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# Molecular Genetic Stock Discrimination of Belugas (*Delphinapterus leucas*) Hunted in Eastern Hudson Bay, Northern Quebec, Hudson Strait, and Sanikiluaq (Belcher Islands), Canada, and Comparisons to Adjacent Populations

B.G.E. de MARCH[1,2] and L.D. POSTMA[1]

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ABSTRACT. Belugas (*Delphinapterus leucas*) harvested from communities on the eastern Hudson Bay (EHB) arc, Sanikiluaq on the Belcher Islands, northwestern Quebec, Hudson Strait, neighboring areas of Hudson Bay, and the St. Lawrence were characterized by differences in the mitochondrial DNA (mtDNA) d-loop sequence and in 15 nuclear microsatellite loci. Results supported the hypothesis that communities outside the EHB arc hunt some EHB belugas, which were strongly differentiated from all neighboring sample populations by mtDNA haplotypes and weakly differentiated by microsatellite data. Belugas genetically most similar to those sampled in EHB comprised 19% of the harvest in Hudson Strait and Ungava, 15% in northwestern Quebec, 9% in western and northern Hudson Bay, 8% in Sanikiluaq, and 5% in Kimmirut (though many were possibly not belugas from EHB, but uncommon genotypes in other stocks). Within EHB, belugas from the Nastapoka River (1984–95) and elsewhere on the EHB arc (1993–97) were very similar. Using simple probabilistic calculations to assign individuals to their most likely sample population, we estimated that 15% of belugas hunted in EHB could be from northern or western Hudson Bay and 3% from Sanikiluaq. St. Lawrence River belugas were strongly differentiated from all other sample populations by both haplotypes and microsatellites. Stocks in Arctic populations were identified by different proportions of alleles and by genetic consistency over several years. Belugas from Sanikiluaq, Kimmirut, and EHB may represent three separate stocks, while large genetic diversities in northern Quebec, northern Hudson Bay, and Arviat confirm that mixtures of stocks were harvested in these areas.

Key words: beluga, *Delphinapterus leucas*, Eastern Hudson Bay, Belcher Islands, stock, molecular genetics, mitochondrial DNA, microsatellite, St. Lawrence, Hudson Strait

RÉSUMÉ. Les bélugas (*Delphinapterus leucas*) prélevés au sein de communautés situées dans l'arc de l'est de la baie d'Hudson (EBH), à Sanikiluaq dans les îles Belcher, au nord-ouest du Québec, dans le détroit d'Hudson, dans les zones jouxtant la baie d'Hudson et dans le Saint-Laurent ont été caractérisés par des différences dans la séquence de la boucle D de l'ADN mitochondrial (ADNmt) et des 15 loci des microsatellites nucléaires. Les résultats appuyaient l'hypothèse selon laquelle les communautés à l'extérieur de l'arc de l'EBH chassent quelques bélugas de l'EBH, qui se différenciaient fortement de toutes les populations d'échantillon voisines par les haplotypes de l'ADNmt et faiblement par les données des microsatellites. Les bélugas les plus semblables à ceux échantillonnés dans l'EBH sur le plan génétique constituaient 19 % du prélèvement dans le détroit d'Hudson et dans la baie d'Ungava, 15 % au nord-ouest du Québec, 9 % dans l'ouest et le nord de la baie d'Hudson, 8 % à Sanikiluaq et 5 % à Kimmirut (bien que nombre d'entre eux aient pu ne pas appartenir à l'EBH, mais être des génotypes inhabituels provenant d'autres stocks). Au sein de l'EBH, les bélugas de la rivière Nastapoka (1984–1995) et ailleurs dans l'arc de l'EBH (1993–1997) étaient très semblables. À l'aide de simples calculs de probabilité pour assigner les individus à leur échantillon de population le plus vraisemblable, on a estimé que 15 % des bélugas chassés dans l'EBH pouvaient provenir du nord ou de l'ouest de la baie d'Hudson et 3 % de Sanikiluaq. Les bélugas du Saint-Laurent se différenciaient nettement de toutes les autres populations de l'échantillonnage, par les haplotypes comme par les microsatellites. Les stocks dans les populations arctiques se distinguent les uns des autres par des proportions différentes d'allèles et par une concordance génétique établie sur plusieurs années. Les bélugas de Sanikiluaq, de Kimmirut et de l'EBH peuvent représenter trois stocks distincts, tandis que les grandes diversités génétiques dans le nord du Québec, le nord de la baie d'Hudson et l'Arviat confirment que, dans ces régions, on a prélevé un mélange de stocks.

Mots clés: béluga, *Delphinapterus leucas*, est de la baie d'Hudson, îles Belcher, stock, génétique moléculaire, ADN mitochondrial, microsatellite, Saint-Laurent, détroit d'Hudson

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[1] Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada
[2] Corresponding author: demarchb@dfo-mpo.gc.ca

## INTRODUCTION

The beluga (*Delphinapterus leucas*) has a discontinuous circumpolar distribution, with the northernmost areas of its range off Ellesmere Island, West Greenland, and Spitsbergen, at about 82˚ N, and the southernmost areas in the St. Lawrence River estuary, White Sea, Okhotsk Sea, Gulf of Alaska, and James Bay (Stewart and Stewart, 1989). Donovan (1992) subdivided the world population of belugas into at least 16 provisional management stocks, 11 of which exist in North America. Four stocks of belugas are currently recognized for management purposes in the Canadian Eastern Arctic (Richard and Pike, 1993). These are 1) the Canadian High Arctic stock; 2) the Southeast Baffin beluga stock, which summers in Cumberland Sound and possibly Frobisher Bay (Brodie et al. 1981; Richard and Orr, 1986); 3) the Western Hudson Bay stock, which summers along the west coasts of Hudson Bay (Sergeant, 1973) and numbered approximately 23 000 belugas in1987 (Richard et al., 1990); and 4) the Eastern Hudson Bay stock, which summers along the east coasts of Hudson Bay and James Bay and numbers at least 2000 belugas (Finley et al., 1982; Smith and Hammill, 1986; Reeves and Mitchell, 1987, 1989). Genetic findings to date have not rejected these divisions and, in fact, suggest the existence of more stocks within some of the above divisions (Brown Gladden et al., 1997, 1999; de March et al., 2002).

Other congregations of belugas also occur, and their relatedness to identifiable stock groups is uncertain. In Hudson Bay, large groups congregate in river mouths and estuaries along the coastal perimeter west of James Bay (near the Winisk, Severn, Nelson, Churchill, and Seal Rivers), and smaller groups congregate to the east of James Bay in the Nastapoka, Little Whale, and Great Whale Rivers (Fig. 1). James Bay has a large summering population, possibly continuous with that of the northern Ontario coast, but its stock status is unknown. Northern Hudson Bay and Foxe Basin may include belugas from western Hudson Bay in early spring and summer, belugas from the High Arctic that pass through Fury and Hecla Straits in late summer, and belugas that spend the summer in Foxe Basin (Richard et al., 1990). Belugas are also seen in Hudson Strait in the summer, and their stock identity is not known. Ungava Bay belugas may be the remains of a separate stock that has been almost extirpated (Finley et al., 1982; Smith and Hammill, 1986; Reeves and Mitchell, 1989; Richard, 1993).

A large proportion of belugas from these areas are suspected to winter in Hudson Strait and southwest Davis Strait, but their migration routes and degree of mixing are unknown (Richard et al., 1990; Reeves and Mitchell, 1989) (Fig. 1). Communities in northwestern Quebec and on Hudson Strait—and possibly Sanikiluaq—are believed to hunt mainly migrating belugas. On the east side of Hudson Bay, reports of southward spring migrations are well documented (Finley et al., 1982). On the west coast of Hudson Bay, belugas are rarely seen or hunted in the spring and might go unnoticed (Richard et al., 1990). The northward migration in the fall occurs along both the east and west coasts of Hudson Bay (Sergeant, 1973; Finley et al., 1982).

