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Re-examining populations of beluga in the Hudson Bay-Strait Complex and assessing the impact on harvests in Nunavik and Sanikiluaq management units

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Belugas from the Hudson Bay-Strait Complex are harvested by hunters from Nunavik and Nunavut communities. In past studies, a genetic mixture analysis (GMA) was used to determine the contribution of animals from the Western Hudson Bay (WHB) and Eastern Hudson Bay (EHB) populations to harvests in the different management units. The population definition of WHB and EHB relied on short haplotypes from the mitochondrial (mt) DNA control region. However, studies with long haplotypes have shown that four populations could be identified in the Hudson Bay-Strait Complex. Here, we aim to 1) revisit the definition of populations within this area by resequencing and comparing short and long haplotypes for the mtDNA control region of 2 861 belugas, and 2) update the relative contribution of the newly-defined reference groups in management units using a GMA. Long haplotypes confirmed the existence of four previously defined populations, WHB, EHB, James Bay (JAM), and Cumberland Sound (CSB). They also allowed for the identification of a fifth population in the Belcher Islands (BEL). For the second objective, we tested the validity of the five populations using a leave-one-out approach and observed a high rate of erroneous assignments between EHB and BEL populations. Misassignments were due to shared genetic matrilineages and possible admixture during summer. Assignments were improved when EHB and BEL populations were combined in as a single reference named BEL-EHB stock. The GMA with the four new reference groups (WHB, JAM, CSB populations and BEL-EHB stock) led to higher proportions of the BEL-EHB stock in the fall harvest in Hudson Strait (5.6%) and Northeastern Hudson Bay (14.9%), and year-round in Sanikiluaq (3.3 to 61.2%), compared to previous studies using only two reference groups. Changes in reference groups, and not resequencing, likely caused most of the variation in the proportional estimate of the BEL-EHB stock in management units. Results from this study have increased the accuracy of the proportional contribution from reference groups to the harvest by the Nunavik and Nunavut (Sanikiluaq) communities.

INTRODUCTION

The beluga is a medium sized cetacean with an Arctic and sub-Arctic circumpolar distribution. Telemetry studies have shown that belugas in some areas undertake seasonal long-distance movements, whereas others can be considered as resident (O’Corry-Crowe et al. 2010). Belugas regularly exhibit philopatry to natal locations, in spite of persistent perturbations (Caron and Smith 1990; Smith et al. 1994; Lewis et al. 2009; Turgeon et al. 2012; Colbeck et al. 2013; Ouellet et al. 2021). The existence of genetic structure among belugas is likely a consequence of cultural and vertical transmission from mothers during repeated use of migratory routes, repeated seasonal movements, and preferred habitat (Brown Gladden et al. 1997; O’Corry-Crowe et al. 1997, 2002, 2010, 2018, 2020; de March et al. 2002, 2004; de March and Postma 2003; Meschersky et al. 2008, 2013; Turgeon et al. 2012; Colbeck et al. 2013; Skovrind et al. 2019). Other studies suggest a structure that is much more complex than just matrilineal dominance (Palsbøll et al. 2002; O’Corry-Crowe et al. 2020). It has been proposed that loss of some population components, particularly older animals, has resulted in loss of ecological knowledge within groups, and consequently limits potential for population recovery (O’Corry-Crowe et al. 2010, 2018, 2020; Colbeck et al. 2013; Whitehead 2017; Brakes et al. 2021; Bonnell et al. 2022).

Within the Hudson Bay-Strait Complex, genetic studies using the mitochondrial (mt) DNA control region (or D-loop) of beluga have identified distinct genetic groups, which are geographically segregated during the summer period (July and August, Fig. 1; de March et al. 2002, 2004; de March and Postma 2003). Early studies using short haplotypes (ca. 234 nucleotides) of the mtDNA control region identified that eastern Hudson Bay (EHB) and western Hudson Bay (WHB) animals had distinct haplotype compositions (Brown Gladden et al. 1997; de March et al. 2002, 2004; de March and Postma 2003). Later studies with longer haplotypes (ca. 609 nucleotides) have also suggested the genetic distinctiveness of individuals summering in James Bay (JAM) and Cumberland Sound (CSB, Turgeon et al. 2009; 2012; Postma et al. 2012; Postma 2017), which are considered to be year-round resident populations in their respective areas, showing little or no seasonal migration (Richard and Stewart 2009; Bailleul et al. 2012; Watt et al. 2020). In the Belcher Islands, both the existence of a local summer population and of an admixture of various beluga populations from Hudson Bay has been suggested (Turgeon et al. 2012; Postma 2017).

Philopatry to summering areas has led to the use of discrete summering aggregations as conservation units in the Hudson Bay-Strait Complex (e.g., Smith and Hammill 1986; Richard et al. 1990; Richard 2010; Mosnier et al. 2017). These conservation units have also been identified as Designatable Units (DUs), namely WHB, JAM, EHB, CSB, by the Committee on the Species of Endangered Wildlife in Canada (COSEWIC). These DUs are considered as discrete and evolutionarily significant units that would, if lost, likely not be replaced through natural dispersion (COSEWIC 2016).

Several Nunavik Inuit communities and some Nunavut communities hunt belugas for subsistence from an admixture of the EHB and WHB populations (Fig. 1). The EHB population numbers around 3,400 animals (Hammill et al. 2021), and was designated as Threatened by COSEWIC (2016). In contrast, the WHB population is an order of magnitude larger with approximately 54,000 animals (Matthews et al. 2017). Beluga harvests in Nunavik (northern Quebec) have been regulated using a combination of Total Allowable Takes (TAT), and seasonal and spatial closures, as defined in management plans, which are re-examined on a regular basis (Lesage et al. 2001).

In both Nunavik and Nunavut, hunters provide tissue samples from some of the belugas they harvest. These samples are haplotyped for the mtDNA control region to estimate the contribution of each population to the harvest in each of the defined management units (Fig. 2, de March and Postma 2003; Turgeon et al. 2009; Doniol-Valcroze et al. 2016; Mosnier et al. 2017). This information is then used to determine removals from the threatened stock summering in the Eastern Hudson Bay to remain within sustainability limits (Mosnier et al. 2017; Hammill et al. 2017; Hammill et al. 2021).

The proportion of belugas from different populations harvested in each of the management units in Nunavik and Nunavut (Sanikiluaq) are estimated using a genetic mixture analysis (GMA). In the past, the GMA was based on short mtDNA haplotypes and assessed the proportions of EHB and WHB populations harvested (Turgeon et al. 2009; Turgeon et al. 2012). This type of analysis was selected due to its robustness even with mtDNA haplotypes shared between populations (Turgeon et al. 2009; Doniol-Valcroze et al. 2016; Mosnier et al. 2017).

Only EHB and WHB populations have been used as references in past GMAs developed for the Nunavik and Sanikiluaq management units. Previous studies using three reference populations, namely WHB, EHB and CSB, suggested that a proportion of the belugas harvested by the southern Hudson Strait were from the CSB population (Turgeon et al. 2009; Turgeon et al. 2012). Those results were considered unlikely as the CSB population is quite small, on the order of ca. 1,000 animals, and is considered to remain in the Cumberland Sound area throughout the year. Instead, those results were attributed to haplotype sharing between WHB and CSB populations (Doniol-Valcroze et al. 2016; Marcoux et Hammill 2016). In recent assessments, WHB and EHB were therefore the only two populations considered in GMAs (Doniol-Valcroze et al. 2016; Mosnier et al. 2017; Hammill et al. 2021).

In this study, we sequenced all available samples collected between 1982 and 2021 to first re-examine the distinctiveness of populations in the Hudson Bay-Strait Complex by comparing short and long mtDNA haplotypes (Fig. 1). Previous studies extended the length of the control region sequenced from 234 to 609 nucleotides, which increased the number of variable nucleotides from 19 to 39 in samples from all of the Canadian DUs (Postma et al. 2012; Postma 2017). Short haplotypes were available on a large proportion of samples from animals harvested in the past four decades in the Nunavik and Sanikiluaq management units. In contrast, long haplotypes were originally only available for a subset of these samples due to time and funding limitations. We then estimated the proportional contribution of each of the newly-defined genetic groups to the harvest conducted in Nunavik and Sanikiluaq management units (Fig. 2). We contrasted these results with those obtained using only two reference populations and short haplotypes, and assessed the effect of resequencing on harvest allocations.

This document presents concepts from evolutionary biology and resource management, that can cause confusion in definitions. The terms “population” and “stock” have been associated with variable meanings in biology (e.g., Waples and Gaggiotti 2006; Stewart 2008; Cadrin 2020). In evolutionary biology, the term “population” is often used to define a group of interbreeding individuals that exist together in space and time (Waples and Gaggiotti 2006). For beluga, this definition of “population” captures the strong family genetic structure present geographically during the summer and the gregarious migration within the Hudson Bay-Strait Complex (Brown Gladden et al. 1997; de March et al. 2002, 2004; de March and Postma 2003; Turgeon et al. 2012). The expression “populations of belugas” also corresponds to the DUs used by COSEWIC for conservation efforts in Canada. In contrast, a stock is defined here as animals located in a management unit and may include more than one population. We consider a management unit as defined by a geographic area, restricted temporally, as used for harvest management. Note that the stock definition varies within the primary literature and DFO documents.

METHODS

SAMPLES

Tissues from 2,861 belugas harvested, biopsy sampled, or tagged between 1982 and 2021 in or close to the Hudson Bay-Strait Complex were selected (Fig. 1). The exact location where each animal was harvested was usually unknown and was attributed to the area in which the harvest event occurred (Table 1, see Table S1 for detailed information on each sample). Sampling metadata is usually provided for each sample but for some, only harvest month and year were available.

Most tissues were preserved in a saturated salt solution containing 20% dimethyl sulphoxide (DMSO) and 0.5 mol/L ethylene diamine tetraacetic acid (EDTA, Seutin et al. 1991). Some samples were only frozen while others were frozen first and preserved later using the DMSO solution.

