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Stock discrimination of belugas (*Delphinapterus leucas*) hunted in eastern Hudson Bay, northern Québec, Hudson Strait, and Sanikiluaq (Belcher Islands), using mitochondrial DNA and 15 nuclear microsatellite loci

Discrimination des stocks de bélugas (*Delphinapterus leucas*) chassés dans l'est de la baie d'Hudson, le nord du Québec, le détroit d'Hudson et à Sanikiluaq (îles Belcher), à l'aide de l'ADN mitochondrial et de 15 loci de microsatellites nucléaires

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Abstract

We examined the possibility that eastern Hudson Bay (EHB) beluga were hunted by the communities outside of the EHB arc. The molecular genetics of 100 belugas hunted from Sanikiluaq on the Belcher Islands, 126 from EHB communities, 137 from north-western Québec and Hudson Strait communities (65/137 from 1983-1997 with complete genetic data, 115/137 from 1998-1999 only mtDNA), and 378 from other geographic areas which might share stocks or are known to be genetically similar were examined. Individuals and sample populations were characterized with a mitochondrial DNA (mtDNA) d-loop sequence of 324 base pairs which described 32 different haplotypes (maternally inherited) and with 15 nuclear microsatellite loci (inherited from both parents).

Stocks could most often be defined from different mixtures of haplotypes in different sample populations. There was weak genetic differentiation among populations on the basis of microsatellites, however, there was considerable overlap of microsatellite alleles frequencies among all populations. All genetic results supported the hypotheses that belugas hunted in EHB and Sanikiluaq are from different stocks. However some individuals from each area had genotypes that strongly associated them with the other stock. Large genetic diversities in samples from Northern Québec and northern Hudson Bay samples may mean that mixtures of stocks were hunted in these areas. On the basis of microsatellite results, it is possible that most examined populations interbreed.

Belugas from both the Nastapoka River (1984-1995) and other locations on the EHB arc (1993-1997) were genetically similar, and were characterized by high frequencies of two haplotypes which are not common elsewhere. Belugas from the Nastapoka River also had low haplotype and microsatellite allelic diversities. Belugas sampled from other locations in the EHB arc in the 1990s had these same haplotypes, but also a low frequency of western haplotypes. These later samples also had a slightly higher microsatellite diversity. 17% of belugas hunted in EHB (all 1984-1997) had genotypes that resemble western Hudson Bay populations. However such belugas were not sampled every year.

The genetic composition of belugas hunted in Sanikiluaq over five years was consistent. These belugas had both a high haplotype and microsatellite diversity, however proportions differed from other western Hudson Bay populations. These belugas may be a different stock or a consistent mixture of other stocks. Beluga males from Sanikiluaq may have a slightly higher genetic diversity than females. Approximately 10% of belugas hunted from Sanikiluaq have genotypes that resemble EHB (1984-1997) more than they resemble other populations.

Since genetic characteristics overlapped among the populations we examined, it was impossible to distinguish with belugas that were outside of their summering range and those that had genetic characteristics more typical of other population. Nevertheless, 31% of belugas from northwestern Québec and Hudson Strait had genotypes that were more probable in EHB, again this value not consistent between communities and years. EHB genotypes comprised 20% in northern Hudson Bay, and 7% in Kimmirut.

Belugas from the Churchill, Nastapoka, and St. Lawrence Rivers have low genetic diversities. This may be a characteristic of populations that frequent estuaries and/or may be due to overhunting in the past.

Some genetic patterns described can be explained by post-glacial dispersion.

Résumé

Nous nous sommes penchés sur la possibilité que des bélugas de l'est de la baie d'Hudson (EBH) aient été chassés par des collectivités de l'extérieur de l'arc de l'EBH. Nous avons étudié la génétique moléculaire de 100 bélugas capturés par les chasseurs de Sanikiluaq (îles Belcher), de 126 bélugas capturés par les collectivités de l'EBH, de 137 bélugas capturés par les collectivités du détroit d'Hudson et du nord-ouest du Québec (données génétiques complètes pour 65 bélugas capturés de 1983 à 1997 et ADN mitochondrial seulement pour 115 bélugas capturés en 1998 et en 1999) et de 378 bélugas provenant d'autres régions qui pourraient avoir des stocks en commun ou dont on sait que les stocks sont génétiquement semblables. Les individus et ces populations d'échantillons ont été caractérisés par une séquence de 324 paires de bases d'une boucle D d'ADN mitochondrial (ADNmt) qui a présenté 32 haplotypes différents (hérités de la mère) et par 15 loci de microsatellites nucléaires (hérités des deux parents).

Dans la plupart des cas, les stocks ont pu être caractérisés à partir de différents mélanges d'haplotypes trouvés dans les diverses populations d'échantillons. L'analyse des microsatellites a indiqué une faible différentiation génétique entre les populations; les fréquences des allèles des microsatellites de toutes les populations se chevauchaient considérablement. Tous les résultats génétiques appuyaient l'hypothèse voulant que les bélugas chassés dans l'EBH et à Sanikiluaq appartiennent à des stocks différents. Toutefois, dans chaque région, certains individus présentaient des génotypes caractéristiques de l'autre stock. Les grandes diversités génétiques des échantillons du nord du Québec et du nord de la baie d'Hudson pourraient indiquer que la chasse a porté sur des stocks mélangés dans ces régions. Selon les résultats de l'analyse des microsatellites, il est possible que la plupart des populations étudiées se croisent.

Les bélugas provenant de la rivière Nastapoka (1984-1995) et d'autres endroits le long de l'arc de l'EBH (1993-1997) étaient génétiquement semblables et caractérisés par des fréquences élevées de deux haplotypes rares ailleurs. Les bélugas de la rivière Nastapoka présentaient aussi de faibles diversités des allèles haplotypiques et microsatellitaire. Des bélugas capturés ailleurs dans l'arc de l'EBH dans les années 1990 présentaient ces mêmes haplotypes, mais aussi une basse fréquence d'haplotypes de l'ouest. Ces échantillons présentaient également une diversité microsatellitaire légèrement plus élevée. Dix-sept pour cent des bélugas capturés dans l'EBH (tous de 1984 à 1997) avaient des génotypes semblables à ceux des populations de l'ouest de la baie d'Hudson. Toutefois, de tels bélugas n'ont pas été capturés chaque année.

Les bélugas capturés à Sanikiluaq sur une période de cinq ans présentaient une composition génétique constante caractérisée par une diversité élevée, tant au niveau de l'haplotype que des microsatellites, mais les proportions étaient différentes de celles des autres populations de l'ouest de la baie d'Hudson. Il peut s'agir d'un stock différent ou d'un mélange constant d'autres stocks. La diversité génétique des mâles capturés à Sanikiluaq pourrait être légèrement supérieure à celle des femelles. Environ 10 % des bélugas de Sanikiluaq ont des génotypes qui ressemblent plus à ceux de l'EBH (1984-1997) qu'à ceux d'autres populations.

Comme les caractéristiques génétiques des populations étudiées se chevauchaient, il était impossible de distinguer entre les bélugas se trouvant à l'extérieur de leur aire d'estivage et ceux dont les caractéristiques génétiques sont typiques d'autres population. Néanmoins, 31 % des bélugas du nord-ouest du Québec et du détroit d'Hudson présentaient des génotypes plus caractéristiques de l'EBH; cette valeur variait selon les collectivités et l'année. Les genotypes de l'EBH ont été trouvés chez 20 % des bélugas du nord de la baie d'Hudson Bay et chez 7 % de ceux capturés à Kimmirut.

Les bélugas des rivières Churchill et Nastapoka et du fleuve Saint-Laurent présentent une faible diversité génétique. Cela pourrait être caractéristique des populations qui fréquentent les estuaires ou attribuable à une chasse excessive par le passé.

La dispersion post-glaciaire peut expliquer certains aspects de la répartition des caractéristiques génétiques.

Introduction

The beluga (*Delphinapterus leucas*) is a toothed whale that is economically and socially important to people in Canada's North. It has a discontinuous circumpolar distribution, with the northernmost areas of its range off Ellesmere Island, West Greenland, and Spitsbergen, about 82 ºN and the southernmost belugas in the St. Lawrence River estuary, White Sea, Okhotsk Sea, Gulf of Alaska, and James Bay (Stewart and Stewart 1989). Hudson Bay has major concentrations of beluga. The use of particular coastal areas is traditional and known for many populations. Large groups congregate in river mouths and estuaries such as the Churchill, Seal, Nelson, Winsk, Severn, Nastapoka, Little and Great Whale Rivers (Figure 1).

The world populations of beluga are subdivided into at least 16 provisional management stocks, 11 of which exist in North America, and seven in Canada (Donovan 1992). These stocks were defined primarily on the basis of morphometric studies, behavioural observations, traditional knowledge, and observations of declines in some areas. Five stocks utilizing Hudson Bay and Hudson Strait are the West Hudson Bay, East Hudson Bay, Baffin Bay, Southeast Baffin Island and Ungava Bay stocks (Donovan 1992, Smith *et al.* 1990). Genetic findings to date (Brown Gladden *et al.* 1997, 1999, de March *et al.* 2002) have not rejected these divisions.

The beluga of Eastern Hudson Bay (EHB) are defined as the population summering in the near-shore waters of Hudson Bay between the Great Whale River and the Nastapoka River (Kingsley 1995) (Figure 1). In the past, this area was often referred to as the "Eastmain". It has been concluded on the basis of aerial surveys that this population has a northern boundary near 58° N (Kingsley 1995). The EHB population was believed to be separate because of its small and stable size. Estuaries frequently used by beluga are those of the Nastapoka and Little Whale rivers, and the inner recesses of Richmond Gulf are also frequented in summer (Kingsley 1995).

