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Molecular genetic relationships among bowhead whales (*Balaena mysticetus*) in Eastern Canadian Arctic and Western Greenland waters

Comparaison de la génétique moléculaire des baleines boréales (*Balaena mysticetus*) des eaux de l'est de l'Arctique canadien et de l'ouest du Groenland

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ABSTRACT

Molecular genetic relationships among bowhead whales (*Balaena mysticetus*) were examined to test the hypothesis that bowheads in the Eastern Canadian Arctic and Western Greenland are from a single population of interbreeding animals. DNA sequencing of the mitochondrial d-loop region and the analysis of 15 nuclear DNA microsatellite loci were completed for 286 individual bowheads sampled at Pelly Bay, Igloolik, Repulse Bay and Pangnirtung in Nunavut, Canada and from Disko Bay in Western Greenland. An additional sample of whales from the Beaufort Sea representing the putative Bering-Chukchi-Beaufort (B-C-B) Sea stock/population was also included in the analysis. While mtDNA haplotype frequency comparisons did not support a rejection of the single population hypothesis, nuclear DNA microsatellite results showed some sub-structuring of the population, specifically the bowheads in Igloolik (Foxe Basin) as compared to the Pangnirtung and W. Greenland (Baffin Bay) samples. Furthermore, the Repulse Bay (Hudson Bay) samples were differentiated from the W. Greenland samples, but not from the Pangnirtung samples. Geographic partitioning of the animals is one possible reason for this result. Other possibilities include sex and/or age class segregation, temporal segregation, selective mating strategies/success or some combination of these factors. Until the possible mechanisms generating this genetic differentiation are more fully investigated and understood, the Hudson Bay-Foxe Basin (HB-FB) bowheads should continue to be considered a separate genetic sub-population from the Baffin Bay-Davis Strait (BB-DS) bowheads.

RÉSUMÉ

Une comparaison de la génétique moléculaire des baleines boréales (*Balaena mysticetus*) a été entreprise pour vérifier l'hypothèse selon laquelle les baleines boréales de l'est de l'Arctique canadien et de l'ouest du Groenland feraient partie d'une seule et même population interféconde. Le séquençage d'ADN dans la région de la boucle D mitochondriale et l'analyse de 15 loci de microsatellites d'ADN nucléaire ont été réalisés chez 286 baleines boréales échantillonnées dans les régions de Pelly Bay, Igloolik, Repulse Bay et Pangnirtung, au Nunavut (Canada) et de Disko Bay dans l'ouest du Groenland. Un échantillon additionnel de baleines de la mer de Beaufort, représentant le stock/population présumé des mers de Béring, des Chukchi et de Beaufort (B-C-B) faisait aussi partie de l'analyse. Bien que la comparaison de la fréquence des haplotypes d'ADNmt n'ait pas confirmé le rejet de l'hypothèse de population unique, les résultats de l'analyse des microsatellites d'ADN nucléaire montraient une certaine sous-structuration de la population, tout particulièrement dans le cas des baleines boréales d'Igloolik (bassin Foxe), comparativement aux échantillons de Pangnirtung et de l'ouest du Groenland (baie Baffin). De plus, les échantillons de Repulse Bay (baie d'Hudson) ont pu être différenciés de ceux de l'ouest du Groenland, mais pas de ceux de Pangnirtung. La répartition géographique des bêtes pourrait expliquer en partie ces résultats. Les autres facteurs pourraient être la ségrégation par sexe ou par classe d'âge, la ségrégation temporelle, le succès ou les stratégies sélectives d'accouplement ou une combinaison quelconque de ces facteurs. D'ici à ce que les mécanismes susceptibles de créer cette différentiation génétique soient mieux connus et mieux compris, les baleines boréales de la baie d'Hudson et du bassin Foxe (BH-BF) devraient continuer à être considérées comme des sous-populations génétiquement distinctes de celles de la baie Baffin et du détroit de Davis (BB-DD).

INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is the largest of three Arctic species of whale inhabiting Canadian waters. Its very size, including a blubber layer which can measure 43 to 50 cm (Montague 1993), made the bowhead a primary target of the European whaling industry in the 18th, 19th and early 20th centuries (Reeves *et al.* 1983, Ross 1993). This intensive and unmanaged commercial hunting resulted in a reduction of numbers of bowheads from a minimum stock size of 452 in Hudson Bay to approximately 100 animals, and from a minimum of 11,759 animals in Davis Strait to approximately 1000 (Woodby and Botkin 1993). These numbers are indicative of the numbers of animals remaining in the stock at the end of the peak harvest decade. As commercial hunting did continue for many years until collapse, the numbers of animals were reduced even further from these estimates of residual stock size.

Since the collapse of the commercial hunt, bowheads have been protected and only a limited aboriginal subsistence hunt is allowed to occur (Reeves 1991). Despite this protection, it is not clear if the eastern Canadian stocks of bowhead whales are recovering (Finley 1990). Some information suggests that the number of animals inhabiting the eastern Canadian Arctic is growing (Hay, 1997), but recovery rates are uncertain and have generally been considered to be slow (Davis and Koski 1980). Slow recovery of bowhead whale populations may be due to continued low-level hunting, instability of ice conditions and predation by killer whales (Mitchell and Reeves 1982, Finley 1990). Also, recovery is difficult to monitor and only a substantial change in numbers would be noticeable. Currently, the bowhead whale is listed as "Endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Campbell 1998), but this is being reviewed.

Because of these questions about the status of the eastern Canadian Arctic bowhead whales and the renewal of subsistence harvests of these animals, there is a need to gather more information about bowhead whale stocks. One approach is the examination of genetic markers. Different classes of markers exist and they are distinct in the type of information that they produce (Milligan *et al.* 1994). Maternally inherited mitochondrial DNA (mtDNA) sequencing can be used for the study of population structure and divergence (Parker *et al.* 1998). Nuclear DNA (nDNA) microsatellite variation can be used to study the above as well as the level of diversity within and among populations (Parker *et al*. 1998), identify individuals (Haig 1998) and when applied over a series of unlinked loci, can even test whether population size has been constant or increasing (Goldstein *et al*. 1999). These types of markers have been applied very effectively to investigate questions of population structure and dynamics for a number of cetacean species (e.g. de March *et al*. 2002; Baker *et al*. 1998; Brown Gladden *et al*. 1997, 1999; Richard *et al*. 1996). Limited work has been done on bowhead whales, and the genetic studies so far have focused mainly on the Bering/Chukchi/Beaufort Sea and Okhotsk Sea animals (Rooney *et al*. 1999; LeDuc *et al.* 1998) and historical samples of bowheads (Rastogi *et al*., 2004). These studies did demonstrate that

DNA analyses are able to reveal a level of variability useful for the examination of bowhead whale stock structure.

The terms population, subpopulation and stock are often used interchangeably. It is important, here, to clearly define what is meant by these terms. A population may be defined as a group of individuals with a higher probability of mating with each other than mating with an individual from another population (Pianka, 1988). However, one problem with definitions of a population is that they often assume that the individuals making up the population have a defined geographical range and are distributed homogeneously (Hartl, 1988). Most populations are actually subdivided by behavioural or environmental parameters. 'Stock', a common term in fisheries biology (Allendorf *et al*., 1987), has been used to label the individual groups making up a subdivided population (or 'sub-population'). For management purposes, these stocks are then defined as groups of animals that are able to be independently exploited and managed (Royce, 1972). Thus, one may consider a population as a biological unit and a stock as an exploited or management unit (Royce, 1972). From a genetics perspective, the key to this approach of defining the stock structure of a species or group of individuals of a species, is that the stock may not be subdivided through additional genetic differences between subgroups (Chakraborty and Leimar, 1987). Thus, within a stock there is a high degree of genetic homogeneity but there are or may be measurable differences in genetic variability between stocks (Allendorf *et al*., 1987).