HAPLOTYPING

DNA was extracted from all samples using DNeasy Blood and Tissue kit (QIAGEN, Valencia, USA). The long (615 nucleotides) sequences of the control region of mtDNA were amplified using primers and PCR conditions from Postma et al. (2012), with Multiplex PCR Kit (QIAGEN, Valencia, USA). Sequencing was processed as in Postma et al. (2012) using an ABI 3130 sequencer (Applied Biosystems Inc., Foster City, USA) at Maurice Lamontagne Institute.

Consensus sequences using the forward and the reverse sequencing outputs were produced and manually edited using Geneious Prime 2020.1 (Biomatters, Ltd, Auckland, New Zealand). Sequences were then aligned using the *muscle* algorithm available for the package Biostrings 2.62.0 (Pagès et al. 2021, penalties for gap opening: 10000, extension: 400) in R (R Core team 2022). The limits of the short and long haplotypes corresponded to the following positions in the complete mtDNA control region (Lillie et al. 1996): 126 and 359 (short), and 38 and 652 (long). Single nucleotide polymorphism (SNPs) were identified using the R package adegenet 2.1.5 (Jombart 2008; Jombart and Ahmed 2011). Haplotypes were defined using sequences without missing base pairs or ambiguities at SNPs. Both short and long haplotype were designated with unique numbers according to sequence libraries (Table S2, Table S3).

DEFINING AND VALIDATING REFERENCE POPULATIONS

To define reference populations, we first characterized the genetic composition of each summering area with a haplotype network (statistical parsimony network, PopART, Leigh and Bryant 2015) and in terms of number of polymorphic sites, number of haplotypes, private haplotypes (i.e., haplotypes specific to a summering area or a reference population), and haplotype diversity (adegenet and pegas 1.1 packages in R, Jambort 2018; Paradis 2010). The genetic distinctiveness between summering areas was also assessed with principal component analyses (PCAs) using haplotype frequencies (ade4 1.7.16 package, Dray and Dufour 2007).

We then evaluated the validity of genetically distinct populations as reference groups for a genetic mixture analysis (GMA). A self-assignment test was performed using the leave-one-out procedure (Anderson et al. 2008), which is available within the rubias 0.3.2 R package (Moran and Anderson 2019). Unique numbers of long haplotypes were used as input to the leave-one-out algorithm. The output is the posterior probability (hereafter, probability) of assigning a specimen to each reference group. We used the results to quantify the proportion of specimens that were correctly assigned to their original reference population at four probability thresholds: ≥95%, ≥80%, ≥60%, and ≥40%. In an ideal system, a well-defined reference population would result in a high accuracy (probability threshold ≥80%) of assignment for a high proportion (e.g. >80%) of the specimens. However, such accuracy is rarely achievable using a single genetic marker.

GENETIC MIXTURE ANALYSES (GMA) OF HARVESTS IN MANAGEMENT UNITS

The proportions of individuals belonging to reference groups per management unit or per period were estimated with a GMA performed using SPAM version 3.7b (Debevec et al. 2000; Alaska Department of Fish and Game 2003) as in Turgeon et al. (2009a).

Standard errors were also computed using a leave-one-out jackknife resampling procedure to remove, at each iteration, individuals hunted on the same date in the same area and account for autocorrelation between samples (as previously done by Doniol-Valcroze et al. 2016).

The Pella-Masuda Bayesian mixture analysis method was selected in SPAM to allow for the possible occurrence of unknown reference groups (see Mosnier et al. 2017). Unknown reference groups may contribute to the harvested belugas, as in previous assessments.

In Hammill et al. (2021), GMA reference groups EHB and WHB were based on 206 and 132 individuals, respectively. In 2022, we used the sequences from 186 and 318 reference individuals for EHB and WHB, respectively. Reference individuals used in Hammill et al. (2021) and this study were identical for 98% for EHB (N = 183) and for 13% (N = 41) for WHB.

RESULTS

HAPLOTYPING

We obtained 2,861 high quality (no ambiguity) haplotypes from samples collected in 12 areas (Fig. 1, Table 1). A total of 43 short and 126 long unique haplotypes were identified from the 2,861 sequences (Table S1, Table S2, Table S3). Individuals from South Hudson Strait (SHS) and South West Hudson Bay (SWH) represented the largest (N = 1,372) and smallest number (N = 17) of individuals per area (Table 1), respectively.

From the 2,861 individuals, a subset of 1,600 individuals were haplotyped for the short control region by both the Freshwater Institute (FWI) and Maurice Lamontagne Institute (MLI) facilities. The FWI and MLI facilities identified 35 and 33 short haplotypes, respectively. Thirty haplotypes, the most common haplotypes, were common to both datasets. Differences in haplotyping increased steeply from 1.5% for the two most abundant haplotypes to 4.9% for the six most abundant haplotypes, and 7.0% for all possible comparisons (i.e., 25 haplotypes with two or more samples; Fig. 3).

REVALUATING POPULATION STRUCTURE IN THE HUDSON BAY-STRAIT COMPLEX

Multiple complementary approaches were used to identify populations of beluga in the Hudson Bay-Strait Complex. Using a subset of 1,136 individuals sampled during July and August from 11 areas (Table 1) we first investigated the haplotypic specificity of animals within summering areas using networks with both haplotype lengths. Eastern and western haplogroups were separated by two and four mutations for the short and the long haplotype networks, respectively (Fig. 4). In both the long and short haplotype networks, the vast majority of Eastern Hudson Bay (EHB) beluga samples had a haplotype from the eastern haplogroup (77% for both lengths).

The western haplogroup included mostly samples from Western Hudson Bay (WHB; North Hudson Bay: NHB, North West Hudson Bay: NWH, and South West Hudson Bay: SWH) but also those from all other summering areas. Haplotypes highly specific to Cumberland Sound (CSB) were observed in both networks in the western haplogroup (e.g., short: HS014; long: HL024; Fig. 4). Haplotypes highly specific to James Bay (JAM) and Long Island (LON) were observed in both haplogroups (e g., short: western HS029, eastern HS017, Fig. 4a; long: western HL070, eastern HL038, Fig. 4b). In all regions, the number of haplotypes, the haplotype diversity, and the number and proportion of private (only present in one summer area, Fig. 1) haplotypes were higher for long than short haplotypes (Table 2). The highest proportion of private haplotypes for both haplotype lengths was observed in CSB (Table 2). The haplotypic diversity in JAM was the lowest using both haplotype lengths. For the short haplotype, only CSB had a proportion of private alleles > 5%. For the long haplotypes, CSB, LON, NWH, and EHB all had proportions of private haplotypes > 5% (Table 2). Using long haplotypes, the high haplotypic specificity of animals within summering areas suggests that WHB, JAM, LON, EHB, and CSB form different populations.

The principal component analyses (PCAs) identified different numbers of distinct summering aggregations using frequencies of short and long haplotypes. For the short haplotypes, the PCA results showed three groups, consisting of EHB, JAM/LON, and all other summer aggregations (Fig. 5a). For the long haplotypes, EHB, JAM, LON, and Belcher Islands (BEL) were each separated from all other summering aggregations (NHB, NWH, SWH, South Hudson Strait: SHS, Ungava Bay: UNG, Frobisher Bay: FRB, CSB), indicating five distinct genetic groups (Fig. 5b). For the long haplotypes, JAM and LON have very similar haplotype frequencies (Table S4). In addition, the two most abundant haplotypes in JAM and LON were the same (HL008, HL070; Fig. 5b, Table S4). These results suggest that JAM and LON form a single population (JAM population will include LON individuals hereafter). In contrast, the two most abundant haplotypes in EHB (HL009, HL016) are different from those of BEL (HL001, HL022; Table S4). We tested further if BEL animals differed from other genetic groups with a third PCA of long haplotype frequencies from populations (EHB, WHB, JAM, CSB) and from management units (considering areas and seasons; Fig. 2). In this PCA, WHB, JAM, EHB, and CSB populations separated from each other (Fig. 6). Haplotype frequencies from BEL across the four seasons formed a separate cluster from other genetic groups in the PCA (Fig. 6), also suggesting that a distinct population inhabits the Belcher Islands.

Five populations were identified within the summering areas with long haplotypes, namely WHB, JAM, EHB, BEL, and CSB. The leave-one-out approach showed an increasing proportion of correct assignment to reference groups with decreasing threshold of posterior probability, except for the CSB population which plateaued at 39.1% at a ≥ 60% probability threshold. Such a result is expected since the CSB population shares multiple haplotypes with WHB (Fig. 6). A large proportion (> 75%) of individuals was assigned correctly to WHB and JAM populations at a ≥ 40% probability threshold (Table 3). In contrast, lower proportions of individuals were assigned to the EHB (69.4%) and BEL (19.7%) populations at a ≥ 40% probability threshold (Table 3). Grouping EHB and BEL populations as BEL-EHB stock increased the proportion of reassignments to BEL-EHB stock (84%) at a ≥ 40% probability threshold (see “Four populations and BEL-EHB stock” in Table 3). Proportions of correct assignments were identical for WHB, JAM and CSB at all probability thresholds for both assignment tests (Table 3).

ESTIMATING HARVESTED PROPORTIONS OF REFERENCE GROUPS IN MANAGEMENT UNITS

We estimated the proportions of new reference groups (WHB population, JAM population, BEL-EHB stock, and CSB population) harvested by the Nunavik and Sanikiluaq communities in the different management units using the long haplotypes. The proportions of animals from the BEL-EHB stock harvested in Hudson Strait (12.3%) and Ungava Bay (4.7%) in spring were similar to previous estimates (Hudson Strait: 11.7%, Ungava Bay: 6.0%, Tables 4 and 5). Increases of proportion EHB beluga harvested were observed in the fall for Hudson Strait (44.0%) and Northeastern Hudson Bay (50.1%), respectively, compared with the previous estimates (Hudson Strait: 29.1%, Northeastern Hudson Bay: 44.5%, Tables 4 and 5). In Hudson Strait, dividing the fall samples into a finer time scale did show that the proportion of BEL-EHB stock in harvest declines late in November (Table 7). We observed the largest increases, ca. 60%, in the proportion of BEL-EHB stock harvested, in samples from the spring and fall from Sanikiluaq (Tables 4 and 5). Similar proportions of harvested BEL-EHB stock were observed between the current estimates and the previous assessments (Tables 4 and 5).

