An overview of genetic relationships of Canadian and adjacent populations of belugas (*Delphinapterus leucas*) with emphasis on Baffin Bay and Canadian eastern Arctic populations

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ABSTRACT

Our current knowledge of the molecular genetics of High Arctic beluga (*Delphinapterus leuca*s) populations (West Greenland, Lancaster Sound/Barrow Strait, Grise Fiord) and populations that are related (southeast Baffin, Beaufort Sea), is presented. In general, genetic analyses confirm the designation of putative stocks and suggest the existence of more stocks than previously described. Comparisons based on mitochondrial DNA haplotypes show that West Greenland (1992) belugas were significantly differentiated from Lancaster Sound/Barrow Strait, Kimmirut, Iqaluit, and/or Pangnirtung but not from Grise Fiord. Grise Fiord haplotypes were not significantly differentiated from Lancaster Sound/Barrow Strait and not from southeast Baffin locations in some years. Lancaster Sound and southeast Baffin collections were not significantly differentiated from each other. These patterns existed for most years within locations, however a few yearly collections within major locations had different patterns. The collections that differed were small groups with few haplotypes, most likely relatives. Patterns in microsatellite differentiation were slightly different than those for haplotypes. This may be due to the fact that individuals in sampled summering populations breed with individuals in other populations during migration or in overwintering areas. West Greenland and Grise Fiord microsatellites were not significantly differentiated from each other. However, Greenland differed from Lancaster Sound and southeast Baffin Island, while Grise Fiord did not. In southeast Baffin Island, Pangnirtung samples differed from Kimmirut using both haplotypes and microsatellites. Iqaluit samples had intermediate genetic characteristics between Pangnirtung and Kimmirut. Patterns of significant differentiation among collections within locations was believed to be due to a combination of temporal patterns, sampling of relatives, chance, seasonal hunting, small sample sizes, and actual differences among populations.

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INTRODUCTION

The beluga (*Delphinapterus leucas*) is a small toothed whale that is economically and socially important to northern people. It has a discontinuous circumpolar distribution, with the northernmost areas of its range in the North Water between Canada and Greenland and at Svalbard, and the southernmost extent in the St. Lawrence River estuary, White Sea, Okhotsk Sea, Gulf of Alaska, and James Bay (Stewart and Stewart 1989). Beluga populations in the Arctic undertake annual migrations between summering and wintering areas, often crossing international boundaries. During the summer, belugas are conspicuous in some coastal areas, particularly in river mouths and estuaries. The main overwintering areas in the eastern North American Arctic are believed to be Baffin Bay, Davis Strait, the Labrador Sea, and Hudson Strait (Fig. 1) and the Bering Sea and Cook Inlet in the west. Belugas probably mate in the early spring (Cosens *et al*. 1993), so they may or may not be mating with the same animals that congregate in their summering areas.

Nearctic populations of belugas are subdivided into at least 16 provisional management stocks, 11 of which exist in North America, and 7 in Canada (Donovan 1992). Stocks have been defined primarily on the basis of morphometric studies, behavioural observations, traditional knowledge, and observations of declines in some areas. Genetic findings to date, described below, have supported these divisions. However, it is already recognised that there are more stocks than described, and some recent co-management decisions in Canada have been made on the basis of recent genetic findings.

The "High Arctic" beluga stock is assumed to be shared by Canada and Greenland (Donovan 1992). It does not have well-defined borders and may in fact consist of several populations or stocks. There are several reasons for developing a better understanding of this wide-rang-

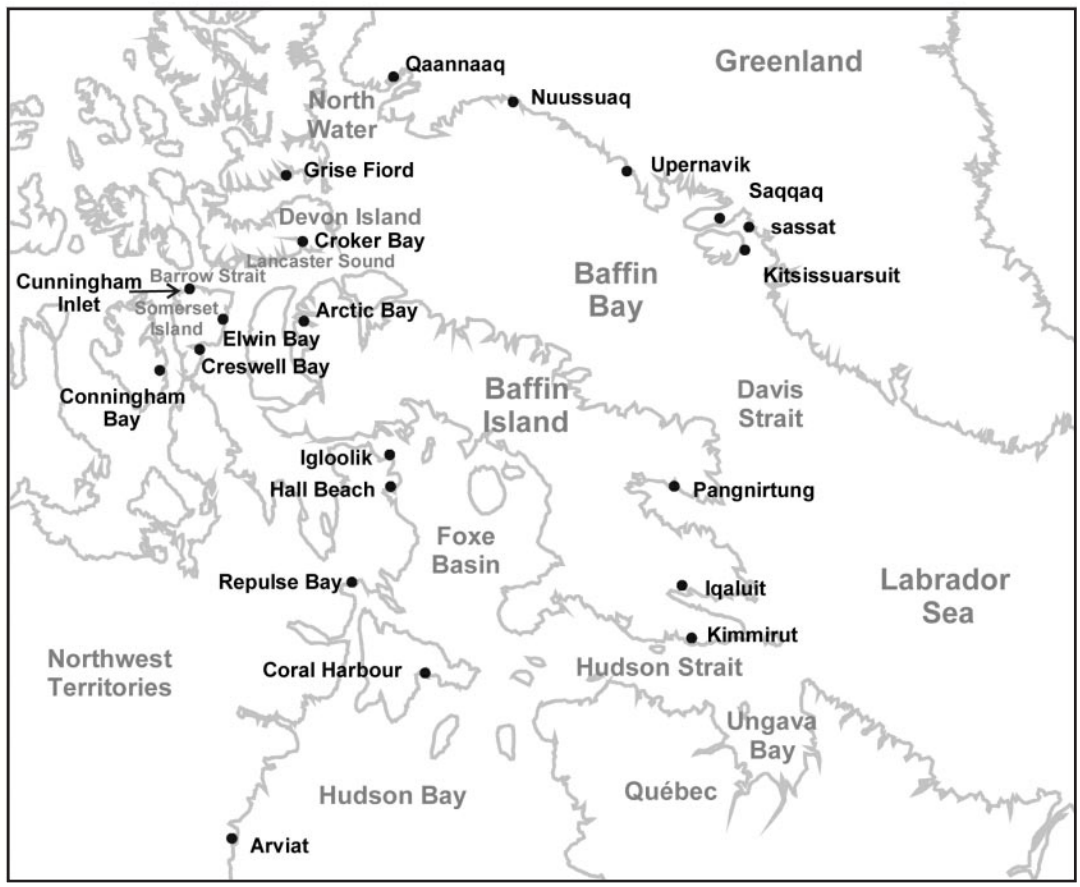

Fig. 1 *Map of localities mentioned in the text.*

ing stock. West Greenland belugas are believed to summer in the Canadian High Arctic. However, recent tracking results of belugas instrumented with satellite transmitters have shown that a large fraction (14/15) of the whales tagged in the Canadian high Arctic travelled to the North Water where they remained in the autumn season, possibly wintering there (Fig. 1, Richard *et al*. 1998, Richard *et al*. 2001). Only one whale has so far been tracked to West Greenland.