In this study, mtDNA control region sequencing analysis and analysis of 15 microsatellite loci were completed for 286 bowhead whale samples collected in the eastern Canadian Arctic and off the coast of western Greenland. The main focus of the study is to investigate whether or not the Hudson Bay/Foxe Basin bowhead whales are in fact genetically distinct from the Davis Strait/Baffin Bay animals. We also examine the genetic variation among these two groups and a sample of bowhead whales from the Beaufort Sea. This information may then clarify the stock designations of bowhead whales in the eastern Canadian Arctic, which are currently based on inferences from information on commercial catches and geographical barriers such as land masses and ice cover (Moore and Reeves 1993), and more recently from satellite telemetry studies (Heide-Jørgensen *et al*., 2003).

MATERIALS AND METHODS

Sample collection

Biopsy samples of bowhead whale skin were obtained during post mortem examinations of beached and hunted animals and during biopsy sample programs targeting free-ranging whales (Table 1). The majority of samples were obtained during biopsy sampling programs of free-ranging bowhead whales in Foxe Basin (Igloolik), Repulse Bay, Pelly Bay and Cumberland Sound (Pangnirtung). Samples from Foxe Basin and Cumberland Sound were collected from June through August, while those in Repulse Bay were collected in August and September.

Based on the assumption that northern Hudson Bay bowhead whales might be distinct from Foxe Basin whales, we avoided collection of samples from Repulse Bay earlier than August to preclude the possibility that whales sampled in Repulse Bay were actually Foxe Basin whales migrating through Repulse Bay. Samples were also obtained during an ongoing program for satellite tracking of bowhead whales from Western Greenland (Heide-Jørgensen *et al.* 2003). A skin biopsy sample was taken for genetic analyses when whales were first approached for attachment of the satellite transmitter. These samples were collected in May in northwest Disko Bay.

All biopsy sampling was conducted from a two-person kayak, boat, or from an ice platform. The majority of whales sampled were initially approached by boat and either pursued and fired at from the boat, or alternatively, a kayak was launched from the floe edge or boat and used to approach the whales to within firing range of the biopsy system. Sampling from the floe edge was conducted opportunistically when bowhead whales were moving along or moving toward and diving beneath the floe edge.

Biopsy tips were cleaned and sterilized using a two stage process involving immersion and cleaning in hydrogen peroxide to dissolve and remove previous genetic material, and then in Betadyne antiseptic solution. Skin samples were transferred from the biopsy tip into vials containing a salt-saturated 20% dimethylsulfoxide (DMSO) solution (Seutin et al. 1991) within 1 to 15 minutes of extraction from the whale. These samples were then kept cool until genetic analyses were initiated.

In addition, a total of n=9 samples was obtained from free-ranging bowhead whales in the Mackenzie Delta area (Shingle Point and King Point) in 1990 and 1992. An additional sample was collected after a bowhead whale hunt in Shingle Point in 1996, bringing the sample total for this area to n=10.

DNA analysis

For earlier samples, total cellular DNA was extracted from bowhead whale skin using the methods described in Maiers *et al*. (1996) with some modifications. The bowhead whale skin has a very tough, rubbery texture after preservation and it required several weeks of incubation at 37°C and repeated additions of proteinase K (20 mg/mL) to digest the tissue to the point where it was suitable for extraction. Once this process was complete, in most samples sufficient quantities of DNA was recovered for analyses. More recent samples (2000 to present) were extracted using commercial DNA tissue extraction kits (DNeasy, Qiagen).

The sex of each of the animals sampled was determined using a PCR-based method for the identification of sex in cetaceans (Bérubé and Palsbøll 1996 or Shaw *et al*, 2003). This method amplifies ZFX-and ZFY-specific regions of nuclear DNA that results in a product that corresponds to a portion of the X chromosome and a product specific to the Y chromosome (if present). Separation and visualization of these products on an agarose gel allows for the reliable assignment of a sex.

Mitochondrial DNA sequencing

A portion of the mitochondrial DNA (mtDNA) d-loop was amplified using primers Dlp 1.5 and Dlp 5 that amplify the majority of variable sites in cetaceans (Rosenbaum *et al.* 2002; Arnason *et al.*, 1993). Automated DNA sequencing of PCR products was performed using an ABI Prism 377 automated DNA sequencer and the dRhodamine fluorescent dye terminator chemistry. The resulting sequences were aligned and variable nucleotide positions assessed using MacVector (ver. 3.5, IBI).

Microsatellite analysis

A total of 15 microsatellite loci were analyzed using primers from a variety of sources (Table 2). The analysis was performed using Applied Biosystems' fluorescence-based technology on a 3100 genetic analyzer. The PCR and primer conditions were as described in the reference papers for each locus with some modifications to the annealing temperatures (Table 2), and were generally analyzed a single locus at a time. Allele sizes for genotypes were determined using Genotyper software (Applied Biosystems) and designations were checked visually with the lanes aligned by scan. Any errors in allele sizing were corrected using a comparison to a set of reference samples that were analyzed with every run of samples.

Statistical analysis

Sample groups that were statistically compared for the purposes of this document were: 1. Mackenzie Delta (Shingle Point and King Point); 2. Gulf of Boothia (Pelly Bay); 3. Foxe Basin (Igloolik samples); 4. Hudson Bay (Repulse Bay); 5. Davis Strait (Pangnirtung); and 6. Baffin Bay (Western Greenland) (Figure 2). Sample groups were also subdivided into males and females as separate test groups for analysis of homogeneity of allele distributions.

Genetic diversity was calculated as $D_h = 1 - \Sigma(p_h)^2$ for each sample group for haplotypes 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 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 (p. 150, Weir 1996).

Homogeneity of allele distributions for all pairs of sample groups (the null hypothesis being "the allelic distribution is identical across populations") was tested using an unbiased estimate of the *P*-value of the probability test or Fisher exact test, when possible (Raymond and Rousset, 1995). Each sample group was also tested at each locus for departure from Hardy-Weinberg equilibrium (HWE) using the U-test (Rousset and Raymond, 1995) with the hypothesis of heterozygote deficiency. These tests were performed using GENEPOP ver 3.4 (Raymond and Rousset, 1995).

An Analysis of Molecular Variance (AMOVA) as described by Excoffier *et al*. (1992) and Michalakis and Excoffier (1996) was performed using methods available in Arlequin (ver. 2.0) (S. Schneider et al.; http://anthropologie.unige.ch/arlequin). AMOVA compares the distribution of alleles at all loci within and among sample groups, and tests whether or not the

observed differentiation is due to chance. Using this analysis, data from both mtDNA sequencing analyses and nDNA microsatellite analyses may be tested separately or combined. AMOVA also yields genetic distances (F_{st} or R_{st} values) between pairs of sample populations. The F_{st} value is a measure of the relative value of between population variation and within population variation (with variation measured as the number of alleles differing among individuals within and between populations). This amounts to a weighted F_{st} statistic over all loci (Weir & Cockerham 1984). The significance of the pairwise F_{st} values are tested using a non-parametric permutation approach, this determining the probability of the observed or a lower F_{st} value being due to chance. 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" which is based on the number of comparisons, the distribution of probabilities, and the chosen table-wide α level (α = 0.05 for this study). Again, for this analysis, the bowhead whale samples were grouped according to sampling location, by year, and by sex and each group tested as a "sample population". If no among year differences or between sex differences were found within a location, the samples were combined for further analysis.

Cavalli-Sforza's "Chord Distance" (Cavalli-Sforza and Edwards, 1967) was used as a measure of genetic distance among sample groups. This was calculated using the GENDIST option in PHYLIP ver. 3.4 (Felsenstein, http://evolution.genetics.washington.edu/) using both microsatellite and haplotype data. The SEQBOOT option in the same package was initially used to generate multiple data sets that are resampled versions of the original data set for bootstrap analysis. This data was then used to in the GENDIST option which generated output files used to construct phylogenetic trees with the Neighbor-Joining Method (Saitou and Nei, 1987). CONSENSE was used to generate a majority rule (extended) tree and DRAWTREE to plot an unrooted tree.

