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Molecular genetics of narwhal (*Monodon monoceros*) from Canada and West Greenland (1982-2001).

Génétique moléculaire des narvals (*Monodon monoceros*) du Canada et de l'ouest du Groenland (1982-2001).

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Abstract

We examined the molecular genetics of 433 narwhals, collected between 1982 and 2001, from hunts in 12 Nunavut communities in Canada and 2 locations in west Greenland. Major sampling locations in Canada were Repulse Bay, Grise Fiord, Broughton Island, Pond Inlet, and Arctic Bay. Narwhals from Repulse Bay were significantly differentiated from most high Arctic locations for both microsatellite alleles and mitochondrial DNA. Narwhals hunted in Igloolik were weakly differentiated from several other locations and most resembled high Arctic, not Hudson Bay, narwhals. Narwhals from Grise Fiord resembled some Greenland locations most and were very weakly differentiated from those hunted in several other locations. Otherwise, no differences could be shown among high Arctic locations in Canada. Narwhals from the Uummannaq district in Greenland may be a stock that differs from narwhal sampled in most locations in Canada. Weak overall differentiation may be due interbreeding and because narwhals may originate from few recent ancestors.

Results do not necessarily negate the existence of stocks that differ for the purposes of management. A study using organochlorine contaminants to discriminate narwhal stocks (de March and Stern 2003) more convincingly showed that different narwhals from several different hunting locations, namely Grise Fiord, Pond Inlet, Broughton Island, and Repulse Bay had different contaminant profiles.

If sample sizes were increased, some comparisons would possibly have sufficient power to distinguish additional differences among stocks. However, we predict that even with larger samples sizes, considerable genetic overlap would exist between locations examined, and that year-to-year differences would continue to be the greatest source of statistical variation.

RÉSUMÉ

Nous avons étudié la génétique moléculaire de 433 narvals capturés entre 1982 et 2001 par des chasseurs de douze collectivités du Nunavut (Canada) et de deux collectivités de l'ouest du Groenland. Les principaux lieux d'échantillonnage au Canada étaient situés près de Repulse Bay, de Grise Fjord, de Broughton Island, de Pond Inlet et d'Arctic Bay. Les allèles microsatellites et l'ADN mitochondrial des narvals de Repulse Bay sont significativement différents de ceux de la plupart des narvals de l'extrême-Arctique. Les narvals capturés à Igloolik sont peu différents de ceux de plusieurs autres endroits et ressemblent le plus aux narvals de l'extrême-Arctique, et non à ceux de la baie d'Hudson. Les narvals de Grise Fjord ressemblent le plus aux narvals de certaines régions du Groenland et sont très peu différents de ceux capturés à plusieurs autres endroits. Aucune autre distinction n'a été observée parmi les narvals de l'extrême-Arctique canadien. Les narvals du district de Uummannaq (Groenland) pourraient appartenir à un stock différent de ceux de la plupart des narvals capturés au Canada. La faible différenciation observée globalement peut être due à des croisements ou au fait que les narvals peuvent être les descendants de quelques ancêtres récents.

Les résultats ne remettent pas nécessairement en question l'existence de stocks définis aux fins de gestion. Une étude axée sur la discrimination des stocks à l'aide des teneurs en contaminants organochlorés (de March et Stern, 2003) a montré de façon plus convaincante que des narvals capturés à plusieurs endroits différents, nommément Grise Fjord, Pond Inlet, Broughton Island et Repulse Bay, ont des profils de contaminants différents.

L'échantillonnage d'un plus grand nombre de narvals permettrait peut-être d'effectuer certaines comparaisons suffisamment puissantes pour différencier davantage les stocks. Cependant, nous estimons que même avec des échantillons plus grands, un chevauchement génétique considérable existerait entre les narvals de différents endroits, et les différences d'une année à l'autre constitueraient encore la plus grande source de variation statistique.