High Arctic populations have been greatly influenced by man in the last century. The numbers of beluga off the west coast of Greenland have decreased during the last 100 years and are still declining probably due to overexploitation (Heide-Jørgensen and Reeves 1996). There are presently no quota restrictions on the harvest in West Greenland. During the period of commercial whale hunting in Canada, whales in the High Arctic were driven into shore in inlets such as Elwin Bay on Somerset Island (Lubbock 1937). Until the last 40 or so years, there were no Inuit settlements that harvested these beluga. There is no quota in the Canadian High Arctic, and about 50 beluga of an approximate summer population of 21,000 are harvested each year (Innes and Stewart 2002, NAMMCO 2000). However, some proportion of this summer population is subject to hunting in West Greenland during the fall, winter and spring, with annual harvests of about 700 (Heide-Jørgensen and Rosing-Asvid 2002). There is evidence of a decline in the numbers of animals wintering off West Greenland (Heide-Jørgensen and Acquarone 2002) that has been attributed to overharvesting (Butterworth *et al*. 2002, Innes and Stewart 2002). Thus, either the High Arctic stock(s) or other stock units with unknown boundaries have been overexploited in West Greenland. Currently, the High Arctic beluga populations in Canada are listed as "vulnerable" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Campbell 1993).

Molecular genetics can now utilise two types of DNA for discriminating stocks, mitochondrial DNA (mtDNA) and microsatellite loci. Both types of loci can be 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, mtDNA, is inherited mainly maternally through egg cell material. The mtDNA locus we used consisted of a string of 234 nucleotides which are found at the beginning of the d-loop region of mitochondrial DNA (Brown Gladden *et al*. 1997). Overall, we have found variability at 22 of 234 nucleotide positions, revealing 54 different "haplotypes" or variations of this sequence. Because mtDNA is maternally inherited, it can identify situations where the female patterns of dispersion are different from the male patterns and/or where social groups are led by females. 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).

Secondly, we analyse 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 to 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.

Interpretation of genetic data requires that differences between populations and/or individuals be evaluated, and there are many opinions and methods available for analyses. Many distance measures between populations and/or individuals are based on multidimensional geo-

metric considerations without reference to any particular evolutionary model. However, most measures of genetic distance between populations used to describe and compare observations for the two types of loci are based on assumptions about the mechanisms that cause changes in allele frequencies. For mtDNA, either distance or parsimony methods can be used. Parsimony methods are based on whether or not mtDNA sequences are identical, and distance methods utilise the number of nucleotide differences to compare mtDNA sequences. Estimators for microsatellites work under the assumption of one of two types of models: the Stepwise Mutation Model (SMM; Kimura and Crow 1964) and the Infinite Alleles Models (IAM; Ohta and Kimura 1973). SMM based models are based on the assumption that the majority of mutations at microsatellite loci are stepwise in nature, changing allelic sizes by one or a few number of repeats. IAM based models assumes changes are due to drift.

Computer simulations of microsatellite mutation patterns indicate that statistical analyses based on the SMM may outperform statistics based on the IAM, particularly over long periods of independent evolution (Goldstein *et al*. 1995). Paetkau *et al*. (1997) in an evaluation of genetic distance statistics in three species of North American bears believed that distance measures based on the IAM are most informative before 20,000 years of separation, while statistics based on the SMM are informative for longer periods of separation. In northern North America, the time frame of deglaciation in the past 10,000 years allows genetic variability due to both mutation and drift in large mammals. Such data are usually analysed under the assumptions of several models or distance measures, and the results examined for trends (Paetkau *et al*. 1994).

This progression of approaches for analysing population genetic data has been reflected in the type and scope of studies and analyses performed with beluga sampled in North America.

Mancuso (1995) examined an mtDNA sequence of 320 base pairs as well as multilocus minisatellite probes (Jeffreys 1985a, 1985b). There were statistically significant differences in haplotype composition among five groups of belugas from Hudson Bay and Hudson Strait. The minisatellite analysis suggested that Mackenzie Delta belugas might be different from all others in eastern Canada but suggested no differences within eastern samples.

Brennin *et al*. (1997) examined population genetic structure in 95 belugas from 12 sampling locations in Canada and Greenland using 10 restriction enzymes. Eight haplotypes were identified among these animals. Two maternal lineages were evident: one from the St. Lawrence estuary and eastern Hudson Bay, 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 populations that colonised the Arctic after deglaciation.

Murray *et al*. (1998a, b) examined genetic variation at the Major Histocompatibility Complex locus *DRB* in 233 belugas from 7 populations. Comparison of allele frequencies among populations showed the High Arctic populations (43 individuals from Grise Fiord, Creswell Bay, Cunningham Inlet) to be different from all others including the St. Lawrence River, the Beaufort Sea, Point Lay in Alaska, Arviat, eastern Hudson Bay and Hudson Strait. No other statistically significant differences were found.

Brown Gladden *et al*. (1997) examined genetic differences among Canadian and adjacent populations using an mtDNA sequence of 324 nucleotides and 624 belugas from 25 sites. Many samples overlapped with those in Brennin *et al*.'s (1997) study. Thirty-nine haplotypes were identified. A higher degree of differentiation than in the previous studies was observed. Brown Gladden *et al*. (1997, 1999) again concluded that North American waters were recolonised by two major groups of belugas, one from the East (Atlantic) and one from the West (Pacific), with only remnants of the eastern belugas evident in the St. Lawrence River and eastern Hudson Bay. Brown Gladden *et al*. (1999) also examined genetic differences among populations using 5 microsatellite loci,

and compared the results with the mtDNA results. Patterns in microsatellite allele distributions were similar to the haplotype patterns, but yielded few statistically significant differences (Brown Gladden *et al*. 1999).

O'Corry-Crowe *et al*. (1997) examined mtDNA control region sequence variation in 324 belugas from 32 locations representing four summering concentrations in Alaska and the eastern Beaufort Sea. The sequence region consisted of 410 base pairs, a region extending past that used in both studies described above. The significance of both Φ_{st} and F_{st} values (ratios of within and between populations variances under different models) was ~ 0.00001 for most pairwise comparisons. It is now believed that there are at least 5 stocks in Alaska. Matching of haplotypes from O'Corry-Crowe *et al*. (1997) with those of Brown Gladden *et al*. (1997) in the overlapping region showed that haplotypes frequencies are very similar to our data (de March, unpublished results).

High Arctic belugas have been examined in two studies. Brown Gladden *et al*. (1997, 1999) showed that 21 Greenland belugas were not significantly differentiated from 26 belugas from Grise Fiord. This study did not include belugas from the Lancaster Sound/Barrow Strait area which are also believed to be part of the High Arctic stocks. Also, Palsbøll *et al*. (2002) examined an mtDNA control region consisting of 244 nucleotides, of which 104 overlapped with our study. Palsbøll *et al*. (2002) concluded that pre- and post-1990 Upernavik samples differed, and the Qaanaq samples differed from others consistently. No samples were significantly different from samples from southeast Baffin and the Canadian High Arctic. However, a larger than expected number of comparisons were significant near $P = 0.05$. The main hypothesis of Palsbøll *et al*. (2002) was that when dealing with small samples sizes, groups of related animals may have been sampled, this possibly leading to deceptive patterns of similarities and differences which should not be extrapolated to larger populations.