RESULTS

DNA analysis

Most of the samples collected were from biopsies of free-ranging bowheads (Table 1). The amount of skin recovered from the biopsy dart was quite variable and ranged from long, "healthy" (dense, rubbery texture) strips of skin, to small amounts of "degraded" (dry, flaky consistency in small bits) sample, to samples that were mostly blubber with only tiny amounts of skin material attached. Sub-samples that were used for DNA extraction were taken from a cross-section of the best quality portion of the sample as possible. However, some samples still yielded degraded DNA and/or extremely small amounts of recovered material. These samples were difficult to amplify and failed to yield results at some loci. Only samples that had information at a minimum of 6 loci were used in the data analysis and haplotype and sex information is missing for some samples. This reduced the sample sizes for analysis from numbers listed on Table 1, though not significantly.

A total of 18 replicate samples were identified on the basis of genetic readings and sex, and removed from the data set. The replicates almost always occurred in the same year X location sample, except in 3 cases where animals were sampled at the same location (Igloolik) in different years. Numbers of males and females were not significantly different within sample groups (Table 1) or in minor sample groups.

Mitochondrial DNA sequence analysis

A total of 40 haplotypes were found in the 286 samples analyzed in this study (Table 3). Of these 40 haplotypes, 30 were found in more than one sample. Within these haplotypes, haplotype 24 was unique to the Western Arctic group (n=10), haplotype 25 was unique to W. Greenland (n=39), and haplotypes 11, 33, 38, 39, 40 and 42 were found only in the Igloolik samples (n=173). Only 3 of the 30 haplotypes with n≥2 were found in the W. Arctic samples and one haplotype was found only in HB/FB (haplotype 22).

When examined more closely no significant genetic differentiation at a table-wide α=0.05 was found among the major sample groups (Table 5).

Haplotype diversity was highest in the W. Greenland samples (0.917) and lowest in Repulse Bay (0.694) (Table 4). Igloolik had a haplotype diversity of 0.885 and the most equitable distribution of haplotypes, most likely due to the significantly larger sample size as compared to the other locations.

Overall haplotype diversity in bowhead was 0.831 (Table 4). This is similar to previously reported results for a smaller bowhead data set used for a comparison to other Arctic marine mammals (de March *et al*., 2002).

Nuclear DNA microsatellite analysis

Nuclear DNA microsatellite analysis was performed at 15 loci using primers from several sources (Table 2). The numbers of alleles detected at each locus ranged from 4 – 18 and the microsatellite diversity of individual loci was lowest for EV37 (0.000 – 0.335) and highest for rw34 (0.758 – 0.890). The lowest numbers of microsatellite alleles were found in Repulse Bay (68 alleles), Pelly Bay (72 alleles) and the W. Arctic (74 alleles) samples and the highest number in the Igloolik samples (118 alleles) (Table 4). Repulse Bay, Pelly Bay and W. Arctic (0.600; 0.608; 0.607) diversities were lower than those from Igloolik, Pangnirtung and W. Greenland (0.657; 0.643; 0.658).

A test for goodness of fit to Hardy Weinberg Equilibrium revealed significant deviations from the HWE at 15 of 90 locus X location tests (marked as **bold** on Table 6). No one locus consistently deviated from HWE, however, Igloolik had the most loci not in HWE (5 out of 15 loci), followed by Pangnirtung (4 out of 15 loci). Inbreeding coefficients (F_{is}) were positive for all except one locus in the Igloolik samples (14 out of 15 loci) and for most loci in samples from Pelly Bay (9 out of 15 loci) and W. Greenland (9 out of 15 loci).

Results of the test for homogeneity among alleles using pairwise comparisons of the major sample groups of bowheads would suggest a high degree of population sub-structuring at a table-wide significance of α=0.05 (most comparisons $p<0.005$ to $p<0.00001$). This test of population subdivision is quite

sensitive to population structure and it is greatly affected if samples are non-random (i.e. are from related individuals) (Paetkau *et al.*, 1998). Even though arguments are made that the sequential von Bonferroni correction is very conservative, especially when the number of tests is large (Weir, 2003; p. 834), it is appropriate here to apply the correction for a table-wide rejection level that is quite stringent (P<0.001) to interpret meaningful results. After application of this correction, the test still resulted in significant differentiation of the Igloolik samples from the W. Arctic, Pangnirtung and W. Greenland sample groups. Igloolik samples were not significantly differentiated from Pelly Bay or Repulse Bay samples.

Analysis of Molecular Variance (AMOVA) for microsatellite data among the 18 minor sample groups (indicated in Table 1; 1998 Repulse Bay not included due to lack of microsatellite data) showed no significant differentiation among years within the major sample groups after applying sequential von Bonferroni criteria (data not presented). Thus, all years were combined within locations and pairwise comparisons made with the 6 major sample groups (Table 1). F_{st} values among the major sample groups ranged from -0.004 to 0.0251 (Table 7). Igloolik was significantly differentiated from Pangnirtung and W. Greenland, and Repulse Bay was significantly differentiated from W. Greenland (though not from Pangnirtung). No other significant differentiation was found among pairs of sample locations.

An unrooted "phylogenetic" tree base on Chord Distance calculated from both haplotypes and microsatellites (Figure 3) reveals a similarity in samples from different years at Igloolik, Pangnirtung and W. Greenland (sample sizes large enough for among year comparisons). However, the 2002 W. Greenland samples were more closely associated with the Pangnirtung samples than with the other W. Greenland samples. Overall, the smaller the sample size, the more unpredictable the branch length so the longer branch lengths may be due to chance. However, the sample groups formed a pattern consistent with geographical distributions.

Male and female samples were separated for analysis at each of the major sample locations. Both Fisher's exact test for population differentiation (Guo and Thompson, 1992) and probabilities of F_{st} values from AMOVA (Michalakis and Excoffier, 1996) revealed similar results (data not presented). In most cases, males and females within a sample location were not significantly differentiated from one another. The exception was the Repulse Bay females. They were significantly differentiated from the Repulse Bay males, females in W. Arctic and Pelly Bay, and were significantly different from the males and females at Igloolik, Pangnirtung and W. Greenland. Igloolik females were also differentiated from Pangnirtung females. The Repulse Bay males did not show this pattern of differentiation and no other significant patterns of differentiation were observed location and sex.

DISCUSSION

The genetic analysis of the bowhead whale samples in this study revealed levels of haplotype diversity higher than diversity found in two other species of

exploited Arctic whales, the beluga and narwhal. Microsatellite diversity was slightly lower in bowhead than for beluga and narwhal, however, this may be a reflection of longer generation times in bowhead. Genetic diversity results are similar to those found for microsatellite analysis of BCB bowheads (Rooney *et al*., 1999) and suggests that bowhead in the Eastern Canadian Arctic also did not undergo a genetic bottleneck due to commercial harvests in the 18th, 19th and early 20th centuries. This level of diversity also shows that patterns of genetic variation, should they be present, will be detectable with the DNA markers used for analysis.

Analysis of haplotype frequencies did not support the rejection of a single bowhead population hypothesis. This result has definitely been an evolving picture as samples were collected over the last 10 years and added in to the analysis. Early in the study, when sample sizes were relatively small and sample collection effort was concentrated in one or two years per location, significant haplotype differences were found, suggesting support for a 2 stock hypothesis. However, as sample sizes were increased and represented multiple years of sampling, these differences disappeared. Considering the high diversity of mtDNA haplotypes found in bowheads, this trend is likely a reflection of movement along a discovery curve of total haplotypes present in the population. The sampling of related individuals within years would also have contributed to this result.

In contrast to the mtDNA haplotype comparisons, both the comparison of allele frequencies (Raymond and Rousset, 1995) and the AMOVA (Michalakis and Excoffier, 1996) revealed a significant difference between Igloolik (Foxe Basin) and Pangnirtung and W. Greenland (Baffin Bay) samples. In addition, these estimates of F_{is} (which measure inbreeding due to nonrandom mating within subpopulations) and F_{st} (which measure inbreeding due to population subdivision) may be indicators of the general breeding structure within a population (Paetkau and Strobeck, 1994). Considering the extremely high proportion of positive F_{is} values for the Igloolik samples, the significant F_{st} *p*-values between Igloolik and the Baffin Bay samples, and the lack of homogeneity among these samples, Igloolik bowheads should be considered a subpopulation, perhaps due to geographic isolation and fragmentation.