The JAM or CSB populations represented small proportions of harvested animals in the Northeastern Hudson Bay, Hudson Strait, and Ungava Bay management units (Table 5). In these management units, the highest proportion of JAM and CSB populations were harvested in Northeastern Hudson Bay in fall and Hudson Strait in spring, respectively. In Sanikiluaq, the JAM population was more frequent in spring and winter harvests compared to those of fall (Table 5). No CSB animals were harvested in Sanikiluaq (Table 5).

In all management areas, the proportion of individuals associated with an unknown population is significantly lower than in the last assessment, especially Sanikiluaq in spring and winter. (Tables 4 and 5). The proportions of unknown were still the highest in the Sanikiluaq management units with the current estimates (Table 5).

QUANTIFYING THE EFFECT OF CHANGES ON GMA

We quantified the effect of resequencing and changes in reference populations on estimates of the proportion of BEL-EHB stock in the harvest per management unit (short haplotypes from 1,517 individuals). The resequencing effect resulted on average in a 4.3% (± SEM 1.0%) change in the estimated proportion of BEL-EHB stock harvested per management unit. The largest resequencing effect (12.0%) on the proportion of BEL-EHB stock harvested was observed in Sanikiluaq during winter (Table 6).

DISCUSSION

In this study, we revisited the short and long mtDNA control region sequences and refined the number of populations from four to five within the Hudson Bay-Strait Complex. Our results using the long haplotypes confirm that WHB, JAM, EHB, and CSB are distinct populations. It also identifies that beluga harvested around the Belcher Islands (BEL), have a genetic composition that is distinct from WHB. From a conservation perspective, the BEL population should be considered as a newly described distinct evolutionary unit, i.e. another Arctic beluga population. However, the performance of the GMA when BEL and EHB populations were used as independent references was reduced by haplotype sharing between the two. It is also currently impossible to separately estimate the abundance of BEL and EHB beluga since they overlap spatially and temporally during summer surveys. Therefore, a more parsimonious approach is to consider the combined abundance of the BEL and EHB populations as a BEL-EHB stock from both stock assessment and management perspectives. The greatest impact of combining the BEL and EHB populations was the increased proportions of BEL-EHB stock animals harvested year-round in Sanikiluaq management unit. In Nunavik, the increase in estimates of BEL-EHB stock harvested over the season is variable, but it is larger in fall in northeastern Hudson Bay compared to the Hudson Strait. Altogether, this study provides a more reliable tool for the management of all of the DUs in the Hudson Bay-Strait Complex (COSEWIC 2016).

FIVE POPULATIONS IN THE HUDSON BAY-STRAIT COMPLEX

Our results confirm that the mtDNA control region can characterize population structure of beluga summering populations in the Hudson Bay-Strait complex (Brown Gladden et al. 1997; de March and Postma 2003; Turgeon et al. 2012; Postma 2017). They also confirm the separation of haplotypes into two haplogroups that are broadly geographically restricted, i.e., western and eastern haplogroups (Postma 2017). WHB and EHB populations were detected, confirming results from past studies (Turgeon et al. 2009; Turgeon et al. 2012). Our findings also highlight the necessity to consider three new populations in the Hudson Bay-Strait Complex, namely JAM, CSB, and BEL. Their genetic composition using the long haplotypes is distinct from those of WHB and EHB.

Analyses of long haplotypes highlighted the specificity of the JAM population, which was also observed in previous studies (Postma et al. 2012; Postma 2017). Our study also showed the similarity between the haplotype frequencies of JAM and LON individuals during summer. Previous studies suggested the presence of individuals with haplotypes from the EHB haplogroup in LON area during summer (Postma et al. 2012; Postma 2017). Although this is consistent with our results, JAM and LON have similar most abundant haplotypes, which are different from those of EHB. JAM and LON have highly specific haplotypes from both western (e.g., HL070, HL072, HL074) and eastern haplogroups (e.g., HL038). Together, those results suggest that the majority of individuals harvested from LON are part of the JAM population. This is consistent with the current management framework which groups catches from the Long Island area with those from James Bay (Fig. 1b).

The CSB population had the highest proportion of private haplotypes with both the short and long haplotypes. There was also a large proportion of haplotypes shared with the WHB population, which is consistent with previous studies (de March et al. 2002, 2004; Turgeon et al. 2009; Turgeon et al. 2012; Postma 2017). Satellite telemetry data indicate that CSB beluga whales form a distinct population that inhabits the area year round (Richard and Stewart 2009). Alternatively, traditional knowledge indicates that different types of beluga whales visit CSB each year (Kilabuk 1998; Watt et al. 2020). The mixed composition observed in the summer in CSB could reflect both telemetry and traditional knowledge information, and may suggest the occurrence of both migratory and resident individuals.

The analyses of the long haplotypes identified BEL individuals as forming a distinct population. With the short haplotype, the BEL population was grouped with the WHB population, mostly due to haplotype sharing. However, the long haplotype showed that the most abundant haplotypes from the western haplogroup differed between the WHB (HL003) and BEL (HL001) populations. Moreover, BEL did not share its two most abundant haplotypes with EHB, although they shared a few non-abundant haplotypes that are part of the eastern haplogroup. These results support those from previous studies showing that 20% of individuals harvested in the Belcher Islands had private or highly specific long haplotypes or mitogenomes (Turgeon et al. 2012; Postma 2017). The larger sample sizes used in the present study show that the Belcher Islands belugas form a distinct population, similar to other DUs of beluga in the Arctic (COSEWIC 2016).

No reference population was identified in other summering areas, namely SHS, UNG and FRB. In these areas, the two most abundant haplotypes were HL001, and HL003, which are abundant haplotypes in the WHB population. There were no or few private haplotypes detected for the long sequences in SHS, UNG, and FRB, suggesting that there are no endemic populations summering in these areas. The Hudson Strait is acknowledged as a migration corridor and a wintering area for the WHB and EHB populations (Finley et al. 1982; Bailleul et al. 2012). However, it also appears that individuals form a mixture of the WHB and EHB populations summer in the Hudson Strait area. These represent very few animals detected in summer aerial surveys in Hudson Strait during the 1980s, 2008 and 2010, but survey effort has been limited in this area (Fig. 7, Finley et al. 1982; Gosselin et al. 2009; Gosselin, J.-F. personal observations).

FOUR REFERENCE GROUPS IN THE HUDSON BAY-STRAIT COMPLEX

We identified four valid reference groups for the GMA when considering a ≥ 40% probability threshold for self-assignment rates: the WHB, JAM, and CSB populations and the BEL-EHB stock. Self-assignment rates were high for WHB and JAM either with five reference populations or four reference groups. These results are in agreement with previous studies highlighting that WHB and JAM populations had distinct genetic compositions (Turgeon et al. 2012; Postma et al. 2012; Postma 2017). With both sets of reference groups, CSB self-assignment rates were lower (39%) than those of WHB and JAM at a ≥ 40% probability threshold. Private haplotypes and a large proportion of haplotypes shared with WHB explain these low self-assignment rates for CSB, which are also consistent with previous studies (Turgeon et al. 2009; Turgeon et al. 2012). Self-assignment rates were poor (19.7%) for the BEL population and acceptable (69.4%) for the EHB population when considering five reference populations. This is likely due to sharing between the BEL and EHB populations of multiple non-abundant haplotypes from the eastern haplogroup. Haplotype sharing between BEL and EHB populations may be due to shared lineages. Alternatively, telemetry research has shown movement between the mainland and the Belcher Islands (Bailleul et al. 2012).

The use of EHB and BEL summering individuals as a single reference group, identified as a BEL-EHB stock, considerably improved the self-assignment rates. The term “BEL-EHB stock” is used here to define the grouping of BEL and EHB populations and describe the genetic composition of animals summering in eastern Hudson Bay that are counted during aerial surveys (St-Pierre et al. in prep.[1]). In past documents (e.g., Hammill et al. 2017; 2021), the animals summering in these areas were described under the term “EHB stock”. The use of the term “BEL-EHB stock” now captures the change in the definition of the genetic composition of those animals, indicating the combination of two populations within a same space (eastern Hudson Bay).

HARVESTED BEL-EHB STOCK INCREASED IN SOME MANAGEMENT UNITS

The large increases in the proportions of beluga harvested from the BEL-EHB stock observed in Sanikiluaq was mainly due to the addition of the BEL population to the BEL-EHB stock. The capacity of the long haplotype to discriminate BEL from WHB populations allowed for an improved genetic definition of belugas summering in the eastern Hudson Bay region. Using short haplotypes, previous assessments identified animals harvested year round in the Belcher Islands mostly as WHB animals (e.g. Hammill et al. 2021). Results from this study using long haplotypes support the hypothesis that harvests of beluga by the Sanikiluaq community are mostly from a population specific to the Belcher Islands (Turgeon et al. 2012; Postma 2017). This analysis also shows that previous analyses have likely underestimated the impact of harvesting on animals summering in the eastern Hudson Bay area.

