other species in our dataset have been adaptively specialized to marine environments for at least several million years. For comparison, the sea otter (*Enhydra lutris*) diverged from its closest terrestrial relative, the Eurasian river otter (*Lutra lutra*) around 5 million years ago (Timm-Davis and Marshall 2021). Given this relatively recent evolutionary transition, polar bears are unlikely to be directly comparable to long-established marine taxa

in terms of ecological and genetic adaptation to marine environments. We repeated all analyses, including polar bear samples, and present those results in the SI.

We imported the data into R using the *adegenet* package (v2.1.11, Jombart 2008). We used the *Hs()* function from *adegenet* to estimate gene diversity and the *allelic.richness()* function in the *hierfstat* package (v0.5.11, Goudet 2004), standardizing for a sample size of 10 alleles, to estimate allelic richness. While gene diversity and allelic richness are expected to be related, gene diversity will be influenced less by the presence of rare alleles than allelic richness. This means that allelic richness will often better detect recent demographic processes as rare alleles are lost first when populations decline. We estimated population-specific F_{ST} using *betas()* function from *hierfstat*.

To test for links between the environment and genetic metrics, we used five environmental factors: (1) mean chlorophyll concentration, (2) mean sea surface temperature, (3) sea surface salinity range, (4) distance to closest coastal population center, and (5) human disturbance index. Marine mammal species richness was used as a sixth variable. For chlorophyll concentration, sea surface temperature, and salinity, we downloaded data layers from the Bio-ORACLE v2.2 database from bio-oracle.org (Figure S2.1a-c; Assis et al. 2017). Mean annual chlorophyll concentration is measured in concentration in mg/m^3 , mean annual sea surface temperature is measured in degrees Celsius and salinity range is measured by the difference in highest and lowest annual salinity concentration on the Practical Salinity Scale (Lewis 1980). All these values are from measurements taken on the sea surface from 2000 to 2014. To download those maps and compile the data corresponding to our sampling sites, we use the R-package *sdmpredictors* (Bosch and Fernandez 2023). For distance to closest coastal population center we used a “distance to market” estimate that measures the distance to the closest provincial capital in kilometers (Figure S2.1d; Yeager et al. 2017). Human impact was measured as the cumulative impact of multiple human-caused stressors on global marine ecosystems, including the effect of settlements, climate change and fishing pressure (Figure

S2.1e; Halpern et al. 2015). The variable for species richness was extracted from mammal species richness map of 2025 from the IUCN Red List website (<https://www.iucnredlist.org/resources/other-spatial-downloads>). The original map included marine as well as terrestrial mammals. To avoid terrestrial species richness influencing our marine mammal species metrics we used the *ne_countries()* function from the *rnaturalearth* v0.3.4 R package (Massicotte and South 2023), which provides polygon layers for all of earth's land masses. These polygons were converted to spatial objects and used as mask to remove all raster cells which overlap with land on the original mammal species richness map (Figure S2.1f). Masking was performed with the *mask()* function from the *raster* v3.6.26 package (Hijmans 2023).

Many processes affect genetic diversity locally. We used distance-based Moran's Eigenvector Maps (dbMEM) to extract and map broad purely spatial patterns in our data. dbMEMs are eigenvectors derived from a spatial distance network among sample sites that represent spatial patterns spanning broad to fine scales. We calculated this distance matrix between sample sites by estimating the shortest marine path between sites using the R-package *marmap* v1.0.10 (Pante and Simon-Bouhet 2013). Before computing the dbMEMs, linear geographic trends were tested for and removed by regressing each variable against latitude and longitude, only keeping model residuals when significant trends were present. dbMEMs were then calculated from the spatial distance matrix and used as explanatory variables in a linear model with the detrended genetic variable. Significant dbMEMs were identified through forward selection from the *SignifReg* package v4.3 (Zambom and Kim 2018), using the adjusted R^2 threshold of the global model. Only dbMEMs with Moran's $I > 0.25$ were kept to represent broad-scale spatial structures. Fitted values from the resulting MEM model were then used to generate spatial prediction maps with *ggplot2* (Hadley 2016) to visualize large-scale spatial patterns.

We tested for links between our environmental variables and metrics describing the genetic composition of populations from each sample site with Bayesian generalized linear mixed effect models using *brms* (Bürkner 2017) in R. All variables were scaled and centered to keep effect sizes comparable. Since we are interested in within-species genetic diversity patterns, we used species identity as a random effect in our models, allowing for random slopes and intercepts. We ran the models assuming a Gaussian error distribution with an identity link function and with a conservative normal prior of zero with standard deviation of one for all fixed effect slope parameters. Data points located closely to each other are often more similar than those farther apart, and our data could therefore exhibit spatial autocorrelation. To account for this, we included the significant dbMEMs identified earlier as explanatory variables in our models. That way we separate effects of geographic proximity or environmental factors not accounted for in our models from those of our tested environmental variables (Borcard and Legendre 2002; Dray, Legendre, and Peres-Neto 2006).

We ran seven models for each genetic metric, one per environmental variable, one for distance to market, one for human impact index and one for species richness, plus one model with only dbMEMs as predictor variables. Models with dbMEMs alone show how much of the variance is explained by spatial variation alone. This yielded 21 models. We calculated the probability of direction of effect for all environmental predictors, using the *p-direction* function from the *bayestestR* package v0.16.1 (Makowski, M. S. Ben-Shachar, et al. 2019; Makowski, M. Ben-Shachar, and Lüdtke 2019). This provides posterior draws with signs (positive or negative) aligned with the estimated effect size. For all models, we also calculated the Bayesian R^2 value with *bayes_R2()* to assess model fit and the widely applicable information criterion (WAIC) with *waic()* to rank the models.

Results

After programmatically searching public databases (following Karachaliou et al. 2025; Chloé Schmidt et al. 2020), we obtained genotypic data for 22,165 individuals sampled at 262 sample sites from 27 species worldwide. The data set used for analyses in the main text, excluding polar bears, comprises a total of 16,013 individuals sampled at 244 sites across 26 species (Figure 2.1, Table S2.1). There were eight significant dbMEMs included in the allelic richness models and six significant dbMEMs in the gene diversity models. For population-specific F_{ST} , there were no significant MEMs (Table 2.1). The dbMEMs provided large-scale global patterns for gene diversity and allelic richness (Figure S2.2 & S2.3). We found a pattern of high genetic diversity in the North Atlantic and low genetic diversity in the North Pacific. While the Northern Hemisphere shows a strong divide into areas with high and low genetic diversity, the Southern Hemisphere has exclusively intermediary genetic diversity.

Our models showed a significant negative relationship between mean temperature and gene diversity and allelic richness and a positive relationship with F_{ST} (Figure 2.2). The same pattern exists regarding species richness. All these models have a smaller WAIC ranking than the null models and therefore better predictive power than models which include only the dbMEMs (Table 2.1). Chlorophyll concentration and distance to market do not show any directional relationship to any of the genetic measures. The directionality in salinity range matches our prediction: negative correlation with genetic diversity but positive correlation with genetic divergence. However, the confidence interval for this model is very wide and therefore does not allow strong conclusions to be drawn. The model testing for relationships with the cumulative human impact index shows weak directionality; however, the relationship is opposite of what we predicted. There was a positive correlation between the human impact index and a negative correlation with population-specific F_{ST} . The directionality of all models was the same in models including polar bears; however, the strength of relationships were less pronounced (Figure S2.4, Table S2.2).

Discussion

Our analyses suggested that despite oceanic interconnectedness, there are global spatial patterns in marine mammal genetic diversity and that, within species, genetic diversity and differentiation are correlated with sea surface temperatures and marine mammals species richness. Allelic richness and gene diversity tended to decrease as mean sea surface temperature increased, and populations became more genetically differentiated in warmer waters. As species richness at a sample site increased, within-population genetic diversity tended to decrease, and genetic differentiation increased. Since our models incorporate individual species as a random effect, the detected pattern represents within-species relationship between environmental variables and genetic metrics. There was no strong evidence for trends in genetic diversity or differentiation associated with measures of human impacts on the environment.

Environmental correlates of genetic diversity

As predicted, environments with lower sea surface temperatures appear to support more genetically diverse populations, which will experience weaker genetic drift compared to smaller populations in warmer waters. Cooler water conditions are correlated with higher productivity waters (Riebesell et al. 2009; Sarmiento et al. 2004) and therefore may support larger populations. A larger population size would act to preserve population-level genetic diversity and explain the negative relationship between temperature and genetic diversity. However, we do not see a link between elevated genetic diversity and higher chlorophyll concentration, even though chlorophyll concentration is a more direct indicator of local productivity (Aruga and Monsi 1963; van de Poll et al. 2013). Although chlorophyll tracks productivity because it reflects photosynthetic biomass (Aruga and Monsi 1963; van de Poll et al. 2013), it is highly variable, fluctuating daily and seasonally, and thus our averaged annual values may not capture variation as it relates to marine mammal population size well (Brown

et al. 1999; Denman, Okubo, and Platt 1977). Productivity is strongly influenced by short-lived bloom events, as well as nutrient and light accessibility, community composition and physical transport (Chavez, Messié, and Pennington 2011), all of which can decouple chlorophyll concentration from carbon fixation, especially when averaging measurements over annual timescales (Lv et al. 2023; Zhai, Beaulieu, and Kudela 2024). Additionally, surface chlorophyll may not adequately reflect the full foraging environment for marine mammals, especially deep-diving species, because productivity varies with depth and stratification (van de Poll et al. 2013). It is therefore possible that the correlation between cold water and higher genetic diversity reflects a link to productivity that is not reflected by chlorophyll-a concentration.

It is also possible that elevated productivity is not driving the increased genetic diversity in colder waters. An alternative explanation can be found in a history of glacial extension and retreat in over the centuries, occurring mostly in colder waters (Polyak et al. 2010). Secondary contact between previously separated populations that have evolved in isolation can result in high genetic diversity in hybrid zones, while retaining elevated divergence between populations. This has been documented in some marine taxa like walrus and harbor seals (Ruiz-Puerta et al. 2023; Westlake and O’Corry-Crowe 2002). However, while these examples are also linked to elevated divergence between conspecific populations, our results show the opposite, a decrease in genetic divergence in regions with lower sea surface temperatures. This could indicate that contemporary processes may exert a stronger influence on population structure than glacial history on a global scale. Large population sizes in productive cold-water regions may result in range expansion, leading to greater overlap with conspecific populations and increased hybridization. This elevated level of gene flow between large populations might counteract the previously strong divergence between these populations. This process can overwhelm the historical signal of glacial population fragmentation. Meanwhile, smaller populations in warm, less productive waters may remain

smaller, more isolated and therefore diverge more rapidly through drift. Warmer waters can also be more heterogeneous than cooler waters at small scales (Brandão et al. 2021; Cao et al. 2025) and it is possible that our observation of increased differentiation is related to local specialization.

While our results do not allow us to distinguish between these different explanations, they do not have to be mutually exclusive. It is possible that correlations with water temperature in the absence of a correlation with chlorophyll concentration is explained by an interplay of admixture of historic refugia populations and elevated productivity of cold water that is not represented by the chlorophyll concentration measures as these explanations are not mutually exclusive.

Human impact

Humans are a major component of wildlife environments. Proximity to ports and human population centers often results in increased exposure to anthropogenic threats, such as vessel traffic, fisheries interactions, noise, and chemical pollution (Ewing et al. 2025; Maxwell et al. 2013; Tyack et al. 2022). Anthropogenic pressures reduce genetic diversity in many taxa, including terrestrial mammals (Schmidt et al. 2020) and marine fishes (Karachaliou et al. 2025). We therefore expected genetic diversity in marine mammals to decline with increasing human proximity and influence. However, none of our genetic diversity measures were strongly associated with distance to ports or with the cumulative human impact index.

The marine environment differs strongly from terrestrial landscapes in how it can be fragmented. Terrestrial fragmentation is dominated by more impermeable physical barriers, like roads and cities, which strongly restrict movement (Shepard et al. 2008; Underhill and Angold 2000). Marine mammals, by contrast, inhabit three-dimensional, continuous environments and their broad movement and seasonal migrations (Lockyer and Brown 1981) allows them to traverse areas that are degraded but not physically blocked. Although human

activities can disrupt marine habitats through noise pollution, chemical pollution, shipping lanes or local sea floor disturbances (Ewing et al. 2025; Maxwell et al. 2013; Tyack et al. 2022), these forms of environmental disruptions often create local and transient avoidance behavior rather than longer-term physical barriers and may not lead to broad-scale reduction in genetic diversity or increase in divergence as seen in terrestrial mammals. In this regard, marine mammals might mirror birds and their ability to fly more than terrestrial mammals, as birds, unlike terrestrial mammals, show the same lack of correlation between human impact and genetic diversity measures (Schmidt et al. 2020).

Finally, both distance to ports and global human impact index are variables that might not capture the specific pressures most relevant to population genetics. Chronic noise, pollution, prey depletion or direct persecution are localized disturbances that may affect different species to varying degrees and therefore might be obscured in a global data set containing multiple species and variables aggregating multiple stressors. Consequently, the proximity to human activities does not result in a net-positive or net-negative effect on their genetic diversity. This does not indicate that human activity does not have an impact on marine mammal genetic diversity; it only indicates that it is not directly driven by the immediate proximity of our sample sites to these animals.

Link to species richness

Environmental conditions such as temperature which shape population-level genetic diversity also influence species richness (Gillman and Wright 2014). This makes it important to examine how these two biodiversity metrics relate to each other. Studies in terrestrial animals on a continental scale (Schmidt, Dray, and Garroway 2022), demonstrate that hotspots of species richness tend to coincide with reduced within-species genetic diversity. This suggests that the processes allowing many species to coexist may also constrain population size within individual species. This does not necessarily require speciation itself to

be strongly linked to genetic differentiation between conspecific populations. Previous studies have already shown that speciation rate does not have to be linked to within-species differentiation (Rabosky and Matute 2013; Singhal et al. 2018, 2022). However, demographic and ecological mechanisms like niche partitioning or habitat fragmentation in species-rich environments can lead to smaller and more spatially structured populations. These conditions then increase drift and reduce within-population diversity. The negative correlation observed between marine mammal species richness and genetic diversity suggests that environments able to support a high number of marine mammal species might do this partly through ecological specialization and demographically smaller populations. At the same time, populations in species-poor systems may grow to larger sizes and maintain higher genetic diversity (Vellend and Geber 2005). This also explains the positive correlation we observe between species richness and population-specific F_{ST} . In regions with many coexisting species, populations diverge and differentiate more strongly from each other, driven by finer ecological structuring and niche-partitioning (Ehrlich et al. 2021; Wagner et al. 2017).

These patterns point towards a trade-off between local biodiversity measured by marine mammal species richness and genetic richness within populations in these regions. This has important management and conservation implications. Although species-rich areas are often prioritized because they support high community-level biodiversity, populations inhabiting these regions may possess reduced adaptive potential due to lower genetic diversity. Consequently, species-rich ecosystems may be less resilient to environmental changes than their taxonomic diversity alone would suggest. Conservation strategies in such regions should therefore emphasize strong species- and habitat-level protections to mitigate additional stressors and prevent further reduction of genetic diversity, while explicitly incorporating genetic indicators alongside species richness in conservation planning.

Conclusion

Marine mammal population genetics are shaped by a complex interaction between environmental conditions, evolutionary processes and human influences. Our results show that colder waters and areas with low marine mammal species richness contain genetically rich and interconnected populations. Meanwhile, species rich and warmer waters tend to facilitate population divergence at the cost of within-population genetic diversity. This has significant consequences for conservation efforts. While in cold waters and areas with low species richness, it is important to maintain connectivity between populations, in warmer and species-rich regions, conservation efforts should prioritize the protection of the existing populations and prevent further fragmentation, as the already existing populations are limited in genetic diversity. As climate change alters marine ecosystems further, integrating population genetic measures into management frameworks will be critical to maintain the long-term evolutionary resilience of marine mammal populations.

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Statements and declarations

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The authors have no relevant competing interests to disclose.

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Author contributions

Claudio Müller: Conceptualization, methodology, analysis, writing – original draft & editing. Chloé Schmidt: Methodology, writing – editing. Eleana Karachaliou: Methodology, writing – editing. Evelien de Greef: Methodology, writing – editing. Stephen D. Petersen: Writing – editing. Steven H. Ferguson: Writing – editing. Colin J. Garroway: Conceptualization, methodology, analysis, writing – editing.

Tables & Figures

Table 2.1: Model results for all variables. The Diversity Variable and Environmental Variable columns show which variables were tested against each other. The MEMs column shows the number of significant MEMs that were used as variables in the model. Mean, lowerCI95 and upperCI95 show the mean and the 95% credible interval results from the model. P-direction shows the probability that the tested diversity variable is strictly positively or negatively correlated (direction depending on the mean value) with the test environmental variable. The null models do not have any coefficient estimates or p_directions, instead they only show how much of the models is explained by the MEMs included in the models.