The degree of inbreeding in the Igloolik samples may also be due to selective and/or variable mating strategies or success. The idea of a generational gene shift has been proposed as a mechanism through which population structure can be influenced by reproductive success (and its influence on the level of genetic diversity, and thus genetic structure) combined with selection by environmental factors in long-lived mammals (Rosenbaum *et al*. 2002). This possibility would need to be tested using modeling techniques comparing genetic variation of different generations of animals (identified by age classes).

The differences in genetic variation between the Igloolik and Baffin Bay samples may be a reflection of the time of year the samples were collected. The W. Greenland samples were collected in the spring, at the start of migration of bowheads west across Baffin Bay and into Canadian waters (Heide- Jørgensen et al., 2003) from mostly adult and some sub-adult animals. The Igloolik samples were taken during mid-summer to early fall and were from a mixture of relatively few adults, mostly sub-adults, juveniles and calves. Correlations between the

numbers of adults and calves in Northern Foxe Basin, consistent over several years, have been suggested to indicate that this area is a nursery for summering females with young-of-the-year calves and a summering area for juveniles (Cosens and Blouw, 2003). Thus, animals may be segregating by migration patterns linked with habitat preferences. An analysis of the data with temporal and age class segregation needs to be done to address these questions and linked with continuing results from satellite tracking studies. It is difficult to predict how this may affect the genetic variation detected in the data analysis completed thus far.

The degree of kinship among the Igloolik bowheads may also affect the genetic variation of the samples. If the Foxe Basin area is used by mostly females and successive age classes of offspring, then the younger animals may have a higher degree of relatedness (full siblings and/or half siblings) than in locations where whales sampled are dominated by likely unrelated adults. A more detailed kinship analysis of the samples needs to be performed to test this hypothesis. This may have some impact on how the results of the genetic differentiation of these samples are interpreted.

The results of the analysis of samples separated by sex and location yielded a noteworthy result with the Repulse Bay samples. When samples were separated by sex at this location, there were n=6 males and n=6 females - equal, but small, sample sizes. The Repulse Bay females were significantly differentiated from almost all other sex and location samples, including Repulse Bay males. It has been suggested that adult males and nonparous adult females, not seen in Foxe Basin during surveys, are found in this area of Hudson Bay (Reeves and Cosens, 2003). Thus, this result may again be due to age class segregation of animals with unrelated adult males and females from different components of the population mixing in this area of Hudson Bay. However, with such small sample sizes, this may also be a chance result.

When combined, the Repulse Bay samples were significantly differentiated from W. Greenland samples but not from Pangnirtung samples. Perhaps there is a gradient of genetic subdivision occurring from W. Greenland to Foxe Basin that increases as animals migrate west across Hudson Bay, through Hudson Strait and north into Foxe Basin. This may be a reflection of different migrations patterns of animals, again perhaps due to age class and or sex segregations.

A better sample size of bowheads from the B-C-B stock of bowhead whales would have provided a better context in which to interpret some of these results. The samples from the Beaufort Sea included in this analysis are likely not representative of the genetic variation present in that population/stock, thus are not providing an accurate comparison to the HB-FB and BB-DS animals. Future analysis of more samples or collaborations to combine data sets will provide a much more rigourous comparison.

CONCLUSIONS

The goal of this study was to assess whether or not bowheads sample in Eastern Canadian Arctic and Western Greenland waters are from a single,

interbreeding population. Based on the results presented here, there is some evidence of sub-structure of the population into the previously hypothesized Hudson Bay-Foxe Basin and Baffin Bay-Davis Strait sub-populations or stocks. However, understanding the mechanisms that are influencing the genetic variation is important as this will define whether the animals in these areas are interbreeding but are segregated at certain times in their migrations, by age class, by family groups, and/or by sex. On the other hand, are they truly from a heterogeneous population that is subdivided by selective mating strategies and success? Combining genetics data with ecological information on reproduction and generation times, satellite tagging data and information from critical habitat studies will be necessary to understand patterns of genetic relationships among bowhead whales.

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REFERENCES

Allendorf, F.W., N. Ryman and F.M. Utter. 1987. Genetics and fisheries management: past, present and future, pp. 1-19. *In* Ryman, N. and F. Utter [eds.] Population Genetics and Fishery Management, University of Washington Press, Seattle and London.

Árnason, Ú., A. Gullberg and B. Widegren. 1993. Cetacean mitochondrial DNA control region: sequences of all extant baleen whales and two sperm whale species. Molecular Biology and Evolution 10: 960-970.

Baker, C.S., L. Flórez-González, B. Abernethy, H.C. Rosenbaum, R.W. Slade, J. Capella and J.L. Bannister. 1998. Mitochondrial DNA variation and maternal geneflow among humpback whales of the southern hemisphere. Marine Mammal Science 14: 721-737.

Bérubé, M. and P. Palsbøll. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Molecular Ecology 5: 283-287.

Brown Gladden, J.G., M.M. Ferguson and J.W. Clayton. 1997. Matriarchal genetic population structure of North American beluga whales *Delphinapterus leucas* (Cetacea: Monodontidae). Molecular Ecology 6: 1033-1046.

Brown Gladden, J.G., M.M. Ferguson, M.K. Friesen and J.W. Clayton. 1999. Population structure of North American beluga whales (*Delphinapterus leucas*) based on nuclear DNA microsatellite variation and contrasted with the population structure revealed by mitochondrial DNA variation. Molecular Ecology 8: 347-363.

Buchanan F.C., M.K. Friesen, R.P. Littlejohn and J.W. Clayton. 1996. Microsatellites from the beluga whale (*Delphinapterus leucas*). Molecular Ecology 5: 571-575.

Campbell, R.R. Editor. 1998. Rare and endangered fishes and marine mammals of Canada: COSEWIC Fish and Marine Mammal Subcommittee Status Reports XII. Canadian Field-Naturalist 112: 94-97.

Cavalli-Sforza, L.L. and A.W.F. Edwards. 1967. Phylogenetic analysis: Models and estimation procedures. American Journal of Human Genetics 19:233-257.

Chakraborty, R., M. and O. Leimar. 1987. Genetic variation within a subdivided population. *In* Ryman, N. and F. Utter [eds.] Population Genetics and Fishery Management, University of Washington Press, Seattle and London. Pp. 89-120.

Cosens, S.E. and A. Blouw. 2003. Size- and age-class segregation of bowhead whales summering in Northern Foxe Basin: a photogrammetric analysis. Marine Mammal Science 19:284-296.

Davis, R.A. and W.R. Koski. 1980. Recent observations of the bowhead whale in the eastern Canadian high Arctic. Report of the International Whaling Commission 30: 439-444.

de March, B.G.E., L.D. Maiers, and M.K. Friesen. 2002. An overview of genetic relationships of Canadian and adjacent populations of belugas (*Delphinapterus leucas*) with emphasis on Baffin Bay and Canadian eastern Arctic populations. NAMMCO Sci. Publ. 4: 17-38.

Excoffier, L., P. Smouse and J. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131: 479-491.

Finley, K.J. 1990. Isabella Bay, Baffin Island: an important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the eastern Canadian Arctic. Arctic 43: 137-152.

Fisher, R.A. 1935. The logic of inductive inference. Journal of the Royal Statistics Society 98: 39-54.

Goldstein, D.B., G.W. Roemer, D.A. Smith, D.E. Reich, A. Bergman and R.K. Wayne. 1999. The use of microsatellite variation to infer population structure and demographic history in a natural model system. Genetics 151: 797-801.

Guo, S.W. and E.A. Thompson. 1992. Performing exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48: 361-371.

Haig, S. 1998. Molecular contributions to conservation. Ecology 79: 413-425.