The present study discusses the genetic relationships of Canadian and adjacent populations of belugas, based on more samples and more genetic markers than previous studies. We now have more recent samples from the Canadian High Arctic and from communities not previously sampled.

METHODS

Beluga samples

The majority of the samples in the present analyses were from summer hunts and some were from scientific collections (see Acknowledgements). In many communities the hunts are seasonal with one or two peaks during spring and/or fall migrations. For this paper, the primary interest is in the eastern High Arctic populations, however, other populations were included. Six locations (West Greenland, Grise Fiord, Lancaster Sound/Barrow Strait, Pangnirtung, Iqaluit, and Kimmirut) were chosen for more detailed analyses. Belugas from the last three communities are referred to as southeast Baffin (SE Baffin) belugas. A total of 504 beluga samples from these 6 locations were grouped into "collections" within locations (Table 1), this term referring to beluga samples collected within a short period of time at one location.

In the 3 High Arctic locations, 65 belugas from Greenland, 37 from Grise Fiord, and 77 from the Lancaster Sound are examined. In the previous study by Brown Gladden *et al*. (1999), 21, 26, and 0 belugas were examined from the same areas. Also, we now analyse for 15 microsatellite loci, whereas Brown Gladden *et al*. (1999) analysed for 5. Samples from the previous study of Brown Gladden *et al*. (1999) were analysed for the additional 10 microsatellite loci.

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

A portion of 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

Table 1. Beluga collections. List of beluga samples split by locality, year, mtDNA haplotypes, microsatellites and sex.

	Location, Year of Sampling, and Number of Samples	n with haplotypes	n with microsatellites	n with both	Sex ratio F:M
West Greenland					
1.	Kitsissuarsuit 1990 (5)	5	5	5	3:2
2.	Saqqaq 1990 (5)	5	5	5	4:1
3.	Nuussuaq 1990 (42)	38	42	38	26:16
4.	sassat (entrapment) near Saqqaq 1990 (13)	13	13	13	5:7
	Total	61	65	61	
Grise Fiord					
5.	Grise Fiord 1984 (17)	13	17	13	9:8
6.	Grise Fiord 1985 (5); 1987 (9)	14	14	14	03:11
7.	Grise Fiord 1993 (5); 1995 (1)	6	6	6	2:4
	Total	33	37	33	
Lancaster Sound and Barrow Strait					
8.	Arctic Bay 1994 (5); 1995 (2)	5	7	5	3:3
9.	Creswell Bay 1993 (5)	5	5	5	1:4
10.	Creswell Bay 1996 (4)	3	4	3	1:3
11.	Croker Bay 1995 (6), 1996 (9)	13	15	13	9:6
12.	Cunningham Inlet 1990 (5); 1991 (5); 1992 (2); 1996 (4)	14	16	14	14:0
13.	Elwin Bay 1992 (12); 1996 (4)	15	16	15	3:1
14.	Conningham Bay 1996 (3), 1997(11)	11	14	11	7:7
	Total	66	77	66	
Pangnirtung (Southeast Baffin)					
15.	Pangnirtung 1982 (10)	10	10	10	1:9
16.	Pangnirtung (Clearwater Fiord) 1983 (5)	5	0	0	5:0
17.	Pangnirtung 1984 (12); 1985 (2); 1986 (23)	37	22	22	10:25
18.	Pangnirtung 1991 (10)	10	10	10	4:6
19.	Pangnirtung1992 (22)	21	21	20	17:15
20.	Pangnirtung 1993 (12)	12	8	8	5:7
21.	Pangnirtung 1994 (18); 1995 (17); 1996 (22)	56	57	52	27:33
	Total	151	128	122	
Iqaluit (Southeast Baffin)					
22.	Iqaluit 1984 (9)	9	9	9	0:7
23.	Iqaluit 1989 (11) ;1991 (4)	15	12	12	7:8
24.	Iqaluit 1992 (18)	18	18	18	9:9
25.	Iqaluit 1993 (24); 1994 (9)	32	32	31	8:25
26.	Iqaluit 1996 (13)	13	13	13	4:7
	Total	87	84	83	
Kimmirut (Southeast Baffin)					
27.	Kimmirut 1989 (8)	8	0	0	5:3
28.	Kimmirut 1990 (4); 1991 (4)	8	1	1	5:3
29.	Kimmirut 1992 (22)	22	22	22	11:11
30.	Kimmirut 1993 (12)	12	12	12	7:5
31.	Kimmirut 1994 (21)	21	19	19	12:9
32.	Kimmirut 1995 (9); 1996 (4)	12	13	12	4:9
	Total	83	67	66	

by Lillie *et al*. (1995). Numerous samples were analysed using asymmetric PCR and manual sequencing as described by 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 260 base pairs of resultant mtDNA sequence for beluga samples were aligned using MacVector ver. 3.5 (IBI) to a reference beluga sequence (Brown 1996). Haplotype ID numbers were designated according to a consensus sequence of variable positions (Brown 1996).

Microsatellite analysis

The 15 sets of microsatellite primers, described by Buchanan *et al*. (1996), Valsecchi and Amos (1996) and Amos *et al*. (1993), were designated according to the species from which the primers were developed and a locus name and number (Table 2). Microsatellites were amplified and visualised 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

Analysis of Molecular Variance or "AMOVA" (Excoffier *et al*. 1992, Michalakis and Excoffier 1996, Goldstein *et al*. 1995) was used to compare six eastern Arctic populations. Also 21 collections within populations were compared (Table 1). Specifically, F_{st} and Φ_{st} values for mtDNA and F_{st} and R_{st} values for microsatellites, both measures of genetic distances, and associated significance levels were obtained for pairwise comparisons of samples.

AMOVA (Excoffier *et al*. 1992, Michalakis and Excoffier 1996) is a linear modelling method in which the final statistics are ratios of variance components, usually the fractions of the total variance described by between- or among- sample variation, and their probabilities of being

Table 2. Details of the fifteen microsatellite loci from belugas. Descriptions are based on all samples 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

drawn from the same sample population. For mtDNA data, F_{st} values are calculated if all haplotypes are considered to be genetically equidistant and Φ_{st} values, if the number of differences between haplotype sequences is considered. For microsatellites, F_{st} values are produced for the IAM model data, and R_{st} values for the SMM model. These values can be converted to several other measures of genetic distance after incorporating rates of mutation or drift. The significance of F_{st} or R_{st} values is determined by using a non-parametric permutation of the difference matrix. The tests were done in the "Arlequin" statistical package (Schneider *et al*. 1997). A total of 100,000 permutations were performed so that low probabilities would be estimated more accurately to apply table-wide statistical criteria. F_{st} values were calculated by differences between mtDNA alleles in two belugas as 0 or 1, and the differences between 2 microsatellite alleles as 0, 1, 2, or 4 ("number of different alleles" choice in Distance Matrix Options in Arlequin). R_{st} values were calculated by choosing the differences between microsatellite alleles ("sum of squared size difference" choice in Distance Matrix Options in Arlequin).

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", calculated based on the number of comparisons and the distribution of probabilities, which is less than the table-wide α level, chosen to be $\alpha = 0.05$ in this study.