Diversity variable	Environmental variable	MEMs	mean	lowerCI95	upperCI95	p_direction	bayes_R2	WAIC
Allelic Richness	null model	8	-	-	-	-	0.7777	367.1
Allelic Richness	chlorophyll mean	8	0.06	-0.07	0.19	0.8387	0.7862	370.4
Allelic Richness	mean temperature	8	-0.25	-0.49	0.00	0.9760	0.8079	344.7
Allelic Richness	salinity range	8	-0.12	-0.62	0.44	0.7274	0.7884	378.9
Allelic Richness	distance market	8	-0.02	-0.18	0.11	0.6438	0.7808	369.8
Allelic Richness	human impact	8	0.10	-0.08	0.28	0.8763	0.8285	325.6
Allelic Richness	Species Richness	8	-0.16	-0.33	0.01	0.9703	0.8190	335.5
Gene Diversity	null model	6	-	-	-	-	0.7390	415.3
Gene Diversity	chlorophyll mean	6	-0.02	-0.16	0.12	0.6188	0.7481	424.9
Gene Diversity	mean temperature	6	-0.23	-0.43	-0.03	0.9859	0.7529	410.8
Gene Diversity	salinity range	6	-0.20	-0.85	0.52	0.7350	0.7742	405.9
Gene Diversity	distance market	6	0.00	-0.13	0.13	0.5393	0.7427	417.3
Gene Diversity	human impact	6	0.12	-0.07	0.31	0.9054	0.7979	372.1
Gene Diversity	Species Richness	6	-0.21	-0.40	-0.02	0.9858	0.8006	369.1
global Fst	null model	0	-	-	-	-	0.1737	669.5
global Fst	chlorophyll mean	0	-0.01	-0.21	0.19	0.5264	0.2201	681.5
global Fst	mean temperature	0	0.19	-0.02	0.43	0.9627	0.2030	666.3
global Fst	salinity range	0	0.32	-0.60	1.29	0.7598	0.2695	690.0
global Fst	distance market	0	-0.12	-0.41	0.11	0.8430	0.2014	671.9
global Fst	human impact	0	-0.14	-0.36	0.08	0.8938	0.2967	647.9
global Fst	Species Richness	0	0.26	0.03	0.49	0.9858	0.3315	662.4

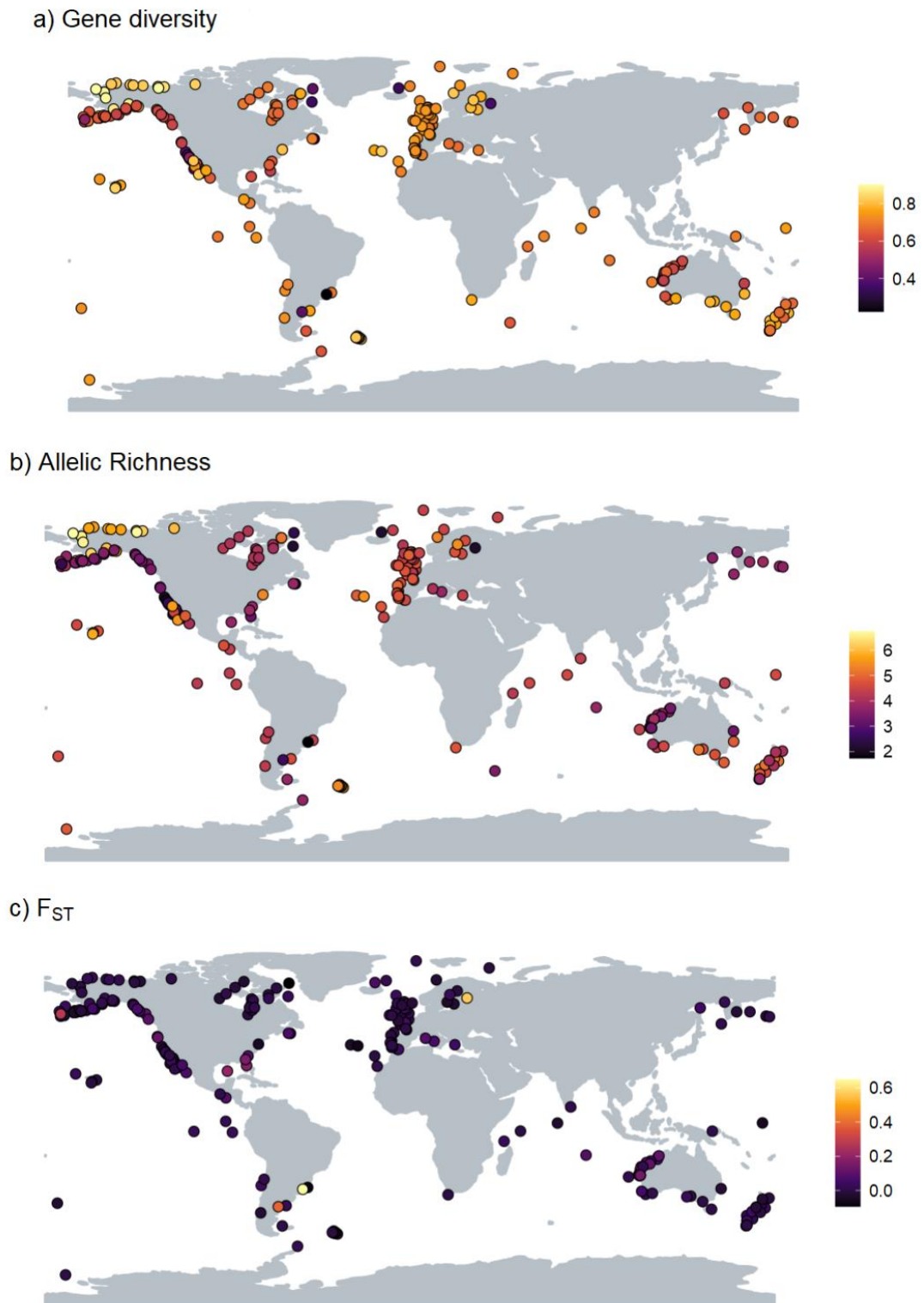


Figure 2.1: Global maps of the raw genetic diversity variables: a) Gene diversity, b) allelic richness and c) population specific F_{ST} of all 244 sampling sites of marine mammal species.

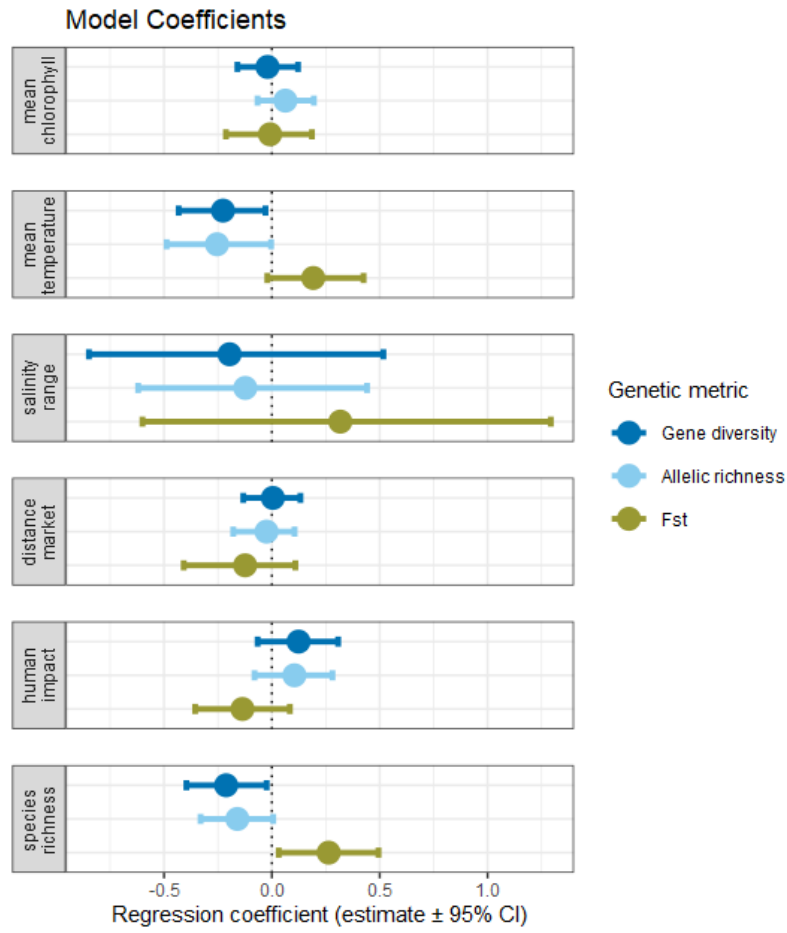


Figure 2.2: Results of generalised linear mixed effects models of marine mammal species. Shows the correlation between gene diversity (GD), allelic richness (AR), and population-specific F_{ST} and environmental variables. Each box represents one of the independent variables we tested. The colors represent the genetic variables. The x-axis shows the resulting coefficient of the model for the corresponding variable. The circles show the mean of each coefficient. The line shows the 95% confidence interval.

CHAPTER 3: EXPLORING CONTEMPORARY AND HISTORIC EFFECTIVE POPULATION SIZES IN ATLANTIC BELUGA WHALE POPULATIONS

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Running head: Beluga effective population size

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Abstract

Maintaining the adaptive capacity of wildlife populations facing rapid environmental change requires understanding the processes that erode genetic diversity. Effective population size governs the rate at which genetic diversity is lost to drift and the efficiency of natural selection, making it an important metric for assessing long-term population viability. Here, we use whole-genome resequencing of 140 beluga whales (*Delphinapterus leucas*) sampled across their eastern Canadian range to reconstruct demographic histories spanning one million years and estimate contemporary effective population sizes across six genetically distinct populations. Effective population size trajectories were shared until approximately 50,000 years ago, after which they began to separate in association with glacial dynamics and post-glacial colonization. These historical processes are reflected in contemporary genomic patterns, including pronounced variation in inbreeding, with the St. Lawrence Estuary population showing extensive runs of homozygosity consistent with long-term isolation that predates recent exploitation. Over the past millennium, population trajectories diverged further, with some populations increasing and others declining, in part reflecting known harvest histories. Contemporary effective population sizes exceed 2,000 in only two populations and fall below 400 in all others. Notably, populations with large census sizes sometimes exhibited low effective population sizes, indicating that apparent demographic stability may obscure reduced adaptive capacity. Our results demonstrate that beluga populations differ substantially in their evolutionary histories and current genetic health, such that whole species-level conservation and management may overlook important variation in vulnerability to future environmental change.

Introduction

Climate warming has altered species' abundances and distributions globally (Díaz et al. 2019; Pörtner, Roberts, and Tignor 2023; Scheffers et al. 2016). Some species have responded to warming through combinations of tracking climatic niches, phenotypic plasticity, and adaptive evolution (Chen et al., 2011; Hoffmann and Sgrò, 2011; Urban et al., 2024). In contrast, many other species face habitat loss, associated population declines, and increased extinction risk (Macleán and Wilson, 2011; Urban et al., 2024; Urban, 2015). In general, this reorganization of biodiversity is substantially altering the ecosystems that sustain wild species and people (Díaz et al. 2018). In the Arctic, the rate of warming is approximately four times the global mean (Rantanen et al. 2022). The threats to Arctic ecosystems associated with rapid warming are compounded by the high degree of specialization of Arctic species on disappearing features of Arctic environments (e.g., sea ice) and increases in industrial development due to growing access to the region (Laidre et al. 2015). Information on the current ecological and evolutionary status of wild populations is necessary to assess the risks posed by warming and understand the possible consequences of future change, especially in highly sensitive ecosystems (Rivkin et al. 2025).

A central goal of conservation and management is to maintain the adaptive capacity of wild populations (Armitage and Plummer 2010; Mcleod et al. 2016). Spatial patterns of genome-wide diversity and the rates at which diversity is lost within populations underlie the microevolutionary processes that shape population mean fitness and resilience to environmental change (Lande and Shannon 1996). All populations lose genetic diversity due to random genetic drift (Li and Graur 1991). The evolutionary concept of effective population size (N_e) estimates the strength of genetic drift and the consequent rate of loss of genetic diversity within a population (Wang, Santiago, and Caballero 2016; Waples 2022, 2025). Additionally, the strength of genetic drift is inversely proportional to the efficiency of natural selection (Charlesworth 2009; Kimura 1983; Ohta 1992). As effective population sizes

decline, the random process of genetic drift can increasingly overwhelm the deterministic process of natural selection. Knowledge of past and present trends in effective population sizes is thus important for prioritizing conservation and management decisions in light of future environmental change.

Beluga whales (*Delphinapterus leucas*) are a vital part of the Arctic food web (Heide-Jørgensen and Teilmann 1994; Kelley et al. 2010; Seaman, Lowry, and Frost 1982; Vachon et al. 2026) and have been identified as an indicator species of environmental change (Wagemann et al. 1995). Belugas also hold cultural importance for northern Indigenous communities, who rely on them for food, materials, and cultural practices (Hoover et al. 2013; Tyrrell 2008). In some regions, they are also important for tourism (Dressler, Fikret, and Mathia 2001), which supports local economies (e.g., Churchill; The Churchill Beluga Whale Tour Operators Association et al., 2015). However, recent centuries have seen a decrease in the number of beluga whales in some regions, driven in most cases by commercial whaling (Harwood, Kingsley, and Smith 2014; Mitchell and Reeves 1981; Reeves and Mitchell 1984; Rugh, Shelden, and Hobbs 2010; Tinker et al. 2024; Watt et al. 2021). While Indigenous communities have hunted beluga whales for millennia, large-scale commercial whaling by European settlers began in eastern Canadian waters in the early 16th century (Loewen 2009; Tuck and Grenier 1981). Commercial beluga whaling peaked in the 19th century (Bockstoe 1986; Reeves and Mitchell 1984) and continued until bans of commercial hunting in 1972 (DFO 1981; International Whaling Commission 1982) and a subsequent complete hunting moratorium in the St. Lawrence Estuary in 1979 (Reeves and Mitchell 1984). An example of the scale of harvest is provided by Stewart (2018), who estimated that at least 14,079 beluga whales were commercially harvested from Cumberland Sound alone between 1860 and 1966. These numbers are likely underestimates because they do not account for whales that were killed but not recovered. Indigenous harvests during this time are not well-documented;

however, commercial harvests in some years were more than 15 times larger than current subsistence catches (Stewart 2018).

The genetic consequences of commercial whaling have been observed in bowhead whales (*Balaena mysticetus*), another endemic Arctic species, demonstrating that overexploitation can reduce genetic diversity (De Greef et al. 2024). Today, only Indigenous communities are permitted to hunt belugas (Meehan et al. 2017), but the small size of some populations may lead to unsustainable harvests (Van de Walle, Tinker, and Sauvé 2025). Beyond hunting, these animals face increasing threats from climate change. Heavily reliant on sea ice to protect them from killer whales (*Orcinus orca*), belugas face heightened predation risk as sea ice melts with rising temperatures (Breed et al. 2017; Ferguson, Higdon, and Chmelnitsky 2010; Higdon, Hauser, and Ferguson 2012; Stafford 2019). Changes in beluga aggregation behaviours have been directly linked to rising sea surface temperatures, leading to fewer whales in warming waters (Rivas, Guirado, and Ortega 2024). Predictive models suggest a northward shift in beluga habitat and a reduction in the range of Arctic whales in general (Chambault et al. 2022; De Greef et al. 2025). This is thought to be related to increases in water temperature and reductions in sea ice (Williams et al. 2021).

Beluga whales in Canada are divided into eight stocks for management purposes. These stocks are based on summering aggregations due in large part to individual beluga whales' high site fidelity to summer locations across years (Finley 1982). These summer areas include shallow coastal estuaries and bays that may offer abundant food (Seaman et al. 1982), warmer waters that facilitate skin moulting (St.Aubin, Smith, and Geraci 2011), and protection from predators during calf birth and nursing (Fraker et al. 1979; Sergeant 2011; Sergeant and Brodie 2011). Seven beluga stocks occur in eastern Canada, and one resides in the western Canadian Arctic in the Eastern Beaufort Sea (COSEWIC 2020) (Figure 1).

The most threatened beluga stocks are Eastern Hudson Bay, Cumberland Sound, Ungava Bay, and St. Lawrence Estuary (COSEWIC 2020; Lesage et al. 2024). The latter three stocks

have been listed as endangered by the Committee on the Status of Wildlife in Canada (COSEWIC) and are now under special management. Several recent aerial surveys of the Ungava Bay stock found no or only a few tens of beluga whales in the region, raising questions about the stock's persistence (Sauvé et al. 2024). It is unclear whether individuals sampled in that region today represent a small remnant of the original stock or consist of individuals that have moved into the region from Hudson Bay and use the area for migration (COSEWIC 2020). Hunting quotas for Eastern Hudson Bay and Cumberland Sound beluga are in place to ensure sustainability and reduce further decline (DFO 2024; Stewart and Lockhart 2005).

The St. Lawrence Estuary stock is of particular interest because it is geographically disjunct south of the Arctic (Brown Gladden, Ferguson, and Clayton 1997), having diverged from other beluga populations after the end of the last ice age (Harington, 1977). The St. Lawrence Estuary stock was subject to substantial hunting and eradication programs following the European colonization of the region (Reeves and Mitchell 1984; Vladykov 1944). Belugas were hunted for their fat, skin, and oil, and in the St. Lawrence Estuary, they were also killed because they were seen as competing with fishermen for fish (Pippard and Malcolm, 1978). Due to large population declines, the hunting of belugas in the St. Lawrence Estuary has been prohibited since 1979 (Kingsley 2002; Reeves and Mitchell 1984).

Despite evidence of demographic stabilization in some of these endangered populations, there is little indication of recovery to previous carrying capacities, and projections suggest further declines (Tinker et al. 2024; Van de Walle et al. 2025; Watt et al. 2021). Generally, beluga population trends are difficult to assess directly because of their remote locations, the considerable time belugas spend underwater and under dense sea ice, and their clumped distribution (St-Pierre et al. 2024).

Most beluga whale populations migrate in the fall and spring (Figure 1). Belugas mate in late winter and early spring while travelling to their summer habitat (O’Corry-Crowe et al.

1997, 2018), which may facilitate gene flow between stocks even when their summer habitats are geographically isolated. Studies using mitochondrial DNA and microsatellites have documented genetic divergence between stocks, maternal site fidelity, and natal philopatry (Brown Gladden et al. 1997; Gladden et al. 1999; Skovrind et al. 2021; Turgeon et al. 2012). A recent whole-genome-scale study identified six genetic beluga whale populations in eastern Canada, located in the Eastern High Arctic-Baffin Bay, Cumberland Sound, Hudson Bay-Strait Complex, Little and Great Whale Rivers, James Bay, and St. Lawrence Estuary (Montana et al. 2024). Contemporary and recent changes in effective population size in these populations have not yet been examined.

To better understand threats to genetic diversity and the adaptive capacity of beluga whales, we used whole genome data from beluga whales sampled across eastern Canada to explore their demographic histories and contemporary effective population sizes. After determining the underlying population structure of our samples, we reconstructed changes in effective population size (N_e) for each population in the deep past (up to 1,000,000 years) and the recent past (up to 3,000 years). Finally, we estimated the contemporary N_e within the context of demographic histories and the future capacity for adaptive change.

Methods

Tissue collection, extraction & sequencing

We used samples from 15 locations spanning seven of the eight Canadian beluga stocks (Table S1): St. Lawrence Estuary, Ungava Bay, Eastern Hudson Bay, Western Hudson Bay, James Bay, Cumberland Sound, and Eastern High Arctic-Baffin Bay (Figure 1). Skin was collected from beluga whales harvested by Indigenous subsistence hunters between 1990 and

2020 (n = 116), or from beluga carcasses found on the beach in the St. Lawrence Estuary (n = 29) or the Strait of Belle Isle (n = 1). DNA from 78 individuals (sampled from Eastern High Arctic-Baffin Bay, Cumberland Sound, Iqaluit, Western Hudson Bay, Sanikiluaq, and St. Lawrence Estuary) was extracted using the Qiagen DNeasy Blood & Tissue kit with the tissue extraction protocol. Samples were sequenced on an Illumina NovaSeq to obtain whole-genome paired-end reads at a target coverage of 10x. The data are available under BioProject ID PRJNA1182041 (De Greef et al. 2025). Data for 68 individuals (sampled from Eastern Hudson Bay, James Bay, Ungava Bay, and named locations within the St. Lawrence Estuary (Table S2)) were obtained from BioProject ID PRJNA984210 (Montana et al. 2024).

Alignment, variant calling & baseline SNP filtering

We trimmed the raw sequences using *Trimmomatic* v0.36 (Bolger, Lohse, and Usadel 2014) and aligned them to the reference genome assembly GCA_029941455.3 (Bringloe and Parent 2023) using Bowtie2 v2.5.2 (Langmead and Salzberg 2012). We removed duplicate reads and added read group information using *Picard* v2.20.6 (Broad Institute 2019). Many methods used in this study are sensitive to the coverage of the genetic data. Given our wide variation in coverage (Table S1), we created two variant call format (vcf) files: one containing only high-coverage individuals (coverage $\geq 10x$) and the other containing all individuals, with down-sampled coverage for the high-coverage individuals. To down-sample high coverage individuals, we used *GATKv4.1.2* (McKenna et al. 2010) to a target modal coverage of 6x (Table S1). Genomic variants were called using *Platypus* v0.8.1 (Rimmer et al. 2014). We then used *vcftools* v1.16 (Danecek et al. 2011) and *bcftools* v1.19 (Danecek et al. 2021) to filter out indels, sites without the PASS flag, low quality sites (QUAL < 50), sites with missingness > 0.25, non-biallelic sites and scaffolds shorter than 100kbp, as well as scaffolds aligned with the sex chromosome to obtain only high-quality autosomal Single Nucleotide Polymorphisms (SNPs).