Hartl, D.L. 1988. A Primer of Population Genetics. Sinauer Associates, Inc., Sunderland, Massachusetts, 305 pp.

Hay, K. 1997. Inuit bowhead knowledge study interim report: Northwest Hudson Bay and High Arctic. Nunavut Wildlife Management Board, Iqaluit, NT.

Heide-Jørgensen, M.P., L.L. Laidre, Ø. Wiig, M.V. Jensen, L. Dueck, L.D. Maiers, H.C. Schmidt and R.C. Hobbs. 2003. From Greenland to Canada in ten days: tracks of bowhead whales, Balaena mysticetus, across Baffin Bay. Arctic 56: 21-31.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statisitics 6: 65-70.

LeDuc, R.G., A. Rosenberg, A.E. Dizon, A.M. Burdin, S.A. Blokhin and R.L. Brownell Jr. 1998. Preliminary genetic analyses (mtDNA and microsatellites) of two populations of bowhead whales. Working paper SC/50/AS11 presented to the scientific working group at the International Whaling Commission meeting, Oman.

Maiers, L.D., M.K. Friesen, A.V. Wiens and J.W. Clayton. 1996. Use of DNA microsatellites in beluga whale (*Delphinapterus leucas*) population genetics. Canadian Technical Report of Fisheries and Aquatic Sciences 2115, v + 17pp.

Michalakis, Y. and L. Excoffier. 1996. A generic estimation of population subdivision using genetic distances between alleles with special reference for microsatellite data. Genetics 142: 1061-1064.

Milligan, B.G., J. Leebens-Mack and A.E. Strand. 1994. Conservation genetics: beyond the maintenance of marker diversity. Molecular Ecology 3: 423-435.

Mitchell, E.D. and R.R. Reeves. 1982. Factors affecting abundance of bowhead whales Balaena mysticetus in the eastern Arctic of North America, 1915-1980. Biological Conservation 22: 59-78.

Montague, J.J. 1993. Introduction, pp. 1-21. *In* J.J. Burns, J.J. Montague and C.J. Cowles [eds.], Allen Press Inc., Lawrence, KS.

Moore, S. and R.R. Reeves. 1993. Distribution and movement, pp. 313-386. *In* J.J. Burns, J.J. Montague and C.J. Cowles [eds.] The Bowhead Whale, Allen Press Inc., Lawrence, KS.

Palsbøll, P., M. Bérubé, A.H. Larsen and H. Jørgensen. 1997. Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. Molecular Ecology 6: 893-895.

Parker, P.G., A.A. Snow, M.D. Schug, G.C. Booton and P.A. Fuerst. 1998. What molecules can tell us about populations: choosing and using a molecular marker. Ecology 79: 361-382.

Paetkau, D., G.F. Shields and C. Strobeck. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7: 1283-1292.

Pianka, E.R. 1988. Evolutionary Ecology. Harper and Row, Publishers, New York, 397 pp.

Rastogi, T., M.W. Brown, B.A. McLeod, T.R. Frasier, R. Grenier, S.L. Cumbaa, J. Nadarajah, and B.N. White. 2004. Genetic analysis of 16th-century whale bones prompts a revision of the impact of Basque whaling on right and bowhead whales in the western North Atlantic. Canadian Journal of Zoology 82: 1647-1654.

Raymond M. and F. Rousset. 1995. GENEPOP (version 3.1b): population genetics software for exact tests and ecumenicism. Journal of Heredity 86: 248-249.

Reeves, R., E. Mitchell, A. Mansfield and M. McLaughlin. 1983. Distribution and migration of the bowhead whale, Balaena mysticetus, in the eastern North American Arctic. Arctic 36: 5-84.

Reeves, R.R. 1991. The bowhead whale. Underwater World, Communications Directorate, Department of Fisheries and Oceans, Ottawa, Canada.

Reeves, R.R. and S.E. Cosens. 2003. Historical population characteristics of bowhead whales (*Balaena mysticetus*) in Hudson Bay. Arctic 56: 283-292.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 41: 223-225.

Richard, K.R., M.C. Dillon, H. Whitehead and J.M. Wright. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Sciences U.S.A. 93: 8792-8795.

Rooney, A.P., R.L. Honeycutt, S.K. Davis and J.N. Derr. 1999. Evaluating a putative bottleneck in a population of bowhead whales from patterns of microsatellite diversity and genetic disequilibria. Journal of Molecular Evolution 49: 682-690.

Rosenbaum, H.C., M.T. Weinrich, S.A. Stoleson, J.P. Gibbs, C.S. Baker and R. DeSalle. 2002. The effect of differential reproductive success on population genetic structure: correlations of life history with matrilines in humpback whales of the Gulf of Maine. Journal of Heredity 93: 389-399.

Ross, W.G. 1993. Commercial whaling in the North Atlantic sector, pp. 511-561. *In* J.J. Burns, J.J. Montague and C.J. Cowles [eds.] The Bowhead Whale, Allen Press Inc., Lawrence, KS.

Rousset, F. and M. Raymond. 1995. Testing heterozygote excess and deficiency. Genetics 140: 1413-1419.

Royce, W.F. 1972. Introduction to the Fishery Sciences. Academic Press, New York, 351 pp.

Saitou, N. and M. Nei. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4: 406-425.

Seutin G., B.N. White and P.T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69: 82-90.

Shaw, C.N., P.J. Wilson and B.N. White. 2003. A reliable molecular method of gender determination for mammals. Journal of Mammalogy 84: 123-128.

Valsecchi, E. and W. Amos. 1996. Microsatellite markers for the study of cetacean populations. Molecular Ecology 5: 151-156.

Waldick, R.C., M.W. Brown and B.N. White. 1999. Characterization and isolation of microsatellite loci from the endangered North Atlantic right whale. Molecular Ecology 8: 1763-1765.

Waser, P.M., and Strobeck, C. 1998. Genetic signatures of interpopulation dispersal. Trends Ecol. Evol. 13: 43-44.

Weir, B.S. and C.C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38: 1358-1370.

Weir, B.S. 1996. Genetic Data Analysis II. Sinauer Associates, Inc. USA. 445 p.

Weir, B.S. 2003. Forensics, pp.830-852. *In* Balding, D.J., M. Bishop and C. Cannings [eds.] Handbook of Statistical Genetics, Second Edition, John Wiley and Sons, Ltd., Sussex, England.

Woodby, D.A. and D.B. Botkin. 1993. Stock sizes prior to commercial whaling, pp. 387-407. *In* J.J. Burns, J.J. Montague and C.J. Cowles [eds.] The Bowhead Whale, Allen Press Inc., Lawrence, KS.

Table 1. Bowhead sample collection information.

Major Sample Group	Sample Location	Minor Sample Group	Year(s)	n samples with Haplotypes	n samples with Microsatellites	n samples with both	Number of Females	Number of Males	Season collected*
1	Beaufort Sea (Mackenzie Delta)	1	1990	2	2	2	1	1	unkn
		2	1992	7	7	7	3	4	unkn
			1996	1	1	1	0	1	unkn^
2	Pelly Bay	3	2000	1	1	1	0	1	unkn
			2001	2	2	2	1	1	unkn
		4	2002	5	5	5	2	3	Sept
3	Igloolik	5	1994	1	1	1	1	0	unkn^
			1995	13	13	13	9	4	4Jul-6Jul
		6	1996	20	20	20	9	11	3Jul-9Jul
			1997	1	1	1	1	0	unkn^
		7	2001	42	42	42	19	23	30Jun-6Jul
		8	2002	65	65	65	32	32	1Jul-15Jul
							(one unknown)		
		9	2003	31	33	31	24	9	unkn
4	Repulse Bay	10	1997	4	5	4	4	1	Aug, Sept
		11	1998	4	0	0	1	3	Sept
		12	2000	4	4	4	3	1	Sept
		13	2001	4	4	4	0	4	Sept
5	Pangnirtung	14	1997	25	25	25	8	17	unkn
		15	2002	10	10	10	7	2	unkn
							(one unknown)		
6	West Greenland	16	2000	7	7	7	2	5	
		17	2001	13	13	13	7	6	28Apr-8May
		18	2002	10	10	10	6	4	4May-13May
		19	2003	9	11	9	11	0	4May-18May
Totals:	286 bowhead			281	282	277	153	134	

* Samples were collected as a biopsy of a free-ranging animal using a crossbow or during satellite tag attachment, unless indicated otherwise.