Genealogies showing patterns of genetic similarities were constructed for 21 collections within major locations using mtDNA haplotype frequencies and microsatellite allele frequencies. Cavalli-Sforza's IAM-based chord distance for both types of loci was used as a measure of genetic distance between and among sample populations (Cavalli-Sforza and Edwards 1967) and Saitou and Nei's (1987) "Neighbor-joining Method" was used to create phylogenetic trees. A total of 1,000 bootstrap samples were generated for the comparison on the basis of microsatellites using the method of Felsenstein (1985), available in the PHYLIP 3.5c computer package (Felsenstein 1993).

RESULTS

Thirteen locations were chosen to represent overall patterns of haplotype frequencies across North America and adjacent areas (Fig. 2). The haplotype network simplified from Brown Gladden *et al*. (1997) (Fig. 3) demonstrates relationships between major haplotypes based on the number of differing nucleotide positions. Haplotypes H18, H17 and H29 are distant from most others. H29 occurs only in the St. Lawrence River, H17 in Hudson Bay, and H18 in both locations. None of these haplotypes were observed in Greenland or Canadian High Arctic populations. Many haplotypes closely related to haplotypes H02, H05 and H07 were common in both the eastern and western Canadian High Arctic and in Greenland (Fig. 2). St. Lawrence, Beaufort Sea (western Canadian Arctic), Point Lay (Alaska), and eastern Hudson Bay haplotypes were strongly differentiated from all other groups (F_{st} and associated probabilities in AMOVA, not shown).

High Arctic beluga

The two sexes were not separated since Fisher's exact test and probabilities of F_{st} values showed that allele frequencies between males and females did not differ significantly with collections or locations. Collections within six locations (Table 1) were reduced from 47 to 32 by pooling collections if 1) they were from the same or adjacent collection years or locations, and 2) there were no significant differences between haplotype frequencies and microsatellite allele frequencies at any loci at $\alpha < 0.05$ using Fisher's exact test (Guo and Thompson 1992).

Comparison of 6 major locations

F_{st} values for mtDNA comparisons ranged from 0.004 to 0.240, with the smallest F_{st} values between the three SE Baffin locations and Lancaster Sound ($F_{st} = 0.004$ to 0.058), between Greenland and Grise Fiord (0.039), and between and Grise Fiord and Lancaster Sound (0.091) (Table 3, above diagonal). There was no significant differentiation in these comparisons. The largest F_{st} values for mtDNA comparisons were between Greenland and Kimmirut ($F_{st} = 0.240$), Greenland and Iqaluit (0.228) and Greenland and Lancaster Sound (0.230), with significant differentiation in all cases. Φ_{st} values

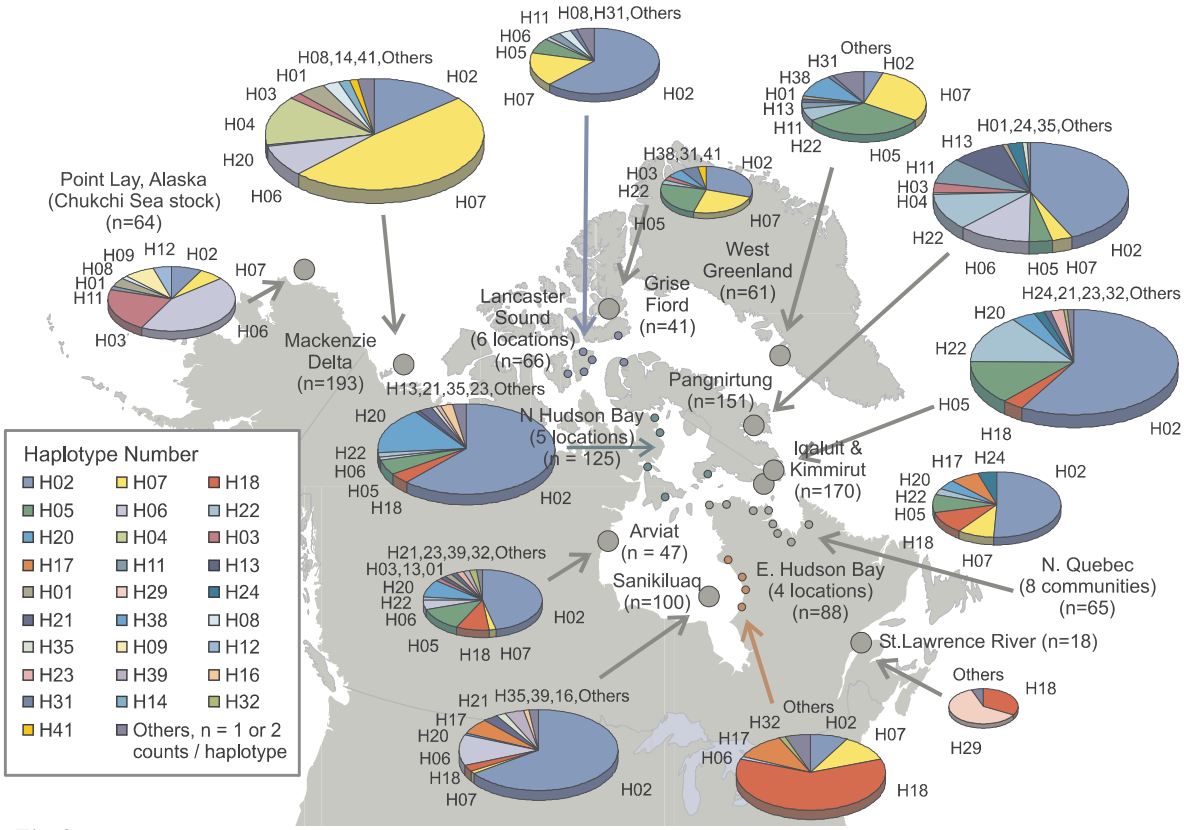

Fig. 2
Beluga mtDNA haplotype frequencies at 13 locations in North America and Greenland. Areas of the pies are proportional to sample size.

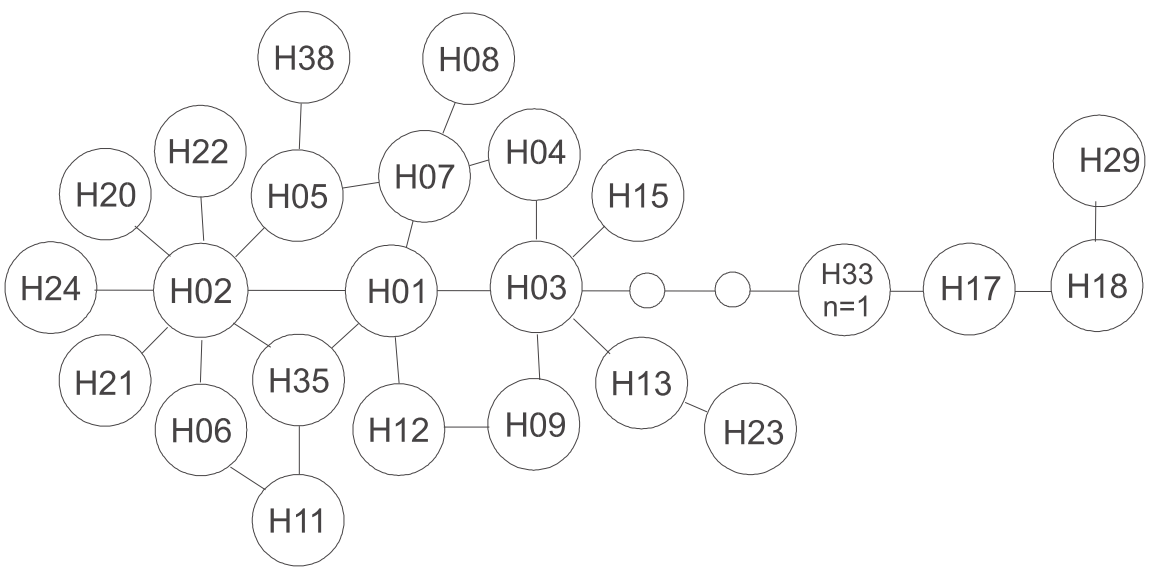

Fig. 3
Haplotype network for common and connecting beluga mtDNA control region sequences reduced from the network in Brown Gladden et al. (1997). Small circles represent halotypes that do not exist or have not yet been found. Each connection line represents a transition