This manuscript addresses the question to what extent communities not on the EHB arc are hunting EHB beluga with the use of molecular genetics techniques. This is an ongoing study, hence recent samples have not been scrutinized as thoroughly as older ones.

There has been a long history of harvesting beluga in EHB, and the subsistence hunt continues to be important. In the past hunts usually occurred in July and August (Francis 1977). In the Little Whale River, whales were driven into more shallow water where they could be easily harpooned. Historic populations levels were high compared to present-day levels (Francis 1977). Robert Hamilton, a member of Governor George Simpson's expedition in 1852, reported that whales were seen by the thousands, whales enough to walk on (Francis 1977).

The commercial catch history of EHB beluga is outlined in Finley *et al* . (1982) and Francis (1977). In the 1800s, the HBC successfully established beluga fisheries in the Little Whale and Great Whale Rivers and at Fort Chimo (Kuujjuaq) on Ungava Bay. This was a land based hunt, using primarily barrier nets. It is estimated that the EHB stock numbered at least 5000 in the late 1840s, before commercial hunting reached high levels. The number of whales killed in the Little Whale River was 423 in 1854, 743 in 1856 and 1500 in 1860. In the Great Whale River 1043 were killed in 1857 and 800 in 1860. By the late 1800s, the fishery experienced a rapid decline. Although numbers may have been reduced, it was believed is that the whales began to avoid the rivers when the whaling company was also there (Francis 1977). The land-based hunt could not survive.

During 1975-1979, communities in EHB, Akulivik, and Povungnituk reported 137-144 beluga landed per year (Finley *et al.* 1982, Kingsley 1995, Lesage 2001, Res Doc 2001/022). Most of these belugas are believed to have been taken in the EHB arc. During 1980-1994 catches in the same communities averaged 90 per year (Kingsley 1995, Lesage 2001, Res Doc 2001/022). In the 1980s, old belugas were still evident in the catch and an overharvesting situation was not evident in spite of large catches (Kingsley 1995, Doidge 1990). Since then, this stock has been designated as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, Campbell 1989, Reeves and Mitchell 1989). In 1990, the Arctic Fisheries Scientific Advisory Committee (AFSAC) (Bodaly *et al* 1992) concluded that harvest from EHB were close to the sustainable yield. There were several concerns. It was believed that occasional high harvests from Hudson Strait could impact the stock. Habitat

modification from the Grand Baleine hydroelectric project was also a concern. A new settlement at Umiujaq placed hunters closer to the Nastapoka River where there is access to whales, and hunting pressures could increase (Bodaly *et al* . 1992). At the Great Whale River, the effects of heavy hunting and small-boat traffic associated with Cree and Inuk communities now established at the river mouth was appeared to account for small numbers of belugas.

A five-year management plan implemented in 1995 limited beluga harvests to 90 animals by hunters from EHB communities and 100 belugas by communities in Hudson Strait (Lesage 2001, Res Doc 2001/022, Hammill 2001, Res Doc 2001/025). There were serious concerns about population size and the structure of the reported landings, particularly in EHB. Also, there was a concern that the community of Sanikiluaq in the Belcher Islands was hunting EHB belugas. In addition, it was believed that communities in northern Québec and Hudson Strait also posed a threat to EHB beluga.

The Belcher Islands lie in the centre of the arc of eastern Hudson Bay (Figure 1). Belugas are hunted from the community of Sanikiluaq mostly on the open water of Hudson Bay. Most of the hunt occurs in late June and early July, when belugas migrate past the islands, and a few are taken in the fall. At least 10 belugas were taken in 1993 and up to 30 in1994 (Kingsley 1995). To determine if EHB belugas were hunted in the Belcher Islands, a directed sampling program was conducted between 1993-1999.

It is not known where beluga hunted in Sanikiluaq spend the summer. There is almost a complete lack of scientific information from southern Hudson Bay. The relation of beluga found in James Bay in the summer, and even their migration, route, and wintering area, and their relationship to with other stocks are not known.

The main wintering areas for Hudson Bay populations are believed to be in Hudson Strait, Davis Strait, the North Labrador Sea, and in unconsolidated ice or open water in Hudson Bay during the winter (Richard *et al.* 1990)(Figure 1). Belugas are assumed to be true to wintering grounds, however the size and extent of the overwintering aggregations is unknown. Although southern Hudson Bay beluga may overwinter in unconsolidated ice south of the Belcher Islands, and traditional knowledge indicates southward movement in fall along the south coast of Richmond Gulf, the main wintering areas are probably unconsolidated ice in Hudson Strait, where stocks may mix and possibly interbreed (Kingsley 1995). The spring movement is believed to be southward from Digges and Mansel Islands. With a 14 month gestation period, and young born in the very early spring, it is possible that belugas might mate while on the wintering grounds or during migrations.

Previous genetics research on Hudson Bay beluga

The following abbreviations will be used: Eastern Hudson Bay (EHB), extending from Long Island to Inukjuak; Western Hudson Bay (WHB) referring to Arviat and Churchill; Sanikiluaq (SAN); Nastapoka River (NaR); North western Québec (NWQu), referring to the western shore of northern Québec including the communities of Puvirnituq, Akulivik, and Ivujivik; Hudson Strait (HS), St. Lawrence River (StLR), Kimmirut (KIM), and northern Hudson Bay (NHB), which includes the communities of Coral Harbour, Igloolik, Hall Beach, and Repulse Bay.

There have been several studies on beluga genetics in North America, most of these include southern Hudson Bay beluga. Several studies have similar results, but represent a progression from weak to stronger stock delineation.

Mancuso (1995) examined an mtDNA sequence of 320 base pairs which had 10 variable sites in common with, and 5 different from, the sites that we examine, and also multilocus minisatellite probes (Jeffreys 1985a, 1985b). Variation was examined in five groups of beluga: Nastapoka River, Eastmain River (James Bay), south Hudson Strait, Kangiqsujjuac (Kangiqsujjuac Bay) , and Ungava Bay. There were significant statistical differences in haplotype composition between EHB (Nastapoka + Eastmain Rivers) (n = 70 belugas) and southern Hudson Strait and Ungava belugas (n = 32). Mancuso (1995) believed that haplotype distribution patterns differed among different estuaries along EHB, but this hypothesis was not supported statistically. The minisatellite analysis suggested that Mackenzie Delta (Western Canadian Arctic) belugas might be different from all others in east. There were no differences within eastern samples.

Brennin *et al.* (1997) examined population genetic structure of 95 belugas from 12 sampling locations by characterizing mtDNA using 10 restriction enzymes. Eight haplotypes were identified. Two maternal lineages were evident: one from the St. Lawrence estuary and EHB, and another which included western Hudson Bay, Baffin Island, western Greenland, the Canadian High Arctic, and the eastern Beaufort Sea. Significant differences could not be shown within the two lineages. Brennin *et al.* (1997) believed that these lineages represented the original “Pacific” and “Atlantic” refugial stocks that colonized the Arctic after deglaciation.

Murray *et al.* (1998) examined genetic variation at the Major Histocompatibility Complex locus DQβ in 233 belugas from 7 sampling locations. Comparison of allele frequencies among populations showed that belugas from southeastern Baffin and the Canadian high Arctic locations (n = 67 belugas) were different from all others including the St. Lawrence River, the Beaufort Sea, Point Lay in Alaska, Arviat, EHB and Hudson Strait (n = 178) . No other statistically significant differences were found.

Brown Gladden *et al.* (1997) found more genetic differences among stocks in a considerably expanded study examining an mtDNA sequence of 234 nucleotides and 624 belugas from 25 sites. Thirty-nine haplotypes were identified. As in previous studies, St. Lawrence River beluga and EHB have several related haplotypes that are distant from those in nearly all other locations. Both of these sample populations were significantly differentiated from other examined. There was very little differentiation among western and northern Hudson Bay samples when table-wide comparison criteria (Rice 1989) were used. Belugas from the Belcher Islands (SAN) were not significantly different from those from western Hudson Bay. Brown Gladden *et al.* (1999) also examined population differentiation using 5 microsatellite loci. Patterns in microsatellite allele distributions were similar to the haplotype patterns, but yielded fewer statistically significant differences (Brown Gladden *et al.* 1999). No genetic differentiation was evident among Hudson Bay populations.

Our genetics database has doubled in size since the studies of Brown Gladden *et al.* (1997, 1999), and methods for molecular genetics analyses have been extended and refined. We now have more and more recent samples, including many from communities from northwestern Québec and Hudson Strait that hunt migrating belugas. Also, we now analyse for 15 microsatellite loci, whereas Brown Gladden *et al.* (1999) analysed for 5 loci.

Both types of DNA loci that we analyse are highly polymorphic, thus there is often a good probability that isolated populations diverge at these loci either due to mutation on a large time scale and/or drift or

migration on shorter time scales.

The first type of DNA locus, mitochondrial DNA (mtDNA), is inherited mainly maternally through egg cell material. The mtDNA locus we used consists of 234 nucleotides which are found at the beginning of the *d*-loop region of mitochondrial DNA (Brown Gladden *et al.* 1997). The mutation rate in the d-loop is high compared to nuclear genes, in the order of 10^{-8}/site/year (Moritz *et al.* 1987). We have found variability at 22 of positions, revealing 54 different "haplotypes" or variations of this sequence. Because mtDNA is maternally inherited, patterns in haplotype distribution can be used to identify situations where the female patterns of dispersion are different from the male patterns and/or where social groups are led by females.