Within Nunavik management units, the proportion of belugas harvested during the spring hunt in Ungava Bay and Hudson Strait pertaining to the BEL-EHB stock were similar to past estimates. The 4.7% BEL-EHB stock estimated in the Ungava Bay spring hunt corresponds approximately to the 6% ratio in abundance estimates between the BEL-EHB stock and WHB populations

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[1] St-Pierre, A.P., Gosselin, J.-F., Mosnier, A. and Hammill, M.O. Abundance estimates for beluga (*Delphinapterus leucas*) in James Bay and the Belcher Islands-eastern Hudson Bay area in summer 2021. DFO Can. Sci. Advis. Sec. Res. Doc. In preparation.

(6% = 3300/(3300+54000), Matthews et al. 2017; Hammill et al. 2021). However, the proportions of BEL-EHB stock estimated in the spring hunt in Hudson Strait and in the fall hunt in Hudson Strait or Northeastern Hudson Bay were larger. In the latter areas, approximately half of the harvested animals are estimated to belong to the BEL-EHB stock, representing a much greater proportion than expected based on the relative size of the BEL-EHB and WHB populations. The estimated proportion of BEL-EHB stock animals in the fall hunt in Hudson Strait and Northeastern Hudson Bay is also higher than in the previous assessment. Considering that the BEL population is now contributing to the definition of the genetic composition of the BEL-EHB stock, this result suggests that a fraction of the BEL population may also migrate out of the Hudson Bay along with individuals from the EHB population. The other fraction of the BEL population likely overwinters in the Belcher Islands, as animals harvested during winter had similar genetic composition to those harvested in summer. In Hudson Strait, sample sizes were large enough to test for changes in the proportion of BEL-EHB stock animals in the hunt during November. Proportions of BEL-EHB stock were high (51.5%; 95% confidence interval: 39.0-63.9%) in early November and decreased to 10.4% late November (95% confidence interval: 0.9-29.5%; Table 7).

PROPORTIONS OF JAM, CSB, AND PUTATIVE OTHER POPULATIONS WERE LOW IN ALL MANAGEMENT UNITS

Small proportions of JAM and CSB populations were harvested in Hudson Strait, Ungava Bay, and Northeastern Hudson Bay, while a larger proportion of the JAM population was harvested by the Sanikiluaq community during the spring and winter. Some individuals of the JAM population may overwinter near Belcher Islands in areas of loose ice (polynya) (McDonald et al. 1997). We also observed smaller proportions of the JAM population in Hudson Strait in spring and in Northeastern Hudson Bay in fall, suggesting the movement of some JAM belugas outside of James Bay and Belcher Island areas. These results contrast with telemetry data obtained from 23 animals tagged in James Bay that showed no seasonal migration (Bailleul et al 2012); however, the number of tagged animals was small relative to the overall estimated population of 19,200 animals and likely captures only a fraction of the possible movement patterns of animals in this population (Hammill et al. in prep.[2]). In contrast, we did not detect any individuals from the CSB population in Hudson Bay, in agreement with a previous study (Turgeon et al. 2012). The presence of CSB animals in Hudson Strait and Ungava Bay is interesting and has been reported elsewhere. This underlines the complexity of beluga social behavior where some animals may be resident, while others may undertake larger scale migrations (Richard and Orr 1986; de March et al. 2004; O'Corry-Crowe et al. 2010, 2020). Note that the GMA may underestimate harvest of the CSB population for individuals bearing frequent haplotypes in the WHB population. We did not encounter a bias from the WHB population towards the CSB population with the GMA, whereas this bias was important for the management regions from the Eastern Hudson Bay in a past study (Doniol-Valcroze et al. 2016). The larger number of reference individuals from WHB has likely limited this effect.

Proportions of unknown reference groups were lower than those from the past genetic mixture analyses in most management units. This can be explained by the incorporation of the BEL population into the BEL-EHB stock. Still, proportions of unknown reference groups were larger in the Sanikiluaq management units. We examined the haplotype frequencies of Sanikiluaq harvest samples in spring, fall, and winter. The large proportion of HL001, BEL's most abundant

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[2] Hammill, M.O., St-Pierre, A.P., Mosnier, A., Parent, G.J., and Gosselin, J.-F. Total abundance and harvest impacts on Eastern Hudson Bay and James Bay beluga 2015–2022. DFO Can. Sci. Advis. Sec. Res. Doc. In preparation.

haplotype, across seasons, suggests that some components of the local population (BEL) may overwinter in the Belcher Islands area. We also identified haplotypes (i.e., HL036, HL037, HL089, HL131, HL132, HL133, HL134, HL135) harvested only in the Sanikiluaq spring, fall, and winter management units, suggesting that additional unknown populations may overwinter around the Belcher Islands. We know of at least two other groups of beluga that have been observed in the south of Hudson Bay, which have little to no genetic data available for analysis. In this study, the SWH summer aggregation is represented by a small sample size (N = 17) and previous studies have suggested some genetic specificity in that region (Turgeon et al. 2009; Postma 2017). There is also a large group of beluga whales often observed in the northwestern part of James Bay during aerial surveys (Gosselin et al. 2013), which has never been characterized genetically.

NEW REFERENCE POPULATIONS/STOCK, NOT RESEQUENCING, HAD THE LARGEST EFFECT ON HARVESTED PROPORTIONS

Resequencing explained a small change in the proportions of the BEL-EHB stock harvested (4.3%). Differences in sequencing results between the two facilities (FWI and MLI) can be explained mostly by changes in methodologies over the last 20 years. The haplotyping program for beluga management started in approximately 2000 at the FWI (de March and Postma 2003). In the early stage of haplotyping, error rates associated with Taq polymerase or sequencing technologies were higher. Consequently, singleton (unique haplotype) grouping with most abundant haplotypes was a procedure undertaken each year to improve the performance of GMA and avoid bias due to rare, potentially erroneous, haplotypes. With the years, Taq polymerase and sequencing technology error rates improved, while reducing haplotype grouping. We did not perform haplotype grouping with the MLI dataset, as error rates were likely negligible since all of the sequences were synthesized in the last year. Furthermore, the error rate was overall lower with the MLI database as all sequences were produced using consensus sequences, with forward and reverse sequencing outputs. To reduce cost, only forward sequencing was conducted for harvest samples at the FWI. Chromatogram interpretation is another potential source of error. At the FWI, a single technician reviewed the chromatograms, which reduces the error rate. At the MLI, we generated a standard operating procedure for the production of consensus sequences that could be transferred to any sequencing facility in the future. Since the resequencing effect was low, we can conclude that the major differences observed between results from previous GMA (Hammill et al. 2021) and those from this study were caused by the change in number of newly-defined reference groups, from two to four.

IMPROVING GENETIC CLASSIFICATION IN THE FUTURE

Genetic characterization of individuals from southern Ungava Bay was not possible in this study. The Ungava population experienced excessive commercial whaling in the late 19th and early 20th century and is currently designated as Endangered (COSEWIC 2016). This population has high site fidelity to the southern part of Ungava Bay in an area where hunting is restricted. A project started in 2018 in collaboration with the Nunavik Hunting, Fishing and Trapping Association (Regional Nunavimmi Umajulirijiit Katujjiqatigininga; RNUK), and conducted a few biopsies (n = 3) on beluga from this area, but there are not enough samples for inclusion in population structure analyses. Environmental DNA sampling is now being developed for beluga haplotying to limit the impact of harvest on these animals.

New genetic markers (mitogenomes, SNPs from the nuclear genome) may improve classification and assignment to reference populations of the Hudson Bay-Strait Complex. The mtDNA sequence cannot discriminate between seasonal migrants (not reproducing with the local population) or effective migrants (reproducing with the local population). Genetic markers derived from nuclear DNA could discriminate between the two types of migrants, if populations are genetically distinct at nuclear loci. Past studies using nuclear markers indicated some genetic differentiation between CSB or JAM with other populations, but not between WHB and EHB populations, which may interbreed (Turgeon et al. 2012).

Other proxies may also improve classification to reference populations of the Hudson Bay-Strait Complex. A previous study combining stable isotopes and trace elements was successful in defining summering stocks and their relative contributions to subsistence harvest in Nunavik (Rioux et al. 2012). Combining the characterization of stable isotopes, trace elements, and mtDNA haplotypes for control regions in each reference individual could help to identify different types of migrants and further reduce the uncertainty around classification of the WHB population and the BEL-EHB stock. Combining proxies while using these new reference populations based on the extended mtDNA sequence may complement genetic assignment and refine classification while reducing uncertainty.