Then, we used PLINK v1.9 (Purcell et al. 2007) to assess kinship and remove the individual with the higher rate of missing data from pairs with $\pi\text{-hat} > 0.4$ to reduce bias from first-degree relatives in analyses. We also removed samples with more than 30% overall missing data. After these filtering steps, 140 samples remained in our final data set and 68 in our high-coverage data set (Table S3). All further analyses will have these filters applied before the analysis-specific filters described in the corresponding method section.

Population structure & runs of homozygosity

Population structure analyses do not require high-coverage data; therefore, we used all individuals, not only those with high coverage, to assess population structure. To estimate genetic population structure, we used SNPs that are not under putative selection and are not strongly linked. We filtered sites for Hardy-Weinberg disequilibrium (heterozygous frequency threshold > 0.6) and low minor allele frequency (< 0.05), then pruned the data set using *vcftools* v1.16 with a minimum distance of 1,000 bp between sites (Table S4). This yielded 1,081,765 SNPs for our population-structure assessments.

We conducted PCAs using the r-package *adeigenet* v2.1.10 (Jombart 2008; Jombart and Ahmed 2011) to examine population structure. We also estimated population structure with admixture analyses with K values 2 through 7, representing the number of ancestral populations, using the *snmf* function from the r-package *LEA* v3.3.2 (Frichot and François 2015). We used *vcftools* v1.16 (Danecek et al. 2011) to estimate pairwise genetic differentiation (F_{ST}) between the identified genetic populations.

Finally, we estimated runs of homozygosity (ROH) as a measure of inbreeding. The greater the number of long homozygous segments in the genome of diploid individuals, the more likely we expect a close relationship between the ancestors that contributed to these regions on the chromosome. Therefore, a greater proportion of ROHs is indicative of a higher degree of inbreeding (Ceballos et al. 2018). To estimate ROHs, we used *PLINK* (Purcell et al.

2007) with a sliding window size of 300kb, requiring at least 50 SNPs and a minimum density of 1 SNP/50kb to define a ROH, and allowing up to 3 heterozygote sites per window. A gap of 1000kb between two SNPs was required for them to be considered in two different ROHs. These parameters were chosen to achieve results comparable to similar studies done with other Arctic whale species (De Greef et al. 2024). Low-coverage data can result in an underestimation of ROHs due to inaccurate variant calling (Taylor, Manseau, and Wilson 2026). We therefore conducted this analysis twice, once using all individuals with down-sampled coverage for high-coverage individuals, and a second time using only high-coverage individuals, to assess the impact of low coverage in our complete data set on these estimates. ROHs also allowed us to estimate an inbreeding coefficient based on ROH (F_{ROH}), calculated as the sum of the lengths of all ROHs divided by the total genome length. This represents the proportion of the genome composed of ROHs. The higher the proportion of the genome that is made up of ROHs, the more of the genome is identical by descent from a common ancestor (McQuillan et al. 2008). We separated all ROHs into four size classes: ROHs shorter than 1 megabase pair (Mb), ROHs between 1 and 5 Mb in length, ROHs between 5 and 10 Mb, and ROHs longer than 10 Mb. Longer ROHs are the result of more recent inbreeding, while short ROHs represent inbreeding further in the past (Pemberton et al. 2012).

Demographic history & contemporary effective population size

Demographic history and effective population size estimates are influenced by coverage levels of the genetic data (Fumagalli 2013; Han, Sinsheimer, and Novembre 2014). Therefore, all analyses in this section were conducted twice, using all individuals with down-sampled coverage as the primary analysis and using only high-coverage individuals as a secondary comparison. Results from the down-sampled analyses are reported in the main text; high-coverage results are provided in supplementary figures and referenced in the text where relevant, though the small number of high-coverage individuals available for most

populations limits inferences from those analyses. For all analyses of N_e , we filtered SNPs to exclude unplaced scaffolds not assigned to a chromosome in the reference genome and sites out of Hardy-Weinberg equilibrium (heterozygote frequency threshold > 0.6 ; Table S5).

To reconstruct changes in N_e over time, we examined models that estimate historic N_e in deep time (over thousands of generations) and in recent history (within the last 100 generations). To estimate deep-time demographic history, we used the coalescent-based method SMC++ (Terhorst, Kamm, and Song 2017). This method allows reconstruction of deep-time demographic history from low-coverage, unphased sequences. To distinguish long runs of homozygosity from missing data, we used *bedops* (Neph et al. 2012) to generate a masked file for inclusion in the SMC++ model. We ran SMC++ for each genetically distinct population. We randomly selected an individual from each population to represent each lineage (Table S2). For SMC++, we set the regularization penalty to 4.0, the non-segregating site cut-off to 100,000, used a thinning of 2,000, and set the timepoints from 10 to 1,000,000 generations. The mutation rate per generation for belugas was set at 1.65×10^{-8} (Westbury et al. 2019). We multiplied the resulting generation numbers by a generation time of 28 years/generation (Lowry, Hobbs, and O’Corry-Crowe 2019) to convert generations into years.

To estimate N_e over the last 100 generations, we used a linkage disequilibrium (LD) based method implemented in the software package *GONE2* (Santiago, Köpke, and Caballero 2025). To get a confidence interval estimate, we ran 50 iterations to get a mean estimate and a 95% confidence interval for each generation. We used *PLINK* (Purcell et al. 2007) to randomly subsample 1,000,000 SNPs 50 times for the error estimation data iterations. For the down-sampled dataset, we conducted the *GONE2* analyses using the `-g 3` flag, which explicitly accounts for low sequencing coverage in linkage disequilibrium estimation (Santiago, Köpke, and Caballero 2025). We conducted parallel analyses using only high-coverage individuals with default settings for validation. Because the down-sampled dataset includes substantially more individuals per population, and *GONE2* accuracy scales with

sample size, the down-sampled analyses are the primary reconstruction for this method. The conversion from generations to years was repeated by multiplying by 28 years/generation.

Finally, to estimate contemporary N_e , we used the LDNe estimator from the R-package *strataG* (Archer, Adams, and Schneiders 2017; Waples and Do 2008). To prepare the SNP dataset for this analysis, we created a VCF file per population containing only individuals from that population. We filtered for biallelic sites and removed all sites with missing data. We used a minor allele frequency cut-off of 0.05 to avoid overestimating N_e due to rare alleles in populations with small sample sizes. We then randomly subsampled 10K SNPs with *PLINK* (Purcell et al. 2007) 10 times to run multiple iterations of the LDNe estimator, then averaged the resulting N_e estimates. Estimates of N_e are sensitive to underlying population structure, the presence of outlier individuals in a sample, and the inclusion of close kin (Macbeth et al. 2013; Novo et al. 2023; Wang 2005). Thus, we estimated contemporary N_e for each genetically distinct population separately. Additionally, for populations with strongly admixed individuals, we ran separate estimates, including and excluding them, to better understand how these factors may affect results. We defined strongly "admixed" individuals as those that did not clearly fall into any cluster according to PC1 and PC2 in our PCA (Figure 2a). Given that all St. Lawrence Estuary belugas were at least second-degree kin, we also estimated N_e for the St. Lawrence Estuary population using a subset of the 10 least related individuals. This was done to create an estimate less affected by the presence of close kin, without reducing the sample size to the point that the results become meaningless.

As with all wildlife genomic datasets, sources of potential bias warrant acknowledgment. Our samples include individuals from different, overlapping generations, and differences in sampling methods (e.g., subsistence harvest versus carcasses from shore) could influence the results of our analyses if these sources systematically differ in their genetic composition. These considerations are discussed in detail in Waples 2025.

Results

Population Structure

We identified six distinct genetic populations using PCA and admixture analyses (Figure 2). The St. Lawrence Estuary population consisted solely of belugas sampled from this region. The remaining individuals clustered into three large groups along PC2 (Figure 2a). PC2 and PC3, as well as admixture analyses with $K=3$ and $K=4$, separated the James Bay and Eastern High Arctic populations from all other individuals (Figures 2a & c, Figure S.1). The James Bay population comprised individuals from James Bay, except those from Bear Island at the northern edge of the bay. It also included five individuals from Kuujjuarapik in Eastern Hudson Bay and Sanikiluaq in the Belcher Islands (Figure S2). The Eastern High Arctic-Baffin Bay cluster comprised individuals sampled in the Eastern High Arctic-Baffin Bay and one individual sampled in Cumberland Sound. One remaining individual sampled in Cumberland Sound was admixed, showing shared ancestry with the Eastern High Arctic-Baffin Bay population and the third cluster, which comprised individuals from several stocks and sampling locations. Specifically, this included all individuals from Western Hudson Bay, Iqaluit and Ungava Bay; the one individual from the Strait of Belle Isle in the eastern Gulf of St. Lawrence; most individuals from Cumberland Sound and Eastern Hudson Bay and Sanikiluaq; and all individuals from Bear Island in northern James Bay (Figure S2). Using PCA on the 84 individuals from this third cluster (Figure 2b) and $K=5$ and $K=6$ admixture analyses, we identified three additional populations. The Cumberland Sound population comprised individuals sampled from Cumberland Sound and one individual from Iqaluit. The Hudson Bay-Strait Complex population comprised all individuals from Western Hudson Bay, Ungava Bay and Bear Island; nine of the ten individuals sampled near Iqaluit (Baffin Island); most belugas harvested in Eastern Hudson Bay and the Belcher Islands; and the one beluga from the Strait of Belle Isle (Figure 2b). The Little and Great Whale Rivers population

(named following Montana et al. 2024) comprised individuals sampled in Eastern Hudson Bay, specifically from the Little Whale River and around Kuujjuarapik at the mouth of the Great Whale River. It also included three individuals from Eastern Hudson Bay for which we had no specific sampling location. Ancestral admixture at $K=7$ did not yield further population distinction and instead showed admixture within the Hudson Bay-Strait Complex population (Figure S3). While fine structure has been documented in the Hudson Bay-Strait Complex in other studies (Parent et al. 2023), our dataset does not distinguish subgroups within this population, which may be due to sample size. Since demographic history and effective population size analyses rely on distinct populations, we treated this complex as a single genetic population.

The St. Lawrence Estuary population was the most distinct, with F_{ST} values > 0.08 relative to all other populations (the highest F_{ST} of 0.12 was between St. Lawrence Estuary and the Eastern High Arctic-Baffin Bay) (Table 1). The Eastern High Arctic-Baffin Bay and James Bay populations had intermediate F_{ST} values compared with the other Arctic populations. The Cumberland Sound, Little and Great Whale Rivers populations, as well as belugas from the wider Hudson Bay-Strait Complex, had the lowest F_{ST} values, indicating less divergence than in the other populations (F_{ST} range: 0.0083 - 0.0109; Table 1). The St. Lawrence Estuary population was the most inbred, with the sum of all ROHs per individual averaging at over 550 Mb; all other populations had a mean ROH of ~ 200 Mb (Figure 3). Using only high-coverage sequences does not change the overall pattern of elevated ROH in the St. Lawrence Estuary population (Figure S4); however, ROHs are increased by ~ 90 Mb compared to low-coverage sequences (Figure S5, Table S6). The longer average sum of all ROHs in the St. Lawrence Estuary population also results in a higher F_{ROH} for St. Lawrence individuals, for both down-sampled (Figure 4, Table 2) and high-coverage samples (Figure S6, Table S7). In the St. Lawrence Estuary, 24% of the genome consists of ROHs, whereas in all other populations this value ranges from 7% to 10%. Across all populations, the majority

of ROHs are shorter than 1 Mb. This category accounts for 16% of the St. Lawrence genome and between 7% and 5% across all other populations. The St. Lawrence population has more ROHs between 1 Mb and 5 Mb long, accounting for 6.6% of the genome, while in all other populations this category accounts for between 2% and 2.3% of the genome. The Little and Great Whale River and the James Bay populations have no ROHs longer than 10 Mb when using the down-sampled data. Only when using the two high-coverage individuals with their original coverage do we find 2% of the genome consisting of ROHs in that length category.

Effective Population Size & Demographic History

Our SMC++ results showed synchronous N_e trajectories across all populations until the middle of the last glacial period, some 50,000 years ago (Figure 5), with a slight mismatch between the James Bay population and the Little and Great Whale River populations, on the one hand, and the remaining four populations, on the other. When only high-coverage individuals are used for the James Bay population (no high-coverage individuals are available for the Little and Great Whale River populations), this mismatch disappears (Figure S7). Around the 50,000-year mark, we observed a decline in N_e for the St. Lawrence Estuary. The remaining populations stayed on the same trajectory for an additional 20,000 to 30,000 years, after which they began to diverge. This divergence coincided with increases in N_e for the Hudson Bay and Strait Complex population and for the Cumberland Sound population in the high-coverage secondary analysis (Figure S7). In contrast, the Eastern High Arctic-Baffin Bay, Cumberland Sound, James Bay, and Little and Great Whale River populations began to decline, with the Cumberland Sound population showing a less pronounced decline than the others. The St. Lawrence Estuary population stabilized around 10,000 years ago, after a steep decline during the last glacial period. It even started increasing slightly again afterwards; however, this increase appears only in the low-coverage data set, whereas the analysis using

only high-coverage individuals does not show such an increase around 10,000 years ago (Figure S7).

To reconstruct demographic changes over the past 3,000 years, we used *GONE2*, which provides higher resolution in the recent past than *SMC++*, whose estimates become increasingly uncertain as they approach the present (Terhorst, Kamm, and Song 2017). Some discrepancy between terminal *SMC++* estimates and initial *GONE2* estimates is expected, given this difference in resolution, and is not interpreted as a biological signal. Within this time frame, demographic trajectories differed substantially among the six populations (Figure 6; Figure S8).

We observed an increase in effective population size across three populations over the past 500-1,000 years. The Eastern High Arctic-Baffin Bay population shows a post-glacial decline according to *SMC++*, but *GONE2* estimates a higher starting effective population size that declines and then recovers (Figure 6). The Hudson Bay-Strait Complex shows the largest increase among populations, reaching its highest effective population size over the last 400 years. The last population to show an increase over the past 100 generations is the St. Lawrence population, which declines to very low numbers after the last glacial period, before increasing rapidly again. While this increase mirrors the Eastern High Arctic population when using all individuals, it is much steeper and more pronounced when considering only high-coverage individuals.

The remaining three populations all show a pattern of decline over the past 100 generations. The N_e for the Cumberland Sound, the Little and Great Whale River, and the James Bay populations decreased until 100-200 years ago, when they reached their lowest point and have remained there. While these declines appear somewhat gradual, the Cumberland Sound and Little Whale River populations show a more pronounced decline around 100 years ago, towards the end of the commercial hunting period.

The estimates for the contemporary N_e suggest that the Eastern High Arctic-Baffin Bay and Hudson Bay-Strait Complex populations have the highest contemporary N_e values, at 2,666 and 3,839, respectively (Table 3). The remaining northern populations all had N_e estimates below 400. The lowest estimate of all populations is found in the St. Lawrence Estuary population, at $N_e = 81$. However, the estimate in that population only reaches such low values if we analyze a low-kinship subset. Using all individuals from the St. Lawrence Estuary, we get much higher estimates, 820 with and 2,430 without admixed individuals.

Discussion

We assessed the demographic history of beluga whale populations in a rapidly warming environment. Our results illustrate a pattern likely common to many wide-ranging species with distinct regional populations. The forces shaping genetic diversity, including glacial history, post-colonial exploitation, gene flow, and drift, have acted differently across the species' range, producing populations that differ in their current genetic health and capacity to respond to future change. Many of the identified populations have lower effective population sizes than they had 2,500 years ago. The effective population sizes of the larger populations (Eastern High Arctic-Baffin Bay and Hudson Bay-Strait Complex) have increased in recent history. Contemporary N_e estimates were small, in the hundreds or below, for all populations except the two with the largest surveyed abundances, which had values above 2,000. The St. Lawrence Estuary population N_e estimate varied depending on which individuals were included in the analysis, ranging from 80 to over 2,000, reflecting sensitivity to sample composition in this highly inbred population. This population also shows a much higher representation of runs of homozygosity, with large proportions of runs falling into the shorter-length categories, indicating substantial long-term inbreeding.

Population dynamics and deep time demographic history

We documented six genetically distinct populations, consistent with the findings of Montana et al. (2024), who used a more spatially resolved dataset. Given the consensus on population structure, we based our demographic analyses on these well-defined genetic populations. Our reconstruction of long-term demographic change suggests that the ancestors of current populations shared a demographic history until approximately 50,000 years ago, near the middle of the last glacial period. Although the Little and Great Whale Rivers and James Bay populations show a slight offset, their trajectories broadly mirror those of the other populations. This mismatch also disappears when conducting the analysis of the James Bay population using only high coverage data (Figure S9). This indicates that the mismatch is caused by the difference in coverage rather than it representing any real discrepancy between the demographic history of these populations.

The divergence of demographic trajectories among populations around 50,000 years ago suggests that the current beluga population's demographics began to diverge during the second half of the last glacial period, with the St. Lawrence Estuary population diverging first. This is consistent with the hypothesis that the St. Lawrence Estuary population was separated from the Northern Beluga populations as glaciers began to retreat, opening new habitats for marine mammal populations (Harington, 1977). Since the retreat of the glaciers began in the south, the St. Lawrence Estuary population would have been the first to establish itself as a distinct population, followed by the divergence of populations that later colonized the Arctic.

The sharp decrease in N_e observed for St. Lawrence Estuary belugas might be attributable to this population colonizing the Gulf of St. Lawrence as the area opened up with the retreat of glaciers (Occhietti et al. 2001). This area increased in size as the Champlain Sea, an inland sea connected to the Atlantic Ocean, covered most of the St. Lawrence lowlands between 13,000 and 10,000 years ago. A beluga whale fossil, dated to $10,700 \pm 90$ years, has been discovered in the Champlain Sea (Harington et al. 2006). The extent of the beluga habitat

grew between 15,000 and 10,000 years ago. It was much larger than it is today, potentially offering this population a new favourable habitat that allowed it to expand in numbers during the warmer post-glacial period, potentially explaining the increase we see after the glacial period (Figure 6). Despite expectations that recent commercial hunting would be the primary driver of elevated inbreeding in this population, the predominance of short ROHs indicates that the bottleneck responsible predates whaling, most likely resulting from post-glacial isolation in the Champlain Sea and subsequent recovery. The well-reported high inbreeding in this population is therefore not solely the result of recent hunting but instead at least partially attributable to a post-divergence bottleneck.

The onset of demographic divergence between populations after the last glacial period also marks a decrease in effective population size for all populations except the Hudson Bay-Strait Complex (Figure 5) and Cumberland Sound, when analyzed using only high-coverage individuals (Figure S9). The decline in N_e across most populations likely resulted from the splitting of one large population into multiple smaller ones. The N_e of the Eastern High Arctic-Baffin Bay, James Bay and Little and Great Whale Rivers populations continued to decline gradually after the last glacial maximum.