We also nalyze for 15 microsatellite loci in beluga (Postma 1995, Maiers *et al.* 1996, Brown Gladden *et al.* 1999, Buchanan *et al.* 1996). Microsatellites are nuclear DNA loci consisting of repeated units of base pairs, with the repeat unit being 1-6 base pairs in length (Ashley, 1999). Alleles are identified by the size, in base pairs, of Polymerase Chain Reaction (PCR) products generated using the microsatellite region as a template. Microsatellite DNA is thought to be non-coding (Ashley, 1999), however there are several hypotheses regarding its possible function (Tautz *et al.,* 1986; Hamada *et al.* 1982). Polymorphism in these regions of DNA arise from a mechanism known as slippage, which causes additions and deletions to the number of repeat units in the microsatellite (Tautz 1989). The rate of this type of mutation, estimated to be 5.6×10^{-4} (Goldstein *et al.,* 1995), is frequent enough to maintain a high degree of polymorphism within populations, but it is not high enough to occur in successive generations (Tautz, 1989). Nuclear loci provide information about the breeding history, mating systems, migrations, and distribution of the population.

There are numerous numerical methods for examining genetic differences and similarities and methods are still changing. Most measures of genetic distance are based on assumptions about the mechanisms that cause changes in allele frequencies. For mtDNA, estimators based on either distance methods or parsimony methods can be used. Distance methods use the number of nucleotide differences to compare mtDNA sequences, parsimony methods are based on whether or not mtDNA sequences are identical. Estimators for microsatellites work under the assumption in one of two types of models: the Stepwise Mutation Models (SMM; Kimura and Crow 1964) and the Infinite Alleles Models (IAM; Ohta and Kimura 1973). SSM based models assume that the majority of mutations at microsatellite loci are stepwise in nature, changing allelic sizes by one or a few repeats. If changes are assumed to be entirely due to drift, parsimony methods or methods using the IAM model are usually more appropriate. Most classical distance measures, however, are based on multidimensional geometric considerations without reference to any particular evolutionary model. In studies motivated by stock management issues, normally with groups closely related animals, the presence of differences is often more important than the source of differences, hence distance measures based on the IAM model or geometric measures are often chosen (Goldstein *et al.* 1995, Paetkau *et al.* 1997, de March *et al.* 2001).

Methods

704 beluga tissue samples, usually skin, were obtained from summer animals between 1984 and 1997 (Table1). Samples from SAN were obtained as part of the Department of Fisheries and Ocean's (DFO) Whale Sampling Program in the Nunavut Land Claim Area. At Churchill, samples were taken by DFO staff during live captures (Churchill). At Arviat, samples were taken from drives and hunter kills. Samples from St. Lawrence River beluga were collected by P. Beland from stranded animals and provided by B.N. White of McMaster University. Samples from hunter-killed belugas from EHB, Hudson Strait, and Ungava were supplied by M. Hammill and M. Kingsley of DFO, Laurentian Region and by B. Doidge, Makivik Corporation.

Hunting patterns are generally known for different eastern communities, however, these may vary in different years, are also known to have changed through the years (Lesage 2001, Res Doc 2001/022). In recent times, hunters from Kuujjuaraapik (previously Great Whale, Poste Baleine) mostly hunt at Little Whale. Some hunters go to Long Island. The recent Umiujaq samples tend to be taken next to the village. However, samples in this study assigned to that community may also be from Nastapoka and the Little Whale River. Inukjuac hunters hunt in Nastapoka in summer and sometimes the Ivujivik area. Early- or late-season samples could be more local. Ivujivik hunts migrating animals in the spring and fall. Most samples from EHB and NWQu provided to us were identified by year from the community that they

came from, and seldom the location where the belugas were hunted. Because of this, genetic compositions are analysed by community. Dates are available only for approximately 50% of the samples.

Skin samples were usually preserved in a saturated salt solution containing 20% dimethyl sulphoxide (DMSO) and 0.5 M EDTA (Seutin *et al.* 1991) at the time when belugas were caught. Other samples were frozen and preserved at later dates.

Previously analysed samples (Brown Gladden *et al.* 1999) were reanalysed for the additional 10 microsatellite loci. Samples from 1998-99 have been analysed only from haplotypes, and are not full discussed here. Most analyses did not include the 129 samples taken in 1998-1999 from NWQu and HS, however, haplotypes from these samples are presented in Table 4. Annual collections from areas distant from the main areas of interest (WHB, NHB, StLR) were not analysed by year (Table 1). The remaining 612 of belugas were grouped as 6 and 9 "sample populations" (Tables 1 and 3) for different comparisons. Also, 21 "collections" with only belugas from EHB, SAN, and HS from before 1998 were examined (Table 1). "Collection" refers to belugas from one location in one year, however some small collections that were geographically close were pooled to increase sample size.

Genetic Analyses

Total DNA extracts were prepared using Amos and Hoelzel's (1991) and Sambrook *et al.*'s (1989) methods with modifications described by Maiers *et al.* (1996). Sex determinations were done by the methods described by Bérubé and Palsbøll (1996).

MtDNA analysis . The control region sequence of mtDNA in beluga samples was amplified using universal primers developed by Kocher *et al.* (1989) and species-specific primers designed by Lillie *et al.* (1995). Numerous samples were analysed using asymmetric PCR and manual sequencing as described in Brown (1996) and others were sequenced from the double-stranded PCR product using dRhodamine terminator cycle sequencing (Applied Biosystems) and an ABI Prism 377 automated DNA sequencer. For both methods, the primer Bel5' (Lillie *et al.* 1995) was used as the sequencing primer.

Approximately 260bp of resultant mtDNA sequence for beluga samples were aligned using MacVector ver. 3.5 (IBI) to a reference beluga sequence (Brown 1996). Haplotype identification numbers were designated according to a concensus sequence of variable positions.

Microsatellite analysis. The fifteen sets of microsatellite primers, described by Buchanan *et al.* (1996), Valsecchi and Amos (1996) and Amos *et al.* (1993) were designated according to species from which the primers were developed and a locus name and number (Table 2). Microsatellites were amplified according to specific conditions (Buchanan and Crawford 1993, Buchanan *et al.* 1994, Maiers *et al.* 1996). Allele lengths were determined by reference to control samples (the original clone that was sequenced) and a M13 sequencing ladder run along side of the samples. Microsatellite alleles were identified by their size in base pairs.

Statistical Analyses

Genetic diversity was calculated as $D_l = 1 - \Sigma_u(p_{lu})^2$ for each microsatellite locus and for haplotypes, and as a mean, $D = 1 - \Sigma_l \Sigma_u(p_{lu})^2/m$ for all microsatellite loci, where p_{lu} is the frequency of the uth allele at the l-th locus, and m is the number of loci (p. 150, Weir 1996).

Analysis of Molecular Variance or "AMOVA" (Excoffier *et al.* 1992, Michalakis and Excoffier 1996, Goldstein *et al.* 1995), available in the "Arlequin" statistical package (Schneider *et al.* 1997) was used to test for significant genetic differentiation among populations, collections, or sexes. AMOVA is a linear modelling method originally designed for genetic data (Cockerham 1973, Long 1986, Weir and Cockerham 1984). AMOVA produces estimates of variance components and F-type statistics which are analogs of several genetic distance measures. The significance of the variance ratios was tested using a non-parametric permutation of the difference matrix. 100,000 permutations were performed so that low probabilities would be estimated more accurately to apply table-wide statistical criteria (Rice 1989, below). F_{st} values were calculated by choosing differences between mtDNA alleles as 0 or 1, and the

differences between 2 microsatellite alleles in 2 belugas was 0,1,2, or 4 ("number of different alleles" choice in Distance Matrix Options in Arlequin). Φ_{st} values for haplotypes and R_{st} values for microsatellites were calculated by choosing the differences between microsatellite alleles as the "sum of squared size difference" in Distance Matrix Options in Arlequin (Schneider *et al.* 1997). These values can be considered to be measures of genetic distance or can be converted to several measures of genetic distance after incorporating rates of mutation or drift (Excoffier *et al.* 1992, Michalakis and Excoffier 1996).

Table-wide statistical criteria for tables with multiple comparisons were calculated using the sequential von Bonferroni correction (Holm 1979, Rice 1989). This correction produces a "minimum significance level" for individual comparisons which is calculated based on the number of comparisons, the distribution of probabilities, and the chosen table-wide α level. A table-wide α =0.05 was chosen.

Genetic relationships among 21 collections (numbered in Table1) from EHB, SAN, and HS were also described with phylogenetic trees. We used Cavalli-Sforza's "chord distance" between populations (Cavalli-Sforza and Edwards 1967) for both microsatellite loci and haplotypes as a measure of genetic distance, and the neighbour-joining method (Saitou and Nei 1987) to construct phylogenetic trees. Chord distance was calculated to 6 significant digits with our own programs and the Neighbour-joining program in the PHYLIP statistical package (Felsenstein 1993), was used to construct the trees.

"Assignment" probabilities (Waser and Strobeck 1999, Paetkau *et al.* 1997, Appendix A) were used to "assign" individuals to their most likely population of origin. Individuals with missing data at more than 2 microsatellite loci were not assigned, although they were included to calculate population summary statistics. Calculations were done with in-house software written in Visual Basic by the first author. The following options were chosen before calculating assignment probabilities to individuals: 1) the individual being assigned was removed from its population of origin, and 2) allele frequencies of "0" in any population were replaced with a frequency of "1" (Appendix A). Individuals in all six sample populations were assigned to one of the three summering populations of EHB, SAN, and WHB. Assignments and misassignments of individuals were then examined to discern possible dispersion and migration patterns.

Results

Nine sample populations

Only 3 haplotypes were observed in StLR belugas, 6-8 haplotypes in each of Churchill, NaR, EHB, NWQu and Kimmirut, 12 in SAN, 14 in NHB, and 15 in Arviat (Tables 3 and 4). Haplotype diversity (D), which is a measure of both the number and the evenness of distribution of alleles, is correlated with the number of haplotypes, but has a slightly different trend. Churchill River beluga, dominated by haplotype H02, had the lowest diversity, but samples from NaR, dominated by H18, and StLR, dominated by H18 and H29, also low diversities (Tables 3 and 4).