Introduction

The narwhal *(Monodon monoceros)* is an ice-associated cetacean that inhabits Arctic seas bordering the Atlantic Ocean. It is the northernmost cetacean common between 70° and 80° N, and occurs less often south to 65° and north to 85° (Reeves and Tracey 1980). The North Atlantic Marine Mammals Commission recognizes 17 aggregations worldwide, which may be discrete or a mixture of stocks (NAMMCO 2000). In the summer months, narwhals visit inshore bays and fiords in the Canadian archipelago, Greenland, and Foxe Basin (Fig. 1). The International Whaling Commission currently recognizes two stocks of narwhals in the Canadian Nearctic. One is centered in northern Hudson Bay and southern Foxe Basin in the summer, and the other in the fjord waters of Northwest Greenland and the Canadian High Arctic archipelago (IWC 1999). IWC also suggests that a working hypothesis in which discrete stocks occupy separate summering areas in the open water season.

In the autumn when fast ice forms, high Arctic stocks of narwhals move from summering areas and spend the winter in areas covered by dense offshore pack ice (Dietz and Heide-Jørgensen 1995). During winter months, narwhals are widely dispersed in Baffin Bay and Davis Strait with high concentrations between 55°-64° W and 68°-71° N and off Disko Bay (Koski and Davis 1994, Heide-Jørgensen *et al.* 1993) (Fig. 1). In spring, narwhals are seen along ice edges on the east coast of Baffin Island, at the entrance of Lancaster Sound and Jones Sound, and in Smith Sound (Bradstreet *et al.* 1982, Koski and Davis 1994). Narwhals from this stock may reach northern Foxe Basin by Fury and Hecla Strait (Stewart *et al.* 1995). Narwhals are also known to move along the ice edges in West Greenland and to concentrate at the entrance of Inglefield Bredning (Born *et al*. 1994).

In Canada, the harvest in the high Arctic takes place from Grise Fiord, Pond Inlet, Arctic Bay, Resolute Bay, Creswell Bay, Taloyoak, Kuugaruk, Broughton Island, Pangnirtung, Clyde River, and several locations in Foxe Basin, namely Igloolik, Hall Beach, and Repulse Bay (Fig. 1) (DFO 1998a). In West Greenland, the hunt takes place in five areas: Qaanaaq, Upernavik, Uummannaq, Disko Bay, Sisimiut, and in the south (Fig. 1).

Heide-Jørgensen e*t al.* (2001) proposed a model of the dispersal of narwhals in Baffin Bay and adjacent area based on satellite tracking, genetic studies, and compilations of local knowledge. Nine coastal summering concentrations of narwhals, proposed to constitute stocks, are identified. Also, nine major hunting grounds in Canada and Greenland are identified and several stocks are hunted on several hunting grounds. Narwhals hunted in Grise Fiord are hypothesized to be part of a “Jones Sound” or possibly a “Smith Sound” stock or aggregation. These narwhals may also be hunted in Qaanaaq, Greenland. Heide-Jørgensen *et al.* (2001) believed that whales hunted in other communities in Canada are most likely not hunted in West Greenland. According to the Heide-Jørgensen *et al.* (2001) model, the narwhals hunted in both Broughton Island and in Clyde River are described as “East Baffin small stocks”. Whales hunted in Pond Inlet are presumed to be part of an “Eclipse Sound Aggregation”. Arctic Bay hunts from the “Admiralty Bay” aggregation, but possibly from the “Eclipse Sound” or “Somerset” aggregations. Narwhals hunted in Creswell Bay and from Resolute are most likely part of “Somerset” aggregation, and it is possible that Arctic Bay also hunts these narwhals.

Two of three hunters from Grise Fiord believed narwhals in Jones Sound to be a different stock from those in the Pond Inlet/Arctic Bay area because of behavioral differences (Stewart *et al*. 1995). Narwhals in the Grise Fiord area are more readily herded into shallow water than those off Lancaster Sound and off Greenland. Visitors from Greenland and Pond Inlet have remarked on how, compared to other areas, narwhals at the floe edge in Jones sound are not alarmed at the sight of hunters. However, many narwhals that frequent the Grise Fiord area are believed to be young (Stewart *et al*. 1995). Hunters in Arctic Bay did not describe different groups of narwhals apart from males and females.