were similar to F_{st} values (Table 3, below diagonal), however more comparisons were statistically significant. In this second AMOVA, the only population pairs which are not significantly differentiated were West Greenland and Grise Fiord, and Iqaluit and Kimmirut.

F_{st} and their probabilities for microsatellite comparisons showed a high degree of differentiation among the 6 locations (Table 4, above diagonal). There was no significant differentiation in the comparisons of the following pairs: Pangnirtung and Kimmirut (0.006), Kimmirut

Table 3. Patterns of mtDNA differentiation among 6 beluga collections in West Greenland and the Canadian High Arctic. F_{st} values are above the diagonal, Φ_{st} values below, and associated probabilities from AMOVA are in parentheses. Minimum significance levels using table-wide criteria and table-wide $\alpha = 0.05$ were $P = 0.006$ and 0.0167, and probabilities below this level are bolded.

	W Greenland	Grise Fiord	Lancaster Sound	Pangnirtung	Iqaluit	Kimmirut
W Greenland		0.039 (0.05)	**0.230 (0.00)**	**0.171 (0.00)**	**0.228 (0.00)**	**0.240 (0.00)**
Grise Fiord	0.028 (0.05)		0.091 (0.00)	**0.079 (0.00)**	**0.106 (0.00)**	**0.112 (0.00)**
Lancaster Sound	**0.224 (0.00)**	**0.081 (0.00)**		0.058 (0.00)	0.044 (0.01)	0.044 (0.01)
Pangnirtung	**0.167 (0.00)**	**0.071 (0.00)**	**0.053 (0.00)**		0.037 (0.00)	**0.049 (0.00)**
Iqaluit	**0.222 (0.00)**	**0.097 (0.00)**	**0.034 (0.01)**	**0.033 (0.00)**		0.004 (0.44)
Kimmirut	**0.235 (0.00)**	**0.103 (0.00)**	**0.038 (0.01)**	**0.044 (0.00)**	-0.002 (0.46)	

Table 4. Patterns of microsatellite differentiation among 6 beluga collections in West Greenland and the Canadian High Arctic. F_{st} values are above the diagonal, R_{st} values below. Associated probabilities from AMOVA are in parentheses. Minimum significance levels using table-wide criteria and table-wide $\alpha = 0.05$ were $P = 0.0125$ and 0.0110, and probabilities below this level are bolded.

	W Greenland	Grise Fiord	Lancaster Sound	Pangnirtung	Iqaluit	Kimmirut
W Greenland		0.006 (0.01)	**0.026 (0.00)**	**0.015 (0.00)**	**0.015 (0.00)**	**0.017 (0.00)**
Grise Fiord	-0.005 (0.84)		**0.011 (0.00)**	**0.020 (0.00)**	**0.010 (0.00)**	**0.013 (0.00)**
Lancaster Sound	0.012 (0.01)	-0.001 (0.57)		**0.009 (0.00)**	**0.028 (0.00)**	**0.033 (0.00)**
Pangnirtung	0.005 (0.07)	0.002 (0.29)	**0.023 (0.00)**		0.003 (0.01)	**0.006 (0.00)**
Iqaluit	0.014 (0.01)	0.006 (0.18)	**0.027 (0.00)**	0.006 (0.06)		0.004 (0.01)
Kimmirut	0.003 (0.20)	0.001 (0.38)	**0.023 (0.00)**	0.004 (0.09)	**0.015 (0.01)**	

and Iqaluit (0.004, and Grise Fiord and Greenland (0.006). The largest genetic distances were between Kimmirut and Lancaster Sound (F_{st} = 0.033), Iqaluit and Lancaster Sound (0.028), and West Greenland and Lancaster Sound (0.026). R_{st} values (Table 4, below diagonal) suggest less differentiation. In this comparison, Lancaster Sound belugas differed from SE Baffin populations, and Iqaluit from Kimmirut.

Comparison of haplotypes among 32 collections (F_{st} values in Table 5 and R_{st} values in Table 6) showed that the general patterns above apply to most collections within locations. In general there was more significant differentiation among collections from different locations than among collections from one location. Among-collection differences (minimum significance level $P < 0.05$) in Greenland were due to 4 of 5 belugas from Kitsissuarsuit which were haplotype H38. This haplotype also occurs three times in other Greenland locations and twice in Grise Fiord. This is reflected in the genealogy where Kitsissuarsuit is a neighbour of, but distant from, other Greenland collections (Fig. 4a). Among Grise Fiord collections, the Grise Fiord 1985-87 collection had weakly significantly different haplotype frequencies than the Grise Fiord 1984 collection, this reflected in the distance between them in Fig. 4a. The Creswell Bay 1993 collection was significantly differentiated from other Lancaster Sound collections, but not from most Greenland and Grise Fiord collections. These 5 Creswell Bay belugas had haplotypes H05, H06, H37, and 2 x H07, which were more common in Greenland than in Lancaster Sound.

The genealogy based on haplotypes (Fig. 4a) has major branches which represented mostly 1) Greenland, 2) Lancaster Sound, Iqaluit, Kimmirut, and 3) western North American locations and Pangnirtung. Both Greenland and Lancaster Sound collections cluster with others from the same location even though they were not significantly differentiated from them. Two of three Grise Fiord collections were on the Greenland branch, but were closer to the other two Grise Fiord branches than most Greenland collections were. Iqaluit and Kimmirut were on the same branch as most Lancaster Sound collections, no doubt due to the high frequencies of haplotypes H02 and H05.

Comparisons of microsatellites among 31 collections based on F_{st} values are shown in Table 7. Within Greenland collections, Saqqaq and the sassat samples were weakly differentiated, this reflected in the genealogy for microsatellites where the two locations are separated (Fig. 4b). There was no significant microsatellite differentiation among the three Grise Fiord collections (Table 7). Two of these three collections are near the vortex of the genealogy. Most Lancaster Sound collections differed from all locations except Grise Fiord and sometimes Greenland (Table 7). Lancaster Sound belugas, apart from Creswell Bay 1993, all clustered closely on the same branch. There was little differentiation among SE Baffin collections (Table 7). SE Baffin collections clustered closely in the genealogy (Fig. 4b) and collections were usually differentiated from Greenland and Lancaster Sound, but not from Grise Fiord (Table 7).