Haplotype diversity is lower in the NaR samples than the other EHB samples (Table 3) . The early NaR samples have the highest frequencies of haplotypes H17, H18, and also two haplotypes not found elsewhere (Table 4). Only one beluga among 41 had haplotype H02, the common western haplotype.

Only 62 microsatellite alleles were observed in StLR belugas, 97 in the NaR, and 104 in the Churchill River (Table 3). The largest number of alleles was observed in NHB (120 alleles) and SAN (114 alleles). Again, diversity measures were correlated with each other but each had a slightly different pattern. Among Arctic belugas, NaR and SAN belugas had the lowest microsatellite diversities (0.6540 and 0.6595), and NHB and NWQu the highest (0.6746 and 0.6745).

AMOVA

There was notable haplotype differentiation based on significance of F_{st} values for mtDNA among the 9 sample populations (Table 5). Haplotype differentiation was significant in 29/36 comparisons after applying sequential von Bonferroni criteria (Rice 1989). 34/36 comparisons were significant at $P \leq 0.05$.

Overall, F_{st} values were largest for comparisons with StLR (Mean F_{st} = 0.39), with NaR (0.35), and then with EHB (0.26), and these three populations were significantly differentiated from most other populations. EHB and NaR were not significantly differentiated from each other (F_{st} = 0.02, Pr = 0.132) . NaR had larger haplotype genetic distances to all other populations than EHB samples did (Table 5). SAN and Churchill differed from most other populations, however the genetic distance between them was not large (F_{st} = 0.05, Pr = 0.004). There was generally little differentiation among samples from KIM, Arviat, NWQu, and NHB (mean F_{st} = 0.025). However, HS and Arviat differed ((F_{st} = 0.03, Pr = 0.034).

A table of R_{st} values (based on distance measure between haplotypes) for the same 9 samples population yielded a very similar pattern of genetic distances as on Table 5, but with fewer significant differences (not shown).

There was notably microsatellite differentiation among 9 groups (Table 6). Only 14/36 comparisons were significant using sequential von Bonferroni criteria (Rice 1989). StLR was the only location that differed from all others. The genetic distance (F_{st}) between StLR and Arctic populations ranged between 0.067 and 0.088, this larger than comparisons among Arctic populations, where F_{st} ranged from 0.000 to 0.011. KIM, Arviat and HS were not significantly differentiated from each other, but differed from NHB, EHB, and SAN. Among Arctic populations, Churchill and NaR did not differ from any other populations. SAN was most often different from other populations, but did not differ from Churchill, NHB, and NaR.

AMOVA under the stepwise mutation model for microsatellite, namely for R_{st} values and their significance, had similar patterns of, but even fewer significant differences (not shown). In this last analysis, StLR was differentiated from all other populations, and SAN from Kimmirut. There were no other significant differences.

F_{st} values for haplotypes and their significance comparing 21 collections in SAN, EHB, and HS (Table 7) shows that the trends among locations (Table 5) do not necessarily apply to all collections within each location. The "phylogenetic" tree of 21 collections (Figure 3) based on chord distance reflects the relationships described below. F_{st} values for haplotypes among SAN collections were small or negative and there was no significant differentiation among these (Table 7). SAN samples cluster closely in Figure 3. There were few significant differences among EHB collections. 1/36 comparisons was significant at Pr<0.00029, the minimum significance level (Rice 1989) and 10/36 at Pr<= 0.05. The differences mostly involved Umiujaq 1997 (n=3) which were all H02, the most common western haplotype. In Figure 3, Umiujaq is close to other collections with a high frequency of this haplotype. Within HS samples, 1/21 sample groups differed at Pr=0.00029 and 5/21 at Pr<= 0.05. All differences involved the Kangiqsujjuaq 1983 collection, which consisted of 3 x H17, 2 x H18, and one H20, the first two haplotypes most commonly associated with EHB and the last with NHB (Table 3). In Figure 3, Kangiqsujuac1983 samples are placed in the middle of EHB collections. Also in Figure 3, most HS collections are placed closer to Sanikiluaq than EHB collections.

Many collections differed from SAN collections. SAN and EHB collections were significantly differentiated (Pr <= 0.00029, minimum significance level, Rice 1989) in 26 /45 = 58% of comparisons. SAN and HS were differentiated in 2/35 = 6%, and EHB and HS in 10/63 = 16% of comparisons. The NaR samples did not differ from other EHB samples, but did differ form HS.

Fisher's exact test (Guo and Thompson 1992) and probabilities of F_{st} values from AMOVA (not shown) showed that alleles frequencies between males and females did not differ significantly with collections or locations. The ratios of the number of haplotypes in females and males observed in five years were 1:4, 3:5, 3:6, 3:3, and 2:4 (overall 5:12). The number of microsatellite alleles observed in the 5 years were 46:67, 75:83, 65:72, 69:71, and 68:69 (overall 97:107). This result is partly due to sex ratios which were 3:7, 15:15, 7:11, 6:12, and 7:8 (overall 38:53), since more diversity is expected in larger samples.

AMOVA for microsatellites (F_{st} values and their significance) for 20 collections that had microsatellite data yielded very few significant differences (not shown). Application of table-wide criterion of α = 0.05 (Rice 1989) suggested there were no differences among any sample groups. In a table with 190 comparisons (20 x 19/2), one would expect 10 differences significant at Pr <=0.05 due to chance, but in fact 18 differences were observed. 8 of 18 differences involved Salluit 1997, which differed from both SAN and

EHB samples groups, but not from Nastapoka and Kangiqsujjuaq, and 4 of 18 differences involved Inukjuac 1994 which differed from mostly from SAN. Nevertheless, there were patterns within F_{st}s. A phylogenetic tree using chord distances for microsatellites only placed all SAN samples on the same branch of a star-like tree (Figure not shown). Also, the two Nastapoka samples had a short distance genetic between them, even though on different branches of the tree. No other patterns are identifiable.

R_{st} values and their significance for microsatellites in these 20 collections showed even fewer differences. Significant differences at $Pr \leq 0.05$, all not significant with table-wide criteria, again involved Salluit 1997 and Inukjuac1994.

Assignment Tests

Results in column "Genotypes Possible?" in Table 8 confirm that many populations have the same alleles, but proportions of alleles differ. Patterns of assignments varied slightly when different methods or different loci were chosen for analyses (Table 8). Method 1, in which the individual tested is removed from the population, and allele frequencies of "0" are replaced with "1", believed to be a conservative method, was used in the summary below.

Among the three summering populations, EHB belugas were most strongly assigned to their population of origin (Figure 3). 82/90 EHB belugas are reassigned to EHB, many with high probabilities. Two EHB individuals, both haplotype H02, are assigned to other locations with high probabilities. Only 67/103 WHB belugas are reassigned to WHB. Many were misassigned, 24/103 to SAN, and 12/103 to EHB (Figure 3).

65/95 Sanikiluac individuals are assigned to Sanikiluaq. A small number (9/65) were assigned to EHB, 8 of these 9 with high probabilities. Four of the misassigned individuals were H17, 3 were H18, and one was H07. Also, all four H17, 2/3 H18, and the one H07 individuals all had high probabilities of being assigned to EHB on the basis of assignments done with microsatellites only (not shown).

HS belugas were mostly often assigned to WHB (33/61), then EHB (19/61), and least often to SAN (9/33) (Figure 3). Assignments to EHB were often with high probabilities. NHB belugas were most strongly assigned to WHB (52/112) and SAN (38/112), and less to strongly EHB (22/112). A number were assigned to EHB, but only a few with high probabilities. Kimmirut belugas were most often assigned to SAN and EHB. The 4 individuals misassigned to EHB with high probabilities are two H18 individuals, one H22, and one H24.

Overall, 72.2 % of individuals from EHB, SAN, and WHB were correctly assigned back to their population of origin (Figure 3). This percentage varied using different methods. When a frequency of ½ rather than 1 for missing alleles was used within populations, the percentage of correct assignments increased slightly to 73.3% (Method 2, Table 8). If no value was substituted for missing alleles, many individuals could not be assigned to any population, thus fewer individuals (65.8%) are correctly assigned (Method 3, Table 8). On the other hand, if the individual being assigned are not removed from the population, and no substitution is made for rare alleles, all individuals with rare or unique alleles are reassigned to their population of origin (Method 4, Table 8). Using this method, 86.3% of individuals are correctly assigned.

If only haplotypes are used for assignments, individuals from HS, NHB, and KIM were assigned mostly to EHB or WHB (Haplotypes, Table 8). Few were assigned to SAN because only one locus was tested – all individuals with H02 or H05 were assigned to WHB and all with haplotypes H07, H17 and H18 were assigned to EHB.

The recent 1998-1999 haplotype data (Table 4) were not used in assignments. In these recent samples, 28/34= 80% of EHB belugas had haplotypes H17 and H18. In northeastern Québec (Akulivik and Puvirnituq) 20/26 belugas were H02, and 1/26 H17 (Table 4). In Hudson Strait communities, 12/69 = 17.39% were H17and H18, and 3/69 = 4.34 % were H07. These percentages of "EHB genotypes" are not all that different than those from the assignments. Of ten samples from Kuujjuac, six are EHB genotypes. The previous small sample from 1997 had 2/7 H07 haplotypes, but not H17 and H18. There were one or two H05 belugas from Kuujjuac in all years. This haplotype was never associated with EHB

or SAN, but with WHB and NHB.