The belugas of eastern Hudson Bay (EHB) are defined as the population summering in the nearshore waters of Hudson Bay from Long Island to Inukjuak (Reeves and Mitchell, 1987, 1989) (Fig. 1). Aerial surveys have determined that this population has a northern boundary near 58˚ N in the summer. The EHB population is believed to be separate because of its small and stable size. Estuaries in the EHB arc that are frequently used by belugas are the Nastapoka and Little Whale Rivers. The inner recesses of Richmond Gulf are also frequented in summer (Reeves and Mitchell, 1989).

Beluga harvesting continues to be an important activity for aboriginal people. Since Sanikiluaq and communities on Hudson Strait (Salluit, Kangiqsujuaq, and Quaqtaq) and northwestern Hudson Bay (Ivujivik, Puvirnituq, and Akulivik) harvest belugas mainly in spring and fall, when belugas migrate past the communities, their harvest may include belugas that summer in EHB. In the EHB communities (Kuujjuarapik, Umiujaq, and Inukjuak) and those of Ungava Bay (Kangirsuk, Aupaluk, Tasiujaq, Kuujjuaq, and Kangiqsualujjuaq), harvesting occurs mainly during summer.

The EHB beluga population was initially reduced by large commercial harvests, which caused the fishery to experience a rapid decline by the late 1800s (Francis, 1977; Finley et al., 1982; Reeves and Mitchell, 1987, 1989). The subsistence hunt continued, but since old belugas were still evident in the EHB harvest in the 1980s, it seemed that overharvesting had not occurred in spite of large catches (Reeves and Mitchell, 1989; Doidge, 1990). After that period, concerns arose about population size, the age structure of the reported landings, and whether hunters from outside the EHB area (e.g., Sanikiluaq and northern Quebec) were harvesting the same beluga stock. Another concern was whether a new settlement at Umiujaq near the Nastapoka River and small boat traffic from Cree and Inuit communities at the mouth of the Great Whale River had increased harvesting pressure (Bodaly et al., 1992). This stock was 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) concluded that harvests from EHB were close to the sustainable yield (Bodaly et al., 1992).

Previous studies of the mitochondrial DNA (mtDNA) sequence of belugas reported that EHB belugas were significantly differentiated from other groups examined (Mancuso, 1995; Murray et al., 1995; Brennin et al., 1997; Brown Gladden et al., 1997, 1999). Brown Gladden et al. (1997), who used the most recent techniques and most samples from the area of interest, described genetic differences in a study using a mtDNA sequence of 234 nucleotides in 624 belugas from 25 geographic locations. As in


FIG. 1. Study area map.

previous studies, St. Lawrence River and EHB belugas had several related haplotypes that were distant from those in nearly all other locations. Both of these sample populations were significantly differentiated from the others examined. The authors hypothesized their common origin from an Atlantic refugium after the last glaciation. This study also showed very little differentiation among western and northern Hudson Bay samples. Belugas from Sanikiluaq in the Belcher Islands were not significantly differentiated from those from western Hudson Bay. Brown Gladden et al. (1999) also examined population differentiation using five microsatellite loci and found no genetic differentiation among Hudson Bay sample populations, including the one from EHB.

Here we test the hypothesis that belugas harvested in the community of Sanikiluaq and the communities in northwestern Quebec and along Hudson Strait and Ungava Bay are from the EHB beluga stock. We analyzed molecular genetic markers and tested the data for significant patterns of variation that might be used to reject the null hypothesis of no stock differences. Sampling efforts during the last several years have been focused to provide information that helps resolve questions of stock identity in these areas. Since the above studies, we now have acquired and analyzed more recent samples, including samples from northwestern Quebec and Hudson Strait communities. Also, we now analyze 15 microsatellite loci, whereas Brown Gladden et al. (1999) analyzed only five loci.

## METHODS

Tissue samples, usually skin, were obtained from 739 belugas sampled between 1984 and 1997, mostly from the subsistence harvest, but a few from tagging studies, biopsies, and beach-cast carcasses (Table 1). Samples from eastern Hudson Bay (EHB) and northwestern Quebec (NWQu) provided by hunters were identified by year and the community that they came from but seldom by the exact location where the belugas were harvested. Because of this, genetic compositions were analyzed by community. Between 10 and 30 belugas were sampled from Sanikiluaq (SAN) hunters each year between 1993 and 1999 as part of a sampling program conducted by the Department of Fisheries and Oceans.

Samples described in Brown Gladden et al. (1999) were reanalyzed for the additional 10 microsatellite loci. Samples from NWQu, Hudson Strait (HS), and Ungava Bay (UN) communities taken in 1998–99 were analyzed only for haplotypes and thus were not included in "assignment" calculations (see Statistical Analyses).

### *Genetic Analyses*

Skin samples were usually preserved in a saturated salt solution containing 20% dimethyl sulphoxide (DMSO) and 0.5 mol/L ethylene diamine tetraacetic acid (EDTA) (Seutin et al., 1991). Some samples were frozen first and preserved later using the salt-saturated DMSO. Total DNA extracts were prepared using the methods of Amos and Hoelzel (1992) and Sambrook et al. (1989), with modifications described by Maiers et al. (1996). Sex was determined using the methods described by Bérubé and Palsbøll (1996).

### *Mitochondrial DNA Analysis*

The mtDNA locus we used consists of 234 nucleotides that are found at the beginning of the d-loop region of the molecule (Brown Gladden et al., 1997). The d-loop region was amplified using the universal primers developed by Kocher et al. (1989) and species-specific primers developed by Lillie et al. (1996). Samples described in the previous study of Brown Gladden et al. (1997) were analyzed using asymmetric PCR and manual sequencing as described in Brown (1996) and samples new to this study 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., 1996) was used as the sequencing primer. The resultant mtDNA sequences were aligned using MacVector Ver. 3.5 (IBI) to a reference beluga sequence (Brown, 1996). Haplotype identification numbers were designated according to a consensus sequence of variable positions.

### *Microsatellite Analyses*

We analyzed for 15 microsatellite loci (Table 2). The 15 sets of microsatellite loci, described by Buchanan et al. (1996), Valsecchi and Amos (1996), and Amos et al. (1993), are designated according to species from which the primers were developed and the person who isolated them. Microsatellites were amplified according to specific conditions (Buchanan and Crawford, 1993; Buchanan et al., 1994; Postma, 1995; Maiers et al., 1996). Allele lengths were determined by reference to control samples (the original clone that was sequenced) and an M13 sequencing ladder run alongside the samples. Microsatellite alleles were identified by their size in base pairs.

### *Statistical Analyses*

Genetic diversity of haplotypes was calculated as $D_h = 1 - \Sigma(p_h)^2$, where $p_h$ is the frequency of the *h*-th allele. Genetic diversity over all microsatellite loci was calculated as a mean of diversity at all microsatellite loci, $D_n = 1 - \Sigma_l \Sigma_u (p_{lu})^2/m$, where $p_{lu}$ is the frequency of the *u*-th allele at the *l*-th locus, and *m* is the number of loci (Weir, 1996:150).

Analysis of Molecular Variance or "AMOVA" (Excoffier et al., 1992; Goldstein et al., 1995; Michalakis and Excoffier, 1996), available in the Arlequin statistical package (Schneider et al., 1997), was used to estimate variance components and calculate F-type statistics to test for significant genetic differentiation among chosen sample groups. $F_{st}$, the measure used here, is both an inbreeding coefficient and a measure of genetic distances (Cockerham, 1973).

Comparisons were made among the 11 major sample populations shown in Table 1, among 35 collections within these populations (Collection # column in Table 1: 34 collections were used for haplotype comparisons, 29 for microsatellite comparisons, and 28 for comparisons using both loci), and between sexes within collections and major sample groups. A collection usually represents different years from one location, but some collections group adjacent locations or years (or both) if sample sizes were small.