In both trees (Figs. 4a and 4b), Beaufort Sea and Alaska samples were on the same branch, and Pangnirtung samples were on a branch close to these. There was no significant differentiation among these 31 collections using the SMM model.

DISCUSSION

Results of molecular genetics findings for belugas from the eastern Canadian High Arctic and from Greenland were examined from several perspectives. These included examining patterns in mtDNA and microsatellite loci alleles, statistical analyses based on different models of temporal changes, and examination of data grouped as sample populations of various sizes. A general picture of population differences in the eastern High Arctic comes from these comparisons.

Several comparisons using pooled location data support the hypothesis that belugas from Grise Fiord and those from Greenland are not genetically differentiated. In pairwise comparison of collections, some differ within locations and some do not differ between locations. The collection from Kitsissuarsuit had several individ-

Table 5. Haplotype differentiation among collections of belugas from West Greenland and the Canadian High Arctic (numbered in Table 1) based on AMOVA F_{st} probabilities. Comparisons significantly differentiated at $P < 0.05$ are marked "+", those significant at a table wide level as "++".

		W Greenland				Grise Fiord			Lancaster Sound							Pangnirtung							Iqaluit					Kimmirut					
Collection Number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
W Greenland	1																																
(4 collections)	2	+																															
	3	+	-																														
	4	+	-	-																													
Grise Fiord	5	+	-	-	-																												
(3 collections)	6	+	+	+	+	+																											
	7		-	-	-	-	-	-																									
Lancaster Sound	8	+	-	+	-	-	-	-																									
(7 collections)	9	+	-	-	-	-	-	-	-																								
	10	+	-	++	++	-	-	-	-	-																							
	11	+	+	+	+	+	-	-	-	-	-																						
	12	+	+	++	++	+	-	+	-	+	-	-																					
	13	+	+	++	++	++	-	+	-	+	+	-	-																				
	14	+	+	+	+	+	-	-	-	+	-	-	-	-																			
Pangnirtung	15	+	+	++	++	+	-	-	-	+	-	-	-	-	-																		
(7 collections)	16	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-																	
	17	++	+	++	++	+	+	-	-	-	-	+	+	+	-	-	-																
	18	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-															
	19	++	+	++	++	++	-	-	-	+	-	-	-	-	-	-	-	-	-														
	20	++	++	++	++	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-													
	21	+	+	++	++	++	-	-	-	+	-	+	+	+	-	-	-	-	-	-	-												
Iqaluit	22	+	+	++	++	+	+	+	+	+	-	+	++	++	+	+	+	++	+	+	+	+											
(5 collections)	23	++	+	++	++	+	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	+										
	24	++	+	++	+	+	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	++	-									
	25	+	++	++	++	+	-	-	-	+	-	+	-	+	-	-	-	+	-	-	-	-	++	-	-								
	26	+	+	++	++	++	+	+	-	+	+	-	-	-	-	-	+	+	-	-	-	+	++	-	-	+							
Kimmirut	27	+	+	++	++	++	-	+	-	+	-	-	-	-	-	-	+	+	+	-	-	+	++	-	-	+	-						
(6 collections)	28	+	+	+	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-					
	29	+	+	++	+	+	-	-	-	+	-	+	-	+	-	-	-	+	-	-	-	+	++	-	-	+	-	+	-				
	30	++	+	++	++	+	-	+	-	+	-	-	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	-	-	-			
	31	++	+	++	+	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	++	-	-	+	-	+	-	-	-		
	32	+	+	+	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	

Table 6. Haplotype differentiation among collections of belugas from West Greenland and the Canadian High Arctic (numbered in Table 1) based on AMOVA R_{st} probabilities. Comparisons significantly differentiated at $P < 0.05$ are marked "+", those significant at a table wide level as "++".

		W Greenland					Grise Fiord			Lancaster Sound							Pangnirtung								Iqaluit					Kimmirut					
Collection Number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32		
W Greenland	1																																		
(4 collections)	2	-																																	
	3	+	-																																
	4	+	-	-																															
Grise Fiord	5	+	-	-	-																														
(3 collections)	6	+	-	-	-		-																												
	7	-	-	-	-		-	-																											
Lancaster Sound	8	-	-	-	-		-	-	-																										
(7 collections)	9	+	-	-	-		-	-	-	-																									
	10	-	-	-	-		-	-	-	-	-																								
	11	+	-	-	-		-	-	-	-	-	-																							
	12	+	+	+	+		+	-	-	-	+	+	-																						
	13	+	+	+	+		+	-	+	-	+	-	-	-																					
	14	+	-	+	+		+	-	-	-	-	-	-	-	-																				
Pangnirtung	15	+	+	++	++		++	+	+	+	+	+	+	-	-	-																			
(7 collections)	16	-	-	+	+		+	-	-	-	-	-	-	-	-	-	-																		
	17	+	-	++	++		++	+	+	-	-	-	+	+	-	-	-	-																	
	18	+	-	+	+		+	-	-	-	+	-	-	-	-	-	-	-	-																
	19	++	+	++	++		++	+	+	-	+	+	+	+	-	-	-	-	+	-															
	20	++	+	++	++		++	+	+	-	+	-	+	-	-	-	-	-	-	-	-														
	21	+	+	++	++		++	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-													
Iqaluit	22	+	+	++	++		++	+	+	+	++	+	+	++	+	++	++	+	++	+	++	+	+													
(5 collections)	23	+	-	++	++		++	+	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	+											
	24	+	+	+	++		++	+	+	-	+	+	+	-	-	-	+	+	+	-	-	-	+	++	-										
	25	+	+	++	++		++	+	+	-	+	-	+	-	-	-	-	-	+	-	-	-	-	++	-	-									
	26	+	+	++	++		++	+	+	-	-	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-								
Kimmirut	27	+	+	++	++		++	-	+	-	+	-	+	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-							
(6 collections)	28	+	-	+	+		+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	++						
	29	++	+	++	+		+	-	-	-	+	-	+	-	-	-	+	-	+	-	-	-	+	++	-	-	-	+	-	-					
	30	+	++	++	++		++	+	+	-	++	+	+	-	-	-	+	+	+	-	-	-	-	++	-	-	-	-	-	-	-				
	31	+	-	++	+		++	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-			
	32	+	+	+	++		++	+	-	-	+	+	+	-	-	-	+	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-		

Table 7. Microsatellite differentiation among collections of belugas from West Greenland and the Canadian High Arctic (Table 1) based on AMOVA F_{st} probabilities. Comparisons significantly differentiated at $P < 0.05$ are marked "+", those significant at a table wide level of $\alpha = 0.05$ as "++".