Microsatellites alone did not assign individuals correctly with high percentages (Table 4). However, individuals that were misassigned on the basis of haplotypes were often misassigned to the same population on the basis of microsatellites. Patterns of assignments using haplotype and using microsatellites differed slightly. Specifically, larger fractions of HS belugas, and increased fraction of belugas from KIM, are assigned EHB and fewer are assigned to SAN and WHB. This may be related to breeding patterns, namely EHB belugas may mate with HS belugas, but not with those from SAN and KIM.

Discussion

The primary objective of this study was to examine whether the community of Sanikiluaq (SAN), and communities from Hudson Strait (HS), from northwestern Québec (NWQu), and those from the eastern Hudson Bay (EHB) arc hunt the same stocks of belugas. Results of various analyses support the hypothesis that there are consistent genetic differences between EHB and SAN belugas, and also among these two populations and other sample populations examined.

EHB arc (1990s) and Nastapoka River (NaR) (1984-1985) belugas are significantly differentiated from all other sample populations tested, but not from each other. Patterns of similarities among collections from the EHB arc and NaR confirm that all communities on the EHB arc hunt the same stock. In addition, EHB belugas are reassigned to their populations of origin more often than other sample populations, and the probabilities associated with reassignment are high. The differentiation is primarily on the basis of haplotypes, however the consideration of microsatellites increases the percent correct assignment, this affecting the credibility of all reassignments.

Belugas hunted in Sanikiluaq are significantly differentiated from all other populations tested, both on the basis of haplotypes and microsatellites. There is a strong consistency among the genetics of belugas hunted in Sanikiluaq over five years. The 5 collections have small genetic distances between them and cluster closely in phylogenetic trees. Several haplotypes, namely H06, H17, H39, H21, occur at low frequencies, but consistently in different collections (Table 3). These animals may be from a stock that is not only different from EHB, but from also from western Hudson Bay. However, both haplotype and microsatellite diversities are high, suggesting that these samples may represent mixed stocks. The possibility that male beluga hunted in Sanikiluaq may have a larger genetic diversity than females may also indicate that a homogenous population was not sampled. Overall, we can conclude that Sanikiluaq hunts (a) different stocks(s).

Within WHB, it is possible that Churchill animals represent a social group that persists through time. The belugas sampled here have a very high frequency of haplotype H02 (84%). This frequency is significantly higher from all other sample populations, and was observed in all five years of sampling.

There is a high degree of genetic overlap in all population comparisons, and statistical differences arise from differences in allele frequencies among populations and not from different alleles. This fact makes it very difficult to determine to what extent different genetic groups actually mix in their summering areas, and which are hunted in different locations. In other words, it is impossible to determine whether the few western HB -type belugas killed in EHB are from the west or whether they are EHB belugas that genes also found in WHB, or both. Similarly, when the occasional haplotype H18 or H17 is landed in any location other than EHB, it is not known whether this was an EHB beluga wandering or migrating a different route, or whether these haplotypes occur at low frequencies in other stocks. To quantify the actual threat to EHB belugas, modelling exercises in which it is assumed that belugas hunted in many locations are mixtures of stocks, and that predict the effects on the entire population may be required.

The second question addressed in this study was the source of migrating animals, particularly in NWQu and HS where communities may be hunting EHB belugas. Assignments suggested that EHB belugas comprise approximately 31% of belugas hunted in NWQu and HS, 20% in NHB, and 8% in KIM (Figure 3, Table 8). Calculating assignments with only haplotypes gives percentages of 27, 11, and 7%, not

notably different from the ones using both haplotypes and microsatellites. Microsatellites do not contribute strongly in differentiating populations.

When only microsatellite loci are used for assignments, a notable higher fraction of belugas in HS and KIM are assigned to EHB, namely 44% and 22%. This result on its own may mean that WHB belugas, but not SAN belugas, breed with EHB belugas.

The relatively small genetic distance between Sanikiluaq and northern Hudson Bay, for both types of DNA (Tables 5 and 6) , and the assignment of NHB belugas to SAN is noteworthy (Figure 3, Table 8). Although haplotype frequencies are not similar in the two areas, NHB and SAN share haplotypes H02, H06, H16, H18, H20, H21 and H35. Haplotype H20 is common in NHB samples, constituting 16% of samples. This haplotype does not occur in EHB and one was sampled in SAN. It is possibly that the SAN "stock" may migrate to northern Hudson Bay. Belugas hunted in NHB have a high genetic diversity, so it is also possible that the belugas in this study were a mixture of stocks.

Are there temporal trends in the EHB genetics data? The Kangiqsujuac 1983 collection had 4/6 EHB haplotypes (Table 4). It is possible that EHB belugas were a larger part of the hunt in the 1980s. Only comparison with more recent samples may give us more insight. In Kuujjuac 1998-1999, 6/10 belugas had EHB haplotypes, but no other HS communities had high frequencies of EHB haplotypes. Also, the differences between NaR (1984-1985) samples and EHB 1990s samples represent a temporal change.

The existence of genetic patterns which can be explained in terms of post-glacial dispersion may confirm that belugas do not change their seasonal feeding and migrating patterns rapidly. The similarity of EHB belugas and St. Lawrence haplotypes is obvious, with both populations having a high frequency of haplotype H18. Haplotype H29 occurs only in the St. Lawrence River, differs from H18 by one nucleotide, and H17, which occurs only in Hudson Bay, also differs by one nucleotide different from H18 (Brown Gladden *et al.* 1997, de March *et al.* 2002). The details of post-glacial events that may have caused this have not yet been fully researched, however some major events in the post-glacial history of Hudson Bay are known (Fulton 1989). Eight thousand years ago, much of the area now covered by Hudson Bay consisted of glacial Lakes Agassiz and Ojibway. Although these two lakes had connected to the St. Lawrence drainage to the south at several earlier dates, it is difficult to believe that these large cold inland lakes could have been a permanent home to beluga over an extended period of time. However, is possible that entrapments or other unusual events may have introduced beluga into these lakes in some years when survival was possible. Lake Agassiz decreased in size very rapidly approximately 8000 years BP when water levels dropped instantaneously by 250 m, with water spilling into the Atlantic after the ice obstruction in Hudson Strait disappeared (Fulton 1989). After that event, beluga could enter Lake Tyrell, now Hudson Bay, through Hudson Strait. The St. Lawrence haplotypes known to be common in EHB today may have already been in Lake Agassiz before this catastrophic event, or they may have been the haplotypes of early belugas to enter this new habitat. The fact that EHB haplotype still resemble St. Lawrence belugas may be an indication of the high degree of site fidelity for females and their families for calving and summer feeding areas. With an average of 13 years per generation (Stu Innes, *pers. comm*), 8000 years represents approximately 600 generations.

Other post-glacial events may be reflected in southern Hudson Bay haplotypes. Both Sanikiluaq and EHB have some western and high Arctic haplotypes which are absent or rare in other Hudson Bay locations. One of these is haplotype H07, which occurs in most EHB collections. This haplotype is not common in other locations in Hudson Bay, however it is common in most Canadian high Arctic populations, West Greenland and the western Canadian Arctic (de March *et al.* 2001). Also, haplotype H06, most common in the Beaufort and Chukchi Sea stocks, occurs in most Sanikiluaq collections and in Arviat. Some of the rare haplotypes in Sanikiluaq and EHB otherwise occur in far removed areas (H16 and H20 in Northern Hudson Bay and H42 in Beaufort Sea). These haplotypes suggest connections to the west and north. It is possibly that these haplotypes occur because both EHB and SAN populations were established earlier than other Hudson Bay populations. Approximately 5 ka BP (five thousand years before present), passage between Fury and Hecla Straits was easier due to higher water levels and warmer temperatures. Northern populations and Hudson Bay populations of beluga may have mixed more than they do today. The area now known as the Gulf of Boothnia would have been considerably larger, and probably would have been home to belugas. Passage became more difficult 3-4 ka BP when

land levels rose. The genetic similarity between Sanikiluaq and NHB remain may also be due to this ancient pattern.

If the above are true, then most of the typical Hudson Bay haplotypes entered Hudson Bay at a later date, possibly with the last 5 thousand years. The hypothesis that Hudson Bay beluga are a mixture of original Atlantic and Pacific colonizers (ref) now seems simplistic. It is probable that EHB haplotypes represent only one of the populations that may have recolonized Hudson Bay from the Atlantic.

The three summering populations associated with estuaries included in this study had low genetic diversities. There is no doubt that in the St. Lawrence this is due to historic overharvesting. In the Arctic, it is also possible that these are populations with a strong site fidelity, and these may interbreed more. However, even if the genetic diversities in the Arctic estuarine populations is low because of past overharvesting, it is evident that belugas from populations with higher diversities have not entered these rivers. This is further evidence that behaviours change slowly.

There were no significant differences between the genotypes of the sexes at any locations sampled. Even when the two sexes were separated as subsamples in larger analyses, they are often neighbors in phylogenetic trees (not shown). Overall, it can be concluded that males and females do not disperse to different summer locations, nor do they migrate at very different times. Richard *et al.* ( ) have shown, with radio telemetry, that most belugas that travel large distances, are males. This is not inconsistent with our observations.

The most obvious shortcomings in this research are sample are small sample sizes from some locations, lack of repeated sampling over several years, lack of seasonal information, and a complete lack of samples from important areas. This problem is being addressed with ongoing a sampling programs in Nunavik and Nunavut. In particular, southern Hudson Bay, James Bay, and several large rivers in both southern and western Hudson Bay, where there is no hunting tradition, will be sampled. Some of these areas may be the summering areas of stocks hunted in EHB, Sanikiluaq, or western Hudson Bay.

It is evident in this study that haplotypes are the strongest individual locus for differentiating stocks. In future research, we will use an extended haplotype region, in which several of the common haplotypes observed now will be subdivided into several. As long as use of the extended region does not lead to a proliferation of rare haplotypes, our ability to delineate stocks may improve. The contribution of different microsatellite loci will also be evaluated. Fewer loci may be as informative as fifteen.