Table-wide statistical criteria for tables with multiple comparisons were calculated using the sequential von

TABLE 1. Beluga major sampling locations, collections within locations, and sample sizes.

| Major Sample Location | Sample Population | Collection # | Year(s) | n samples with Haplotypes | n samples with Microsatellites | n samples with both | No. of Females | No. of Males | Season |
|---|---|---|---|---|---|---|---|---|---|
| 1 & 2 | Western Hudson Bay (WHB) | | | | | | | | |
| 1 | Arviat | 1 | 1985 | 34 | 30 | 29 | 16 | 19 | July 17 to Aug 24 |
| | | 2 | 1987 | 22 | 20 | 20 | 7 | 15 | July 19 to Aug 23 |
| 2 | Churchill River (ChR) | 3 | 1988 to 1993 | 55 | 53 | 53 | 22 | 22 | late July, early Aug |
| 3 | Northern Hudson Bay (NHB) | | | | | | | | |
| | Cape Dorset | 29 | 1990, 96 | 4 | 4 | 0 | 4 | 4 | October |
| | Coral Harbour | 4 | 1994, 95, 96 | 9, 2, 29 | 9, 2, 32 | 40 | 16 | 19 | Aug to Nov, mostly Sept |
| | Hall Beach | 5 | 1994, 96 | 5, 2 | 7, 3 | 7 | 0 | 10 | September |
| | Igloolik | 6 | 1994, 95 | 19, 30 | 22, 20 | 36 | 7 | 39 | late Aug, mostly Sept |
| | Repulse Bay | 7 | 1983, 95 | 13, 11 | 0, 13 | 11 | 11 | 13 | late Aug, mostly Sept |
| 4 | Sanikiluaq (SAN) | 8 | 1993 | 10 | 10 | 10 | 3 | 7 | late June, early July |
| | | 9 | 1994 | 30 | 27 | 27 | 15 | 15 | late June, early July |
| | | 10 | 1995 | 23 | 23 | 23 | 7 | 11 | as above, 3 in Aug & Sept |
| | | 11 | 1996 | 18 | 19 | 16 | 6 | 12 | as above, 6 in Sept, 1 in Nov |
| | | 12 | 1997 | 19 | 19 | 19 | 7 | 8 | June, 1 in Oct |
| 5 & 6 | Eastern Hudson Bay (EHB) | | | | | | | | |
| 5 | Nastapoka River (NaR) | 13 | 1984 | 18 | 18 | 18 | 12 | 6 | June-Sept, mostly July |
| | | 14 | 1985 | 23 | 23 | 23 | 12 | 12 | mostly July, Aug |
| 6 | EHB 1990s | | | | | | | | |
| | Kuujjuarapik | 15 | 1993, 94, 97, 98 | 2, 5, 5, 8 | 2, 5, 5, 9 | 20 | 7 | 10 | July, August, September |
| | Great Whale R. | 15 | 1995 | 6 | 6 | 6 | 3 | 3 | not known |
| | Little Whale R. | 16 | 1995 | 2 | 2 | 2 | 0 | 2 | not known |
| | Richmond Gulf | 16 | 1995 | 2 | 2 | 2 | 1 | 1 | not known |
| | Umiujaq | 17 | 1994, 95 | 3, 2 | 3, 2 | 5 | 2 | 3 | June and July |
| | | 17 | 1997, 99 | 4, 1 | 4, 0 | 3 | 3 | 1 | June and July |
| | Inukjuaq | 18 | 1994, 97, 98, 99 | 7, 10, 10, 15 | 7, 10, 0, 0 | 17 | 10 | 7 | mostly July |
| 7 | Northwestern Quebec (NWQu) | | | | | | | | |
| | Puvirnituq | 30 | 1998, 99 | 9, 14 | 0 | 0 | | | not known |
| | Akulivik | 30 | 1999 | 1 | 0 | 0 | | | not known |
| | Ivujivik | 19 | 1995, 98 | 6, 17 | 6 | 6 | | | not known |
| 8 | Hudson Strait (HS) | | | | | | | | |
| | Salluit | 20 | 1997, 98 | 7, 5 | 8, 0 | 7 | 4 | 4 | June & July |
| | Kangiqsujuaq | 31 | 1983 | 6 | 0 | 0 | 2 | 4 | Oct 21–23 |
| | | 21 | 1994, 95, 97, 98, 99 | 10, 9, 7, 8, 16 | 10, 9, 7, 0, 0 | 26 | 13 | 13 | June & July |
| | Quaqtaq | 32 | 1995, 98, 99 | 2, 4, 2 | 2, 0, 0 | 2 | 0 | 2 | October |
| 9 | Ungava Bay (UN) | | | | | | | | |
| | Kangirsuk | 22 | 1994, 95, 97, 98 | 1, 2, 7, 1 | 1, 2, 7, 1 | 11 | 9 | 2 | Jan to July, mostly July |
| | Aupaluk | 33 | 1989, 99 | 2, 7 | 0 | 0 | | | not known |
| | Tasiujaq | 33 | 1994, 99 | 1, 4 | 1,0 | 0 | 1 | 1 | not known |
| | Kuujjuaq | 23 | 1997, 98, 99 | 6, 1, 1 | 6, 0, 0 | 6 | 2 | 4 | June, July, Oct, Nov |
| | Kangiqsualujjuaq | 23 | 1998 | 1 | 1 | 1 | 1 | | December |
| 10 | Kimmirut (KIM) | 34 | 1984 | 8 | 0 | 0 | 5 | 3 | August |
| | | 35 | 1990 | 4 | 0 | 0 | 2 | 2 | not known |
| | | 35 | 1991 | 4 | 1 | 1 | 3 | 1 | Feb to May, Oct |
| | | 24 | 1992 | 22 | 22 | 22 | 11 | 11 | not known |
| | | 25 | 1993 | 12 | 12 | 12 | 7 | 5 | not known |
| | | 26 | 1994 | 20 | 19 | 19 | 12 | 9 | not known |
| | | 27 | 1995 | 9 | 9 | 8 | 3 | 6 | not known |
| | | 27 | 1996 | 3 | 3 | 3 | 0 | 3 | not known |
| 11 | St. Lawrence River (StLR) | 28 | 1988, 89, 91 | 18 | 18 | 18 | 11 | 7 | not applicable |
| | Total = 739 belugas | | | 714 | 555 | 530 | | | |

Bonferroni correction (Holm, 1979; Rice, 1989). This correction produces a "minimum significance level," which is based on the number of comparisons, the distribution of probabilities, and the chosen table-wide $\alpha$ level ($\alpha = 0.05$ in this study). To estimate low probabilities accurately enough to apply table-wide statistical criteria, the significance of the variance ratios was calculated from 100 000 permutations of the difference matrix in AMOVA.

TABLE 2. Details of the 15 microsatellite loci based on all individuals (> 1300) analyzed in genetic studies.

| Microsatellite Locus[1] | 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 | Buchanan et al., 1996 | 9 | 170–188 | 184 | 0.44 |
| DlrFCB3 | 61 | Buchanan et al., 1996 | 25 | 141–207 | 141, 157, 165 | 0.85 |
| DlrFCB4 | 63 | Buchanan et al., 1996 | 14 | 155–183 | 159, 163 | 0.69 |
| DlrFCB5 | 61 | Buchanan et al., 1996 | 10 | 106–132 | 108, 124 | 0.60 |
| DlrFCB8 | 63 | Buchanan et al., 1996 | 9 | 163–185 | 171, 177 | 0.73 |
| DlrFCB10 | 61 | Buchanan et al., 1996 | 10 | 171–189 | 183 | 0.79 |
| DlrFCB11 | 61 | Buchanan et al., 1996 | 13 | 110–138 | 114, 134 | 0.48 |
| DlrFCB13 | 61 | Buchanan et al., 1996 | 8 | 270–294 | 286 | 0.17 |
| DlrFCB14 | 61 | Buchanan et al., 1996 | 9 | 289–329 | 309 | 0.61 |
| DlrFCB16 | 61 | Buchanan et al., 1996 | 11 | 276–302 | 278, 296 | 0.67 |
| DlrFCB17 | 64 | Buchanan et al., 1996 | 24 | 139–205 | (167 + 169), 177 | 0.84 |
| Gme464/465 | 45 | Schlötterer et al., 1991 | 6 | 130–142 | 134 | 0.56 |
| EV37Mn | 59 | Valsecchi and Amos, 1996 | 15 | 177–215 | 195, (205–209) | 0.84 |
| EV94Mn | 65 | Valsecchi and Amos, 1996 | 16 | 202–244 | 202, 208, 214 | 0.77 |

[1] The 15 sets of microsatellite loci are designated according to species from which the primers were developed or the person who isolated them or both. Dlr = *Delphinapterus leucas*; FCB = Fiona C. Buchanan; Gme = *Globicephala melaena*; EV = Elena Valsecchi; Mn = *Megaptera novaeangliae*.