Recent demographic history patterns

One significant threat to belugas in recent centuries has been human hunting associated with commercial whaling in the post-colonial era, beginning in the early 16th century. While early commercial whaling did not often target belugas and was primarily focused on bowhead and right whales (Loewen 2009), belugas were intensively harvested in some regions. Commercial beluga whale harvests in Cumberland Sound, the Little and Great Whale rivers in Eastern Hudson Bay, and in the St. Lawrence Estuary resulted in intense exploitation of these populations (Béland 1996; Mitchell and Reeves 1981). We therefore expected to see a substantial decline in the N_e of these populations, coinciding with commercial whaling

activities. However, our reconstruction does not provide such clear results. While all of these populations show a decrease in effective population size over the last 1,000 years, it appears this decline began before the onset of commercial whaling. The mismatch is present only in the down-sampled estimates, despite the use of the low-coverage correction in *GONE2*, suggesting residual uncertainty in the timing of demographic events. Analyses restricted to high-coverage individuals for Cumberland Sound and James Bay place the decline as a sharper, more pronounced event coinciding with the commercial whaling period (Figure S10), consistent with documented harvest histories. However, the low sample size for high coverage Cumberland Sound and James Bay makes these results less reliable.

Alternatively, the decline observed before the commercial whaling period might not be the result of commercial whaling by European settlers, but rather of pre-colonial whaling conducted by Indigenous populations. While the peak period of beluga whale removal in the Little and Great Whale River area occurred during the 1850s and 1860s, Inuit hunters had already been hunting them before the onset of commercial whaling (Reeves and Mitchell 1987). The same is likely true for Indigenous communities on Baffin Island (McCartney 1980), making Indigenous hunting a plausible explanation for the decline in effective population size in Cumberland Sound over the last 1,000 years.

The James Bay population has not been subject to commercial whaling and remains in or near James Bay year-round (Bailleul et al. 2012) which has likely limited both gene flow into this population and harvest removals. Nevertheless, at least some James Bay beluga could have been taken by whaling in Hudson Bay, which could explain their similar trajectories to the Cumberland Sound and Little and Great Whale River populations over the last centuries. While there is no evidence of commercial hunting in James Bay itself, many samples from this genetic population have been collected outside James Bay, at Kuujjuarapik and Belcher Island (Figure S2, Table S2). It is therefore conceivable that hunting in the Eastern Hudson Bay could also affect the James Bay population.

While an increase in N_e was noted for both the Eastern High Arctic-Baffin Bay and Hudson Bay-Strait Complex populations over the last 1,000 years, the reasons behind these increases are likely to differ between the two populations. Left largely undisturbed, the Eastern High Arctic-Baffin Bay population seemed to have slowly recovered from the decline in N_e following the last glacial period, probably furthered by suitable environmental conditions and lack of natural or anthropogenic disturbances. Other factors might explain the rapid increase in the population of the Hudson Bay-Strait Complex. Studies with larger sample sizes and higher resolution have detected finer structure in this population (Parent et al. 2023), and our admixture analysis reveals that the Hudson Bay and Strait Complex population comprises a diverse range of genetic combinations from different ancestries (Figure S3). The increase we observe in our demographic history reconstruction over the last centuries could indicate mergers between previously more distinct populations. This could result in a large, genetically distinct cluster containing substructure from previously distinct populations, with large spikes in their demographic histories indicating the onset of gene flow between them.

Finally, the St. Lawrence population shows the most surprising result among the six populations. The suggested increase in this population's effective population size over the past centuries was unexpected, given that commercial harvests removed thousands of individuals during this period. This signal likely reflects occasional gene flow from Arctic populations rather than population growth, a hypothesis further supported by contemporary admixed individuals in the estuary and discussed further in the context of contemporary N_e below.

Contemporary N_e

Both historical and contemporary N_e can help inform conservation and management. Modern conservation and management efforts have started to consider N_e as a measure for the adaptive capacity of wildlife populations. The 2022 Kunming-Montreal Global Biodiversity

Framework designated an effective population size of 500 as a headline indicator of genetic health, representing the minimum size that theory predicts populations need to maintain long-term evolutionary potential (Franklin 1980; Hoban et al. 2020; Jamieson and Allendorf 2012). However, this threshold should be considered in light of a population's full demographic history, including past bottlenecks and expansions, rather than as a standalone criterion. The large contemporary N_e estimates for the Eastern High Arctic-Baffin Bay and Hudson Bay-Strait Complex populations, and the continued increase in N_e , suggest these populations are stable in their genetic diversity. This could indicate a steady or substantial adaptive capacity, which may help provide resilience to future changes, such as a warming climate. In the Eastern High Arctic-Baffin Bay population, this will likely be a requirement for its persistence in the future, as this region is predicted to require a higher degree of genetic adaptation to environmental changes over the next decades, according to current climate change models (De Greef et al. 2025).

The N_e estimates of the St. Lawrence population varied depending on which individuals were included in the analysis (Table 3). The estimates range from 81 to 2,430. The low-end estimate of 81 matches previous estimates for this population (Best 2022) and is obtained when kinship is minimized among samples. The elevated ROH burden in this population, with 24% of the genome made up of ROHs compared to 7-10% in all other populations, is consistent with long-term inbreeding. The pervasive close kinship among all sampled individuals is most parsimoniously explained by high inbreeding, given the breadth of sampling locations and years represented in our data (Table S1). Together, these patterns indicate that the St. Lawrence Estuary population has low genetic diversity and a high ongoing risk of further loss through drift, regardless of which N_e point estimate is used.

While this population is clearly distinct and geographically segregated, some gene flow from Arctic populations appears to have occurred, which may partly account for the increase in N_e noted in the demographic history reconstruction. We found two individuals in the St.

Lawrence estuary that are admixed with the Hudson Bay and Hudson Strait population, indicating recent gene flow from the Arctic into the St. Lawrence estuary. The literature (Vladykov 1944) reports at least episodic influxes of Arctic beluga into the St. Lawrence estuary. The relative proximity of wintering areas of some Arctic populations in southern Labrador (Bailleul et al. 2012) as well as reports of vagrant beluga each summer in Newfoundland waters, the northwestern and southern Gulf of St. Lawrence, Scotian Shelf, or eastern U.S. (Curren and Lien, 1998; R. Michaud, unpublished data), with some identified genetically or from their contaminant loads as coming from the Arctic, provide additional evidence for potential gene flow from northern populations (Lesage et al. 2024). The genetic identity of the Strait of Belle Isle beluga in this study (attributed to the Hudson Bay-Strait Complex population), although beach-cast and therefore with some uncertainty about its location while still alive, further supports the presence of Arctic beluga in southern waters. However, low levels of gene flow may not mitigate inbreeding stress in this population. Studies on inbreeding and mutation load have supported the conclusion that this population is inbred (DFO Canadian Science Advisory Secretariat Science Advisory Report 2024; Orton et al. 2025).

The Little and Great Whale Rivers populations have a N_e estimate which is not far higher than the low end of the St. Lawrence Estuary. This population has experienced a substantial decline in N_e in recent years, with a very low contemporary N_e that falls well below the recommended 500. The observed low N_e must be carefully considered, given the small sample size for this population and the low sequence coverage for these individuals. However, low coverage tends to be linked to an overestimation of N_e (Han et al. 2014; Waples 2025) meaning that higher-coverage analyses would likely yield even lower estimates. Combined with the recent decline in this population, this suggests it may be susceptible to further declines and future environmental changes (Reed 2005; Waples 2022).

The Cumberland Sound population has a contemporary N_e estimate of 250-400. The exclusion of admixed individuals results in lower estimates. Low aerial survey numbers and the decline this population has undergone during the last centuries provide evidence that it currently has much lower numbers than it was historically able to maintain. Despite that, this population does not exhibit elevated ROH, indicating much less inbreeding than expected. This might result from gene flow from surrounding populations. Our population structure analysis shows that one individual from Cumberland Sound clusters genetically with the Eastern High Arctic-Baffin Bay population. At the same time, another appears to be admixed between the Cumberland Sound and Eastern High Arctic-Baffin Bay populations. Additionally, although the neighbouring belugas at Iqaluit are identified as Hudson Bay and Strait Complex individuals, one individual found there belongs to the Cumberland Sound cluster. Together, these patterns indicate ongoing dispersal and gene flow between Cumberland Sound and neighbouring populations, consistent with the absence of elevated inbreeding in this population.

The population with the highest ROH, aside from the St. Lawrence Estuary population, is the James Bay population, although it is not significantly higher than those of the remaining populations. This population has an estimated abundance exceeding 10,000 belugas (Sauvé et al. 2024). However, because our population structure analysis reveals Hudson Bay individuals in James Bay and James Bay individuals along the eastern Hudson Bay coast, it is uncertain whether this estimate represents the genetic James Bay population or a combination of James Bay and eastern Hudson Bay individuals. The contemporary N_e for the James Bay population is also below 500. Reconstruction of demographic history indicates a decline over the last centuries; this population appears to have plateaued over the last 500 years. Climate change projections predict greater environmental changes linked to local adaptation in beluga whales in James Bay than in most other regions inhabited by this species (De Greef et al. 2025). Despite its demographic stability over the last centuries, its low N_e in an environment

predicted to change strongly in the near future suggests a population more at risk than its census data alone would indicate.

Across all populations, the most recent generation in the *GONE2* analysis consistently yields higher N_e estimates than contemporary N_e estimates. This pattern is especially notable in the St. Lawrence population, which is currently experiencing a bottleneck due to centuries of intensive hunting. Despite this decline, there is no clear signal in the *GONE2* analysis, nor is there an increase in large ROHs. This suggests that the genetic data do not yet fully reflect the consequences of recent whaling activities. Because beluga whales are long-lived, genetic signatures of demographic change may take time to become apparent. However, populations like the Eastern High Arctic-Baffin Bay population and the St. Lawrence population also demonstrate that these animals can be rather resilient against genetic bottlenecks. Both of these populations have declined strongly in the past, the St. Lawrence population to an extent that we still detect signals of long-past inbreeding, and yet both of them recovered after an initial bottleneck after the last glacial period. This suggests that populations like Cumberland Sound and the St. Lawrence Estuary, which are currently struggling to recover from a very recent decline over the last century (Hammill et al. 2007; Watt et al. 2021), may retain some capacity for recovery if anthropogenic pressures are reduced and suitable habitat conditions are maintained. Although the long-term genetic consequences of sustained small N_e should not be discounted.

Implications

Our findings reveal substantial variation in the genetic health and demographic trajectories of beluga whale populations across eastern Canada, with direct implications for their management. The Eastern High Arctic-Baffin Bay and Hudson Bay-Strait Complex

populations, with contemporary N_e values above 2,000 and increasing demographic trajectories, appear to retain meaningful adaptive capacity. Nonetheless, the Eastern High Arctic-Baffin Bay population occupies a region predicted to experience disproportionate environmental change, making continued genetic monitoring a priority.

The remaining four populations, Cumberland Sound, Little and Great Whale Rivers, James Bay, and the St. Lawrence Estuary, all have contemporary N_e well below the 500-individual threshold recommended by the Convention on Biological Diversity. For Cumberland Sound and Little and Great Whale Rivers, where recent demographic declines are most pronounced, current harvest levels warrant careful reassessment. For the St. Lawrence Estuary, the combination of high inbreeding, small N_e , and limited recovery trajectory argues for continued harvest prohibition and exploration of whether facilitated gene flow from Arctic populations could provide demographic or genetic benefit without disrupting population identity. The James Bay population presents a particular challenge. Despite an apparently large census size, its low N_e and the substantial environmental changes projected for its habitat suggest it is more genetically vulnerable than abundance estimates alone would imply.

Each of these populations has a distinct evolutionary history that uniform management approaches are unlikely to adequately reflect. This is not unique to belugas. Wherever a species comprises populations with divergent histories of isolation, exploitation, and gene flow, species-level assessments risk obscuring the variation in genetic vulnerability that determines which populations are most exposed to losing the capacity to adapt.

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Statements and declarations

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Competing interests:

The authors have no relevant competing interests to disclose.

Data availability

Data have been deposited to BioProject under ID PRJNA1182041 and ID PRJNA984210. All scripts are available under https://github.com/MuellerC-UoM/Beluga_PopStructure-DemographicHistory/

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Author contributions

Claudio Müller: Conceptualization, methodology, analysis, writing – original draft & editing. Evelien de Greef: Methodology, writing – editing. Cortney A. Watt: Writing – editing, Steven H. Ferguson: Conceptualization, writing – editing. Veronique Lesage: Methodology, writing – editing. Geneviève J. Parent: Methodology, writing – editing. Colin J. Garroway: Conceptualization, methodology, analysis, writing – editing.

Tables & Figures

Table 3.1. Weighted pairwise F_{ST} between genetically distinct populations.

EHA=Eastern High Arctic-Baffin Bay, CS=Cumberland Sound, HBSC=Hudson Bay-Strait Complex, LGR=Little and Great Whale Rivers, JB=James Bay and SLE=St. Lawrence Estuary.

Pairwise F_{ST}	EHA	CS	HBSC	LGR	JB
CS	0.0206				
HBSC	0.0238	0.0083			
LGR	0.0362	0.0203	0.0109		
JB	0.0497	0.0359	0.0269	0.0426	
SLE	0.1217	0.1055	0.0876	0.1129	0.1191

Table 3.2. F_{ROH} by length category in mega base pairs. The numbers represent the relative proportion runs of homozygosity of the corresponding length category make up in the total length of the genome. EHA=Eastern High Arctic-Baffin Bay, CS=Cumberland Sound, HBSC=Hudson Bay-Strait Complex, LGR=Little and Great Whale Rivers, JB=James Bay and SLE=St. Lawrence Estuary.

Pop	<1Mb	1-5Mb	5-10Mb	>10Mb	F_{ROH} mean
EHA	0.0594	0.0229	0.0052	0.0135	0.1010
CS	0.0571	0.0122	0.0043	0.0067	0.0803
LGR	0.0603	0.0148	0.0026	0.0000	0.0777
HBSC	0.0552	0.0120	0.0065	0.0109	0.0846
JB	0.0708	0.0183	0.0031	0.0000	0.0922
SLE	0.1611	0.0657	0.0052	0.0071	0.2391

Table 3.3. Effective population size estimates of the six genetic populations.

Populations with "w/o A" are populations that we tested excluding admixed individuals. "low kinship" refers to the estimates where we only used ten individuals with the lowest degree of relatedness for estimation of N_e . " n " represents the number of genomic samples. " N " represents the estimated size of the entire population based on aerial surveys, which are extracted from the most recent COSEWIC or DFO status reports (COSEWIC 2020; Sauvé et al. 2024; Tinker et al. 2024). The HBSC abundance estimate N represents the combined estimates for Western Hudson Bay beluga and the Eastern Hudson Bay - Belcher Islands stock and thus, include beluga from LGR. " N_e " is the average estimated effective population size, based on 10 iterations of a random subsampling of 10,000 SNPs from our data. The average lower and upper 95% confidence limits (CI) are for N_e estimates of each population.

Population	n	N	N_e	Lower 95% CI	Upper 95% CI
EHA	16	21,213	2,666	2,106	3,655
CS	12	1,090	394	378	412
CS, w/o A	11	1,090	272	263	282
LGR	9	Na	138	135	142
HBSC	62	58,292	3,839	3,559	4,167
JB	15	11,455	304	295	313
SLE	26	1,850	820	786	856
SLE, w/o A	24	1,850	2,430	2,137	2,817
SLE, low kinship	10	1,850	81	80	82

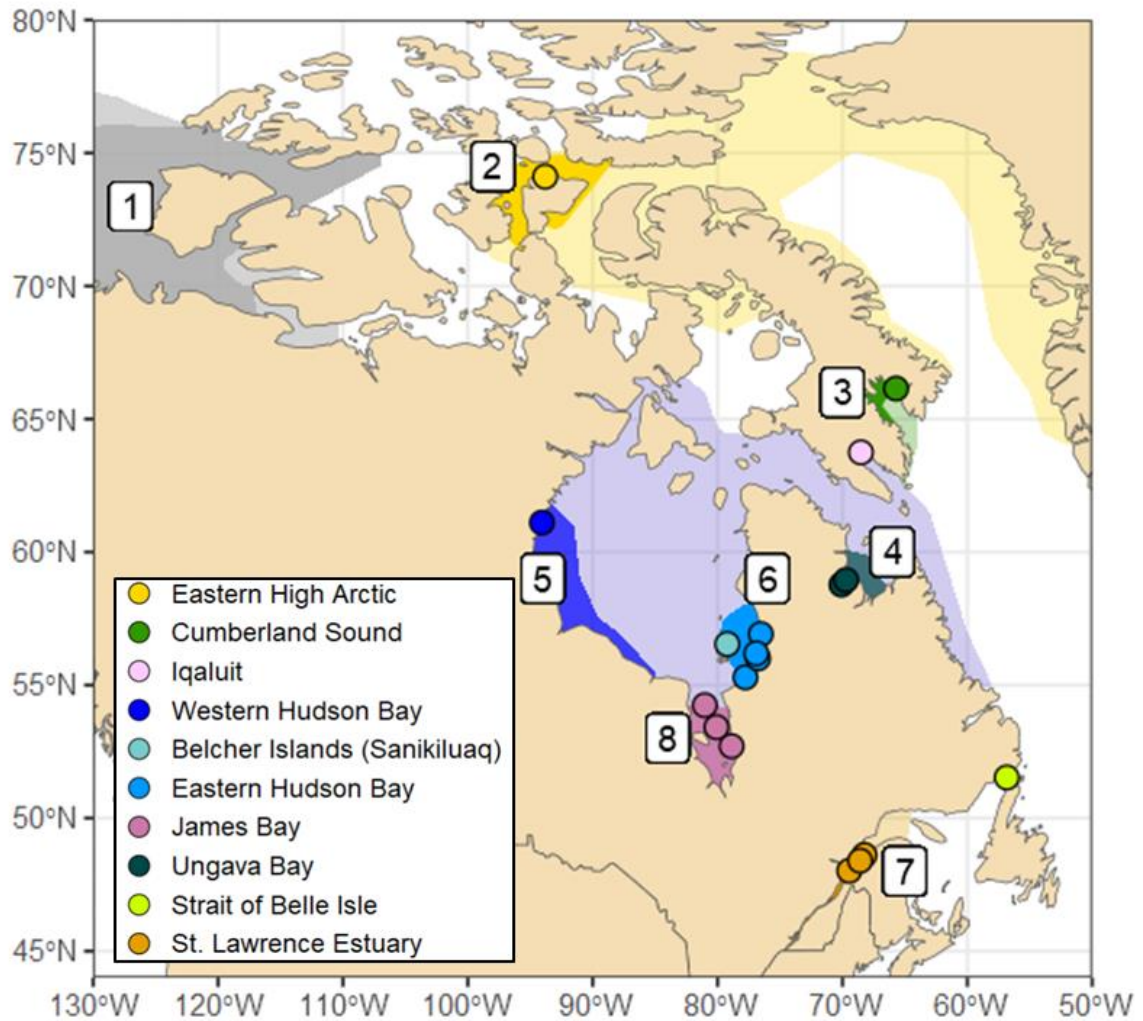


Figure 3.1: Canadian beluga stocks and range (COSEWIC 2020). Dark colored areas show summer habitats; lightly colored areas show seasonal migration range. Designated stocks are: (1) Eastern Beaufort Sea, (2) Eastern High Arctic-Baffin Bay, (3) Cumberland Sound, (4) Ungava Bay, (5) Western Hudson Bay, (6) Eastern Hudson Bay, (7) St. Lawrence Estuary and (8) James Bay. The dots show the sampling locations: Eastern High Arctic-Baffin Bay (n=15), Cumberland Sound (n=13), Iqaluit (n=10), Western Hudson Bay (n=15), Sanikiluaq (n=15), Eastern Hudson Bay (n=29), James Bay (n=16), Ungava Bay (n=3), Strait of Belle Isle (n=1) and St. Lawrence Estuary (n=29).