The summer range of northern Hudson Bay narwhals includes the waters surrounding Southhampton Island, with the largest aggregations in Repulse Bay, Frozen Strait, Western Foxe Channel, and Lyon Inlet (Richard 1991; DFO 1998b) (Fig. 1). These narwhals are assumed to winter in eastern Hudson Strait or in open leads and polynas of northern Hudson Bay and western Hudson Strait. They are assumed to be a separate stock because of their apparent year-round discontinuous distribution with Baffin Bay narwhals. Unlike the hunters from Arctic Bay and Grise Fiord, no hunters from Repulse Bay had killed a tusked narwhal and found it to be female (Stewart *et al.* 1995). Hunters in Igloolik did not describe different groups of narwhal.

Several hypothesized stock differences and existing scientific knowledge and traditional knowledge have been confirmed by comparing organochlorine contaminant (OC) profiles from narwhals hunted in different communities (de March and Stern 2003). Canonical discriminant function analysis using 14 OC groups separated narwhals hunted in Repulse Bay, Broughton Island, Pond Inlet and Grise Fiord. While narwhals from all sample locations had overlapping OC contaminant concentrations, OC ratios differed among sample locations. These differences are assumed to be due to food web differences. Canonical functions were most strongly correlated with the concentrations of several PCB congeners and DDT compounds. Narwhals from Repulse Bay were the most distinct, with overall lower OC levels and high PCB/DDT ratios. Narwhals from Broughton Island had relatively high OC levels and high PCB/DDT ratios. Narwhals hunted in Pangnirtung may be from the same stock as those hunted in Broughton Island. Narwhals from Clyde River are not convincingly associated with or separated from other groups; however this may be due to the small sample size of six animals. Among the 4 major sample groups, narwhals from Pond Inlet and Grise Fiord are the most similar. However, narwhals from Pond Inlet had a notably lower PCB/DDT ratio than those from Pond Inlet (de March and Stern 2003).

Palsbøll *et al.* (1996) examined 406 narwhals from Greenland and 28 from Canada using a mitochondrial DNA (mtDNA) sequence of 287 base pairs. This genetic marker is maternally inherited. They found differences based almost entirely on the ratios of the two most common haplotypes (a described sequence of mtDNA). On the basis of this evidence, Palsbøll *et al.* (1996) suggested that there are three aggregations in West Greenland: the Avanersuaq district; Melville Bay and the Upernavik district; and the Uummannaq district. Twenty-eight (28) narwhals from Canada, a cluster of 19 from Pond Inlet and the remainder from Pangnirtung, Broughton Island, Grise Fiord, and Pond Inlet, were included in this study. This cluster from Canada was not significantly differentiated from narwhals from the Avanersuaq district, but they were significantly differentiated from narwhals from the other two aggregations. In the samples from Canada, the ratio of the two common haplotypes, Mm01:Mm02, was 22:4 (=5.5); 125:44 (=2.84) in the Avanersuaq district; and 94:26 (=3.62) in Disko Bay. The ratios were 81:7 (11.5) in the Uummannaq district; 15:16 (=0.94) in Melville Bay and Upernavik; and 0:28 (=0.0) in East Greenland (frequencies also listed in Table 6). Mm005 had three occurrences in the Avanersuaq district, one in Disko Bay and one in Canada. Besides these three haplotypes, two different unique haplotypes were found, one in Canada and one in the Avanersuaq district.

The Freshwater Institute in Winnipeg, Manitoba, Canada, has performed molecular genetics analyses on narwhals since 1998. Over these years the main objective of the project was to find and use loci with sufficient diversity to detect differences in allele frequencies among narwhals hunted at different locations. Sample sizes that were large enough for rigorous statistical analyses took several years to accumulate. In this paper, we will present and compare the results of additional mtDNA sequence information from a larger set of Canadian narwhal samples.

Methods

Samples were collected from summer hunts and scientific collections (Table 1, Fig. 1). Narwhal samples were included in this study if they had an mtDNA reading or had results at 6 or more of the 9 microsatellite loci.