We used Cavalli-Sforza's "Chord Distance" between sample populations (Cavalli-Sforza and Edwards, 1967), using both microsatellite and haplotype data, as a measure of genetic distance among Collections 1 to 28 in Table 1. The Neighbor-Joining Method (Saitou and Nei, 1987) was used to construct phylogenetic trees.

Individual belugas from all sample populations except northwestern Quebec (Sample population 7, Table 1) were "assigned" to one of three summering areas, using probabilistic calculations as described by Waser and Strobeck (1998) and Paetkau et al. (1997). Specifically, Baye's formula is used to assign each individual to the sampling population most likely for its genotype. Sample groups to "assign from" and to "assign to" were chosen to best elucidate possible stock affiliations in the main areas of interest. "Assignments" and "misassignments" of individuals were then examined to discern possible dispersion and migration patterns. Only individuals for which we had obtained both haplotype and microsatellite data were used. NWQu samples were not included because of the small sample size and because we felt we could not confidently combine these data with the data from any geographic neighbour. Calculations were done with in-house software written in Visual Basic.

## RESULTS

Possible parent-offspring relationships between individuals, identified by at least one allele in common at each microsatellite locus, were identified to determine whether sampling was unduly clustered because samples included family groups. A slightly larger than expected number of parent-offspring-like relationships was found in the Churchill River (in 7 of 1378 pairwise comparisons of individuals; expected number is 4.55/1378 comparisons), Coral Harbour (7/903, expected 2.1/903), Kuujjuaq 1997 (2/21, expected 0.2/21), Kimmirut (KIM) (5/231, expected 1.8/231), and the St. Lawrence River (StLR) (6/153, expected 2.9/153). Although some of these were no doubt true parent-offspring pairs, samples were not eliminated from analyses.

### *Major Sample Populations*

Thirty-five haplotypes were found in the area encompassed by this study (Table 3). The number of haplotypes and haplotype diversity varied among the 11 major sample populations (Table 4). Belugas from the ChR and NWQu had the lowest haplotype diversities (0.294 and 0.370) because of the high frequency of haplotype H02 in both locations (Table 3). Samples from the Nastapoka River (NaR), dominated by H18, but with H05 and H17 at notable frequencies, had a slightly higher diversity of 0.510. Haplotype diversity was slightly higher in EHB 1990s than in the NaR. Samples from the StLR, dominated by haplotypes H18 and H29, had a similar diversity of 0.512 (Tables 3 and 4). The highest haplotype diversities were observed from Arviat (0.747) and Hudson Strait (HS) (0.692). KIM had an intermediate haplotype diversity due to a more equitable distribution of haplotypes, but relatively few haplotypes given the large sample size from this location (Table 3). Among uncommon haplotypes, haplotype H06 occurred primarily in SAN, H07 and H17 in EHB, H21 in northern Hudson Bay (NHB), H22 in KIM, and H05 in WHB and KIM (Table 3).

The lowest numbers of microsatellite alleles were observed in StLR (62 alleles), NWQu (70 alleles, n belugas = 6), UN (90 alleles), and the NaR (97 alleles) (Table 4). The largest numbers of alleles were observed in NHB (120 alleles) and SAN (114 alleles). Among Arctic belugas, NaR and UN belugas had the lowest microsatellite diver-

TABLE 3. Haplotype frequencies in sample populations.

| Haplotype Name (H) | 02 | 04 | 05 | 06 | 07 | 13 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 26 | 29 | 32 | 35 | 39 | 44 | 53 | Others[1] | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Arviat | 26 | – | 7 | 3 | 1 | 1 | – | – | 5 | – | 5 | 1 | 1 | 1 | – | – | – | 1 | – | 1 | 1 | – | 1, 1 | 56 |
| Churchill River | 46 | 1 | 4 | – | – | – | – | – | 1 | – | 1 | – | 1 | – | – | – | – | – | – | – | 1 | – | – | 55 |
| N Hudson Bay | 77 | – | 6 | 1 | – | 1 | 3 | – | 5 | – | 21 | 3 | 2 | 1 | – | – | – | – | 1 | – | – | – | 1,1,1 | 124 |
| Sanikiluaq | 65 | – | – | 12 | 1 | – | 1 | 6 | 3 | – | 1 | 3 | – | – | – | – | – | – | 2 | 4 | – | – | 1,1 | 100 |
| Nastapoka River | 1 | – | – | – | 5 | – | – | 2 | 28 | 2 | – | – | – | – | – | 2 | – | 1 | – | – | – | – | – | 41 |
| Kuujjuarapik | 1 | – | 1 | 1 | 2 | – | – | 5 | 9 | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 20 |
| Umiujaq, Whale Rivers | 5 | – | – | – | 3 | – | – | 4 | 7 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 19 |
| Inukjuak | 3 | – | – | – | 1 | – | – | 2 | 35 | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | 42 |
| Puvirnituq, Akulivik | 20 | – | – | 1 | – | – | – | 1 | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | 1 | 24 |
| Ivujivik | 17 | – | 1 | – | 1 | – | – | 3 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 23 |
| Salluit | 5 | – | 1 | – | 3 | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | 1 | – | 12 |
| Kangiqsujuaq 1983 | – | – | – | – | – | – | – | 3 | 2 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | 6 |
| Kangiqsujuaq 1994 on | 31 | – | 4 | – | 2 | – | – | 1 | 4 | – | 2 | – | 3 | – | 2 | – | – | – | – | – | – | 1 | – | 50 |
| Quaqtaq | 4 | – | 1 | – | – | – | – | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 8 |
| West Ungava | 15 | 3 | – | – | 2 | – | – | 1 | 1 | – | 1 | – | – | – | 1 | – | – | 1 | – | – | – | – | – | 25 |
| Kuujjuaq, Kangiqsualujjuaq | 5 | – | 2 | – | 1 | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | 9 |
| Kimmirut | 49 | – | 14 | – | – | – | – | – | 2 | – | – | – | 12 | 1 | 2 | – | – | – | – | – | – | – | 1,1 | 82 |
| St. Lawrence River | – | – | – | – | – | – | – | – | 6 | – | – | – | – | – | – | – | 11 | – | – | – | – | – | 1 | 18 |
| Total | 370 | 4 | 41 | 18 | 22 | 2 | 4 | 29 | 110 | 2 | 35 | 7 | 20 | 3 | 5 | 2 | 11 | 4 | 3 | 5 | 2 | 2 | 13 | 714 |

[1] Haplotypes observed only once in this study.

TABLE 4. Genetics descriptions for 11 major sample populations in Table 1.

| Sample Population | n different haplotypes | Haplotype Diversity (Dh) | n different Microsatellite Alleles | Microsatellite Diversity (Dn) |
|---|---|---|---|---|
| Arviat | 15 | 0.747 | 111 | 0.672 |
| Churchill River | 7 | 0.294 | 104 | 0.661 |
| Northern Hudson Bay | 14 | 0.580 | 120 | 0.675 |
| Sanikiluaq | 12 | 0.555 | 114 | 0.660 |
| Nastapoka River 1984–1985 | 7 | 0.510 | 97 | 0.654 |
| Eastern Hudson Bay | 8 | 0.567 | 107 | 0.660 |
| NW Quebec | 8 | 0.370 | 70 | 0.611 |
| Hudson Strait | 10 | 0.692 | 100 | 0.672 |
| Ungava | 10 | 0.630 | 90 | 0.658 |
| Kimmirut | 8 | 0.591 | 109 | 0.670 |
| St. Lawrence River | 3 | 0.512 | 62 | 0.592 |
| Combined | 35 | | 150 | |

sities (0.654 and 0.658), suggesting an uneven distribution of alleles, and NHB, ARV, and HS had the highest diversities (0.675, 0.672, and 0.672).