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FIGURES

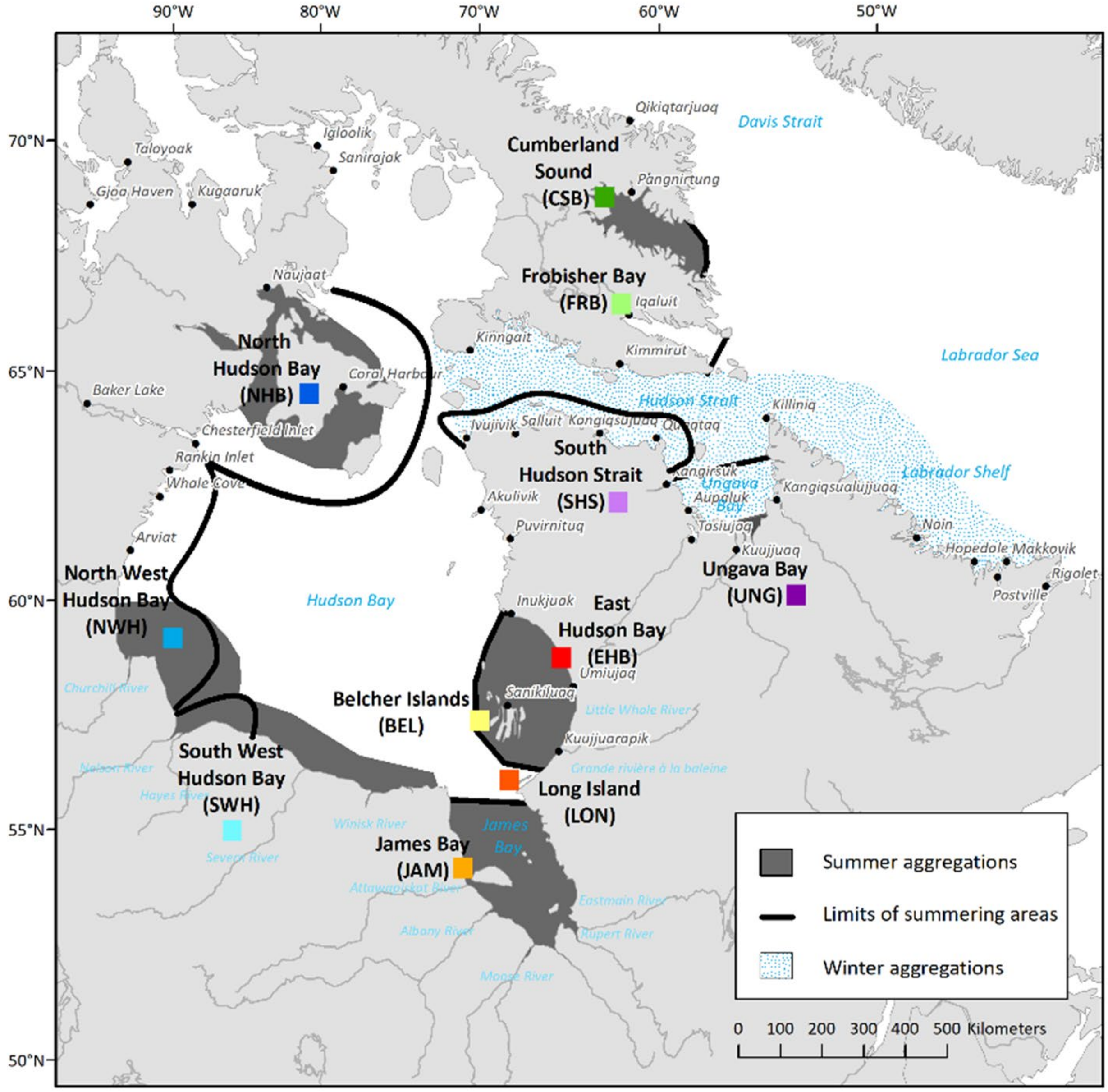

Figure 1. Geographic delimitation of summering areas investigated for population structure of beluga in the Hudson Bay-Strait Complex. Major Inuit communities (also harvest locations in Table 1) considered in each area are indicated but may not reflect all of the hunting regions of Inuit communities. The four largest summering aggregations indicated in dark grey (a) are western Hudson Bay (WHB), James Bay (JAM), eastern Hudson Bay (EHB) and Cumberland Sound (CSB, see Table 1 for all acronyms for summering areas). The WHB and the EHB are migrating through the Hudson Strait to the hypothetical winter area (dotted blue). Summering and wintering aggregations adjacent to Hudson Bay are reproduced from DFO (2002) or Hobbs et al. (2019).

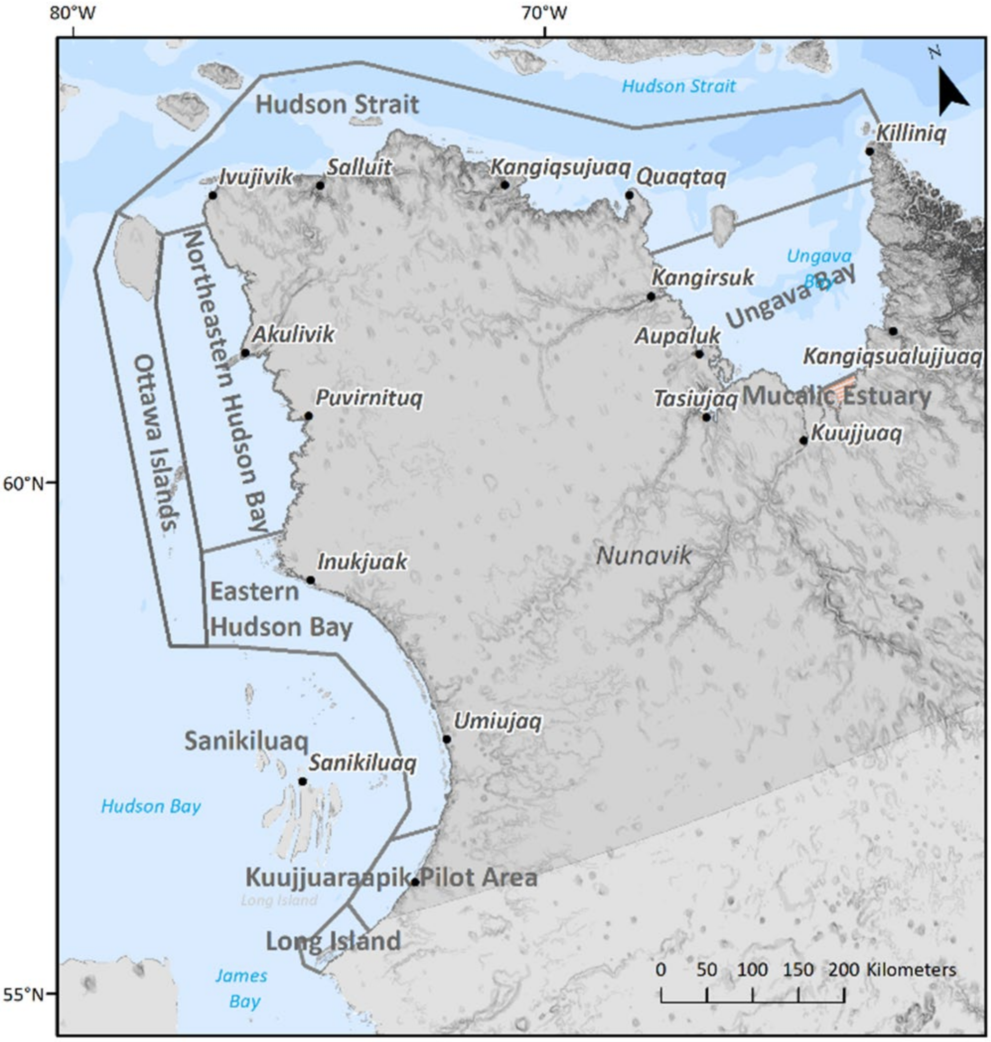

Figure 2. Nunavik management areas. The smaller management areas of the Nastapoka River and Little Whale River are not presented due to the scale of the map. There are no official geographic limits to the Sanikiluaq management area.

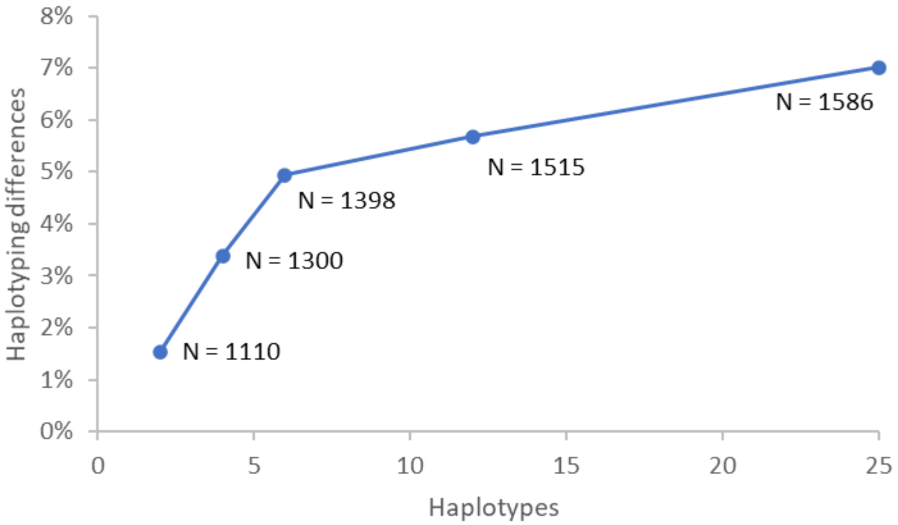

Figure 3. Increasing haplotyping differences with haplotype rarity between databases from the FWI and MLI facilities. Sample size are indicated as cumulative values for more abundant haplotypes (to the left) and combined with rarer haplotypes (to the right). This figure shows that haplotype discrepancies between both databases are not for the two most abundant haplotypes (N = 1110 samples) but for the 3 to 6 more abundant haplotypes. Rarer haplotypes also increase haplotyping differences but to a lesser extent due to their low sample sizes.