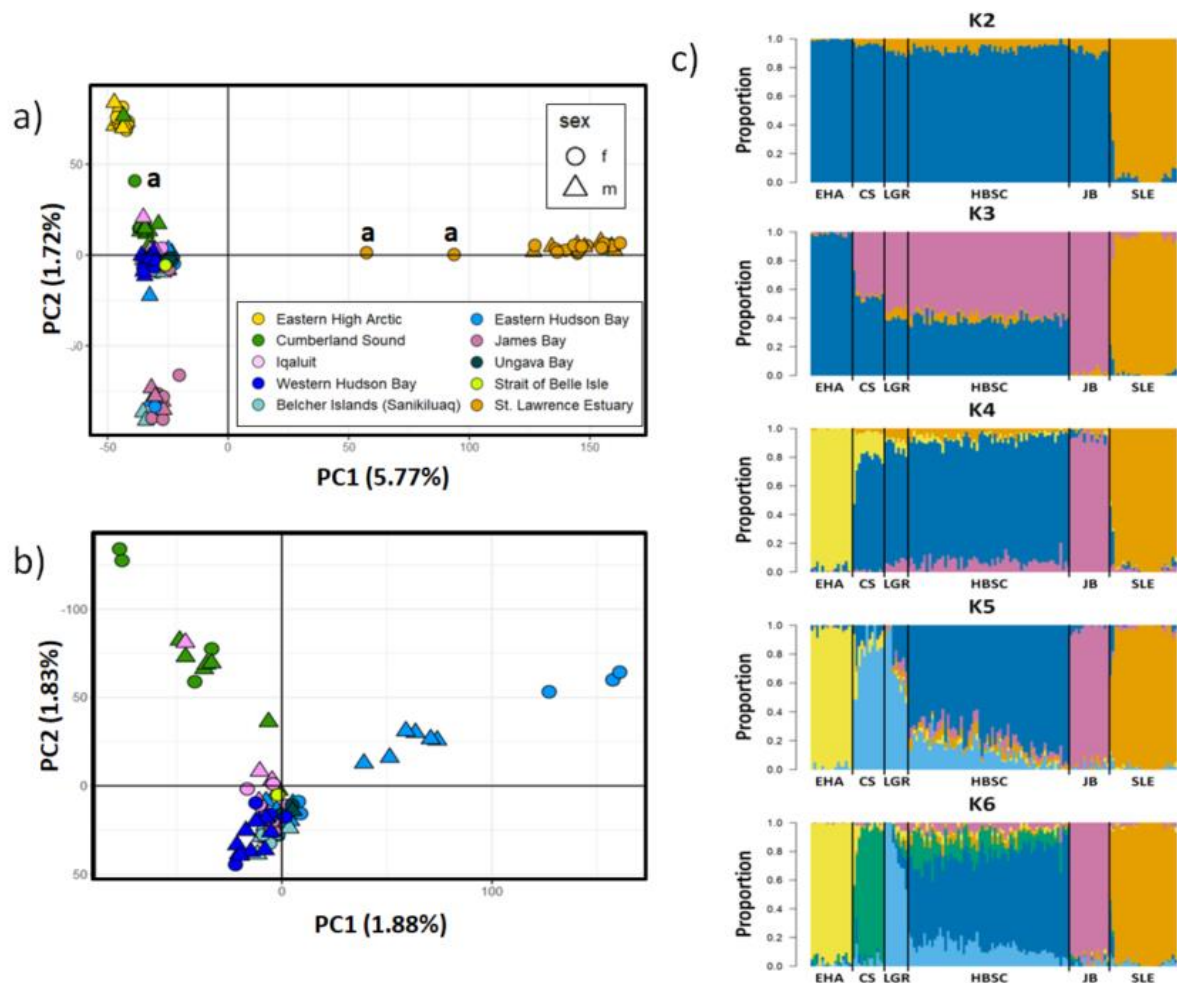


Figure 3.2. Population structure. a) PCA showing the population structure of all sampled individuals (n=140). Individuals treated as “admixed” for further analysis are labeled in the PCA with an “a”. b) PCA of population structure within the largest, highly heterogeneous cluster from Figure 2a (n=84). c) Admixture plot with K=2–6. EHA=Eastern High Arctic-Baffin Bay, CS=Cumberland Sound, LGR=Little and Great Whale Rivers, HBSC=Hudson Bay-Strait Complex, JB=James Bay and SLE=St. Lawrence Estuary.

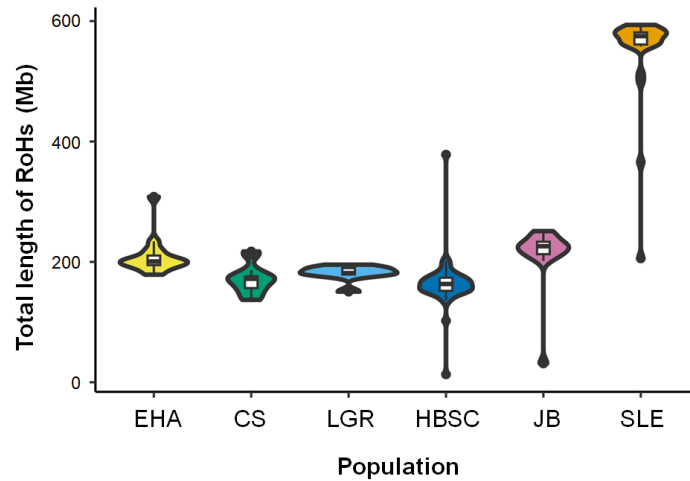


Figure 3.3. Runs of homozygosity estimates for all populations. EHA=Eastern High Arctic-Baffin Bay, CS=Cumberland Sound, LGR=Little and Great Whale Rivers, HBSC=Hudson Bay-Strait Complex, JB=James Bay, SLE=St. Lawrence Estuary.

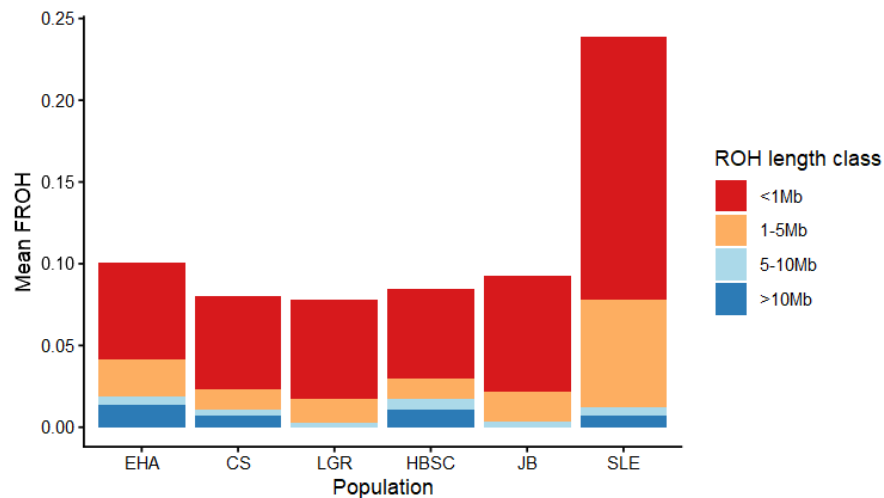


Figure 3.4. Proportions of genome in runs of homozygosity by length class. Average total length of runs of homozygosity represented as a proportion of total genome length. The colors show the ratio of the total runs of homozygosity made up of runs of different length ranges in mega base pairs. The x-axis shows the different populations: EHA=Eastern High Arctic-Baffin Bay, CS=Cumberland Sound, LGR=Little and Great Whale River, HBSC=Hudson Bay-Strait Complex, JB=James Bay, SLE=St. Lawrence Estuary.

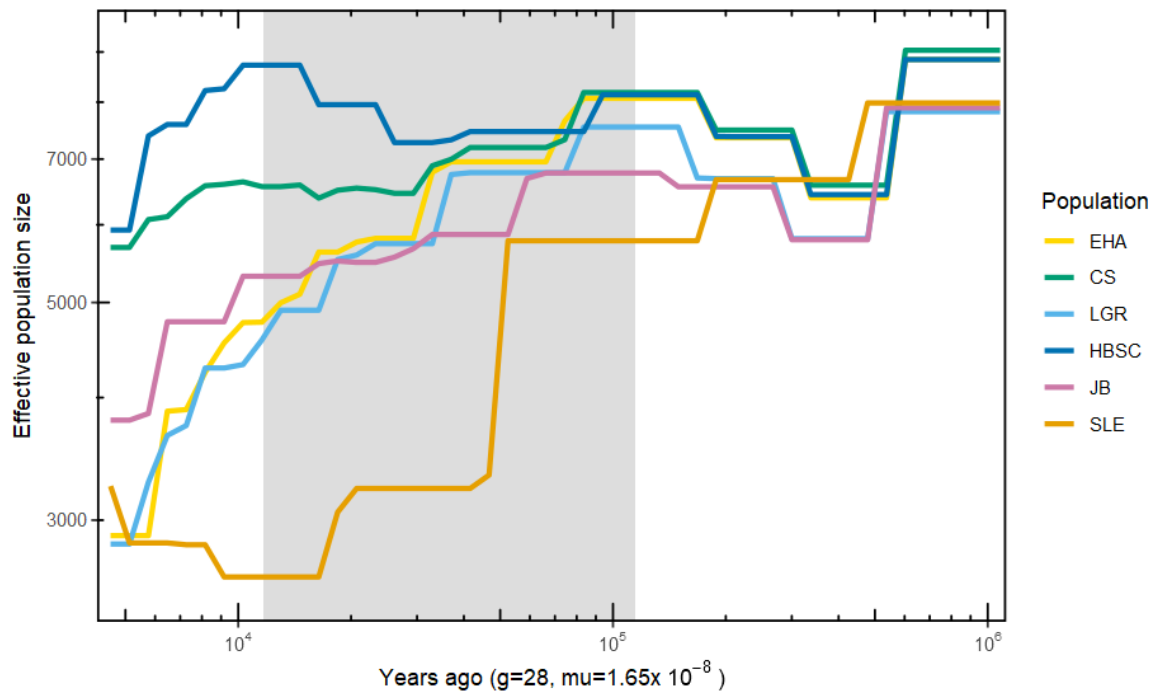


Figure 3.5. Demographic history reconstruction with SMC++. Changes in beluga whale effective population size (N_e) over time shown by the median of 20 SMC++ iterations per population. The grey bar marks the last glacial period (115 – 11.7 thousand years ago) and axes are log10-scaled. CS=Cumberland Sound, EHA=Eastern High Arctic-Baffin Bay, SLE=St. Lawrence Estuary, JB=James Bay, HBSC=Hudson Bay-Straits Complex, LGR=Little and Great Whale Rivers.

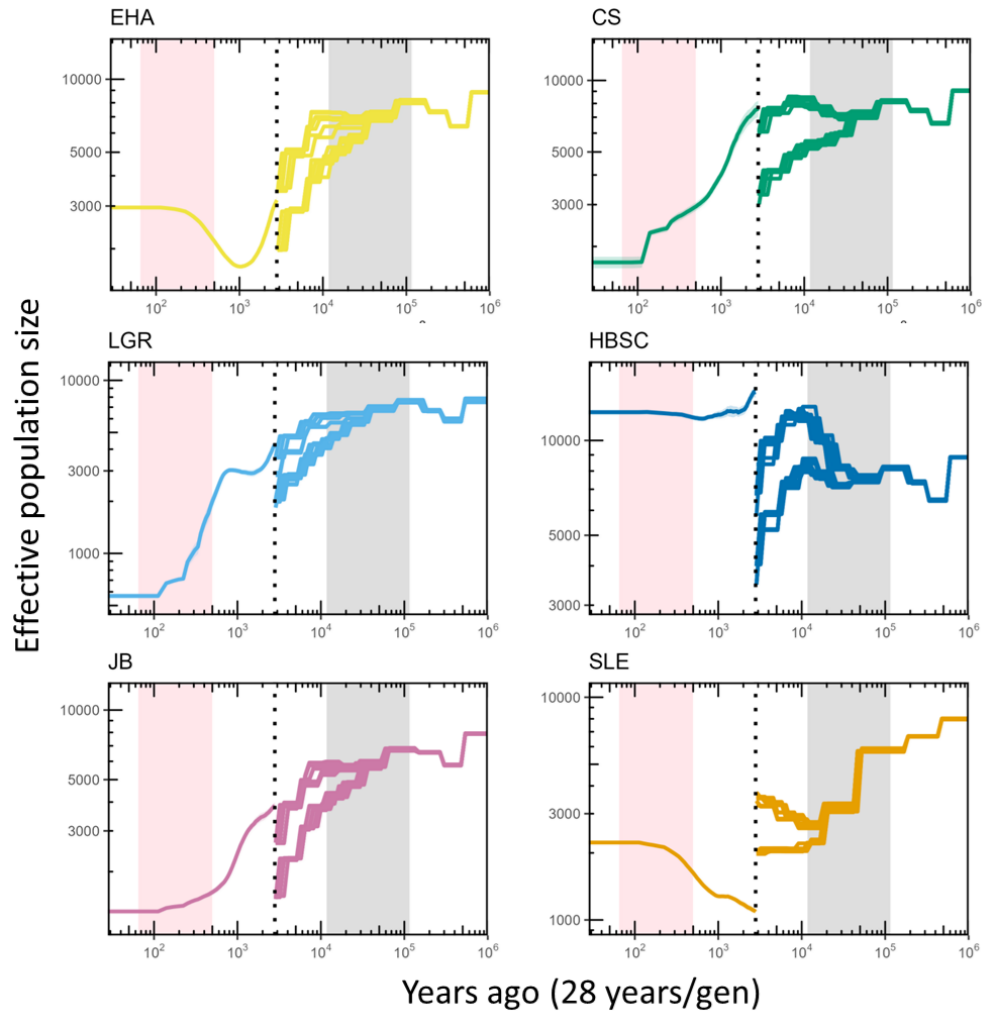


Figure 3.6. Demographic history reconstruction. Shows the past trajectory of the effective population size using a linkage disequilibrium-based methods SMC++ and *GONE* of the six genetic populations. EHA=Eastern High Arctic-Baffin Bay, CS=Cumberland Sound, LGR=Little and Great Whale Rivers, HBSC=Hudson Bay-Strait, JB=James Bay and SLE=St. Lawrence Estuary. Results to the right side of the dotted line show the demographic history older than 100 generations, estimated with SMC++. They show the totality of all 20 iterations. The grey bar marks the last glacial period (115 – 11.7 thousand years ago). The results to the left of the dotted line are the last 100 generations, estimated with *GONE*. Results are presented as the median (solid line) and 95% confidence interval (light shading). The pink shaded area represents the time of commercial hunting from early 16th century (500 years ago) to the end of commercial whaling in Canada (60 years ago).

CHAPTER 4: GENOMIC EVIDENCE FOR LOCAL ADAPTATION IN CANADIAN BELUGA WHALE POPULATIONS

Running head: Local adaptation in belugas

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Abstract

Understanding the genomic basis of local adaptation is critical for conserving species that occupy heterogeneous environments, particularly in rapidly changing marine ecosystems. Canadian beluga whales (*Delphinapterus leucas*) inhabit a broad environmental range, from the temperate St. Lawrence Estuary to Arctic coastal waters, and exhibit strong site fidelity and natal philopatry. We investigated patterns of adaptive divergence among six genetically distinct beluga populations using genome scans conducted with two complementary methods. We identified candidate single nucleotide polymorphisms (SNPs) showing elevated divergence beyond what would be expected under neutral population structure. Nearly 6,000 loci were detected by both methods, providing robust evidence for local adaptation. Environmental association analyses revealed that the strongest adaptive signals were linked to ice thickness, chlorophyll concentration, and an Arctic versus non-Arctic population contrast, highlighting ecological drivers of population differentiation. The St. Lawrence Estuary population stood out as uniquely adapted, consistent with its historic and geographic isolation. A structural variant on chromosome 19 associated with this population suggests a potential genomic mechanism facilitating local adaptation. In contrast, relatively few SNPs were associated with migration distance or water temperature, suggesting the possibility of culturally transmitted migratory behavior and polygenic adaptation with subtle genomic signatures. Combined, our results demonstrate the contribution of local adaptation to the population structure of Canadian beluga whales and the importance of both ecological and historical factors on adaptive divergence.

Introduction

Adaptation is a central process in evolutionary biology, explaining how populations evolve traits that enhance survival and reproduction within their environments. Through natural selection, genetic variants that create a fitness advantage under specific environmental conditions become more common over generations, shaping the phenotypic and genomic traits of species (Cook and Saccheri 2013; Fisher 1930). Many conspecific populations can experience heterogeneous environmental pressures that vary spatially, such as differences in temperature, salinity, or prey availability. Under such conditions, populations may diverge genetically as they adapt to their local conditions, a phenomenon known as *local adaptation* (Savolainen, Lascoux, and Merilä 2013; Williams 1966). Local adaptation arises when gene flow among populations is insufficient to counterbalance divergent selection, allowing alleles that are advantageous in one environment but potentially neutral or maladaptive in another to increase in frequency (Kawecki and Ebert 2004). This process generates population-specific genomic signatures of selection and can ultimately lead to ecological specialization (Savolainen et al. 2013; Wadgymar et al. 2022). Understanding the genetic basis of local adaptation and identifying locally adaptive genetic regions provides insight into the evolutionary mechanisms that allow populations to persist in rapidly changing environments (Atkins and Travis 2010; Bocedi et al. 2013). These insights are particularly valuable because locally adapted populations may harbour genetic variants that could facilitate species persistence through adaptation to altered environments.

In the Arctic and along the Canadian coast, where climate change is rapidly altering marine habitats (Laidre et al. 2015; Rantanen et al. 2022), identifying locally adapted populations is important for understanding the capacity of species to respond to ongoing environmental change. The eastern Canadian Arctic is home to a significant proportion of Canada's beluga whales (*Delphinapterus leucas* (Hobbs et al. 2019)). Beluga whales exhibit

strong site fidelity, consistent seasonal migration routes, and natal philopatry, while exhibiting complex population structures, shaped by both ecological and behavioural factors (Finley 1982). Recent studies identified at least six distinct genetic populations in eastern Canada, five of which reside in the Arctic, with the southernmost beluga whale population occurring in the St. Lawrence River estuary (Montana et al. 2024; Müller et al. 2026, Figure 4.1). The eastern Canadian populations are genetically differentiated despite evidence for historical connectivity and ongoing gene flow (Montana et al. 2024; Müller et al. 2026; O’Corry-Crowe et al. 2018). Since even low levels of gene flow homogenize populations, the persistence of genetic structures suggests that mechanisms beyond geographic isolation contribute to the maintenance of population structure (Tigano and Friesen 2016).