*Analysis of Molecular Variance (AMOVA)*

Haplotype differentiation was significant in 36 of 55 pairwise comparisons among 11 major sample populations after applying sequential von Bonferroni criteria for multiple comparisons (Rice, 1981) (Table 5). Overall, $F_{st}$ values were largest for pairwise comparisons with belugas from StLR (Mean $F_{st}$ = 0.409), NaR (0.370), and EHB (0.318). These three sample populations were significantly differentiated from all other sample populations except EHB 1990s and NaR, which were not significantly differentiated from each other ($F_{st}$ = 0.005, $p$ = 0.267). NaR samples had greater genetic distances from all the other populations than EHB 1990s samples did (Table 5).

The sample populations UN, SAN, NWQu, and ChR were not significantly differentiated from each other, nor were the sample populations UN, HS, NHB and ARV from each other (Table 5). Sample populations were mostly differentiated between these two groups. NWQu was significantly differentiated from ARV, and ARV from both HS and NHB. KIM was differentiated from SAN, NWQu, NHB, and the ChR.

There was considerably less microsatellite differentiation than haplotype differentiation among the 11 major sample groups (Table 6). Only 17 of 55 pairwise comparisons were significant after applying sequential von Bonferroni criteria (Rice, 1989). StLR was the only location that differed from all others. $F_{st}$ values between the StLR and Arctic sample populations ranged from 0.067 to 0.106, while values among Arctic populations ranged from –0.002 to 0.013. The locations KIM, HS, ChR, NaR, NWQu, UN, and NHB were not significantly differentiated from each other. ARV and KIM were significantly differentiated from EHB 1990s and SAN, which were differentiated from each other. SAN was also significantly differentiated from NHB, and ARV was differentiated only from NHB.

AMOVA tables comparing the 35 Collections in Table 1 are not presented because they generally confirmed patterns

TABLE 5. $F_{st}$ values (above diagonal) and associated probabilities for mtDNA differentiation (below diagonal). Differentiation significant at $p < 0.0024$, the minimum significant level for a table-wide $\alpha = 0.05$ is marked with an asterisk (*).

| | Arviat | Churchill River | N Hudson Bay | Sanikiluaq | Nastapoka River | E Hudson Bay | NW Quebec | Hudson Strait | Ungava Bay | Kimmirut | St. Lawrence River |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Arviat | | 0.115* | 0.021 | 0.041 | 0.300* | 0.255* | 0.088* | -0.001 | 0.010 | 0.026 | 0.307* |
| Churchill River | 0.000* | | 0.056* | 0.050 | 0.585* | 0.497* | 0.002 | 0.085* | 0.062 | 0.069* | 0.618* |
| N Hudson Bay | 0.037 | 0.002* | | 0.031* | 0.414* | 0.360* | 0.041 | 0.017 | 0.015 | 0.042* | 0.421* |
| Sanikiluaq | 0.005 | 0.003 | 0.004* | | 0.431* | 0.369* | 0.018 | 0.030* | 0.017 | 0.052* | 0.440* |
| Nastapoka River | 0.000* | 0.000* | 0.000* | 0.000* | | 0.005 | 0.533* | 0.319* | 0.388* | 0.416* | 0.312* |
| E Hudson Bay | 0.000* | 0.000* | 0.000* | 0.000* | 0.267 | | 0.448* | 0.267* | 0.331* | 0.360* | 0.289* |
| NW Quebec | 0.000* | 0.300 | 0.010 | 0.077 | 0.000* | 0.000* | | 0.053 | 0.034 | 0.065* | 0.559* |
| Hudson Strait | 0.456 | 0.000* | 0.032 | 0.008* | 0.000* | 0.000* | 0.004 | | -0.006 | 0.021 | 0.339* |
| Ungava Bay | 0.169 | 0.009 | 0.108 | 0.096 | 0.000* | 0.000* | 0.048 | 0.609 | | 0.016 | 0.391* |
| Kimmirut | 0.032 | 0.002* | 0.001* | 0.001* | 0.000* | 0.000* | 0.003* | 0.035 | 0.126 | | 0.417* |
| St. Lawrence R. | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | |

TABLE 6. $F_{st}$ values (above diagonal) and associated probabilities for microsatellite differentiation (above diagonal). Differentiation significant at $p < 0.0012$, the minimum significance level for a table-wide $\alpha = 0.05$ is marked with an asterisk (*).

| | Arviat | Churchill River | N Hudson Bay | Sanikiluaq | Nastapoka River | E Hudson Bay | NW Quebec | Hudson Strait | Ungava Bay | Kimmirut | St. Lawrence River |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Arviat | | 0.004 | 0.007* | 0.008* | 0.003 | 0.011* | 0.001 | 0.005 | 0.012 | 0.004 | 0.088* |
| Churchill River | 0.058 | | 0.000 | 0.004 | -0.002 | 0.003 | 0.000 | 0.004 | 0.004 | 0.000 | 0.067* |
| N Hudson Bay | 0.000* | 0.500 | | 0.003 | 0.000 | 0.003 | 0.008 | 0.005 | 0.012 | 0.005 | 0.080* |
| Sanikiluaq | 0.000* | 0.024 | 0.009 | | 0.002 | 0.009* | 0.011 | 0.008* | 0.013 | 0.008* | 0.077* |
| Nastapoka River | 0.084 | 0.856 | 0.562 | 0.144 | | 0.002 | 0.002 | 0.004 | 0.006 | 0.003 | 0.083* |
| E Hudson Bay | 0.000* | 0.043 | 0.031 | 0.000* | 0.197 | | 0.010 | 0.005 | 0.005 | 0.009* | 0.084* |
| NW Quebec | 0.437 | 0.493 | 0.215 | 0.157 | 0.376 | 0.123 | | 0.005 | 0.001 | 0.004 | 0.106* |
| Hudson Strait | 0.036 | 0.092 | 0.012 | 0.001* | 0.097 | 0.032 | 0.321 | | 0.005 | 0.002 | 0.082* |
| Ungava Bay | 0.014 | 0.294 | 0.005 | 0.002 | 0.173 | 0.153 | 0.795 | 0.231 | | 0.013 | 0.080* |
| Kimmirut | 0.022 | 0.523 | 0.003 | 0.000* | 0.083 | 0.000* | 0.364 | 0.225 | 0.005 | | 0.079* |
| St. Lawrence R. | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | 0.000* | |

of similarities and differences shown in Tables 5 and 6. However, an overall lower amount of differentiation and some spurious $F_{st}$ values and probabilities occurred when small samples were compared. There was no significant differentiation at $p < 0.05$ among collections within ARV, KIM, SAN, NaR, NWQu, and UN, either for mtDNA or for microsatellites. This similarity of collections within locations is evident in the "phylogenetic" tree of 28 collections based on Chord Distance calculated from both haplotypes and microsatellites (Fig. 2). Most NHB collections were significantly differentiated from each other, except that Igloolik and Repulse Bay were not significantly differentiated from each other for loci of either type (Fig. 2). Inukjuak (EHB) samples differed weakly from other EHB 1990s collections, and strongly resembled the NaR collections for both haplotypes and microsatellites. All SAN collections were significantly differentiated from most of the EHB 1990s collections on the basis of both haplotypes and microsatellites. HS collections mostly resembled western Hudson Bay collections. Significant differences among HS collections involved the Kangiqsujuaq 1983 collection (haplotype data only). This collection of six individuals had three haplotypes (2 × H18, 3 × H17, and 1 × H20), of which the first two are most commonly associated with EHB and the last with NHB (Table 3).