Numerical techniques to address stock issues such as these will continue to evolve. The comparison of collections with small sample sizes can both create false differences and obscure differences. Because there may be many comparisons, significant differences will occur due to chance, and findings cannot necessarily be extrapolated to the whole population. Also, belugas in small collections may be relatives, and if they contain several uncommon alleles, it may appear very different from all their neighbours. It is also possible that small collections may actually be a group of belugas from another stock, but the small sample size will not allow us to detect differences. Increasing the sample sizes by pooling samples is only a partial solution. More “significant differences” by any one of a number of statistical test can be described by pooling collections and increasing sample size (de March *et al.* 2001). Again the fact that larger collections contain groups of relatives may contribute to the ability to describe significant differences. Valuable information from small collections may be lost by pooling. Thus we are faced with trying to interpret the meaning of small-scale patterns and to find large-scale patterns at the same time. Marine mammal scientists are grappling with this problem, and a variety of approaches are still being examined. Future modelling studies may be the best way to work with both small and larger scale variation. In case such as this, where important stocks are being examined, it is best to examine data from a variety of viewpoints.

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Appendix A. Assignment Statistics. "Assignment" probabilities (Waser and Strobeck 1999, Paetkau *et al.* 1997) were used to describe the genetic affiliation of individual belugas in six sample populations to three sample populations where they might have originated. This was done for all individuals which had haplotypes and valid data at at least 13 microsatellite loci as follows. The probability of sampling the individual's geneotype in a random sample from each of *n* populations of interest was first calculated. These *n* probabilities were calculated from allele frequencies in each population. These probabilities can be used as they are, however they are usually standardized to add up to 1 (Baye's Formula). The original or the standardized probability can be used to describe an individual's affiliation to different population or to determine the population with which the individuals is most likely affiliated. This method is particularly useful in that it may identify individuals which could be in different geographic locations at different times of the year. The patterns assignments or misassignments are then viewed in terms of knowledge about individual belugas, sex, date, knowledge of the migration or hunt in particular years, or the alleles which caused the misassignment

In assignment calculations, slight differences in assumptions about rare alleles, removing or not removing animals to be assigned from its population of origin, and the choice of performing calculations with simulations or with actual individuals, can all affect overall outcome. We chose to remove the individual being assigned from its population of origin, to replace alleles frequencies of "0" in any population with "1". Paetkau *et al.* (1997) replaced missing alleles with a frequency of ½. If frequencies are left at "0", all animals with unique alleles are no assignable, hence the assignment statistics are weak. We chose the value "1" for missing allels because we believed assignments would be conservative. Specifically, individuals with unique alleles would be less likely to be reassigned to their population of origin on the basis of the presence of one allele.

Figure 1. Place Names.

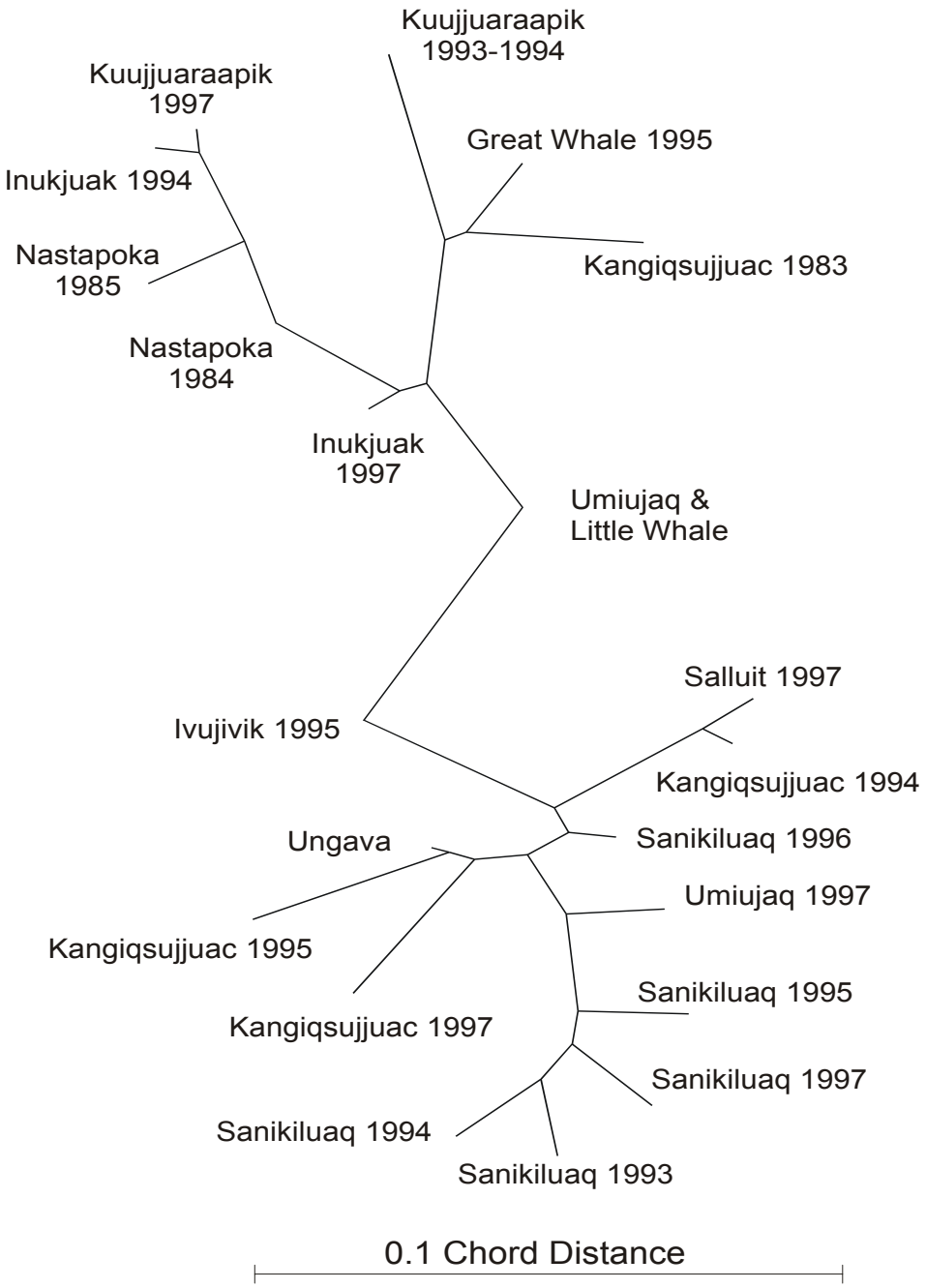

Figure 2. Phylogentic tree of 21 beluga collections form eastern Hudson Bay, Belcher Islands, and Hudson Strait, calculated from Chord distances and constructed with the neighbor-joining method.

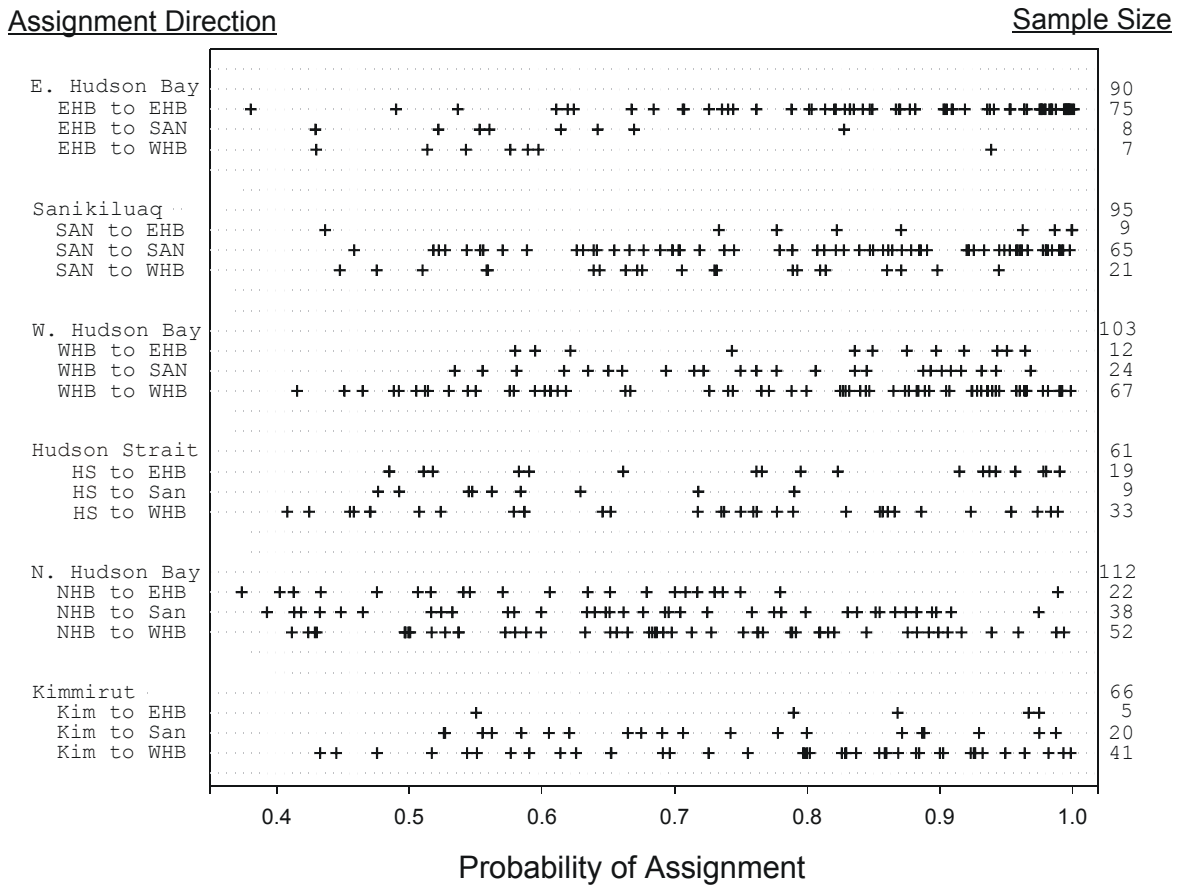

Figure 3. Assignment of individual beluga from 6 locations to EHB, Sanikiluaq, and WHB. Each beluga was assigned a most-likely population of origin based on both haplotype and microsatellites, and the probability that gave this assignment is plotted.