In addition to differences in feeding ecology and demographic history (Bailleul et al. 2012; Béland 1996; Müller et al. 2026), these populations occupy a variety of distinct environments. Their habitats range from temperate waters in relatively isolated estuaries of the St. Lawrence in the south to large, migratory groups in the Arctic waters of Baffin Bay and the Beaufort Sea (Béland 1996; COSEWIC 2020; Gosselin et al. 2002). Perhaps the most striking difference between the environments of these populations occurs along a latitudinal gradient. Due to upwelling and nutrient influx from the St. Lawrence River and the connecting lakes, the southern waters of the St. Lawrence Estuary are warmer, with less annual ice coverage, more nutrient-rich and more species rich than the Arctic marine environments (Assis et al. 2017; Greisman and Ingram 1977; Therriault and Lacroix 2011; Figure S4.1). While genetic divergence among Canadian beluga populations is well documented (Brown Gladden et al. 1997; Gladden et al. 1999; Montana et al. 2024; Müller et al. 2026; Skovrind et al. 2021; Turgeon et al. 2012), it is unclear whether this structure has arisen primarily through neutral processes such as genetic drift or whether local adaptation associated with heterogeneous environments has contributed to the rise and the persistence of region-specific genetic identities. However, recent studies have revealed strong evidence for

local adaptation to heterogeneous environments in the common dolphin (*Delphinus delphis*) (Barceló et al. 2022), bottlenose dolphin (*Tursiops aduncus*) (Louis et al. 2021; Pratt et al. 2021) or bottlenose whales (*Hyperoodon ampullatus*) (De Greef et al. 2022). These findings raise the possibility of similar processes having shaped Canada's beluga populations.

In this study, we identify genomic loci associated with environments and behavioural traits. For the environmental factors, we focus on sea surface temperature, ice thickness and chlorophyll concentration. Population-specific adaptations linked to thermal tolerance in cetaceans (Barceló et al. 2022; Pratt et al. 2021; Yeates and Houser 2008) and diet specialization (Teixeira et al. 2023) have already been identified in other species. These traits are strongly linked to environmental conditions and resource availability (Schluter 1996) and are therefore candidates for environmental factors shaping populations' genetic identity. Additionally, we assess local adaptations associated with the broad ecological divide between non-Arctic and Arctic individuals (St. Lawrence Estuary compared to all other populations). The split between the St. Lawrence Estuary population and Arctic populations occurred at the end of the most recent glacial period, when the southern population got isolated from its conspecific neighbours in a separate refugium, creating a distinct evolutionary history compared to the remaining Arctic populations (Brown, Ferguson and Gladden 1997). This population also exists at the southern edge of the beluga's range. Population at species range edges often experience environments that put more selection pressure onto them than on conspecific populations closer to the range center (Johannesson and André 2006). This makes the St. Lawrence population a strong candidate for local adaptation. Our behavioral trait of interest was migration distance during the fall and winter. Beluga whales are migratory mammals, spending the summer months in shallow coastal environments and then migrating into deeper water to avoid being trapped by ice (Lockyer and Brown 1981). However, migration distances can vary significantly among populations. While individuals from the Cumberland Sound, James Bay and St. Lawrence Estuary populations only migrate short

distances, barely leaving their estuaries (or bay, in the case of the James Bay population), their conspecific counterparts in the Eastern High Arctic-Baffin Bay and Hudson Bay travel long distances, up to thousands of kilometers each winter. While much of cetacean behavior is determined culturally through social learning (Carroll et al. 2015; Filatova 2024; Rendell and Whitehead 2001), it is possible that there are underlying genetic factors that facilitate these differences in lifestyle.

Here, we investigate the genomic basis of local adaptation across Canada's beluga whale populations using a whole-genome single nucleotide polymorphism (SNP) dataset, encompassing samples collected from across the Canadian Arctic and sub-Arctic coast. These samples include individuals from multiple management stocks and represent six genetic populations (Müller et al. 2026). This provides an opportunity to evaluate how evolutionary processes have shaped adaptive variation across heterogeneous marine environments. As Arctic ecosystems undergo rapid transformations driven by climate change, cetaceans will have to adapt to new environmental conditions (e.g., De Greef et al. 2025). The past relationship of these animals with their environment will inform how they will survive into the future.

Methods

Tissue collection, extraction & sequencing

We obtained tissue samples from 15 locations representing seven Canadian management stocks (St. Lawrence Estuary, Ungava Bay, Eastern Hudson Bay, Western Hudson Bay, James Bay, Cumberland Sound, and Eastern High Arctic-Baffin Bay) and six genetically distinct populations (Müller et al. 2026). While there is significant overlap between the

genetic populations and the designated management-defined stocks, these two designations do not precisely match. For this study, it was important to account for genetic population structure in our analyses, and we will therefore refer to the six genetically distinct populations for the rest of this study. We will continue using the naming conventions established in Montana et al. (2024) and used in Müller et al. (2026) to distinguish between these six genetic populations: St. Lawrence Estuary (SLE), Eastern High Arctic-Baffin Bay (EHA), James Bay (JB), Hudson Bay and Strait Complex (HBSC), Cumberland Sound (CS) and Great and Little Whale River (GLR).

The skin tissues were collected from individuals harvested by indigenous subsistence hunters, with additional samples obtained from stranded or deceased individuals in the St. Lawrence Estuary and the Strait of Belle Isle (Figure 4.1a). We extracted DNA using the Qiagen DNeasy Blood & Tissue Kit protocol. We performed whole-genome sequencing on an Illumina NovaSeq platform, generating paired-end reads targeting an average coverage of 10x.

Alignment, variant calling & filters

We trimmed the raw sequences for quality with Trimmomatic v0.36 and aligned them to a beluga reference genome (GCA_029941455.3) (Bringloe and Parent 2023) using Bowtie2 v2.5.2 (Langmead and Salzberg 2012). We removed duplicate reads and added read group information using Picard v2.20.6 (Broad Institute 2019). To ensure consistency across samples, we down-sampled high-coverage individuals to a target modal coverage of 6x using GATK v4.1.2 (McKenna et al. 2010). We called variances with Platypus v0.8.1 (Rimmer et al. 2014). To keep only high-quality reads, we used vcftools v1.16 (Danecek et al. 2011) and bcftools v1.19 (Danecek et al. 2021) to filter out indels, sites without the PASS flag, low quality sites (QUAL<50), sites with missingness >0.25 and non-biallelic sites. We used PLINK v1.9 (Purcell et al. 2007) to calculate kinship and removed one individual from each

close-kin pair ($\pi\text{-hat} > 0.4$) to avoid bias from first-degree relatives. We then excluded alleles with low frequency (minor allele frequency < 0.5), sites with missingness > 0.1 and we then removed all scaffolds for which the reference genome has no chromosome-specific annotation, as well as scaffolds aligned to sex chromosomes. Finally, we used beagle v5.2 (Browning, Zhou, and Browning 2018) to impute missing data since lfmms cannot be run with missing values in the data set.

Regions under selection

We used two methods to test for evidence of selection on SNPs: PCAdapt and Latent Factor Mixed Models (LFMM). Both methods perform genome-wide association scans aimed to detect loci that deviate from neutral expectation, but with different statistical approaches. PCAdapt uses principal component analysis to identify axes of genetic variation that reflect population structure, and then tests if allele frequency variation at each locus is more strongly associated with those axes than expected by chance. SNPs identified with PCAdapt are SNPs with large contribution to population structure. LFMM uses a latent factor mixed-model regression, in which genetic variation at loci is modelled as a function of environmental covariates and uses latent variables to account for unobserved population structure. The two methods used here provide a robust framework for identifying putative adaptive loci while minimizing false positives due to population structure or demographic history. By integrating results from both methods, we identified patterns of outliers that were consistent across methods, providing evidence for selection-driven differentiation. Additionally, we were able to use LFMM to identify regions that, while statistically accounting for underlying population structure, are linked to environmental factors or migration distances.

We also fitted an LFMM model without an environmental variable, accounting for the underlying structure of our dataset by setting $K=6$ to represent the six genetic populations. For further discussion, we will refer to this analysis as LFMM-K6. These two models addressed

whether there is evidence for general differentiation between the populations through adaptation. In the absence of significant outlier SNPs, the divergence between populations across the entire genome can be explained by genetic drift. We then tested for correlations between allele frequencies and four environmental variables: mean annual sea surface water temperature, mean annual surface chlorophyll-a concentration, and mean annual ice coverage (Figure S4.1), and finally between non-Arctic and Arctic populations. Additionally, we tested one behavioural variable, migration distance.

The environmental data for each sampling location were downloaded from Bio_ORACLE v2.2 (Assis et al. 2017) and extracted using the r-package *sdmpredictors* v0.2.14 (Bosch and Fernandez 2023). We averaged environmental variables within a 100 km buffer for each sampling location. We ran an LFMM analysis using a binary variable to separate Arctic and non-Arctic individuals. The non-Arctic individuals comprise individuals genetically assigned to the St. Lawrence population, while all other individuals were assigned as non-Arctic. We used this distinction to test for adaptations to broad general differences between the environments.

To estimate migration distances, we used the *marmap* package in R v1.0.10 (Pante and Simon-Bouhet 2013) to calculate the shortest distance through water from each sampling location to the most distant point of the corresponding population's migration route as described by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Figure S4.2)(COSEWIC 2020): Individuals from the Cumberland Sound population migrate only short distances to the opening of the Cumberland Sound (Richard 2002). All individuals belonging to the Hudson Bay and Strait Complex and the Little and Great Whale River population leave the Hudson Bay during the winter and travel down the Hudson Strait along the Newfoundland Coast (Colbeck et al. 2013; Lewis et al. 2009). James Bay individuals remain in James Bay year-round (Postma, Lianne D. 2012; Reeves and Mitchell 1987), probably retreating further into the bay or moving into Hudson Bay proper. Individuals from

the St. Lawrence estuary move towards the opening of the estuary during the winter (Béland 1996; Kingsley 2002). For individuals sampled at Iqaluit, we do not have good data to estimate their migration distances. Genetically, most of these individuals cluster with the Hudson Bay and Strait Complex, which also contains an individual from Cumberland Sound (Müller et al. 2026). We also lack telemetry movement data for individuals summering in this region, and we therefore do not know their winter range. Given the uncertainty of their migratory status, we excluded those individuals from this part of the analysis. Additionally, we used two different migration distances for individuals from the Eastern High Arctic-Baffin Bay, since COSEWIC has identified two possible migration destinations: Sarvarjuaq (the North Water) or along the West Greenland coast (COSEWIC 2020; Heide-Jørgensen et al. 2003; Richard et al. 1998). We fit two LFMMs for migration distances, assuming the North Water for one and the West Greenland coast for the other. This resulted in a total of eight distinct models to identify potentially adaptive SNPs: PCAdapt, LFMM-K6, temperature, chlorophyll, ice thickness, Arctic/non-Arctic, short migration (assuming short migration distance for the Eastern High Arctic-Baffin Bay) and long migration (assuming long migration distance for the Eastern High Arctic-Baffin Bay).

Each model produced a p-value per SNP, representing the likelihood that the distribution of the SNP was explained by the underlying population structure (PCAdapt and LFMM-K6), or that the environmental or behavioural variable we tested for did not significantly contribute to the distribution of these SNPs. The resulting p-values per SNP were transformed to q-values using the *qvalue()* function from the *qvalue* R-package v4.5 (Storey et al. 2025). This approach estimates the proportion of true null hypotheses from the empirical p-value distribution and controls the false discovery rate (FDR), providing an FDR-adjusted measure of significance that corrects for the multiple SNPs tested per model. We then applied a q-value of 0.05 as the cutoff for significant outliers, meaning any SNP with a q-value < 0.05 is

considered a significant candidate SNP for a site under adaptive selection via the tested variable.

Gene Ontology preparation

To explore the putative functions of the candidate SNPs, we established a Gene Ontology (GO). This linked SNPs to genes for which one or multiple functions have already been identified (Figure S4.4). Because the beluga reference genome used for alignment and variant calling does not have comprehensive functional annotation, we mapped candidate SNPs to the annotated genome of the most closely related species (*Monodon monoceros*; narwhal) (Bringloe and Parent 2023) to assign gene identities and perform GO analysis, assuming identical functions among genes present in both species. Gene annotation for the narwhal genome was originally done by combining RNA-seq data, protein homology and repeat libraries.

All candidate SNPs from all the previous analyses were compiled into a single list. SNP positions were converted from VCF to BED format and expanded to +/-100 bp windows. Genomic sequence for each window was extracted from the beluga reference genome using *getfasta* from *bedtools* v2.31.0 (Quinlan and Hall 2010). These sequences were aligned to the narwhal genome using *BLAST+* v.2.15.0 (Camacho et al. 2009), after generating a narwhal nucleotide database with the *makeblastdb* command from *BLAST+*. We kept only high-confidence alignments, filtering for $\geq 95\%$ sequence identity, $\geq 80\%$ query coverage and $e\text{-value} \leq 1e-10$. For SNPs with multiple matches, the best alignment per site was selected based on $e\text{-value}$ and bit score. Then we identified overlaps between the BLAST-file and the narwhal genome annotation (GFF-file) using *bedtools intersect* (Quinlan and Hall 2010). Gene identifiers were extracted and compiled into a list representing the set of genes containing putative SNPs or overlapping with regions in close proximity (+/-100bp) of the adaptive SNPs. To generate functional annotations for GO enrichment analysis, we used

gffread (Pertea and Pertea 2020) to extract protein sequences from the narwhal genome. We submitted the resulting protein *FASTA* to *PANNZER2* (Törönen, Medlar, and Holm 2018), which returned a GO-file and functional categories for use in enrichment testing.

We ran separate GO analyses for each set of adaptive SNPs from each model we fit earlier: (1) PCAdapt, (2) LFMM-K6, (3) chlorophyll, (4) water temperature, (5) ice thickness, (6) Arctic/non-Arctic, (7) long migration and (8) short migration. For each analysis, we reduced the BLAST file to include only the adaptive SNPs from the corresponding model. Functional annotations were obtained from the GO-file. Since *PANNZER2* provides multiple types of annotation predictions with varying confidence levels, we only kept entries predicted using ARGOT ontology-predictors. ARGOT predictions use sequence similarities and statistical weighting to assign high-confidence Gene Ontology categories, thereby avoiding low-support predictions for a given gene's function. From the narwhal GFF-file we kept only rows annotated as mRNA. These entries correspond to complete transcribed gene models and provide the correct gene identifiers for functional annotation. Using only mRNA rows avoids redundantly counting overlapping sequences, such as exons. This ensures that SNPs are mapped to full genes that can be clearly linked to the Gene Ontology terms. Next, we identified overlapping genes from the BLAST and gff files, excluding adaptive sites that are not assigned to any functional gene. The remaining genes were then matched to a matching GO-term, general descriptors of the gene's functions. It is important to note that one gene can be linked to multiple GO-terms; the total number of functions assigned to each model we ran can exceed the number of identified genes for that model.

GO-enrichment analysis

Finally, we conducted a GO-enrichment analysis. This analysis uses the identified functional groups to detect whether each group is statistically overrepresented relative to a background genome. In our case, we tested the above-identified functions and their

corresponding genes against the narwhal genome, represented by the GFF-file. Again, we ran one analysis per adaptive SNPs set from the different models. We imposed a cut-off size of at least 15 corresponding genes to provide meaningful results (Table S4.1), since with a smaller number of genes, any gene will almost automatically represent a very high ratio in any given functional group, not because of the overrepresentation of that functional group among the adaptive genes, but because of the low number of genes being tested.

To run the enrichment analysis, we used the *enricher()* function from the *clusterProfiler* R-package (Xu et al. 2024; Yu et al. 2012). The maximum number of genes per GO category was kept at its default of 500. GO categories with more genes are usually very broad (e.g., "nucleus") and don't provide much specific insight into a gene's function (Geistlinger et al. 2021; Xu et al. 2024); however, they can overpower signals from more specific categories. It is important to keep in mind that this does not mean that genes associated with them are automatically discarded, as the hierarchical nature of GO means most genes linked to any of the broader GO categories are usually also linked to more narrow functions.

Results

Regions under selection

With PCAdapt, we identified 12,888 significant candidate SNPs. LFMM-K6 run identified 25,081 significant candidates. Five thousand nine hundred and forty-two (5,942) SNPs were identified in both analyses, representing SNPs that, independent of analysis method, showed a significantly higher degree of divergence than the background divergence resulting from the underlying population structure.

Among the environmental variables we tested, we found the most SNPs linked to ice thickness (4,178) and Arctic vs non-Arctic environments (4,947). The significant SNPs associated with ice thickness were mostly absent in the two comparison SNP sets (PCAdapt and LFMM-K6). On the other hand, approximately 66% of all SNPs associated strongly with Arctic vs non-Arctic environments are present among the PCAdapt and LFMM-K6 SNPs. 1,062 SNPs were significantly linked to chlorophyll concentration. Eighty-six percent of those were also present in the PCAdapt and LFMM-K6 results (Table 4.1).

Four of our results, the PCAdapt, the LFMM-K6, the mean chlorophyll and the Arctic/non-Arctic analysis had a grouping of outliers in close proximity to each other (Figures 4.2 & 4.3). When looking at this region in detail, we found it to be located in the center of one arm of chromosome 19, consisting of closely clustered outlier SNPs (Figure S4.3).

Despite some evidence for adaptation linked to ice thickness, there was no detectable signal of local adaptation linked to water temperature. Only a few SNPs met our significance threshold, and those were primarily linked to the structural anomaly on Chromosome 19. There were also relatively few SNPs linked to migration distances. This does not necessarily mean that there are no genetic adaptations facilitating different migratory strategies. Instead, if genetic adaptations are guiding this behaviour, they may not be detectable in our samples.

Gene Ontology & Gene Ontology Enrichment

We were able to align most regions containing significant SNPs from the original data sets (98+%) to the narwhal reference genome. The five models with the highest numbers of significant SNPs also yielded a sufficient number of genes (>15) to enable meaningful GO-enrichment analysis (Table S4.1): PCAdapt, LFMM-K6, chlorophyll concentration, ice thickness, and Arctic/non-Arctic. The analyses testing for genes linked to sea surface temperature and migration distances (assuming both short and long migration distances for

Eastern High Arctic-Baffin Bay individuals) yielded only a small number of significant SNPs, which could not be meaningfully tested for enrichment.

The gene ontology enrichment results suggested that three of the five models had a large number of functional groups overrepresented in their significant candidate SNPs compared to the background of the narwhal genome: PCAdapt, LFMM-K6 and the Arctic/non-Arctic comparison all showed a significant difference in the ratio of functional groups (Figure 4.4, Tables 4.2, S2, S3 & S4). There was no sign of enrichment in the candidate SNPs linked to chlorophyll concentration and ice thickness. In all models, the ratio between significant SNPs detected and genes linked to those SNPs was in a very narrow range (10%-18%).

Discussion

We identified SNPs exhibiting levels of divergence beyond those expected under neutrality. The convergence of candidate loci across independent analytical methods provides strong evidence that selection has contributed to shaping population-specific genetic variation. Associations between genetic variation and environmental variables further suggest that ecological heterogeneity, particularly along the Arctic/non-Arctic gradient, has played an important role in maintaining genetic differentiation. The St. Lawrence Estuary population appears to be distinctly adapted, consistent with its unique evolutionary history and environmental conditions. However, not all environmental variables showed strong links to signals of local adaptation.