Both Fisher's Exact Test for population differentiation (Guo and Thompson, 1992) and probabilities of $F_{st}$ values from AMOVA showed that allele frequencies between males and females did not differ significantly within collections or locations (not shown). When the two sexes were treated as separate collections, they were often neighbors in phylogenetic trees. Although slightly higher haplotype and microsatellite diversities were observed in males, this was believed to be an artifact of the larger size of the male sample.

*Assignment Tests*

Belugas hunted in EHB were the only summering population strongly assigned (82%, or 79/96, with high probability for many individuals) to its actual origin (Fig. 3). None of the 79 EHB belugas assigned to EHB was haplotype H02. Of 17 belugas not assigned to EHB, eight were H02, one was H17, and three were H18.

Of belugas sampled in WHB (Arviat and Churchill River), 74% (75/102) were assigned to WHB or NHB, 18% (18/102) to SAN, and 9% (9/102) to EHB (Fig. 3). Five of the nine assigned to EHB were haplotype H18. One other H18 from WHB was assigned to NHB.

Of belugas harvested at SAN, 53% (50/95) were assigned to SAN, 39% (37/95) to WHB/NHB, and 8% (8/95) to EHB. Seven of those assigned to EHB, with probabilities greater than 0.80, were haplotype H17 or H18, and the eighth was H07. When those assignments were made using microsatellites alone (not shown), all four H17, two of

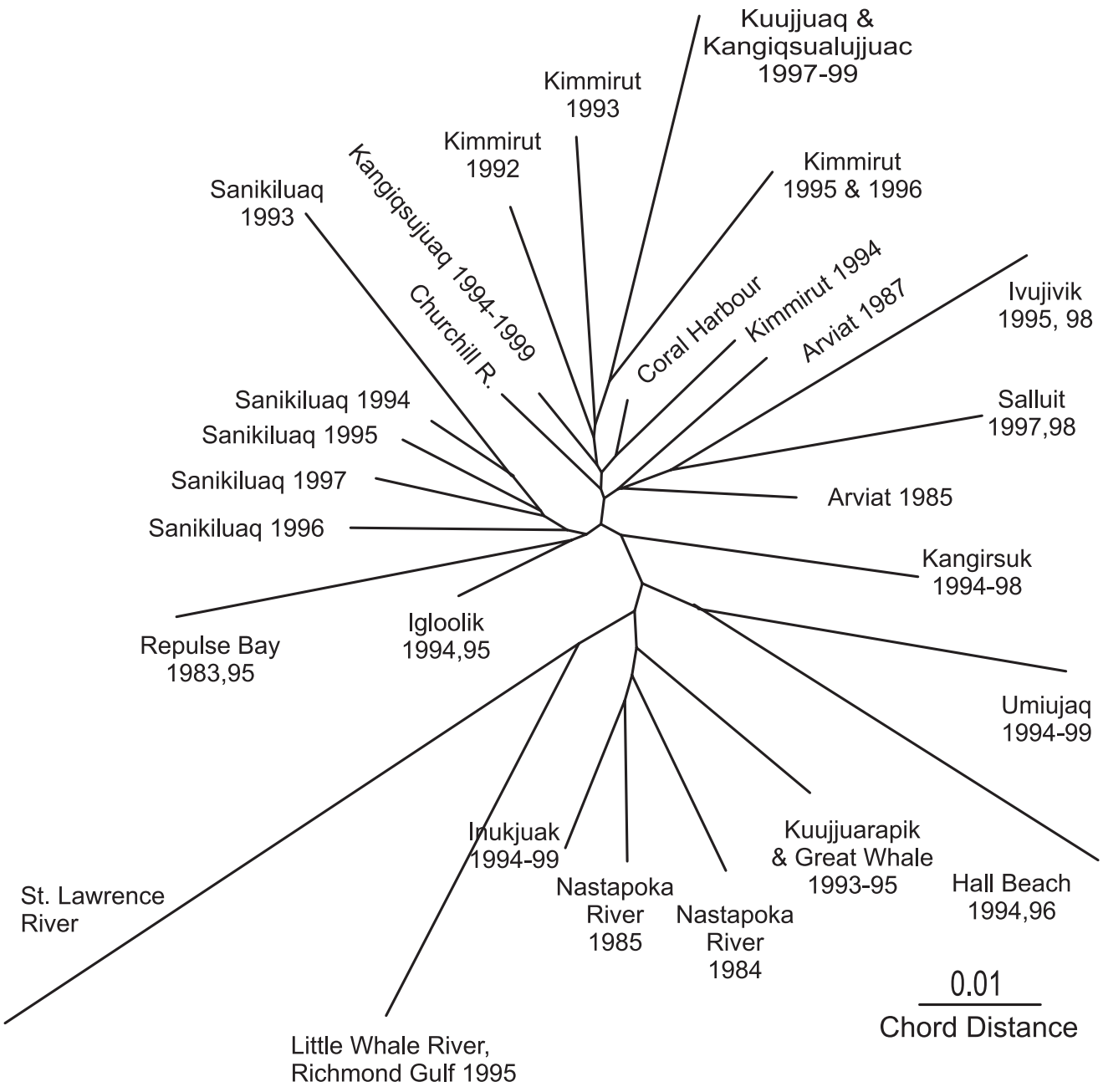


FIG. 2. Phylogenetic tree of Collections 1 to 28 in Table 1. Cavalli-Sforza's Chord Distance between sample populations (Cavalli-Sforza and Edwards, 1967), using both microsatellite and haplotype data, was used as a measure of genetic distance. The Neighbor-Joining Method (Saitou and Nei, 1987) was used to construct the trees.

three H18, and the one H07 individuals all maintained high probabilities of being assigned to EHB.

Of belugas sampled at HS, 69% (37/54) were assigned to WHB or NHB, 19% (10/54) to EHB, and 13% (7/54) to SAN (Fig. 3). Of individuals sampled at NHB, 74% (70/94) were assigned to WHB/NHB, 17% (16/94) to SAN, and 9% (8/94) to EHB. Assignments from NHB to EHB all had probabilities less than 0.63. Of belugas sampled at KIM, 83% (54/65) were assigned to WHB/NHB, 12% to SAN, and 5% (3/65) to EHB. The three KIM belugas assigned to EHB are one H22 and two H18 individuals, the only H18 individuals sampled in KIM.

Many belugas for which we have only haplotype data can be assigned if we assume that H18, H17, and H07 are EHB genotypes and H02 and H05 are WHB genotypes. Of 25 belugas from 1998 and 1999 Inukjuak (EHB) samples, 21 (84%) were haplotype H18, one was H17, two were H02, and one was H32. Thus 88% (22/25) are EHB haplotypes. Of 23 belugas from Akulivik and Puvirnituq (NWQu) samples, 20 were H02, one was H17, one was H20, and one had a unique haplotype. The 23 Ivujivik (HS) samples from 1995 and 1998 had 17 H02, two H17, one H18, three H07, and one H05. Thus these locations had 83% western haplotypes. Also, three of six samples from