Table 1. Beluga samples and collections (numbered) used in this study. Some individuals were analysed for only 1 type of locus, hence the total number in any collection may exceed the number analysed for haplotypes or microsatellites.

Collection # in Table 7.	Sample Populations	Year(s)	n with Haplotypes	n with Microsat. Loci	F:M ratio	Dates
	Western Hudson Bay (WHB)					
	Kimmirut	1989-1996	82	66	43 : 40	mainly June and fall
	Arviat	1985	34	30	16 : 19	mainly mid July and mid august
		1987	22	20	7 : 15	early August
	Churchill	1988-1993	55	53	22 : 22	late July, early August
	Northern Hudson Bay (NHB)					
	Cape Dorset	1990,1996	4	4	4 : 4	October
	Coral Harbour	1995,1996	40	43	16 : 19	Aug to Nov, mostly September
	Hall Beach	1994,1996	7	10	0 : 10	September
	Igloolik	1994-1996	49	42	7 : 39	late Aug, mostly September
	Repulse Bay	1983, 1995	24	13	11 : 13	late Aug, mostly September
1	Sanikiluac (SAN)	1993	10	10	3 : 7	late June, early July
2		1994	30	27	15 : 15	late June, early July
3		1995	23	23	7 : 11	as above, 3 in Aug & Sept
4		1996	18	16	6 : 12	as above, 6 in Sept, 1 in Nov
5		1997	19	19	7 : 8	June, 1 in Oct
6	Nastapoka River (NaR)	1984	18	18	12 : 6	June-Sept, mostly July
7		1985	23	24	12 : 12	mostly July, Aug
	Eastern Hudson Bay (EHB)					
8	Kuujjuaraapik	1993	2	2	2 : 0	July
8	Kuujjuaraapik	1994	5	5	1 : 0	August
9	Kuujjuaraapik	1997	5	5	1 : 4	July and Sept
	Kuujjuaraapik	1998	8	0		
10	Great Whale River	1995	6	6	3 : 3	August
11	Richmond Gulf	1995	2	2	1 : 1	July
11	Little Whale River	1995	2	2	0 : 2	September
11	Little Whale River	1995	2	2	0 : 2	September
11	Umiujaq	1994	3	3	2 : 1	June and July
11	Umiujaq	1995	2	2	0 : 2	June and July
12	Umiujaq	1997	3	4	3 : 1	June and July
	Umiujaq	1999	1	0		
13	Inukjuak	1994	7	7	4 : 3	mostly July
14	Inukjuak	1997	10	10	6 : 4	mostly July
	Inukjuak	1998,1999	25	0		

Table 1. Continued

Collection # in Table 7	Sample Populations	Year(s)	n with Haplotypes	n with Microsat. Loci	F:M ratio	Dates
	Northern Québec (NQu)					
15	Ivujivik	1995	6	6	3 : 3	June and July
	Ivujivik	1998-1999	17			
	Puvirnituq	1998-1999	25	0		
	Akulivik	1998-1999	1	0		
	Hudson Strait (HS) and Ungava					
16	Salluit	1997	7	8	4 : 4	June, July, August
	Salluit	1998	5	0		
17	Kangiqsujjuac	1983	6	0	2 : 4	October
18	Kangiqsujjuac	1994	10	10	2 : 8	unknown
19	Kangiqsujjuac	1995	9	9	8 : 1	June&July
20	Kangiqsujjuac	1997	7	7	3 : 4	June&July
	Kangiqsujjuac	1998-1999	18	0		
21	Quaqtaq	1995	2	2	0 : 2	October
	Quaqtaq	1998	5	0		
21	Kangirsuk	1994	1	1	1 : 0	unknown
21	Kangirsuk	1995	2	2	2 : 0	July
21	Kangirsuk	1997	7	7	6 : 1	June and July
	Aupuluk	1998-1999	9	0		
21	Tasiujaq	1994	4	2	1 : 1	unknown
21	Kuujjuaq	1997	7	7	3 : 4	July
	Kuujjuaq	1998-1999	10	0		
	Kangirsualujjuaq	1998	1	0		
	St. Lawrence River (StLR)	1988,1989,1991	18	18	11 : 7	
	Total = 741 belugas		694	547		

Table 2. Details of the fifteen microsatellite loci. Descriptions are based on all samples (>1300) we have analysed.

Microsatellite Locus	*Annealing Temperature*	*Reference*	*n Alleles*	*Range of Sizes*	*Major Modes*	*Observed Heterozygosity*
DlrFCB1	64	Buchanan et al 1996	9	107-127	117	0.73
DlrFCB2	63	"	9	170-188	184	0.44
DlrFCB3	61	"	25	141-207	141,157,165	0.85
DlrFCB4	63	"	14	155-183	159,163	0.69
DlrFCB5	61	"	10	106-132	108,124	0.60
DlrFCB8	63	"	9	163-185	171,177	0.73
DlrFCB10	61	"	10	171-189	183	0.79
DlrFCB11	61	"	13	110-138	114,134	0.48
DlrFCB13	61	"	8	270-294	286	0.17
DlrFCB14	61	"	9	289-329	309	0.61
DlrFCB16	61	"	11	276-302	278,296	0.67
DlrFCB17	64	"	24	139-205	(167+169),177	0.84
Gme464/465	45	Schlötterer et al 1991	6	130-142	134	0.56
MnoEV37Mn	59	Valsecchi and Amos 1996	15	177-215	195,(205-209)	0.84
MnoEV94Mn	65	"	16	202-244	202,208,214	0.77

Table 3 . Genetics descriptions for 9 sample populations 1993-1997.

Note	Sample Population	n beluga	n beluga with Haplotypes	n beluga with Microsatellite data	n beluga with both	n different haplotypes	Haplotype Diversity	n different Mic Alleles	Microsatellite Diversity
	Kimmirut	83	82	66	65	8	0.591	109	0.670
[1]	Arviat	57	56	50	49	15	0.747	111	0.672
[1]	Churchill	55	55	53	53	7	0.294	104	0.661
	Northern Hudson Bay	142	124	112	94	14	0.580	120	0.675
[2]	Nastapoka River 1984-1985	42	41	42	41	7	0.510	97	0.654
[2]	Eastern Hudson Bay 1990-1997	48	47	48	47	6	0.637	104	0.661
	Northern Québec, Hudson Strait	67	65	61	59	8	0.703	110	0.675
	Sanikiluaq	100	100	95	95	12	0.555	114	0.660
[3]	St. Lawrence River	18	18	18	18	3	0.512	62	0.592
	Total					32		150	

[1] combined as West Hudson Bay (WHB) in 6 population analyses

[2] combined as East Hudson Bay (EHB) in 6 population analyses

[3] omitted in 6 population analysis

Table 4. Haplotype frequencies in 9 locations and from 13 communities in northern Québec and eastern Hudson Bay locations in 1998 and 1999. "Others" are frequencies of unnamed haplotypes which occur in only one location.

Haplotype Name	H02	H04	H05	H06	H07	H13	H16	H17	H18	H20	H21	H22	H23	H24	H29	H32	H35	H39	H44	Others	Total
Nine Locations																					
Kimmirut	49	-	14	-	-	-	-	-	2	-	-	12	1	2	-	-	-	-	-	1,1	82
Arviat	26	-	7	3	1	1	-	-	5	5	1	1	1	-	-	1	-	1	1	1,1	56
Churchill R.	46	-	4	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	1	1	55
N. Hudson Bay	77	-	6	1	-	1	3	-	5	21	3	2	1	-	-	-	1	-	-	1,1,1	124
Nastapoka R.	1	-	-	-	5	-	-	2	28	-	-	-	-	-	-	1	-	-	-	2,2	41
E. Hudson Bay	6	-	-	1	5	-	-	8	26	-	-	-	-	-	-	-	-	-	-	1	47
Hudson Strait	33	-	6	-	6	-	-	5	7	3	-	2	-	3	-	-	-	-	-	0	65
Sanikiluaq	65	-	-	12	1	-	1	6	3	1	3	-	-	-	-	-	2	4	-	1,1	100
St. Lawrence R.	0	-	-	-	-	-	-	-	6	-	-	-	-	-	11	-	-	-	-	1	18
																					588
Northern Quebec and Eastern Hudson Bay Samples from 1998-1999																					
Kuujjuaraapik	1	-	1	-	-	-	-	2	4	-	-	-	-	-	-	-	-	-	-	0	8
Umiujaq	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1
Inukjuak	2	-	-	-	-	-	-	1	21	-	-	-	-	-	-	-	-	-	-	1	25
Puvirnituq	19	-	-	1	-	-	-	1	-	-	-	3	-	-	-	-	-	-	-	1	25
Akulivik	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1
Ivujivik	14	-	1	-	-	-	-	2		-	-	-	-	-	-	-	-	-	-	0	17
Salluit	1	-	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	5
Kangiqsujjuaq	13	-	1	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	1	18
Quaqtaq	4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	0	5
Aupuluk	6	2	-	-	1	-	-	-	-	-	-	-	-	-		-	-	-	-	0	9
Tasiujaq	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4
Kuujjuaq	3	-	1	-	-	-	-	2	4	-	-	-	-	-	-	-	-	-	-	0	10
Kangirsualujjuaq	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1
																					129

Table 5. F_{st} values and associated probabilities for mtDNA differentiation. F_{st} values are above the diagonal, probabilities are below. Differentiation significant at Pr < 0.006, the minimum significant level for a table-wide α = 0.05, is marked with an *.