Local adaptation across populations

Our results provide strong evidence that local adaptation contributes to the population structure of Canada's beluga populations. Both PCAdapt and LFMM-K6 identified a large number of SNPs with levels of divergence beyond those expected from population structure alone. The large number of potentially adaptive SNPs across the entire genome indicates that adaptation-facilitated divergence among populations is not driven solely by a small number of genes but instead involves widespread genetic differentiation, potentially shaped by selection.

Notably, almost 6,000 SNPs were identified as significant outliers in both methods. This overlap represents loci that are consistent across methodologies and therefore very unlikely to be an artifact of model assumptions. Instead, this substantial overlap among methods supports the conclusion that adaptive processes have shaped population structures, despite evidence for gene flow among populations (Müller et al. 2026; O’Corry-Crowe et al. 1997, 2018). At the same time, the incomplete overlap between methods is expected, given their distinct statistical approaches and sensitivities. Although both methods aim to distinguish selection from neutral demographic processes, their differing test statistics and sensitivities to allele frequency patterns mean that each method might detect distinct sets of candidate loci (Hoban et al. 2016). The overlap between the two therefore represents a conservative set of robust candidates for selection, while the non-overlapping SNPs likely represent method-specific sensitivity, rather than false positives. Many of these SNPs overlap strongly with selection signatures for specific environmental factors: 66% of those SNPs can be found amongst SNPs linked to an Arctic/non-Arctic differentiation, and 86% are linked to chlorophyll concentration. One striking finding, evident in both methods, is a dense cluster of highly differentiated SNPs localized to a restricted region on one arm of chromosome 19. The physical clustering of significant outlier loci is difficult to reconcile with independent, locus-specific selection alone. Instead, this pattern is consistent with a chromosomal inversion or

another form of structural variation that reduces recombination across a large genomic segment (Schaal et al. 2022).

Combined, the convergence of PCAdapt and LFMM-K6 results provides strong evidence that a considerable number of observed genetic differentiation among Canada's beluga whale populations cannot be explained by drift alone and is consistent with widespread local adaptation.

Local adaptation specific to the St. Lawrence Estuary beluga whale population

Our results provide strong evidence for local adaptation in beluga whales specific to life in the southern estuary of the St. Lawrence. This pattern is consistent with the unique evolutionary history of this population that has been geographically separated from the Arctic beluga populations for approximately 50,000 years, since the last glacial period (Brown Gladden et al. 1997). Previous studies comparing the marine ecosystem of the Baltic sea with the Atlantic have revealed strong signs of local adaptation, driven by environmental factors over 8,000 years, a lot shorter time than what we see in the St. Lawrence population, but consistent for multiple marine species including mammals (Johannesson and André 2006). The geographic isolation experienced by the St. Lawrence Estuary population created similar conditions and likely imposed selective pressures that differed significantly from those experienced by conspecifics. Our data provide some evidence for weak gene flow from the north, yet this population has remained genetically distinct (Müller et al. 2026).

Despite living in an environment that is very distinct from the Arctic, this population flourished until the onset of commercial whaling (Béland 1996). The substantial similarity between the patterns of significant adaptive SNPs linked to the Arctic/non-Arctic divide and to chlorophyll concentration (Figure 4.3) most likely results from the fact that chlorophyll concentration in St. Lawrence is strongly elevated (Winkler et al. 2003) compared to the waters of the Arctic (Figure S4.1) and the most significant split for this variable therefore also

reflects the Arctic/non-Arctic divide. Consequently, we expect SNPs significantly correlated to one environment type to be present in the results of the other one as well. The fact that, aside from the PCAdapt and LFMM-K6 results, only the adaptive SNPs associated with the Arctic/non-Arctic contrast show enrichment for specific Gene Ontology categories suggests that this environmental divide captures a biologically meaningful shift in selective pressure, strong enough to leave a detectable footprint on gene function. The genes that differentiate the St. Lawrence Estuary population from the Arctic groups are not scattered randomly across the genome. They cluster along certain functional lines, implying adaptive responses to environmental conditions.

The most obvious signal of divergence beyond what would be expected from drift is a large, structural variation, most likely an inversion, on one arm of chromosome 19. Recombination suppression arising from structural variants like this can lead to the joint inheritance of multiple linked loci, causing genomic regions to diverge collectively between populations (Kirkpatrick and Barton 2006). This can facilitate population differentiation by maintaining sets of alleles that are advantageous under particular environmental regimes (Wellenreuther and Bernatchez 2018). While our data do not directly demonstrate the existence of an inversion, nor identify the phenotypic traits potentially affected, the repeated detection of this region across independent methods suggests that it may be an important contributor to genomic divergence. While the functionality of this structural variation is not yet resolved, its strong association with the St. Lawrence Estuary makes it a compelling candidate for further targeted investigation using linkage disequilibrium, haplotype structure, or long-read or cytogenetic approaches. It might represent a genomic feature associated with adaptive responses to the distinct environmental conditions in the south compared to those of their Arctic conspecifics.

Ice Thickness, temperature and migration

In comparison to the Arctic/non-Arctic adaptive SNPs, the SNPs linked to annual ice thickness show much weaker overlap with the main divergence through adaptation signal from PCAdapt and LFMM-K6. This likely reflects that ice thickness varies most strongly not between the St. Lawrence and the Arctic, but rather between the Eastern High Arctic-Baffin Bay, where we have by far the most annual ice coverage, and the rest of the species' range (Parkinson and Cavalieri 2008). This indicates that while multiple environmental factors independently shape the population genetics of Canada's beluga whales, large-scale, generalized genome scans will only detect the strongest signal. The large number of significant SNPs linked to ice thickness we uncovered still provides strong evidence for local adaptation shaped by this environmental variable. Beluga whales show a strong ecological association with sea ice, which plays a central role in shaping their seasonal distribution (Hauser et al. 2016; Hauser et al. 2017), habitat use including foraging (Heide-Jørgensen et al. 2010; Watt, Orr, and Ferguson 2016) and development (Noren and Suydam 2022). Belugas routinely occupy ice-covered and ice-edge habitats, using leads, polynyas and areas of dynamic ice for access to prey (Asselin et al. 2011; Gilchrist and Robertson 2000), predator avoidance (Westdal et al. 2017), and navigation (Ferguson, Higdon, and Chmelnitsky 2010; Laidre et al. 2015; Stafford 2019). Therefore, the presence and seasonal dynamics of sea ice strongly influences habitat selection and population differentiation, underscoring the importance of ice-related ecological processes in shaping beluga whale ecology.

The SNPs associated with chlorophyll concentration and ice thickness show no signs of enrichment. This indicates that although selection is related to these variables, the underlying genes are not linked to any particular biological function. This lack of enrichment in SNPs linked to ice thickness compared to the Arctic/non-Arctic divide indicates that the broad Arctic/non-Arctic divide reflects a more cohesive adaptive shift. In contrast, other environmental factors may drive more scattered and less functionally focused responses

across the genome. However, the large number of significant SNPs linked to ice thickness indicates that local adaptation driven by differences in annual ice thickness remains significant, especially in the Eastern High Arctic-Baffin Bay compared to other populations (Figure S4.1). Further targeted investigation into local adaptation of this population compared to its southern counterparts is therefore warranted.

Water temperature is a variable that is very commonly linked to patterns of local adaptation in marine mammals. Most studies showing evidence for local adaptation in cetacean have candidacy loci linked to differences in water temperature (Barceló et al. 2022; De Greef et al. 2022; Louis et al. 2021; Pratt et al. 2021). In our study, only a small number of SNPs showed signs of adaptive selection linked to water temperature. However, the overall pattern of divergence does not look dissimilar to the patterns seen in significant SNPs linked to chlorophyll concentration or the Arctic/non-Arctic split (Figure S4.4), only with much higher q -values, therefore many fewer SNPs meeting the significance threshold of 0.05. Thermal adaptation is generally expected to be highly polygenic (Healy et al. 2018; López-Hernández and Cortés 2019; Way and Oren 2010), which might produce subtle allele frequency shifts across many loci rather than strong outlier signals detectable by genome scans. It also might reflect a strong covariance between water temperature and broader latitudinal and ecological gradients as well as population structure, making it challenging to disentangle temperature-specific effects from other correlated environmental variables.

We only detected a few SNPs significantly associated with migration distance, regardless of whether we used the long or short migration route for the Eastern High Arctic-Baffin Bay population. It is possible that the variation in migratory behaviour in beluga whales is neither genetically determined nor facilitated by genomic factors. Instead, this behavior is largely shaped by cultural transmission and social learning, like in many other cetacean species (Katona and Beard 1990; O’Corry-Crowe et al. 1997). Additionally, migration distances are not necessarily static over evolutionary timescales. Migration distances may have shifted in

response to environmental or demographic changes. Studies in terrestrial mammals have shown that a decline in population size can result in a reduction in migration distances (Lamb et al. 2025). It is therefore conceivable that the decrease in some of the beluga populations might have changed their migration behavior. Such temporal variability would weaken associations between genotype and migration distance, as their contemporary migration paths no longer reflect the migration to which the population was originally adapted.

Finally, methodological limitations could further contribute to the lack of a detectable signal. Some genomic regions might be underrepresented in the dataset, potentially obscuring adaptive variation. Additionally, adaptation related to migratory behaviour may involve many loci with minor individual effects, as is likely for most complex traits. Such polygenic adaptations are inherently difficult to detect using outlier-based approaches, which are most sensitive to loci under very strong and recent selection (Barghi, Hermisson and Schlötterer 2020, Pritchard and Di Renzo 2010). Additionally, a larger sample size might reveal additional patterns that have remained undetected, given that our sample sizes for some of the populations are rather small.

Implications

Our findings add to a growing list of studies that support the idea of genetic local adaptation in cetaceans (Barceló et al. 2022; De Greef et al. 2022; Johannesson and André 2006; Louis et al. 2021; Pratt et al. 2021; Zhou et al. 2018). Our results suggest that the long separation of the St. Lawrence beluga whales from Arctic populations that occurred during the last glaciation (Kingsley 2002) has allowed them to adapt to the very different conditions of a temperate estuarine environment. This evolutionary history provides important context

for the future. Rapid climate change is reshaping ecosystems globally, nowhere more than in the Arctic where warming happens approximately four times the global average (Rantanen et al. 2022). A consistent pattern throughout studies uncovering local adaptation in cetaceans is the link of adaptive SNPs to heterogeneity in water temperature. Given how much global warming is causing water temperatures around the world's oceans to rise, it will be essential to understand in what ways this environmental variable shapes these animals. As the Arctic continues to warm and undergo rapid environmental change, many beluga populations will soon face conditions that diverge sharply from those they have experienced in the recent past. This will increase the requirements to adapt (De Greef et al. 2025). The long-term persistence of beluga populations in markedly different habitats indicates that local adaptation has contributed to population divergence over evolutionary timescales. This history of adaptation suggests that belugas possess some capacity to respond to environmental change, including conditions that overlap with those projected for parts of the Arctic under continued warming. The St. Lawrence Estuary population demonstrates that beluga whales can adapt to environmental shifts, at least when populations are stable and free from major external pressures. The St. Lawrence Estuary population is now small and endangered, likely as a result of a drastic reduction in numbers during commercial whaling (Reeves and Mitchell 1984; Vladykov 1944). Before these targeted hunts, this population was larger (DFO Canadian Science Advisory Secretariat Science Advisory Report 2024), suggesting that its transition from the Arctic to the non-Arctic conditions was successful. This evolutionary precedent suggests that, if Arctic beluga whales are protected from additional stressors, and given enough time, they may potentially have the capacity to adapt to the changing climate they will encounter in the decades to come. However, adaptive responses occur over generational timescales and are shaped by population size, connectivity, and the rate of environmental change, meaning that past adaptation does not guarantee future resilience (Pelletier and Coltman 2018; Razgour et al. 2019). Understanding how local adaptation has

shaped beluga populations therefore provides important context for assessing their vulnerability and adaptive potential in a rapidly changing Arctic and highlights the need to incorporate evolutionary processes into conservation and management planning.

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Competing interests:

The authors have no relevant competing interests to disclose.

Data availability

Data have been deposited to BioProject under ID PRJNA1182041 and ID PRJNA984210.

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Author contributions

Claudio Müller: Conceptualization, methodology, analysis, writing – original draft & editing. Jaanus Suurväli: Methodology, writing – editing. Evelien de Greef: Methodology, writing – editing. Cortney A. Watt: Writing – editing, Steven H. Ferguson: Writing – editing. Colin J. Garroway: Conceptualization, methodology, analysis, writing – editing.

Tables & Figures

Table 4.1: Significant SNPs linked to environmental variables for Canadian beluga whale populations. The “SNPs total” column indicates the total number of significant SNPs linked to the “Variable”. The three “Overlap” columns indicate how many of the SNPs were also among the significant SNPs present among the candidate SNPs based on the two models without environmental variables, and how many were present in both. The “Complete overlap” column indicates the Overlap with PCAdapt & LFMM-K6 as a percentage of the SNPs total column.

Variable	SNPs total	Overlap with PCAdapt	Overlap with LFMM-K6	Overlap with PCAdapt & LFMM-K6	Complete Overlap
Temperature	10	8	7	7	70.0%
Chlorophyll	1,062	921	1,007	918	86.4%
Ice thickness	4,178	1,132	218	206	4.9%
Arctic	4,947	3,329	4,648	3,271	66.1%
Migration (long)	22	22	4	4	18.2%
Migration (short)	7	7	2	2	28.6%

Table 4.2: Output from Gene Ontology enrichment analysis for Canadian beluga whale populations. signSNPs shows the number of significant adaptive SNPs identified in each model. The GO-terms and genes columns show how many functional terms and how many genes linked to at least one GO-term were in the dataset compared to the background narwhal genome environment (one gene can cover multiple GO-terms; therefore, the GO-term count can exceed the number of actual genes). Significant GO-terms and significant genes columns show how many functional terms and genes from that data set showed a significant degree of enrichment amongst the adaptive SNPs. genes/signSNPs shows the relative numbers of genes in the enrichment analysis compared to the number of significant genes found in the model, while enrichGenes/signSNPs shows how many percentage of the original SNPs were associated with a gene that was significantly overrepresented.

model	sign SNPs	GO-terms	genes	significant GO-terms	significant genes	genes/signSNPs	enrichGenes/signSNPs
PCAdapt	12,888	3,573	1,699	85	692	13.18%	5.37%
Ifmm_K6	25,081	3,856	2,507	57	933	10.00%	3.72%
Chlorophyll	1,062	1,276	190	0	0	17.89%	0.00%
Ice thickness	4,178	2,467	585	0	0	14.00%	0.00%
Arctic	4,946	2,765	758	37	123	15.33%	2.49%

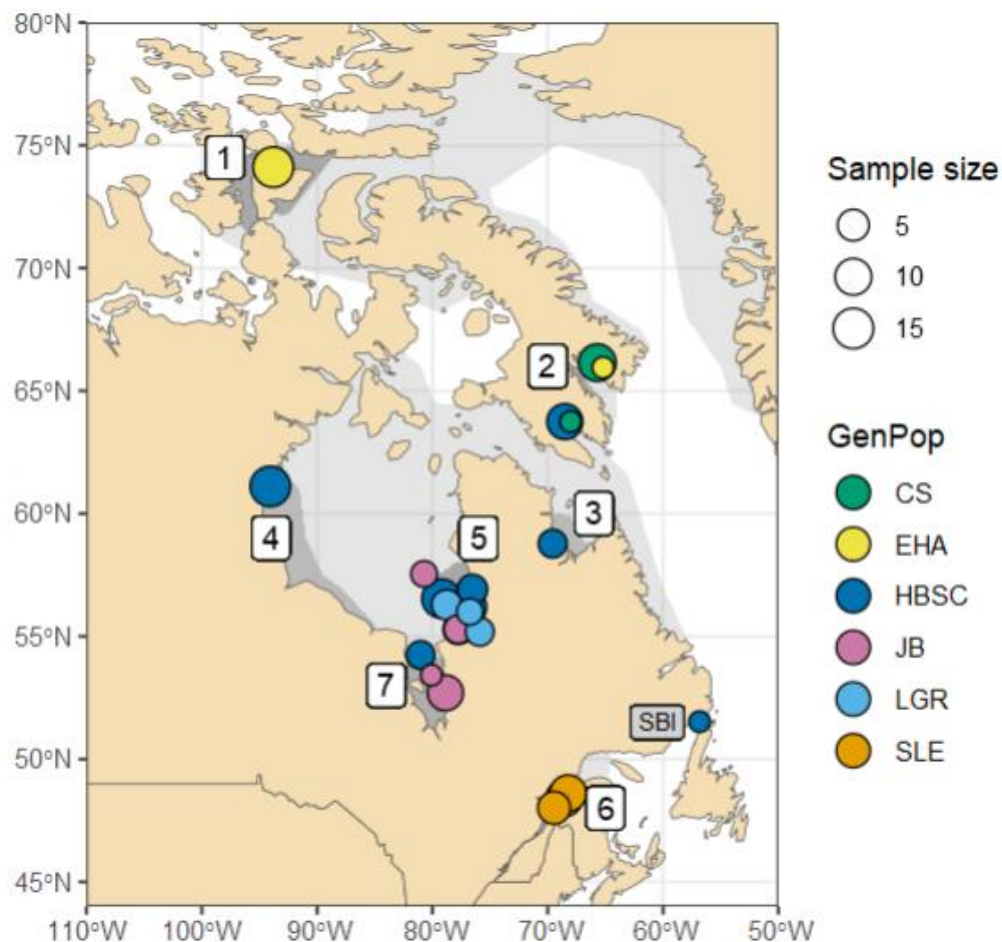


Figure 4.1: Canadian beluga stocks and range. Dark grey areas show summer habitats; light grey areas show seasonal migration range. Designated stocks are: (1) Eastern High Arctic-Baffin Bay, (2) Cumberland Sound, (3) Ungava Bay, (4) Western Hudson Bay, (5) Eastern Hudson Bay, (6) St. Lawrence Estuary and (7) James Bay (COSEWIC 2020). The dots show the sampling locations; their sizes reflect the number of samples coming from each location. The colors represent the genetic populations the samples belong to based on Müller et al. 2026 (CS=Cumberland Sound, EHA=Eastern High Arctic-Baffin Bay, HBSC=Hudson Bay and Strait Complex, JB=James Bay, LGR=Little and Great Whale River, SLE=St. Lawrence Estuary). SBI shows the Strait of Belle Isle.