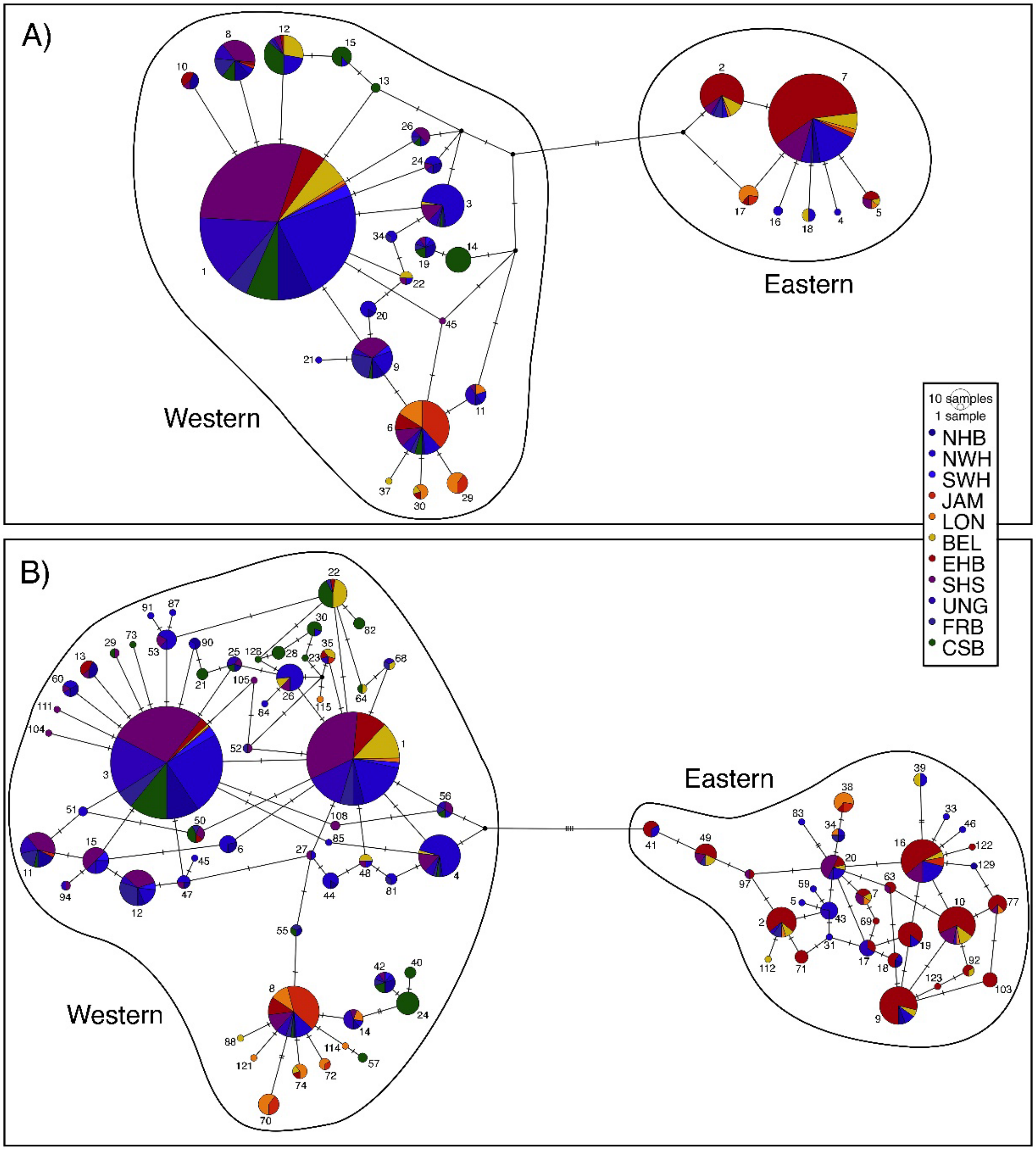

Figure 4. Haplotype networks of the mitochondrial DNA control region short (234 nucleotides, A) or long (615 nucleotides, B) haplotypes for belugas from the summering areas in the Hudson Bay-Strait Complex. Geographic limits of summering areas are described in Fig. 1 and acronyms defined in Table 1. A statistical parsimony (TSC) network using PopArt is presented. Small perpendicular bars along lines between two haplotypes indicate the number of mutations between haplotypes. Black circles lacking haplotype numbers indicate missing haplotypes in the evolution of the network. In both panels, the western and the eastern haplogroups are presented in the left and right, respectively.

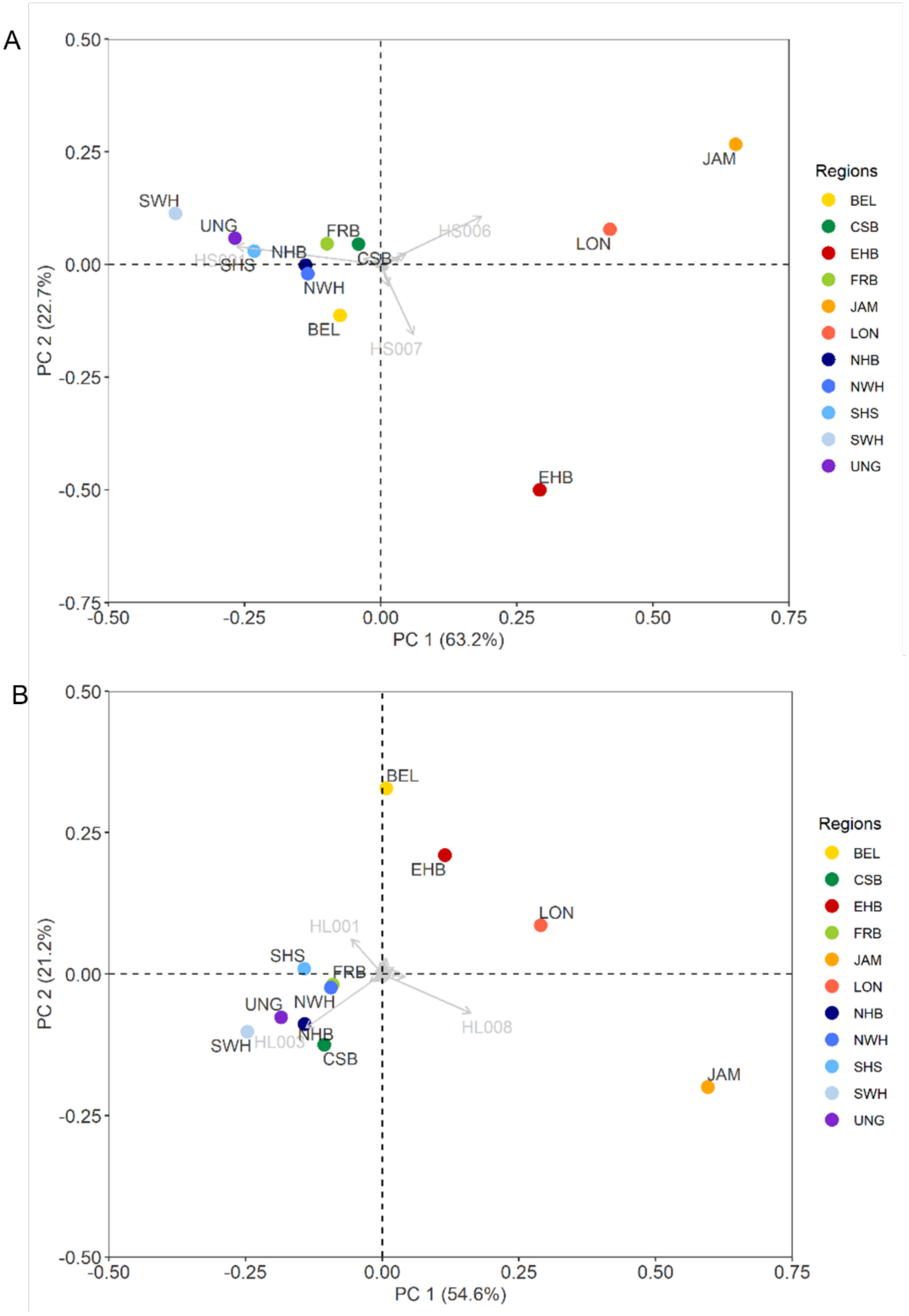

Figure 5. Biplot from the principal component analyses (PCA) using haplotype frequencies of the short (A, 234 nucleotides) or long (B, 615 nucleotides) mitochondrial DNA control region for belugas from the summer areas in the Hudson Bay-Strait Complex (see Table 1 for acronyms). The length and direction of arrows explain the effect of the haplotypes on the distance between summer aggregations.

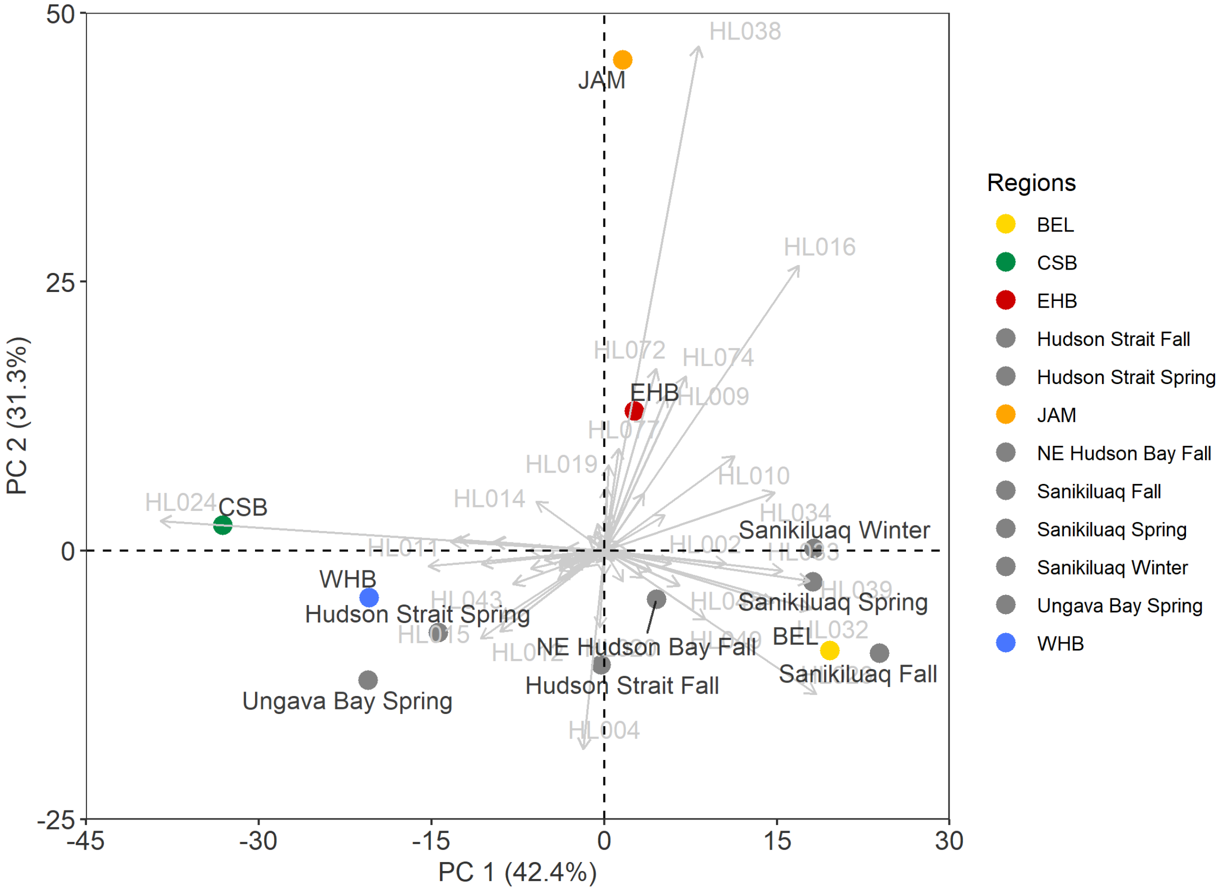

Figure 6. Biplot from the principal component analysis (PCA) using haplotype frequencies of the long haplotype (615 nucleotides) for the mitochondrial DNA control region for belugas from five populations (in color; WHB, JAM, EHB, BEL, CSB; see Table 1 for acronyms) and from Nunavik or Sanikiluaq management units (in grey, see Fig. 1b for locations, NE: Northeastern). The length and direction of arrows explain the effect of the haplotypes on the distance between summer aggregations.