^ Sample collected from harvested animal.

Table 2. Details of the 15 microsatellite loci based on all individuals (n=286) analyzed in this study.

Microsatellite Locus[1]	Annealing Temperature	Reference	n Alleles	Range of Sizes (base pairs)
EV1*Pm*	48°C / 53°C	Valsecchi & Amos, 1996	13	137 - 195
EV37*Mn*	48°C / 53°C	Valsecchi & Amos, 1996	5	181 - 195
EV76*Mn*	48°C / 53°C	Valsecchi & Amos, 1996	4	152 - 162
EV104*Mn*	48°C / 53°C	Valsecchi & Amos, 1996	9	147 - 165
TexVet11	64°C /59°C / 54°C	Rooney *et al*., 1999	7	242 - 256
TexVet16	62°C / 57°C / 52°C	Rooney *et al*., 1999	6	184 - 196
TexVet17	56°C / 51°C / 46°C	Rooney *et al*., 1999	11	192 - 214
rw18	48°C / 53°C	Waldick *et al*., 1999	5	187 - 195
rw31	48°C / 53°C	Waldick *et al*., 1999	6	114 - 132
rw34	50°C / 55°C	Waldick *et al*., 1999	18	84 - 128
rw48	50°C / 55°C	Waldick *et al*., 1999	10	129 - 149
DlrFCB4	48°C / 53°C	Buchanan *et al.*, 1996	18	150 - 206
DlrFCB11	48°C / 53°C	Buchanan *et al*., 1996	6	120 - 130
GATA028	48°C / 53°C	Palsboll *et al*., 1997	9	118 - 186 (tetramer)
GATA098	48°C / 53°C	Palsboll *et al.*, 1997	6	86 - 110 (tetramer)

[1] The 15 loci are designated as listed in the reference (usually according to species and/or by the initials of the person who developed the primers; or, in Palsboll *et al*., as the repeat unit and locus identifier.).

Table 3. Haplotype frequencies in sample populations.

Location	Haplotype Name (B) 02	04	05	06	08	09	11	12	13	14	16	17	21	22	23	24	25	27	28	31	32	33	34	35	36	37	38	39	40	42	Others[1]	Total
Western Arctic	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1,1,1	10
Pelly Bay	2	-	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	1	8
Igloolik 1995	2	1	-	2	2	-	1	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	14
Igloolik 1996	8	-	1	-	4	-	1	-	-	-	-	2	-	1	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	1	21
Igloolik 2001	11	-	3	-	5	2	-	1	-	1	4	2	2	2	1	-	-	-	-	-	2	1	1	1	1	1	-	1	-	-	-	42
Igloolik 2002	17	1	4	1	7	1	-	1	1	-	4	3	2	2	-	-	-	1	2	-	-	4	-	3	1	-	2	2	3	3	-	65
Igloolik 2003	11	-	1	1	2	-	-	-	-	1	5	2	1	1	-	-	-	1	2	-	-	-	3	-	-	-	-	-	-	-	-	31
Repulse Bay	7	-	-	1	1	-	-	-	-	-	1	1	-	2	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	16
Pangnirtung 1997	1	-	1	1	3	3	-	2	-	2	3	-	1	-	1	-	-	1	2	1	1	-	-	1	-	-	-	-	-	-	1	25
Pangnirtung 2002	3	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1	10
West Greenland 2000	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	1, 1	7
West Greenland 2001	-	-	-	1	1	1	-	-	-	-	2	1	-	-	-	-	1	-	1	-	-	-	1	1	2	1	-	-	-	-	-	13
West Greenland 2002	3	-	-	-	1	-	-	-	-	-	2	-	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	10
West Greenland 2003	2	-	1	-	2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	9
Total	72	2	13	8	31	9	2	4	2	4	22	15	8	9	3	2	2	4	11	2	5	5	11	7	4	3	2	3	3	3	10	281

[1] Haplotypes observed only once in this study.

Table 4. Genetics descriptions for 6 major sample locations listed in Table 1.

Sample Location	n Different Haplotypes	Haplotype Diversity (D_h)	n Different Microsatellite Alleles	Microsatellite Diversity (D_n)
Western Arctic (n=10)	6	0.760	74	0.607
Pelly Bay (n=8)	6	0.813	72	0.608
Igloolik (n=175)	30	0.885	118	0.657
Repulse Bay (n=17)	6	0.694	68	0.600
Pangnirtung (n=35)	18	0.916	97	0.643
West Greenland (n=41)	17	0.917	97	0.658

Table 5. F_{st} values (above diagonal) and associated probabilities for mtDNA differentiation (below diagonal). Differentiation significant at $p<0.0030$, the minimum significant level for a table-wide $\alpha=0.05$, is marked with an asterisk (*).

	Western Arctic	Pelly Bay	Igloolik	Repulse Bay	Pangnirtung	West Greenland
Western Arctic		0.0163	0.0168	-0.0109	0.0555	0.0413
Pelly Bay	0.3332		-0.0041	0.0298	0.0216	0.0007
Igloolik	0.1837	0.4640		0.0089	0.0179	0.0040
Repulse Bay	0.4546	0.2430	0.2472		0.0708	0.0520
Pangnirtung	0.0178	0.1770	0.0252	0.0069		-0.0027
West Greenland	0.0484	0.4446	0.2134	0.0231	0.5572	

Table 6. Microsatellite information for genetic analysis of bowhead samples. N = number of individual samples scored; A = number of alleles; H_o = observed heterozygosity; H_e = expected heterozygosity; F_{is} = inbreeding coefficient and test for goodness of fit to Hardy Weinberg Equilibrium (deviations from HWE are **bolded**).