	Kimmirut	Arviat	Churchill R.	N Hudson Bay	Nastapoka R.	E Hudson Bay	Hudson Strait	Sanikiluaq	St. Lawrence R.
Kimmirut		0.03	0.07 *	0.04 *	0.42 *	0.32 *	0.03	0.05 *	0.42 *
Arviat	0.032		0.11 *	0.02	0.30 *	0.20 *	0.00	0.04 *	0.31 *
Churchill R.	0.002 *	0.000 *		0.06 *	0.59 *	0.47 *	0.10 *	0.05 *	0.62 *
N Hudson Bay	0.002 *	0.034	0.002 *		0.41 *	0.32 *	0.03	0.03 *	0.42 *
Nastapoka R.	0.000 *	0.000 *	0.000 *	0.000 *		0.02	0.30 *	0.43 *	0.31 *
E Hudson Bay	0.000 *	0.000 *	0.000 *	0.000 *	0.132		0.20 *	0.32 *	0.26 *
Hudson Strait	0.029	0.384	0.000 *	0.010	0.000 *	0.000 *		0.04 *	0.33 *
Sanikiluaq	0.001 *	0.005 *	0.004 *	0.003 *	0.000 *	0.000 *	0.005 *		0.44 *
St. Lawrence R.	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	

Table 6. F_{st} values and associated probabilities for microsatellite differentiation.Fst values are above the diagonal, probabilities are below. Differentiation significant at Pr < 0.003, the minimum significance level for a table-wide a = 0.05, is marked with an "*".

	Kimmirut	Arviat	Churchill	N Hudson Bay	Nastapoka R.	E Hudson Bay	Hudson Strait	Sanikiluaq	St. Lawrence R.
Kimmirut		0.004	0.000	0.005 *	0.003	0.009 *	0.004	0.008 *	0.079 *
Arviat	0.022		0.004	0.007 *	0.003	0.011 *	0.006	0.008 *	0.088 *
Churchill R.	0.526	0.056		0.000	-0.002	0.003	0.002	0.004	0.067
N Hudson Bay	0.002 *	0.000 *	0.497		0.000	0.002	0.006 *	0.003	0.080
Nastapoka R.	0.079	0.080	0.860	0.559		0.001	0.003	0.002	0.083 *
E Hudson Bay	0.000 *	0.000 *	0.066	0.147	0.315		0.004	0.008 *	0.085 *
Hudson Strait	0.028	0.017	0.272	0.001 *	0.175	0.068		0.009 *	0.081 *
Sanikiluaq	0.000 *	0.000 *	0.023	0.008	0.142	0.000 *	0.000 *		0.077 *
St. Lawrence R.	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	

Table 7. Genetic distances (F_{st} values) above diagonal, and probabilities below diagonal. Differentiation significant at Pr <= 0.00029, the minimum significant level, is marked as "+++", at Pr <= 0.05, is marked as "+". The 21 collections can be identified on Table 1.

		Sanikiluaq 1993-1997					Nastapoka R. 1984-1985		Eastern Hudson Bay 1993-1997							Hudson Strait 1983-1997						
	Collection #	Sani..93	Sani..94	Sani..95	Sani..96	Sani..97	Nast..84	Nast..85	Kuuj...93,94	Kuuj...97	GWhale 95	Umiu…94,95	Umiu…97	Inuk...94	Inuk...97	Ivujivik95	Salluit 97	Kangiq...83	Kangiq...94	Kangiq...95	Kangiq...97	Ungava
Collection #		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
n =		10	30	23	18	19	18	23	7	5	6	11	3	7	10	6	7	6	10	9	7	20
Sani..93	1		-0.05	-0.05	0.02	-0.06	0.48	0.37	0.22	0.37	0.28	0.22	-0.01	0.51	0.45	-0.05	0.00	0.28	0.02	-0.02	-0.03	-0.01
Sani..94	2	-		-0.02	0.05	-0.01	0.46	0.38	0.27	0.39	0.31	0.25	0.00	0.49	0.43	-0.02	0.03	0.31	0.05	0.00	0.00	0.02
Sani..95	3	-	-		0.01	-0.02	0.44	0.35	0.25	0.36	0.29	0.21	-0.04	0.47	0.41	-0.05	0.01	0.29	0.02	-0.03	-0.04	-0.01
Sani..96	4	-	-	-		0.00	0.54	0.44	0.43	0.49	0.46	0.31	-0.11	0.60	0.53	0.01	0.04	0.47	0.06	-0.01	-0.01	0.01
Sani..97	5	-	-	-	-		0.52	0.43	0.35	0.45	0.40	0.30	-0.06	0.56	0.50	0.02	0.03	0.40	0.05	-0.02	-0.02	0.01
Nast..84	6	+++	+++	+++	+++	+++		0.01	0.28	0.01	0.27	0.01	0.66	-0.09	-0.04	0.34	0.47	0.29	0.38	0.51	0.40	0.38
Nast..85	7	+++	+++	+++	+++	+++	-		0.12	-0.05	0.09	-0.02	0.51	-0.02	0.00	0.20	0.34	0.12	0.27	0.40	0.28	0.29
Kuuj...93,94	8	+	+	+	+++	+++	+	+		0.14	-0.12	0.06	0.46	0.27	0.21	0.09	0.26	-0.12	0.21	0.31	0.21	0.22
Kuuj...97	9	+	+++	+++	+	+++	-	-	-		0.09	-0.05	0.62	-0.01	0.09	0.15	0.28	0.16	0.21	0.41	0.27	0.28
GWhale 95	10	+	+	+	+++	+++	+	-	-	-		0.04	0.52	0.28	0.22	0.08	0.27	-0.15	0.21	0.35	0.24	0.24
Umiu…94,95	11	+	+	+	+	+	-	-	-	-	-		0.38	0.02	-0.02	0.02	0.19	0.06	0.12	0.25	0.11	0.14
Umiu…97	12	-	-	-	-	-	+++	+	+	+	+	-		0.79	0.68	0.04	0.05	0.52	0.06	-0.07	-0.01	-0.01
Inuk...94	13	+++	+++	+++	+++	+++	-	-	-	-	-	-	+		-0.06	0.36	0.50	0.30	0.40	0.55	0.43	0.40
Inuk...97	14	+	+++	+++	+++	+++	-	-	+	-	-	-	+	-		0.30	0.46	0.22	0.36	0.49	0.36	0.34
Ivujivik95	15	-	-	-	-	-	+	+	-	-	-	-	-	+	+		-0.10	0.11	-0.09	-0.03	-0.10	-0.08
Salluit 97	16	-	-	-	-	-	+	+++	+	+	+	+	-	+	+	-		0.30	-0.12	-0.03	-0.03	-0.04
Kangiq...83	17	+	+	+	+++	+++	+	-	-	-	-	-	+	-	-	-	+		0.24	0.35	0.22	0.24
Kangiq...94	18	-	-	-	-	-	+++	+++	+	+	+	-	-	+	+	-	-	+		-0.02	-0.03	-0.05
Kangiq...95	19	-	-	-	-	-	+++	+++	+	+	+++	+	-	+++	+	-	-	+++	-		-0.07	-0.05
Kangiq...97	20	-	-	-	-	-	+	+	+	+	+	-	-	+	+	-	-	+	-	-		-0.08
Ungava	21	-	-	-	-	-	+++	+++	+	+	+	+	-	+++	+	-	-	+	-	-	-	

Table 8. Assignments using different options.

Assignment Direction	Genotype Possible ?	Method 1	Method 2	Method 3	Method 4	Haplotype	Microsatellites (15 loci)
EHB to EHB	91/91	75/91	77/90	64/90	83/90	80/88	50/90
SAN to SAN	95/95	65/95	64/95	60/95	79/95	19/95	59/95
WHB to WHB	103/103	67/103	69/103	65/103	86/103	83/102	53/103
Mean % Correct		72.3	73.3	65.8	86.3	64.1	56.4
NQu to EHB	48/61	19/61	16/61	10/61	10/61	16/59	27/61
NQu to SAN	50/61	09/61	08/61	07/61	07/61	00/59	10/61
NQu to WHB	56/61	33/61	37/61	32/61	32/61	43/59	24/61
NHB to EHB	80/112	22/112	17/112	11/112	11/112	11/94	39/112
NHB to SAN	101/112	38/112	39/112	37/112	37/112	03/94	37/112
NHB to WHB	106/112	52/112	56/112	54/112	54/112	80/94	36/112
KIM to EHB	38/66	05/66	05/66	04/66	04/66	05/65	15/66
KIM to SAN	38/66	20/66	18/66	12/66	12/66	00/65	21/66
KIM to WHB	64/66	41/66	43/66	40/66	40/66	60/65	30/66
cannot be assigned		0	0	61/527	32/527	0	0

Methods

Genotype Possible?	Number of genotypes that are possible in the test population.
Method 1	Allele frequencies of "0" within populations are replaced with "1". Individual tested is removed from population.
Method 2	Allele frequencies of "0" within populations are replaced with "1/2". Individual tested is removed from population.
Method 3	Allele frequencies of "0" within are not changed. Individual tested is removed from population.
Method 4	Allele frequencies of "0" are not changed. Individual tested remains in the population.
Haplotypes	Only haplotypes are used to assign individuals. Methods as in Method 1
Microsatellites	15 Microsatellites are used to assign individuals. Methods as in Method 1