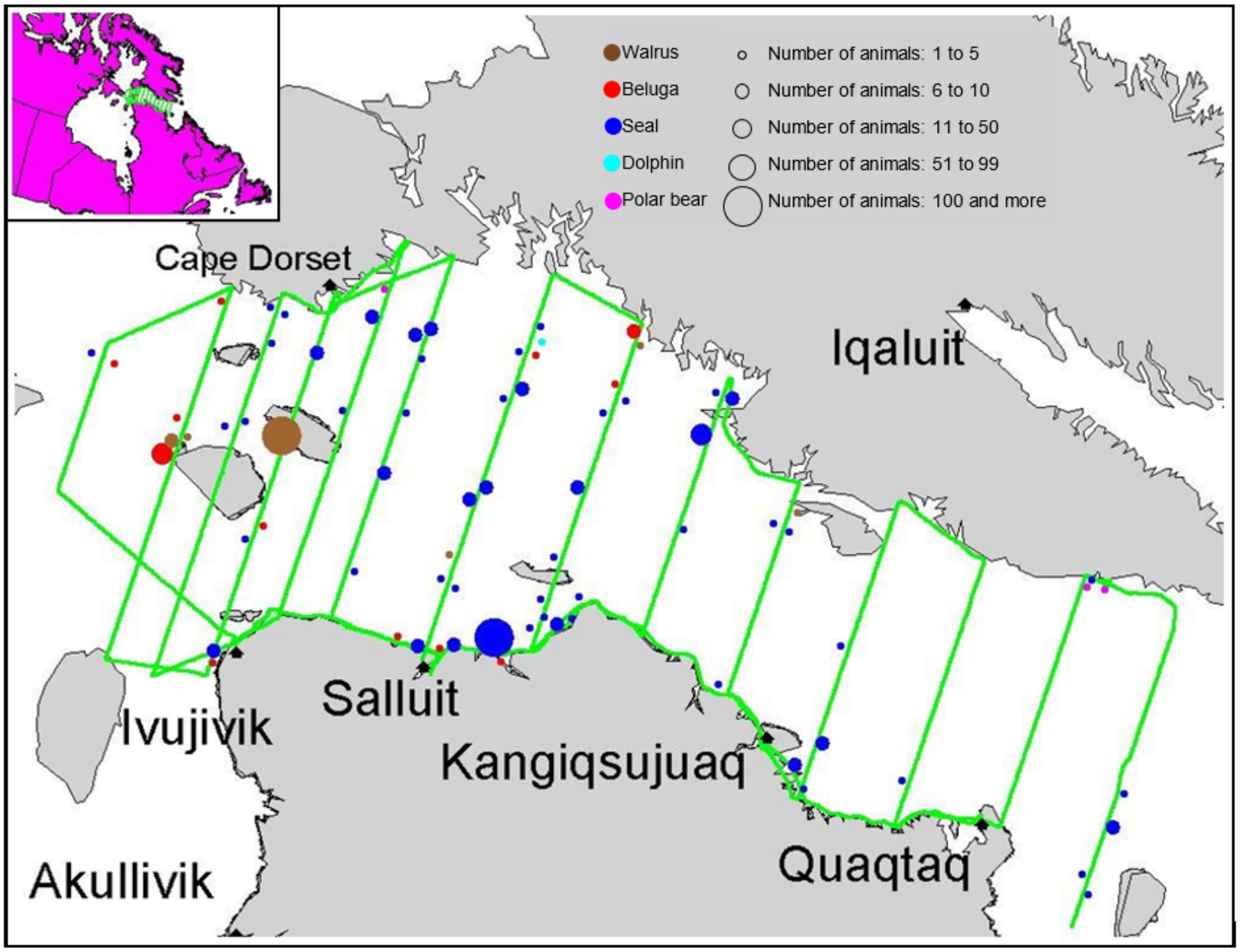

Figure 7. Marine mammal observations from systematic aerial surveys flown 9-12 August, 2010. A total of 69 belugas were counted (J-F Gosselin, personal observations).

TABLES

Table 1. Summarized metadata of all samples and a subset of summer samples. Table S1 provides more details on each individual.

Areas	All samples			Summer aggregations		
	Month range	Year range	N	Month range	Year range	N
North Hudson Bay (NHB)	Apr.–Nov.	1989–2009	90	Jul.–Aug.	1993–2009	67
North West Hudson Bay (NWH)	Jun.–Oct.	1985–2015	264	Jul.–Aug.	1985–2015	234
South West Hudson Bay (SWH)	Jul.–Aug.	2002–2005	17	Jul.–Aug.	2002–2005	17
James Bay (JAM)	Jul.–Oct.	2002–2016	45	Jul.–Aug.	2003–2016	38
Long Island (LON)	Jun.–Oct.	2003–2018	59	Jul.–Aug.	2003–2018	37
Belcher Islands (BEL)	Jan.–Dec.	1993–2021	422	Jul.–Aug.	1994–2020	66
South East Hudson Bay (EHB)	May–Oct.	1990–2020	230	Jul.–Aug.	1994–2019	183
North East Hudson Bay (NEH)	May–Oct.	1998–2019	48	-	-	0
South Hudson Strait (SHS)	May–Nov.	1994–2021	1372	Jul.–Aug.	1995–2020	241
North Ungava Bay (UNG)	Jun.–Dec.	1994–2020	157	Jul.–Aug.	1994–2020	113
Frobisher Bay (FRB)	Jun.–Aug.	1991–2004	53	Jun.–Aug.	1991–2004	53
Cumberland Sound (CSB)	May–Aug.	1982–2018	104	Jun.–Aug.	1982–2018	87
Total		-	2861		-	1136

Table 2. Genetic composition from the 11 summering areas of belugas from or close to the Hudson Bay-Strait Complex using short (234 nucleotides) and long (615 nucleotides) mtDNA control region sequences (haplotype). See table 1 for acronyms of summer aggregations and sample sizes. Polymorphic sites (S) were quantified with adegenet 2.1.5 (Jombart 2008; Jombart and Ahmed 2011), haplotype diversity (Pi) was estimated with the hap.div function of pegas 1.1 (Paradis 2010), whereas the number of haplotypes (H), private haplotypes (i.e., only present in one summering aggregation, Hp) and the proportion of private haplotypes (Hp%) were calculated manually.

Summering aggregations	Short haplotype					Long haplotype				
	S	H	Pi	Hp	Hp%	S	H	Pi	Hp	Hp%
NHB	13	11	0.61	0	0.0	22	20	0.81	1	1.5
NWH	16	20	0.66	3	1.7	31	42	0.87	12	5.6
SWH	5	3	0.32	0	0.0	8	5	0.74	0	0.0
JAM	9	6	0.52	0	0.0	19	8	0.56	0	0.0
LON	11	9	0.85	0	0.0	23	15	0.91	3	8.1
EHB	13	10	0.61	0	0.0	23	29	0.92	5	6.6
BEL	12	10	0.71	1	1.5	21	21	0.83	2	3.0
SHS	15	16	0.52	1	0.4	25	34	0.80	4	2.1
UNG	12	12	0.46	0	0.0	22	21	0.75	0	0.0
FRB	13	11	0.72	0	0.0	20	17	0.86	0	0.0
CSB	10	11	0.76	2	19.5	19	22	0.84	9	34.5
Total	17	29	0.72	7	2.0	39	90	0.89	36	5.8

Table 3. Estimating robustness of the reference groups for harvested belugas from the Hudson Bay-Strait Complex using the package rubias in R (more details in methods; Moran and Anderson 2019). Results should be read in rows, i.e., 15.1% of the WHB reference individuals were reassessed to WHB at probability equal or greater than 95%. Random probabilities of reassignment are 25 and 20% for 4 and 5 reference groups, respectively.

Reference groups	N	≥95%	≥80%	≥60%	≥40%
Five populations					
WHB population	318	15.1	27.0	71.4	87.1
JAM population	75	28.0	70.7	74.7	77.3
EHB population	183	0.0	11.5	26.8	69.4
BEL population	66	0.0	0.0	3.0	19.7
CSB population	87	13.8	35.6	39.1	39.1
Four populations and BEL-EHB stock					
WHB population	318	15.1	27.0	71.4	87.1
JAM population	75	28.0	70.7	74.7	77.3
BEL-EHB stock	249	2.4	23.3	43.0	84.7
CSB population	87	13.8	35.6	39.1	39.1

Table 4. Past genetic mixture analysis (1982-2018) using the Pella-Masuda model to determine the proportions of beluga from WHB or BEL-EHB stock in the harvest of Nunavik and Sanikiluaq management units (format modified, from Hammill et al. 2021; BEL-EHB stock was identified as EHB population in the original document). Ns: number of individual samples; Nv: number of different hunt dates (events); P: proportion; WHB: Western Hudson Bay, EHB: Eastern Hudson Bay, UNK: Unknown; CI: confidence interval based on variance among hunting events; CV: coefficients of variation based on individual samples (CVs) / hunting events (CVv). ND: not determined (sample size < 10).