Sample Group	Variable	EV104	TV16	GATA28	EV1	EV37	EV76	FCB4	RW18	RW31	RW48	TV11	TV17	RW34	FCB11	GATA98	overall
Western	N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Arctic	A	6	2	4	3	3	3	8	3	4	7	3	8	12	4	4	74
	H_o	0.7778	0.6000	0.6667	0.6000	0.6000	0.1000	0.8571	0.5000	0.4444	1.0000	0.3333	0.9000	1.0000	0.5000	0.5714	0.6301
	H_e	0.8086	0.4200	0.5139	0.6150	0.5800	0.3350	0.8061	0.4600	0.4444	0.8150	0.4861	0.8200	0.8900	0.5750	0.5306	0.6067
	F_{is}	0.0620	-0.3970	-0.0830	0.0260	-0.0240	**0.4070**	-0.0100	-0.0950	-0.0190	-0.1200	0.3290	-0.0200	-0.0400	0.1730	-0.0370	
Pelly Bay	N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	A	6	5	7	4	4	2	6	3	4	5	3	7	8	5	3	72
	H_o	0.5000	0.5000	0.8571	0.8750	0.5714	0.2500	0.6250	0.2857	0.5000	0.7500	0.2857	0.8571	0.8750	0.8571	0.4000	0.5993
	H_e	0.7578	0.6875	0.8265	0.7109	0.6633	0.2188	0.5781	0.2551	0.5625	0.7656	0.4388	0.8163	0.8438	0.6531	0.3400	0.6079
	F_{is}	**0.3210**	**0.3320**	0.0230	-0.1430	0.1070	-0.0820	-0.0140	-0.0070	0.2860	0.0890	0.3360	0.0830	0.0200	-0.1100	-0.0160	
Igloolik	N	175	175	175	175	175	175	175	175	175	175	175	175	175	175	175	175
	A	9	6	9	8	4	4	14	5	5	9	7	10	16	6	6	118
	H_o	0.8047	0.6587	0.8286	0.6982	0.4821	0.1951	0.7029	0.5829	0.5930	0.8229	0.4368	0.7914	0.7412	0.5679	0.5814	0.6325
	H_e	0.8181	0.6036	0.8636	0.7193	0.5753	0.1912	0.6975	0.5919	0.5984	0.7760	0.5391	0.7977	0.7808	0.6887	0.6070	0.6565
	F_{is}	0.0200	**0.2660**	**0.0650**	0.0090	0.0480	0.0120	0.0060	0.0130	0.0030	-0.0360	**0.1600**	**0.0850**	0.0010	**0.0750**	0.0120	
Repulse Bay	N	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
	A	6	4	6	8	3	1	6	3	4	4	2	5	8	3	5	68
	H_o	1.0000	0.7273	0.6154	0.8462	0.6667	0.0000	0.5833	0.6667	0.7692	0.7273	0.4545	0.5455	0.6923	0.5455	0.7143	0.6369
	H_e	0.7574	0.6157	0.7574	0.7722	0.5312	0.0000	0.6528	0.5313	0.5680	0.7273	0.3512	0.6983	0.8077	0.4835	0.7449	0.5999
	F_{is}	-0.1640	-0.1250	0.1680	-0.0440	-0.1310	**n/a**	0.0630	-0.1980	-0.2030	0.1330	-0.2590	0.1810	0.0830	-0.0950	0.1920	
Pangnirtung	N	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35
	A	9	3	8	12	3	3	8	4	4	8	6	7	12	4	6	97
	H_o	0.8824	0.4000	0.6286	0.9412	0.6286	0.2500	0.4412	0.5882	0.4118	0.7714	0.4706	0.7879	0.6000	0.7188	0.5926	0.6075
	H_e	0.8157	0.5159	0.8082	0.7872	0.5629	0.2222	0.6631	0.5887	0.4035	0.7318	0.6306	0.7842	0.7584	0.6982	0.6797	0.6434
	F_{is}	-0.0610	**0.2480**	**0.1300**	-0.0630	-0.0870	-0.0560	**0.1420**	-0.0100	-0.0150	-0.0160	**0.1350**	-0.0110	0.0500	-0.0520	0.1540	
W. Greenland	N	41	41	41	41	41	41	41	41	41	41	41	41	41	41	41	41
	A	8	3	8	10	5	3	8	5	4	7	4	9	13	4	6	97
	H_o	0.9000	0.4634	0.5854	0.9000	0.5122	0.3415	0.6250	0.5641	0.5128	0.7750	0.3902	0.7692	0.9000	0.6970	0.6571	0.6395
	H_e	0.8087	0.5446	0.8096	0.7850	0.5181	0.2965	0.7331	0.6160	0.4895	0.7656	0.5535	0.8008	0.8269	0.6515	0.6747	0.6583
	F_{is}	-0.0390	0.1170	**0.2230**	-0.0480	0.0030	-0.0880	**0.1040**	0.0930	-0.0180	-0.0120	**0.3420**	0.0170	-0.0510	0.0840	0.0390	

Table 7. F_{st} values (above diagonal) and associated probabilities for microsatellite differentiation (below diagonal). Differentiation significant at p <0.0042, the minimum significant level for a table-wide α = 0.05, is marked with an asterisk (*).

	Western Arctic	Pelly Bay	Igloolik	Repulse Bay	Pangnirtung	West Greenland
Western Arctic		-0.0221	-0.0040	-0.0026	-0.0082	-0.0072
Pelly Bay	0.7593		0.0043	0.0053	0.0181	0.0198
Igloolik	0.7239	0.2998		0.0146	0.0101	0.0093
Repulse Bay	0.4084	0.2745	0.0087		0.0215	0.0251
Pangnirtung	0.8497	0.0656	**0.0005***	0.0082		0.0057
West Greenland	0.8103	0.0416	**0.0020***	**0.00267***	0.0763	

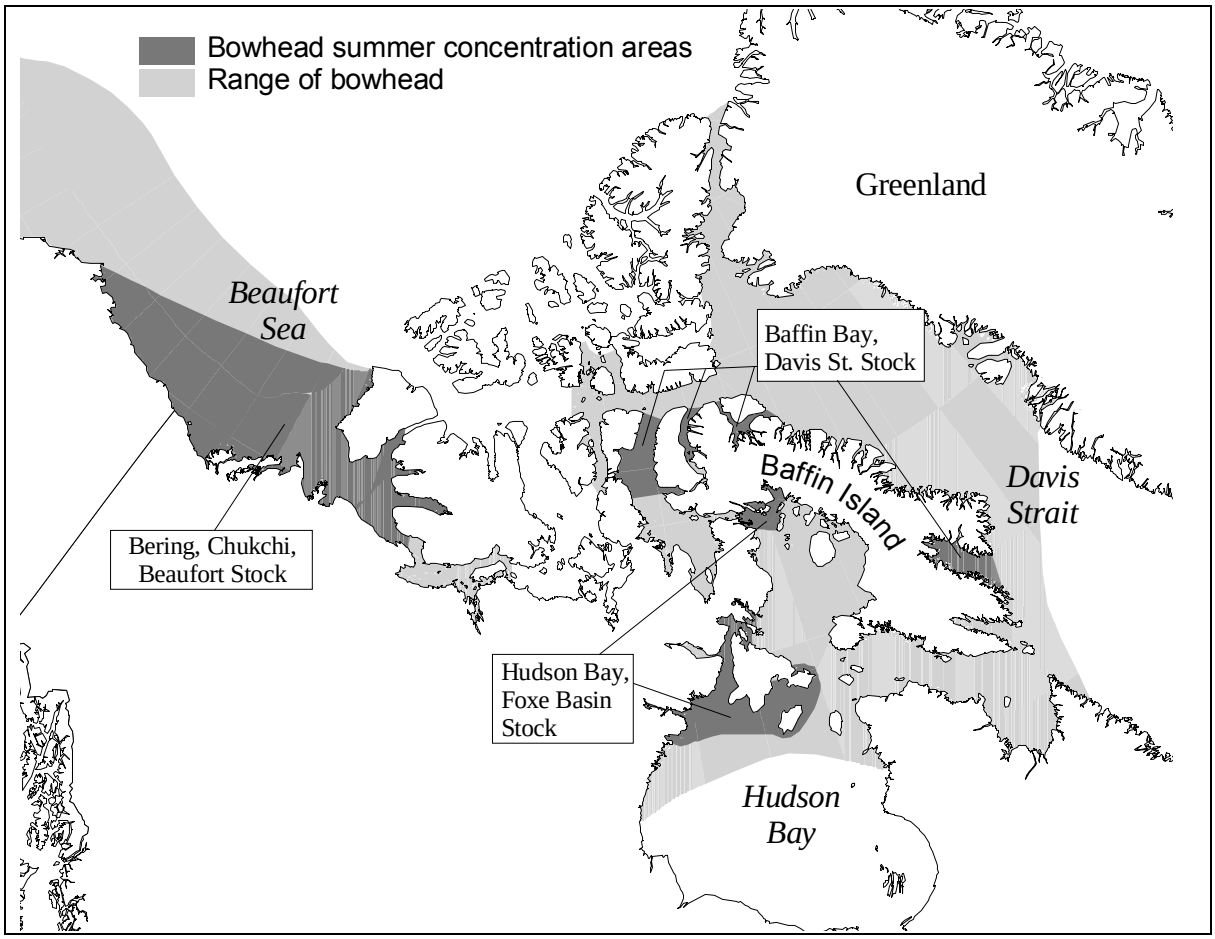

Figure 1. Distribution and summer concentrations of bowhead whales in Canadian and western Greenland waters.