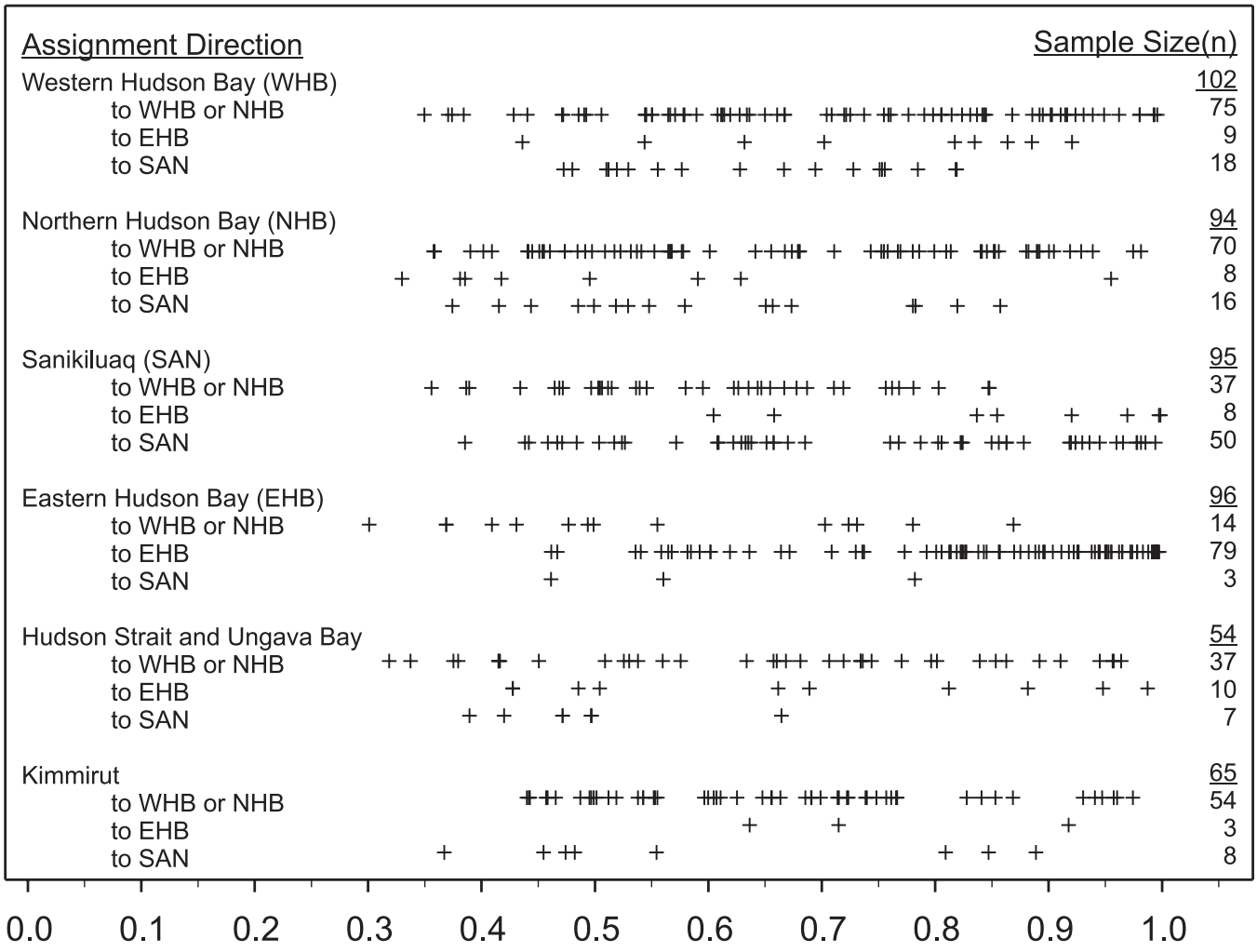


FIG. 3. Assignment of individual belugas from six sample populations into one of three summering areas: a) eastern Hudson Bay (Locations 5 and 6, Table 1); b) Sanikiluaq, and c) western and northern Hudson Bay combined (Locations 1–3, Table 1). The six sample populations are from four summering areas—1) Western Hudson Bay (Locations 1 and 2, Table 1); 2) Northern Hudson Bay; 3) Sanikiluaq; and 4) Eastern Hudson Bay (Locations 5 and 6, Table 1)—and two areas that hunt migrating belugas—5) Hudson Strait and Ungava Bay (Locations 8 and 9, Table 1); and 6) Kimmirut. We calculated the probability of belonging to each of the three summering areas for every beluga, and assigned each individual to its most probable summering area. The probability associated with the assignment is plotted.

1983 from Kangiqsujuaq had "EHB" haplotypes (last paragraph). The 24 Kangiqsujuaq samples from 1998 and 1999 had 16 H02, two H18, two H22, and one each of H17, H20, H05, and H53. Twenty-one other samples from Quaqtaq, Aupulak, Tasiujaq, Kuujjuaq (UN), all collected in 1998 and 1999, had 12 H02, one H17, two H04, and others with a frequency of 1. Eight KIM belugas from 1984, for which we have only haplotype data, were all haplotype H02, a western haplotype.

## DISCUSSION

The primary objective of this study was to examine whether communities from the eastern Hudson Bay arc (EHB), Hudson Strait (HS), Ungava Bay (UN), northwestern Quebec (NWQu), and the community of Sanikiluaq (SAN) harvested the same beluga stocks. The threatened EHB stock was of primary interest. St. Lawrence belugas were also examined as an outgroup.

All genetic results confirm that EHB belugas are distinct and that all communities on the EHB arc harvest mostly these belugas. Samples obtained only from the Nastapoka River (NaR) in 1984 and 1985 and samples taken from EHB arc communities in the 1990s were not significantly differentiated from each other, but were significantly different from most sample collections from other areas. Both EHB 1990s and NaR belugas were assigned to their same population of origin more often than other sample populations were, and the probabilities associated with these assignments were generally higher than those of other major sample populations assigned to their same source. Also, sample collections within EHB cluster closely on a phylogenetic tree (Fig. 2). Some belugas from other locations, namely SAN and HS, were assigned to EHB with high probabilities, and some EHB belugas were

assigned to Sanikiluaq and to WHB and NHB, but not with high probabilities. The consistent differentiation between EHB and NaR and other locations is due primarily to haplotype differences, namely, high frequencies of haplotypes H18, H17, and H07 in EHB and high frequencies of H02 in other locations.

Belugas from EHB, SAN, and KIM were significantly differentiated from each other and most of their geographic neighbours, and comparison of communities or years (or both) within these locations revealed that samples from the same location were similar. These sample locations will be considered to represent different stocks of belugas. However, belugas at each of these locations are most likely not all from the same stock.

Belugas harvested in Sanikiluaq (SAN) are significantly differentiated on the basis of both haplotypes and microsatellites from those sampled in all other locations examined. There was no significant genetic differentiation among collections of samples from SAN over five years. Collections from different years are not significantly differentiated and cluster closely on the phylogenetic tree (Fig. 2). SAN samples were dominated by haplotype H02 (65% of total over all years), and H06 was also present in all years (12% total). Several haplotypes, namely H17, H18, H21, H35, and H39, occurred at low frequencies, but all were sampled more than once. This genetic consistency indicates that SAN belugas may be a separate stock. However, it is also possible that a consistent mixture of stocks was sampled. Sources for these belugas may include the Nelson River, southern Hudson Bay, northern Hudson Bay, James Bay, and EHB. It is notable that some individuals from SAN were assigned to EHB with high probabilities; thus, it is highly probable that these really were EHB belugas. Both haplotype and microsatellite diversities are high compared to EHB and Churchill, also suggesting that the Sanikiluaq sample population represents an admixture of populations.

Kimmirut beluga collections had no significant genetic differentiation among years, and these collections clustered closely on a phylogenetic tree (Fig. 2), suggesting that they may be a separate stock. The relatively few haplotypes for the sample size also confirm that these Kimmirut belugas may be a separate stock. Haplotype H02 was not as dominant as in western Hudson Bay samples, and haplotype H22 was common in Kimmirut. Haplotype H22 was otherwise most common in samples from Iqaluit and Pangnirtung (de March et al., 2002). Kimmirut belugas are most likely from a stock or summering location in Hudson Bay that has not yet been sampled.

Belugas from the Churchill River differ from neighboring sample populations only on the basis of haplotypes. Samples consist of 84% haplotype H02 (46/55 belugas), 9% H05, and others that occur only once. The frequency of H02 was high in all five years of sampling (not shown). This genetic consistency suggests that Churchill belugas may also be a separate stock. Their composition of microsatellites is not significantly differentiated from that of any other sample population except the StLR. The only other sample collections that have a high frequency of H02 are Ivujivik, Puvirnituq, and Akulivik (37/47 samples or 79%); however, belugas from these northwestern Quebec locations also had a low frequency of H17 and H18.