		W Greenland				Grise Fiord			Lancaster Sound							Pangnirtung							Iqaluit					Kimmirut					
Collection Number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
W Greenland (4 collections)	1																																
	2	-																															
	3	-	-																														
	4	-	+	-																													
Grise Fiord (3 collections)	5	-	+	-	-																												
	6	+	+	-	-	-																											
	7	-	-	-	-	-	-																										
Lancaster Sound (7 collections)	8	+	-	++	+	+	-	-																									
	9	-	-	-	-	-	-	-	-																								
	10	+	+	++	++	++	+	+	+	+																							
	11	++	++	++	++	+	+	-	+	-	+																						
	12	+	+	+	+	-	-	-	+	-	+	-																					
	13	+	+	+	+	-	-	-	+	-	+	-	-																				
	14	+	++	++	++	+	-	-	-	-	+	-	-	-																			
Pangnirtung (7 collections)	15																																
	16	+	+	+	+	+	+	-	+	+	++	+	+	+	+																			
	17	+	+	++	+	-	+	-	+	-	+	++	+	++	++		-																	
	18	+	-	+	-	-	-	-	-	-	+	++	+	+	+		-	-																
	19	++	+	++	+	-	+	-	+	-	+	++	++	++	++		+	-	-															
	20	+	+	-	-	-	-	-	-	-	+	-	-	-	+		-	-	-	-														
	21	+	++	+	+	-	+	-	+	-	++	++	+	++	++		-	-	-	+	-													
Iqaluit (5 collections)	22	+	+	+	+	-	-	-	+	-	+	++	++	++	++		+	+	-	+	-	+												
	23	+	+	+	-	-	-	-	+	-	++	++	+	++	+		-	-	-	+	-	-	-											
	24	+	+	+	+	-	+	-	+	-	++	++	++	++	++		-	-	-	-	+	+	+	-										
	25	+	+	++	++	-	-	-	-	-	++	++	+	++	++		+	+	-	-	-	+	+	-	-									
	26	+	+	++	+	+	+	-	+	+	+	++	++	++	++		-	-	-	-	+	+	++	+	-	-								
Kimmirut (6 collections)	27																																
	28																																
	29	+	+	++	+	+	+	-	+	-	+	++	++	++	++		++	++	+	-	-	++	+	+	-	+	+							
	30	+	+	++	-	+	+	-	-	+	++	++	++	++	+		-	-	-	+	-	-	+	+	+	-	-		+				
	31	+	+	++	-	-	+	-	+	-	++	++	++	++	+		+	-	-	+	-	-	+	-	-	-	+		-	-			
	32	+	+	+	+	-	-	-	-	-	+	+	+	+	+		+	-	-	+	-	-	+	-	-	-	+		-	-	-	-	

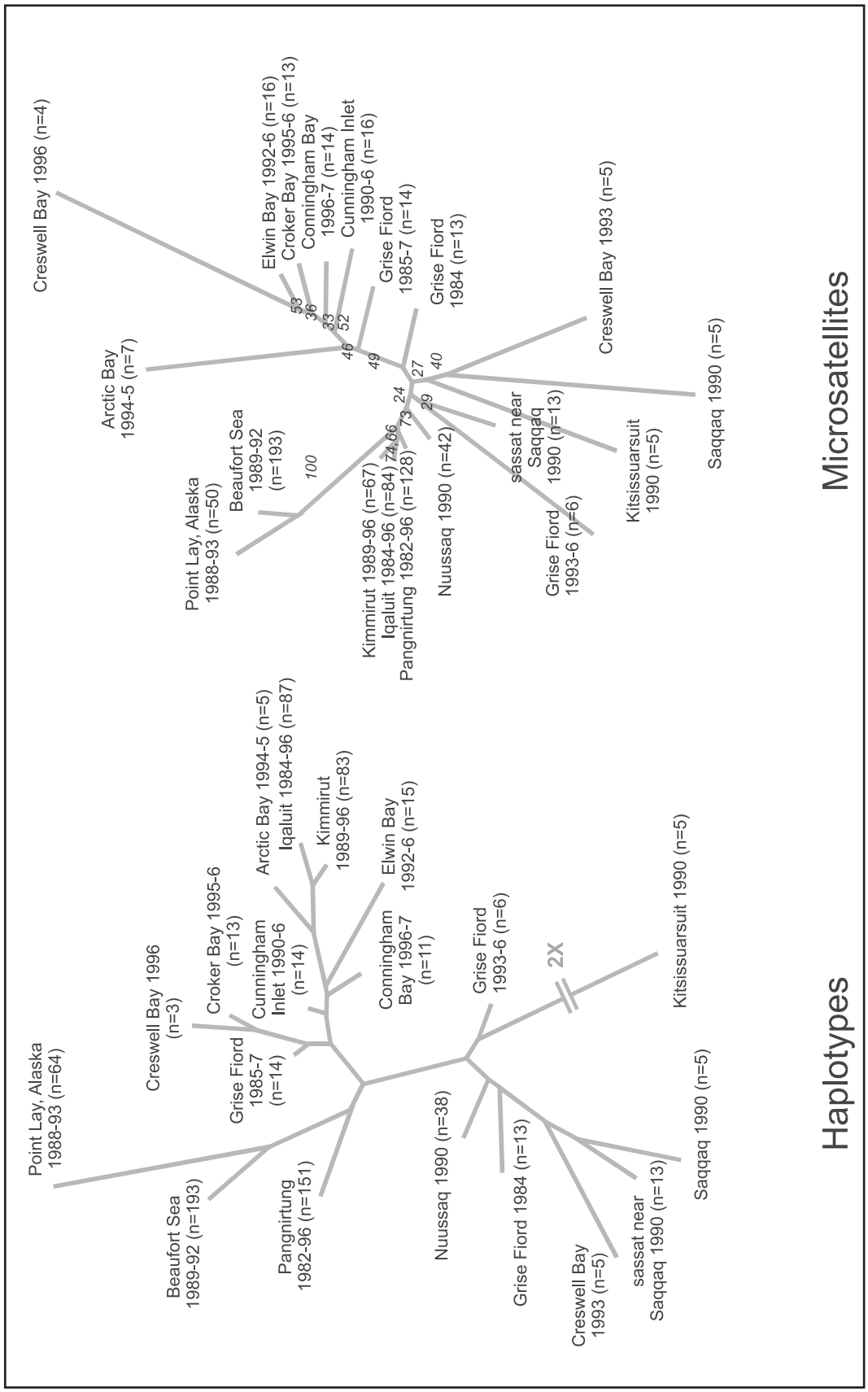

Fig 4.
Unrooted Tree Diagrams for High Arctic subsamples and related populations. Trees were constructed using Cavalli-Sforza's chord distance (Cavalli-Sforza and Edwards 1967) as a measure of genetic distance among sample populations for both microsatellite loci and haplotypes, and the Neighbor-joining Method of Saitou and Nei (1987) for constructing trees.

uals with an uncommon haplotype (H04), thus this collection differed from other Greenland collections. It did not differ from the Grise Fiord 1993-1996 collection, where the same haplotype occurred. However, individuals from Kitsissuarsuit had similar microsatellite allele frequencies as individuals in other Greenland collections. The Grise Fiord 1985-1987 collection stood out from other Greenland and Grise Fiord collections due to 4/5 individuals being haplotype H02, thus they were grouped with Lancaster Sound and SE Baffin collections. This same collection had microsatellite allele frequencies similar to Lancaster Sound.

The belugas grouped as Lancaster Sound belugas differ from both Greenland and Grise Fiord samples in several comparisons. Haplotype H02, which is otherwise common to SE Baffin and Hudson Bay, is common in Lancaster Sound belugas. Haplotypes H05 and H07, common in Greenland and the Beaufort Sea, occur at lower frequencies. However, the Creswell Bay 1993 individuals are similar to Greenland samples on the basis of both mtDNA and microsatellites.