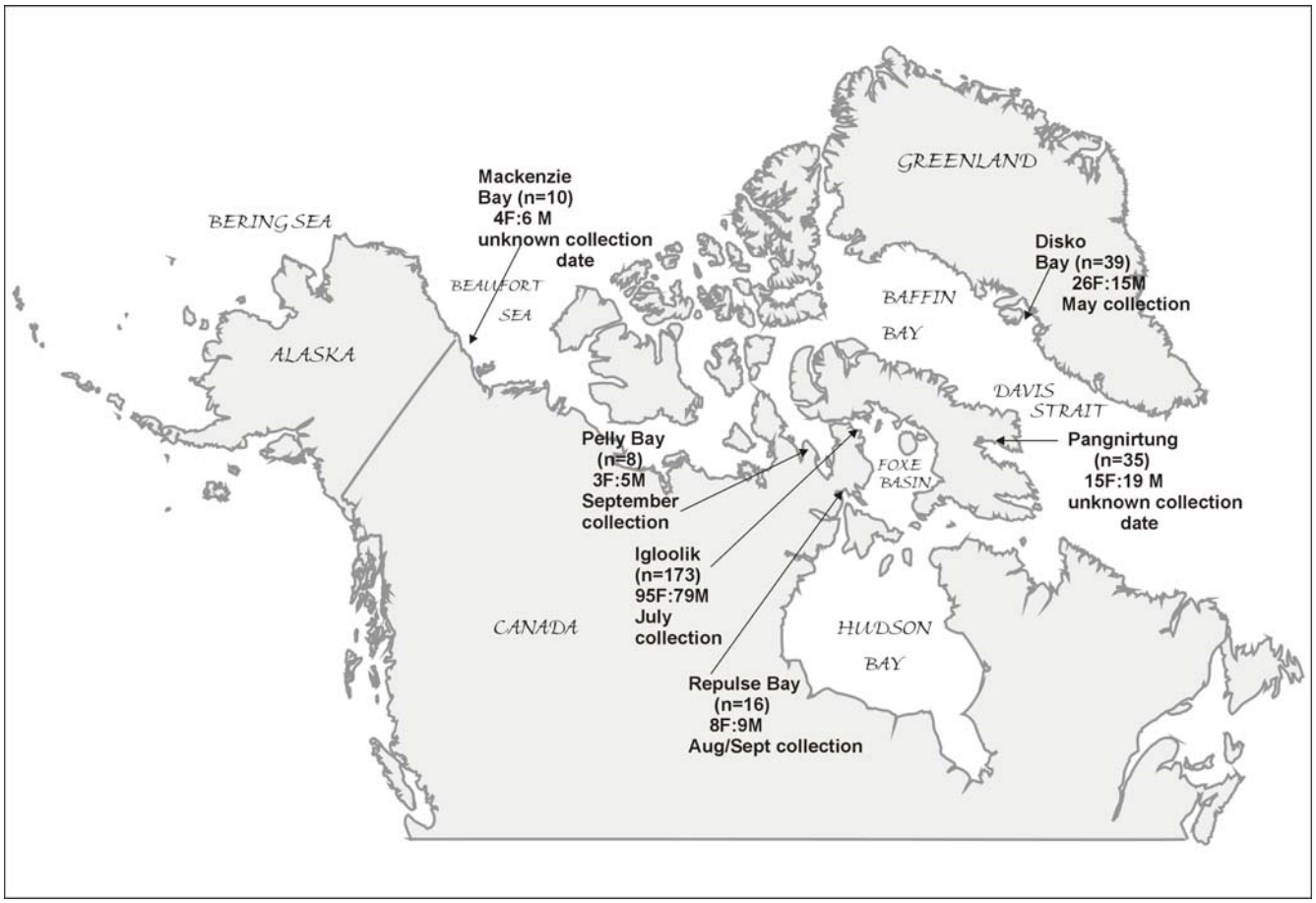

Figure 2. Sampling locations and sample summary for bowheads (n=281) analyzed for molecular genetic markers.

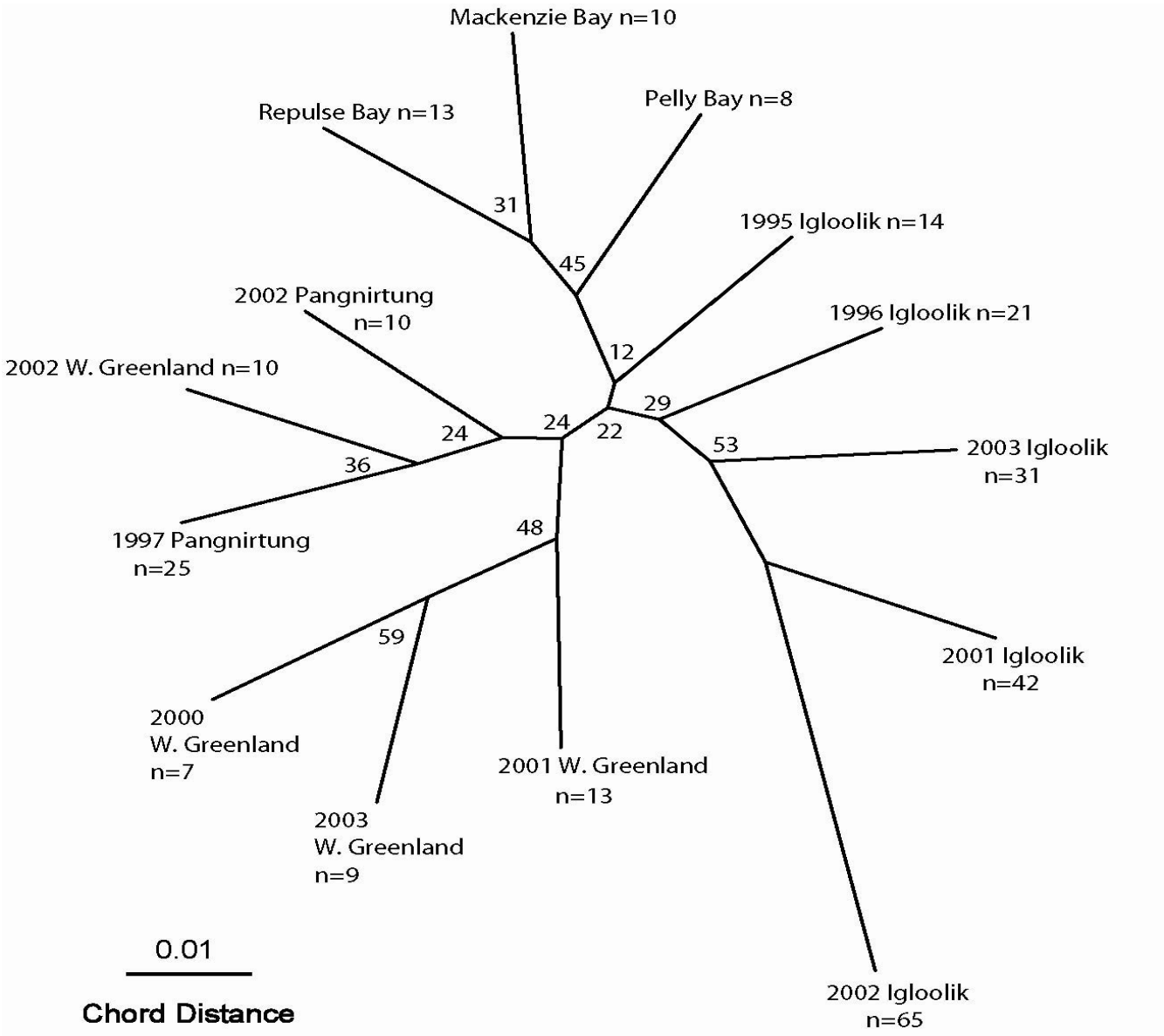

Figure 3. Consensus phlogenetic tree of major sample groups 1 to 6 from Table 1 with groups 3, 5 and 6 separated into minor sample groups. Cavalli-Sforza's Chord Distance between sample groups (Cavalli-Sforza and Edwards, 1967), using both microsatellite and haplotype data, was used as a measure of genetic distances in 1000 bootstrap replicates. The Neighbor-Joining Method (Saitou and Nei, 1987) was used to construct the trees and a consensus tree determined using the Majority Rule (extended) option. Numbers at nodes of the branches indicate percent support of the branch separation.