Belugas sampled at Arviat have a high genetic diversity, as expected with migrating belugas. Samples from 1985 and from 1987 have a similar genetic composition. Haplotypes at Arviat are significantly differentiated from those found at ChR, NaR, and EHB, discussed as possible different stocks above, but also from those found in NWQu. Arviat haplotypes are not significantly differentiated from those of NHB, SAN, HS, UN, and KIM. Microsatellites are significantly differentiated only from those found in NHB, SAN, and EHB. Samples from other areas where migrating belugas are hunted—namely, HS, UN, and possibly NHB—also have high genetic diversities.

Samples from NHB remain most problematic, since genetic results gave no clear picture about their stock status. They were similar to other Hudson Bay collections and had a relatively high genetic diversity; however, collections within NHB were often significantly differentiated from each other.

Genetic distances ($F_{st}$ values) and assignment patterns support the hypothesis that Sanikiluaq and other communities in Nunavut and Nunavik hunt some EHB belugas. EHB belugas may comprise 19% of belugas harvested in HS and UN, 15% in NWQu (assuming H18, H17, and H07 are EHB belugas), 9% in NHB, 9% in WHB, 8% in SAN, and 5% in KIM (Fig. 3). Thus, the hunting pressure on EHB belugas is spread among several communities. However, 18% of belugas hunted in EHB are assigned to WHB or NHB and 3% to SAN. At this point, we believe that some of the above estimates are still based on too few samples to calculate the relative importance of different hunts. Also, methods of "assigning" individuals remain problematic. Although individuals can be assigned to various stocks on the basis of simple probabilistic calculations, such calculations do not take into account the fact that different populations are most likely at breeding equilibrium. Thus, when comparing populations that differ in frequencies of the same genetic loci, we will find individuals in every population that resemble those in other populations more than they resemble individuals in their own population. These individuals would be wrongly assigned using simple methods like the one used here. Model-based assignment methods similar to that described by Pritchard et al. (2000), but modified to use both haploid and diploid data, may be more appropriate for assigning individuals.

The three summering sample populations associated with estuaries included in this study had low genetic diversities. In the St. Lawrence and Nastapoka Rivers, this is no doubt due in part to past overharvesting. Both the Churchill and Nastapoka Rivers may have populations with strong site fidelity. Also, these populations may reach their summer feeding areas early in the season, which

might lead to more inbreeding than is found in a population that spends more time in open water.

There were no significant differences between the genotypes of the sexes at any locations sampled. Even when the two sexes were separated in analyses, they were often neighbors in phylogenetic trees (results not shown). There were more haplotypes and microsatellite alleles in males than in females, but this result may have been caused by the fact that more males were sampled. 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. (1990) has shown, using radio-telemetry, that most belugas that travel large distances are males. One would therefore expect a higher genetic diversity, caused by wandering males, for males from some locations. In these data, males do not have a higher diversity than females.

There is little microsatellite differentiation among Hudson Bay sample populations, including that of EHB. The few cases of significant differentiation that were demonstrated among Hudson Bay populations make little sense in terms of geographic distance or migration (Table 6). It is possible that most Hudson Bay populations examined interbreed. With a 14-month gestation period, and young born mainly in late May and early June (Doidge, 1990; R.E.A. Stewart, pers. comm. 1999), belugas might mate either while in mixed stocks on wintering grounds or during migrations, thus leading to mixing of nuclear alleles. It is also possible that interbreeding occurs at a slow rate among populations, so that geographic differences can still be demonstrated. When only haplotypes are used to draw phylogenetic trees, collections within Sanikiluaq do not cluster together as they do when microsatellites are also included in the analysis. This suggests that using the entire genotype rather than only haplotypes is better for characterizing sample populations and thus also for characterizing individual belugas.

Male dispersion is also a possible explanation for the lack of microsatellite differentiation; however, the comparisons of genetic characteristics of males and females mentioned above give no evidence that males disperse more than females.

St. Lawrence belugas were highly differentiated from all other sample populations for both types of loci. Both EHB and StLR have high frequencies of haplotype H18, and the StLR has a high frequency of H29, which has not been found elsewhere (Table 2). Haplotype H17, one nucleotide different from H18 and two different from H29, occurs mainly in belugas sampled from EHB, SAN, and Hudson Strait communities (Brown Gladden et al., 1997; de March et al., 2002). Haplotypes H18, H17, and H29 differ from H02 at 6, 7, and 9 nucleotides, while other haplotypes differ from H02 at 1 to 4 nucleotides. The EHB belugas may have been the first colonizers from the Atlantic after the ice obstruction in Hudson Strait disappeared approximately 8000 years ago (Fulton, 1989). Colonization directly from the south at earlier dates is also a possibility that merits investigation. However, it is difficult to believe that belugas could have overwintered in glacial Lakes Agassiz and Ojibway, or other glacial lakes that were intermittently connected to the Champlain Sea or the St. Lawrence River between approximately 10 000 and 18000 years ago. The fact that EHB haplotypes still resemble those of St. Lawrence belugas indicates the high degree of site fidelity shown by females and their families to calving and summer feeding areas. With an average of 13 years per generation (Stu Innes, pers. comm. 1999), 8000 years represents only about 600 generations.

Both Sanikiluaq and EHB contain some western Arctic and High Arctic haplotypes that are absent or rare in other Hudson Bay locations. Haplotype H07 occurs in EHB but is not common in other locations in Hudson Bay; however, it is common in most Canadian High Arctic populations, in West Greenland, and in the western Canadian Arctic (de March et al., 2002). Haplotype H06, which occurs in SAN and at a low frequency in Arviat in this study, is common in the Chukchi Sea stock (sampled in Alaska and Russia), but it is also found in the Beaufort Sea and Pangnirtung (de March et al., 2002). Some of the uncommon haplotypes in Sanikiluaq and EHB also occur in far removed areas (H16 and H20 in northern Hudson Bay and H42 in the Beaufort Sea). This infiltration of western genes may be occurring now, but it may also have occurred at a greater rate in the past. Approximately 5000 years ago, passage through Fury and Hecla Strait was facilitated by higher water levels and warmer temperatures, and the Gulf of Boothia was also connected to Repulse Bay. The Gulf of Boothia would have been considerably larger and may have been home to belugas. Passage became more difficult 3000-4000 years ago when land levels rose.

There is a high degree of genetic overlap in all sample populations except the StLR samples. Statistically significant differentiation among Arctic populations is mostly due to differences in allele frequencies, and not to the presence or absence of different alleles. Examination of the usefulness of different microsatellite loci (unpublished results) have led us to believe that population discrimination would not improve with the use of more microsatellite loci. In fact, 10 random loci out of the 15 used would give the same amount of differentiation as 15 loci. Even when samples can be shown to be genetically consistent over the years, as is the case for SAN, EHB, and KIM, it is still impossible to determine whether the group constitutes a separate stock or whether the mixtures of stocks or social groups sampled happened to be consistent. We need additional information, including traditional knowledge, biological parameters, contaminant profiles, and radio tagging studies, to better understand where migrating belugas originate.

Our ability to define stocks is also limited by small sample numbers (or no samples) from many locations, non-random sampling, lack of repeated sampling, and the need for accompanying information such as dates, locations, and population data. We have no information about the genetics of some

major summer congregations, such as those in the Seal, Nelson, Winisk, and Severn Rivers, in James Bay, and along the southern Hudson Bay coast. Also, northern Hudson Bay and Foxe Basin locations have been sparsely sampled. It may be impossible to sample adequately in some areas of interest, such as James Bay and the Nelson River, because of difficulty in obtaining samples.

Given the large variation in genetic results and the fact that it may be next to impossible to obtain adequate samples from many summering and migrating populations, model-based methods that incorporate different types of knowledge may be the most appropriate for understanding Arctic beluga populations. These models would include existing scientific knowledge of population parameters and migration routes, traditional knowledge, and new information on stock discrimination from studies of genetics and contaminants.

## ACKNOWLEDGEMENTS

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