It is apparent that patterns of genetic similarities and differences change depending on whether or not annual collections are pooled. When annual collections are compared, they often resemble collections from other locations. Possible explanations are: 1) different stocks may have been sampled in different years; 2) groups of relatives that did not have the most common alleles or haplotypes were sampled; and 3) there were more false significant differences because more comparisons were made. These possible explanations cannot be separated.

The consistent difference between Lancaster Sound and Greenland samples suggests that although Lancaster Sound belugas may overwinter in Greenland, they are not the same genotypes as were sampled in Greenland in 1990.

Patterns in microsatellite differentiation generally resembled those for mtDNA, with one exception. Lancaster Sound belugas differed from SE Baffin Island belugas on the basis of microsatellite loci, but not based on mtDNA. We can conclude that these two populations do not interbreed, not unexpected on the basis of the geographic distance between them and possible different overwintering locations.

Analyses under the SMM and IAM models for haplotypes differ slightly. Lancaster Sound belugas are more distant from Greenland and Grise Fiord under the SMM than the IAM. This is probably entirely due to the relationship between H02 and H07 which differ by two nucleotides, hence contributing more "genetic distance" under assumptions of the SSM models. Similarly, SE Baffin samples are more distant from High Arctic samples when analysed under the SMM model. This is due to the relationships between H02, H05 and H07. There are several haplotypes in SE Baffin which are one nucleotide different from H02 but 3 nucleotides different from H07 (thus two different from H05), again these differences contribute to the genetic distance. In addition, some SE Baffin locations have a low frequency of H18, which is 8 to 9 nucleotides different from most others examined, and this increases Kimmirut's genetic distance from others considerably under this model. H18 is common in eastern Hudson Bay, and some of these belugas may migrate past Kimmirut where they are hunted.

In contrast, in analyses of microsatellite data, comparisons under the IAM model show a high degree of differentiation among sample populations while analyses under the SMM model show little or none. Within-sample variation is very high under the SMM model because several of microsatellite loci have a bimodal distribution of allele frequencies, and alleles in both modes occur in many sample locations. Under the IAM model, all major sampling areas are significantly differentiated from each other except for the pairs (Grise Fiord and Greenland), (Iqaluit and Pangnirtung), and (Iqaluit and Kimmirut). Under the SMM, only Lancaster Sound samples are significantly differentiated from SE Baffin, and Iqaluit from Kimmirut, and all others are not differentiated from each other.

Palsbøll *et al*. (2002) concluded that samples from Greenland were not significantly differentiated from samples from SE Baffin and the Canadian High Arctic on the basis of mtDNA haplotypes. The mtDNA region that was used was shorter than the one used in this study.

Because of this, the most common haplotype in Palsbøll *et al*.'s (2002) study, DL02, included our haplotypes H02, H05, H06, H11, and H22, three of which we found to be important for discriminating stocks in the High Arctic. Thus Palsbøll *et al*.'s (2002) study could not detect some important differences. The second most frequent haplotype, DL01, overlapped primarily with our haplotype H07, and this haplotype was important in discriminating High Arctic stocks in both studies. The haplotype that distinguished Qaanaaq samples in Palsbøll *et al*.'s (2002) study was not found in our samples.

To make appropriate decisions about stock management, we must understand whether patterns of differences and similarities represent patterns that persist over time, or whether they represent a snapshot in time. The fact that collections from different years within locations generally cluster together in tree diagrams provides some evidence that patterns do not change rapidly within approximately a decade.

Some patterns in genetic distributions can be explained by post-glacial dispersion. Greenland haplotypes resemble both Beaufort Sea and Pangnirtung in that haplotypes H07, H02, H06, H05 and several others closely related to H05 occur in all three locations (Fig. 2). Analysis of mtDNA under the SMM model shows a high degree of similarity between the Beaufort Sea and Greenland, and less between the Beaufort Sea and Point Lay (Brown Gladden *et al*. 1997). Beluga movement through the High Arctic islands probably does not occur at the present time, however it was possible approximately 10 kyr (thousand years) BP (before present), and also 5 kyr BP, when land was lower and/or ice plugs did not exist in M'Clintock Channel (Dyke *et al*. 1996). Thus Beaufort Sea beluga may have eastern origins. Also, it is possible that the haplotype similarities between Lancaster Sound and Hudson Bay may be explained by post-glacial dispersion. Movement through Fury and Hecla Straits may have been easier approximately 5 kyr BP, when land levels were lower. Both locations have relatively high frequencies of H02 and other closely related haplotypes.

Interpretation of genetics data will continue to be difficult for many marine mammals species such as beluga because adequate sampling designs are difficult to achieve. Numerical alternatives in analysing results from small samples will continue to be problematic, and is confounded in social species by the fact that sampled animals could be close relatives. The use of small samples sizes can lead to patterns of significant differences not necessarily representative of the larger picture, and thus can lead to wrong conclusions about genetic differentiation. When many such small non-random samples are pooled to obtain a large sample size and then compared, other problems arise. Small differences in allele frequencies when comparing large samples will often be statistically "significantly different" since the null hypothesis is that samples were randomly sampled from the same population, which they were not. Interpretations also tend to be difficult due to the fact that some statistical tests are very responsive to small differences in allele frequencies, and others are not. Dizon *et al*. (1997) suggest that data-driven models may not be a useful approach for detecting population substructure. Model-based approaches may be more desirable, but it may be difficult to construct a model for a marine mammal population where the behaviour is not well understood. One advantage of alternative approaches is that they may better elucidate the possibilities of falsely detecting population structure (Dizon *et al*. 1997).

An important challenge for stock assessment scientists is to determine the population dynamics that contribute to maintaining the observed gradients and differences. The data here and additional data will be re-examined in the future. Using simulation techniques, we will determine what levels of population mixing and selection could maintain the type of genetic gradients observed here. Also, we will examine the degree of genetic relatedness within and among collections to gain insight about the social structure of beluga populations.

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Wildlife Fund and from the Fisheries Joint Management Committee, as part of the Inuvialuit Land Claims Agreement, that provided funds to develop methods and examine Beaufort Sea and Alaska belugas. L.D. (Postma) Maiers and J. Brown Gladden were involved in both methods development and sample analysis. F.C. Buchanan developed 10 microsatellite markers from beluga to expand the scope of our analytical capabilities.

Most samples from before 1990 were provided by R.E.A. Stewart, and later ones by the cooperative "Whale Sampling Program" in which the Department of Fisheries and Oceans (DFO), local Hunters and Trappers Organisations and the Nunavut Wildlife Management Board worked together to obtain samples. Many other individuals contributed samples from their research, and these have been invaluable. M.P. Heide-Jørgensen and R. Dietz contributed samples from Greenland; B. White from the St. Lawrence River; W. Doidge from Nunavik; K. Frost and L. Lowry from Alaska; and T. Smith (EcoMarine Corporation) from the Canadian High Arctic. Nunavut Implementation Funds provided funds for the analysis of archived samples. Many DFO employees have obtained samples or been helpful in obtaining samples. We also thank several anonymous reviewers who made very helpful suggestions.

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