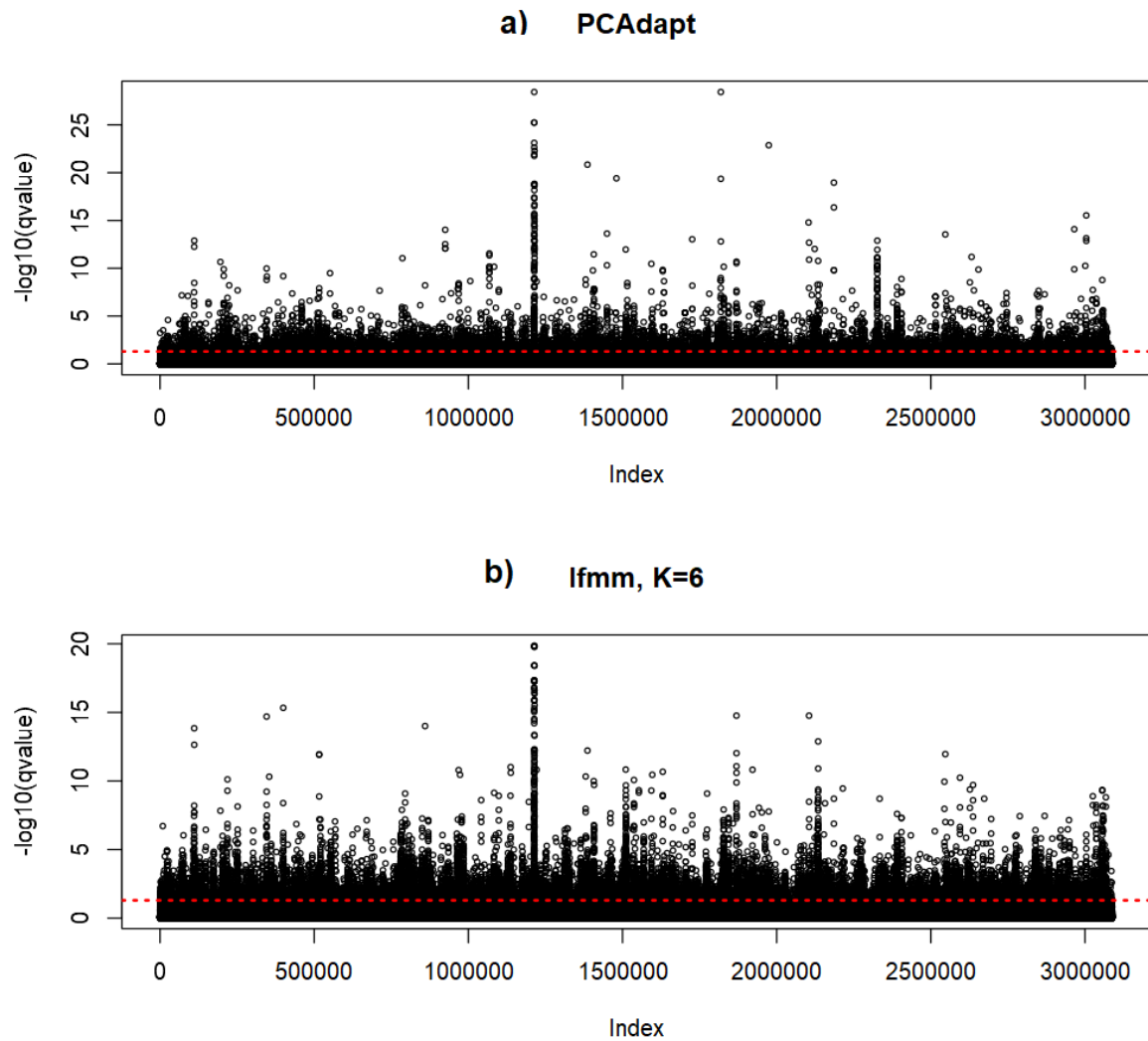


Figure 4.2: Genome scan results. Using a) PCAdapt and b) lfmm using K=6 for Canadian beluga whale populations. The x-axis shows the SNP index number for each SNP, grouped by chromosome. The red line shows the cut-off value for significant outliers (q -value=0.05).

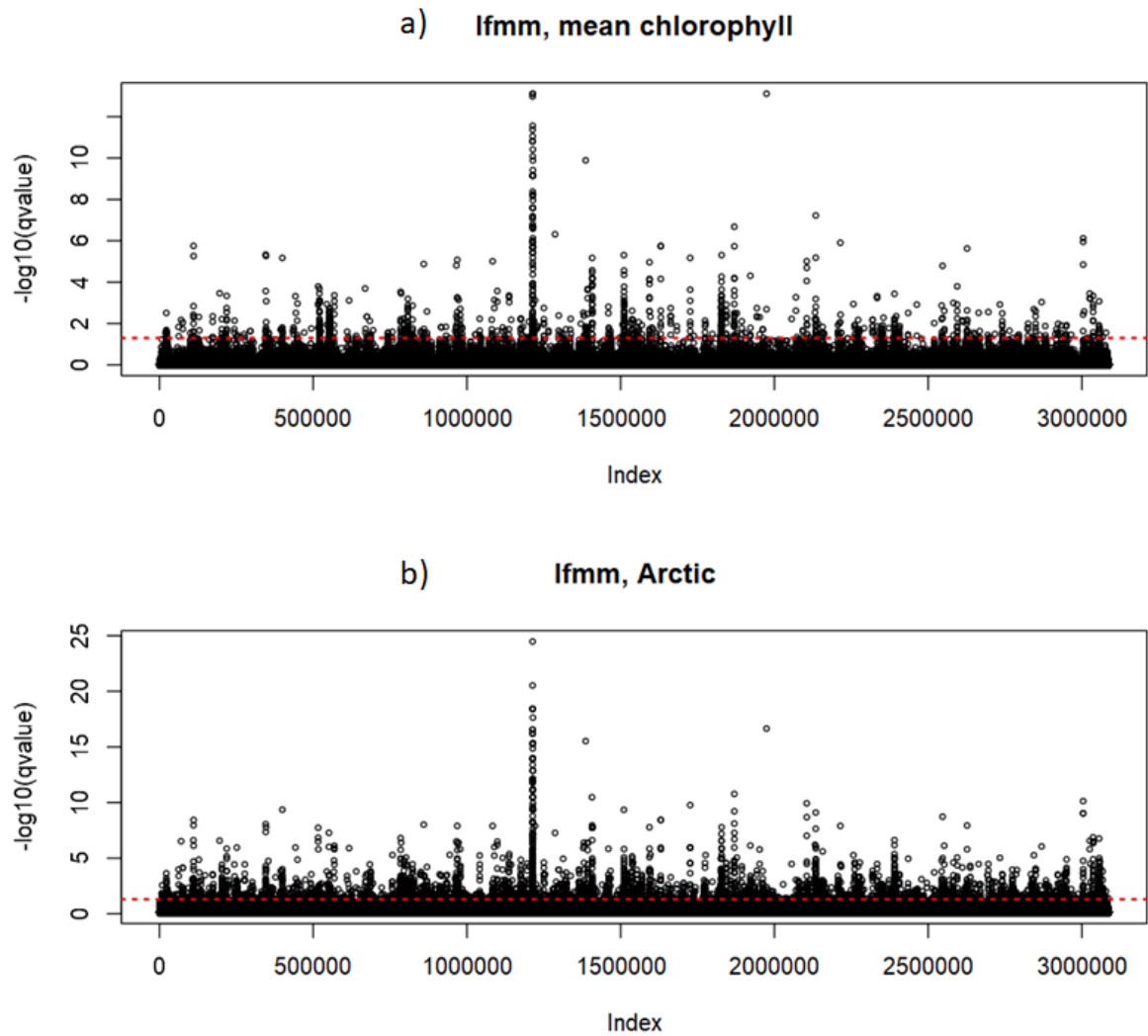


Figure 4.3: Results of LFMMs. Testing for links to a) chlorophyll concentration and Arctic vs non-Arctic environment for Canadian beluga whale populations. The x-axis shows the index number for each SNP, grouping each SNP by chromosome. The red line shows the cut-off value for significant outliers ($q\text{-value}=0.05$).

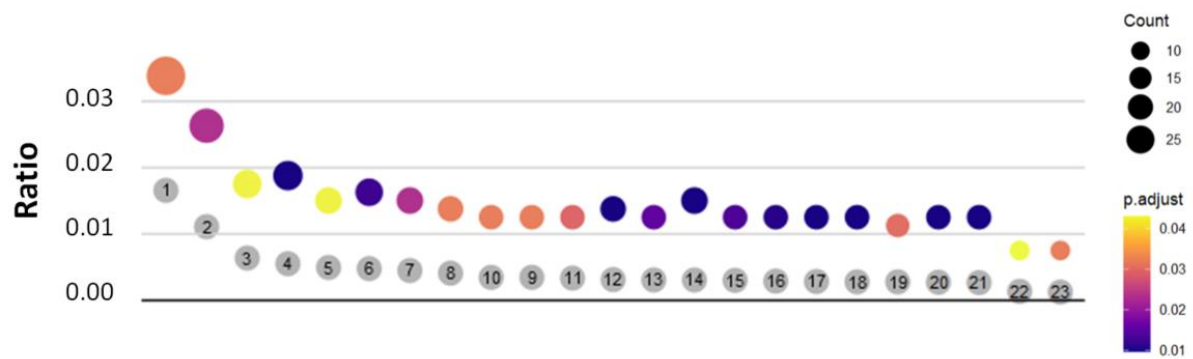


Figure 4.4: Gene Ontology enrichment results for the Arctic/non-Arctic model for Canadian beluga whale populations. The grey dots show the ratio of genes associated with the corresponding GO-terms relative to the total number of genes in the background gene of the narwhal. The numbers correspond to GO-terms and corresponding functions: (1) GO:0005925, function: focal adhesion; (2) GO:0005516, function: calmodulin binding; (3) GO:0008013, function: beta-catenin binding; (4) GO:0005201, function: extracellular matrix structural constituent; (5) GO:0008543, function: fibroblast growth factor receptor signaling pathway; (6) GO:0032869, function: cellular response to insulin stimulus; (7) GO:0048009, function: insulin-like growth factor receptor signaling pathway; (8) GO:0048013, function: ephrin receptor signaling pathway; (9) GO:0035176, function: vascular endothelial growth factor signaling pathway; (10) GO:0035176, function: social behavior; (11) GO:0038063, function: collagen-activated tyrosine kinase receptor signaling pathway; (12) GO:0048012, function: hepatocyte growth factor receptor signaling pathway; (13) GO:0031547, function: brain-derived neurotrophic factor receptor signaling pathway; (14) GO:0038145, function: macrophage colony-stimulating factor signaling pathway; (15) GO:0035791, function: platelet-derived growth factor receptor-beta signaling pathway; (16) GO:0005021 and GO:0038109, functions: vascular endothelial growth factor receptor activity and kit signaling pathway; (17) GO:0005005-GO:0005007 and GO:0005019, functions: transmembrane-ephrin receptor activity, epidermal growth factor receptor activity, fibroblast growth factor receptor activity, platelet-derived growth factor beta-receptor activity; (18) GO:0005008-GO0005011

and GO:0005018 and G:0005020 and GO:0008288 and GO:0035790 and GO:0036332 and GO:0038062, functions: hepatocyte growth factor receptor activity and insulin receptor activity and insulin-like growth factor receptor activity and macrophage colony-stimulating factor receptor activity and platelet-derived growth factor alpha-receptor activity and stem cell factor receptor activity and boss receptor activity and platelet-derived growth factor receptor-alpha signaling pathway and placental growth factor receptor activity and protein tyrosine kinase collagen receptor activity; (19) GO:0140789, function: histone phosphatase activity; (20) GO:0036323, function: vascular endothelial growth factor receptor-1 signaling pathway; (21) GO:0005004 and GO:0060175, functions: GPI-linked ephrin receptor activity, brain derived neurotrophic factor receptor activity; (22) GO:0043401, function: steroid hormone receptor signaling pathway; (23) GO:0010906, function: regulation of glucose metabolic process. The colored dots show the same ratio of candidate SNPs for adaptation to Arctic vs non-Arctic environments from the beluga whales. The size of the colored dots represents the number of genes associated with each corresponding GO-term. The color represents the adjusted p-value for the deviation from the background ratio for each GO-term. Dots associated with multiple GO-terms indicate ratios made up by genes that correspond to the same set of GO-terms.

CHAPTER 5: CONCLUSION

As we leave the first quarter of the 21st century, it has become increasingly apparent that, as my supervisor once phrased it, we seem to be "committed to climate change now".

Although we keep setting new goals for the reduction of greenhouse gas emissions (Seo 2017; UN Climate Change Secretariat 2025) and new limits on global temperature increases (Cointe and Guillemot 2023; Gao, Gao, and Zhang 2017), it is undeniable that anthropogenic climate change has become a noticeable reality in most parts of the world. Mitigating the effects of human-caused climate change is and will always be an essential part of research fields dedicated to environmental conservation. However, we also need to turn our attention to the question of how conservation efforts should look when we have already changed the planet to such an extent that it no longer provides the conditions to which most life was originally adapted. We also have to consider what it takes to maintain the unique beauty of our planet's biodiversity. Population genetics is one field that offers significant insight into biodiversity to answer this question. Genetics is one of the major frameworks underpinning the mere existence of biodiversity. It has shaped life on earth as it exists today, and it will continue to shape life under the new environmental conditions we are currently creating (De Greef et al. 2025; Markham and Malcolm 1996). Therefore, understanding this aspect of life better will be crucial if we want to be successful in our attempt to conserve earth's biomes.

My work aims to add to this complex undertaking. The first chapter of this thesis provided a framework to understand genetic diversity in marine mammals on a more holistic level than has been done before. One of the benefits of the study of biology in our modern age is the fact that I have been provided with more access to data for my field of study than any generation of researcher before me. Online data repositories allowed me to compile a data set of marine mammal populations and their genetic diversity that exceeds anything that any single researcher or even an entire laboratory of researchers could have collected only a

generation ago. It is impossible to gather genetic material from dozens of marine mammal species from hundreds of populations around the world, unless one has direct access to the work and data of countless dedicated researchers that came before; fortunately, this was a privilege I had for this project. This allowed me to discover previously unknown large-scale patterns in marine mammals. The inverse correlation between genetic diversity in marine mammal populations and sea surface temperature is a pattern that will probably become essential to keep in mind as the oceans warm with rising global temperatures. Meanwhile, it is important to understand the relationship between species-level genetic diversity and community level species richness. Understanding that these variables are negatively correlated puts the goal of preserving biodiversity into a new context, as it sheds light on the question of what metrics we should even use to define our goals. After all, if preserving the number of species in a given area does not correlate with preserving the genetic diversity of these species, all our preserved wildlife populations may not be resilient enough to withstand even small fluctuations in their environment.

This chapter can also be seen as a further piece in a long-standing project to map out the genetic diversity of the world's wildlife, as it builds and expands on the work of scientists that studied the genetic diversity of other animal groups on a global scale (Karachaliou et al. 2025; Schmidt 2022; Schmidt et al. 2020). Seeing where different ecosystems, taxonomic groups, and wildlife communities show the same genetic patterns is just as important as learning where they differ. Marine mammals fill a very unique niche in wildlife biodiversity, consisting of species that are often more closely related to other taxa on land than in their current environment (Shafer 2023; Timm-Davis and Marshall 2021). These animals have gone through very extreme changes. They evolved from life in the ocean to life on land, just to then return to the ocean (Uhen 2007). Given the environmental requirements of marine mammals and how much the world's oceans absorb a large part of the anthropogenic effects

on the climate (Heinze et al. 2015), the future of these animals holds the need for even more adaptation.

My first chapter also sheds light on a phenomenon that has become very apparent during previous studies on similar scales (Karachaliou et al. 2025): global distribution of research resources. While the data set I compiled for this chapter covered many species around the globe, it did so mainly in the northern hemisphere. This left massive gaps in the data set as only half of the planet is properly represented. While these gaps are not ideal for any study on global terrestrial patterns, it is arguably even more of an issue in the study of marine animals. After all, while most of earth's land is located in the northern hemisphere of our planet, most of its marine environment is in the southern hemisphere. If we really want to understand global biodiversity on a holistic level, then it is important to start allocating more of our research resources to the global south.

For the following chapters of this thesis I turned from broad patterns across marine mammals at the global scale to the narrower and more specific examination of Canada's beluga whales. This shift helps us to understand how these large-scale principles connect to a real conservation issue. By shifting from a global to a single-species level, these chapters showed how the genetic processes that shape biodiversity at a global holistic scale are equally important, though often more complex, within a single species' evolutionary history. The reconstruction of the demographic history of different Canadian beluga populations revealed that past environmental changes, like glacial cycles and recent anthropogenic pressures, have left an undeniable mark on these animals. However, the effect of these changes cannot be easily summarized. While some of the detected beluga populations have remained stable or even grown over time, others have exhibited sharp declines, depending on their geographic, historic, and environmental context. These findings demonstrate how genetic diversity is both a reflection of environmental history and a determinant of contemporary and future resilience toward environmental changes. While demographic history reconstruction and contemporary

effective population size of belugas have been studied before (Brown Gladden, Ferguson, and Clayton 1997; Gladden et al. 1999; Montana et al. 2024; Skovrind et al. 2021; Turgeon et al. 2012), the focus has always either been on a single genetic population or on the species in general. This is the first study that is not limited to individual, isolated groups but instead creates a complete picture of western Atlantic belugas that accounts for detailed population structure. Understanding genetic drift is absolutely vital for management and conservation efforts. It is the one evolutionary force that still shapes and alters the genetic make-up of a population, even if one reduces all selection pressures, all hunting, and all population reduction. Therefore, expressing the history and the current state of a population in terms of its genetic drift will become an important undertaking as we incorporate genetic metrics into conservation efforts.

My final data chapter dealt with local adaptation, a mechanism that, aside from genetic drift, is vital to understand this underlying population structure in beluga whales. We found clear evidence for local adaptation. There are many genetic regions that have clearly diverged more strongly between the Arctic and the St. Lawrence Estuary populations than mere drift would explain. Many of these regions are linked to functional genes that are overrepresented compared to their background frequency, pointing towards more targeted selection. In the case of Chromosome 19 they are part of a large, structural variance, potentially a huge genetic inversion sitting on the longer arm of that chromosome. There is even more evidence for local adaptation, as seen in the potentially adaptive SNPs linked to ice thickness. Given that ice thickness varies strongly between the Eastern High Arctic and the remaining Arctic populations (Parkinson and Cavalieri 2008), there is potential for more local adaptation between the Arctic populations themselves, once the strong signal from the St. Lawrence Estuary population is accounted for. Meanwhile, the results from the GO-enrichment analysis indicate that the local adaptation we have discovered so far is likely driven by specific functions which is worth investigating further. And as already seen in the first chapter, one of

the big, crucial environmental variables we have to take into account when it comes to marine mammal genomics is water temperature. It keeps appearing as a central variable linked to the genetic make-up of marine mammal genetic diversity, be it on a global, cross-species scale measured in neutral genetic markers, or in more local, species specific studies of genetic adaptation.

These results point to enormous potential for more discoveries yet to be made regarding the functional adaptation of these animals. Given how young these populations are on an evolutionary timescale, and the long generation time of beluga whales, such strong evidence for local adaptation potentially shaped by environment-specific selection warrants further investigation. While a lot of research in Arctic ecosystems often results in a pessimistic outlook for the future of the wildlife in this region, it is somewhat of a silver lining to know that these animals have already undergone significant adaptation to very different ecosystems in the past, and managed to adjust. It is surprising to find this silver lining in the St. Lawrence Estuary, where today, the local beluga population is of most concern due to excessive hunting in the recent past (Reeves and Mitchell 1984; Vladykov 1944). This just shows how essential it is to protect not just this species, but its distinct populations. After all, their unique genetics evidently holds a lot of potential for their future.

In its entirety, this thesis demonstrates the importance of a complete understanding of the vulnerability and resilience of wildlife populations. While large scale studies can provide important insight into the big picture of wildlife genetics and ecology, it is also essential to understand species on a more immediate, species- and population-scale level, where evolutionary history meets the pressures of the present and where conservation efforts can have the largest impact.

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