Nunavik communities

Season	Ns/Nv	WHB population (%)		BEL-EHB stock (%)		CVs/CVv	UNK P (%)
		P	95% CI	P	95% CI		
<u>Spring (Feb.1–Aug.31)</u>							
Hudson Strait	770/347	82.9	78.5–87.0	**11.7**	8.1–16.0	0.2/0.2	5.3
NE Hudson Bay	2/1	ND	-	**ND**	-	-	-
Ungava Bay	122/76	87.4	77.8–94.6	**6.0**	0.8–15.8	0.6/0.7	6.6
<u>Fall (Sep.1–Jan.31)</u>							
Hudson Strait	454/180	67.6	60.3–74.5	**29.1**	22.4–36.3	0.1/0.1	3.3
NE Hudson Bay	31/14	49.1	26.4–72.0	**44.5**	23.5–66.5	0.3/0.3	6.5
Ungava Bay	4/4	ND	-	**ND**	-	-	ND

Sanikiluaq

Season	Ns/Nv	WHB population (%)		BEL-EHB stock (%)		CVs/CVv	UNK P (%)
		P	95% CI	P	95% CI		
Spring (Apr.1–Jun.30)	301/107	76.8	69.2–83.7	**1.6**	0.0–6.6	0.1/0.1	12.6
Ext. Spring (Apr.14–Jul.1)	31/18	75.1	67.2–82.2	**4.6**	1.1–10.2	0.4/0.5	20.4
Summer (Jul.1–Aug.31)	45/30	61.5	32.8–86.2	**25.6**	4.9–56.0	0.4/0.5	12.9
Fall (Sep.1–Nov.30)	45/30	97.8	91.8–99.9	**0.0**	-	-	2.2
Winter (Dec.1–Mar.31)	56/7	31.3	6.1–65.6	**36.6**	9–70.7	0.2/0.5	32.1

Table 5. Updated genetic mixture analysis using the long haplotypes (MLI database) and new reference groups for harvested belugas from Nunavik communities, and Sanikiluaq. NE Hudson Bay: Northeastern Hudson Bay; Ns: number of individual samples; Nv: number of different hunt dates (events); P: proportion; WHB: Western Hudson Bay, EHB: Eastern Hudson Bay, JAM: James Bay, CSB: Cumberland Sound, UNK: Unknown; CI: confidence interval based on variance among hunting events; CV: coefficients of variation based on individual samples (CVs) / hunting events (CVv). ND: not determined (sample or event size < 10).

Nunavik communities

Season	Ns/Nv	WHB population (%)			BEL-EHB stock (%)			JAM population (%)			CSB population (%)			UNK P (%)
		P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	
Spring (Feb.1–Aug.31)														
Hudson Strait	824/364	75.7	70.5–80.6	0.0/0.0	**12.3**	8.6–16.5	0.1/0.2	2.6	0.6–5.9	0.5/0.6	6.5	3.6–10.2	0.2/0.3	2.9
NE Hudson Bay	2/1	ND	-	-	**ND**	-	-	ND	-	-	ND	-	-	-
Ungava Bay	143/87	87.8	76.5–95.7	0.1/0.1	**4.7**	0.8–11.8	0.6/0.6	1.1	0.0–8.1	2.3/2.2	5.1	0.7–13.3	0.6/0.7	1.3
Fall (Sept 1–Jan. 31)														
Hudson Strait	512/202	49.6	40.0–59.2	0.1/0.1	**44.0**	35.1–53.0	0.1/0.1	0.0	-	-	2.8	0.7–6.1	0.5/0.5	3.6
NE Hudson Bay	45/19	37.3	18.0–59.0	0.3/0.3	**50.1**	23.9–76.2	0.2/0.3	8.2	0.4–26.3	0.8/0.9	-	-	-	4.4
Ungava Bay	6/6	ND	-	-	**ND**	-	-	ND	-	-	-	-	-	ND

Sanikiluaq

Season	Ns/Nv	WHB population (%)			BEL-EHB stock (%)			JAM population (%)			CSB population (%)			UNK P (%)
		P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	
Spring (Apr.1–Jun.30)	229/99	7.2	2.1–14.8	0.5/0.5	**62.8**	51.5–73.4	0.1/0.1	17.4	9.4–27.2	0.2/0.3	-	-	-	12.6
Fall (Sep.1–Nov.30)	49/35	28.4	9.6–52.6	0.4/0.4	**61.0**	35.1–83.9	0.2/0.2	2.4	0.0–16.1	2.3/1.9	-	-	-	8.2
Winter (Dec.1–Mar.31)	76/11	43.7	20.1–69.0	0.3/0.3	**39.9**	13.0–70.8	0.3/0.4	13.7	2.6–32.0	0.5/0.6	-	-	-	2.7

Table 6. Quantifying the effect of resequencing on proportions of beluga from each population and unknown (UNK) harvested in Nunavik and Belcher Islands managements units. Note that the proportions of Eastern Hudson Bay (EHB) population presented in this table are not reliable due to the low number of reference individuals in the Western Hudson Bay (WHB) population (n = 41, see methods for more details) or low sample size per management unit (using only samples in common to FWI and MLI databases). DIFF are the absolute difference between EHB proportions from simulations with FWI samples until 2019 and same or different reference samples for MLI samples until 2019, respectively.

Management units		FWI samples until 2019 (%)			MLI samples until 2019 (%)			
	N	WHB	**EHB**	UNK	WHB	**EHB**	UNK	**DIFF (%)**
Hudson Strait								
Spring	621	81.6	**13.3**	5.2	78.2	**12.6**	9.2	**0.7**
Fall	359	71.7	**25.5**	2.8	64.8	**30.2**	5.0	**4.7**
Ungava Bay								
Spring	96	90.2	**3.6**	6.3	83.5	**10.2**	6.3	**6.6**
Northeastern Hudson Bay								
Fall	22	50.9	**44.6**	4.6	47.2	**48.3**	4.6	**3.7**
Sanikiluaq								
Spring	181	55.3	**23.1**	21.6	51.4	**26.5**	22.1	**3.4**
Fall	31	86.2	**10.6**	3.2	85.8	**11.0**	3.2	**0.4**
Winter	48	59.6	**38.3**	2.1	20.5	**50.3**	29.2	**12.0**

Table 7. Genetic mixture analysis using the long haplotypes and new reference groups for harvested belugas from the Hudson Strait at different periods. September-October represents harvested proportions during the usual hunt closure period. Ns: number of individual samples; Nv: number of different hunt dates (events); P: proportion; WHB: Western Hudson Bay, EHB: Eastern Hudson Bay, JAM: James Bay, CSB: Cumberland Sound, UNK: Unknown; CI: confidence interval based on variance among hunting events; CV: coefficients of variation based on individual samples (CVs) / hunting events (CVv). ND: not determined (sample or event size < 10).

Period	Ns/Nv	WHB population (%)			BEL-EHB stock (%)			JAM population (%)			CSB population (%)			UNK P (%)
		P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	P	95% CI	CVs/CVv	
May	6/6	ND	-	-	**ND**	-	-	ND	-	-	ND	-	-	ND
Jun.	577/230	71.3	64.977.3	0.0/0.0	**12.4**	7.9–17.7	0.2/0.2	4.8	2.0–8.8	0.4/0.4	8.6	4.7–13.5	0.2/0.3	2.9
Jul.	223/114	84.7	77.2–90.9	0.0/0.0	**11.0**	5.6–18.0	0.3/0.3	0.0	-	-	1.6	0.0–6.7	1.0/1.1	2.7
Aug.	18/14	75.8	46.8–95.3	0.2/0.2	**13.7**	0.0–57.4	0.8/1.2	4.7	0.0–33.2	1.9/1.9	0.3	0.0–0.6	0.5/0.6	5.6
Sept.	26/7	ND	-	-	**ND**	-	-	ND	-	-	ND	-	-	ND
Oct.	223/104	49.5	37.5–61.6	0.1/0.1	**47.3**	34.7–60.1	0.1/0.1	0.0	-	-	0.0	-	-	3.1
Nov.	263/91	45.9	32.3–59.8	0.1/0.2	**45.1**	33.0–57.6	0.1/0.1	0.0	-	-	4.4	1.1–9.7	0.5/0.5	4.6
Nov. 1–10	167/62	41.2	27.8–55.2	0.2/0.2	**51.5**	39.0–63.9	0.1/0.1	0.0	-	-	4.4	0.5–12.2	0.6/0.7	3.0
Nov. 11–20	96/29	50.1	22.5–77.6	0.2/0.3	**33.9**	13.9–57.6	0.2/0.3	4.5	0.5–12.5	1.0/0.7	4.3	0.5–12.1	0.8/0.7	7.3
Nov. 21–30	49/13	71.9	47.9–90.6	0.1/0.2	**10.4**	0.9–29.5	0.5/0.7	0.0	-	-	7.5	0–35	1.0/1.3	10.2

SUPPLEMENTARY MATERIAL

Table S1

Metadata for each beluga from this study (N = 2861)

Table S2

Sequence library of short control region in the mtDNA of belugas from the Hudson Bay-Strait Complex

Table S3

Sequence library of long control region in the mtDNA of belugas from the Hudson Bay-Strait Complex

Table S4

Long haplotype frequencies per summering area

All tables are available at this link: Reexamining populations of beluga in the Hudson Bay-Strait Complex and assessing the impact on harvests in Nunavik and Sanikiluaq management units