Genetic analyses

Due to inconclusive results in analyses of preliminary data, we changed our methods for genetic data collection several times. For more robust results, we increased our analysis from five to thirteen microsatellite loci in 1999. Increasing the number of loci had been helpful for discriminating beluga populations and we hoped it would also be so for narwhals. In 2000, we decided to examine a longer region of sequence within the mtDNA d-loop than had been previously analysed (Table 2). This change was made for several reasons. First, haplotypes were the most informative locus in exploratory analyses with narwhals (de March 2002b). Second, Palsbøll *et al.* (1996) had found genetic differences among narwhal stocks using a portion of mtDNA sequence that was adjacent to the one we had been analysing. Finally, analysis of an extended region had been more successful in differentiating beluga sample populations that the original sequence.

The extended mitochondrial DNA sequence was determined for a portion of the d-loop region (Table 2). Target amplification was carried out using the MT3R and MT4F primers (Arnason *et al*. 1993) and reaction conditions described in Palsbøll *et al*. (1996). Sequencing reactions were prepared using Applied Biosystems dRhodamine dye terminator kits according to the manufacturer's instructions and the MT4F amplification primer as the sequencing primer (Palsbøll *et al*. 1996). Sequencing was performed on an ABI Prism 377 automated DNA sequencer and was optimized to yield long reads of clean sequence.

The resulting DNA sequences allowed the alignment of 501 base pairs of information and spanned the combined overlapping regions of sequence evaluated by Palsbøll *et al.* (1996) and the shorter sequence that we analysed for in the earlier stages of this study. This allowed for the comparison of variable sites found by different studies and the identification of shared haplotypes (Table 3). Our original haplotypes, based on 347 base pairs, were designated as "N-Types", for example N01, N05, and N16. The extended haplotypes, with 501 base pairs, were designated as "M-Types". All "M-Types" can be converted to "N-Types" and "Mm-Types" described by Palsbøll *et al*. (1996) since these haplotypes sit within the region of the M-Type. Also, the "Mm-Type" sequence, with 287 base pairs, overlaps 258 positions of the N-Type sequence (Table 3), hence some comparisons are possible.

As a result of analyses conducted between 2001 and 2003, it became evident that microsatellite loci would only weakly differentiate narwhals sampled at most different locations. We therefore modified the emphasis of our laboratory analyses. Three of 13 microsatellite loci were dropped from the processing of new samples, either because they had low diversity, because they appeared to yield redundant information, or because there were technical problems in their analysis. More resources were then focused on completing the analysis of the longer portion of mtDNA sequence (the M-Types) in our archive of narwhal samples.

Genetic methods for microsatellite analyses used are described in de March *et al.* (2002a and 2002b). We believe the nine chosen loci (Table 4) to be as informative as 13 in the de March *et al.* (2002b) progress report.

Statistical methods.

Analysis of Molecular Variance or "AMOVA" (Excoffier *et al. 1992*) was used to compare sample populations. F_{st} values, a measure of genetic distance among populations, and associated significance levels, were obtained for both mtDNA and microsatellite data. To estimate low probabilities accurately enough to apply table-wide statistical criteria (Rice 1989), the significance of the variance ratios was calculated from 100,000 permutations of the difference matrix in AMOVA.

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

Many exploratory comparisons of sample groups were made before deciding which comparisons best summarized the overall results. This exploration was motivated by few patterns of significant differences among sample groups. Microsatellite and haplotype information were analysed both separately and combined if samples had both types of data. Also, the ability of both N-Type and M-Type haplotype data to discriminate among sample populations was examined. In addition, data were analysed as many (year x location) sample groups and as fewer location sample groups, with data from different years pooled.

Results

N- and M-Type haplotypes

The M-Type sequence was 154 nucleotides larger than the N-Types and 5 variable positions were gained by analysing for the longer region (Tables 2 and 3). Among these 5 haplotypes, M13 and M18 were sampled only once, M12 twice, M09 three times, and M08 15 times. Position 55 was problematic (Footnote 2, Table 3); hence we eliminated it from all haplotypes. Specifically, Mm003 described by Palsbøll *et al.* (1996) was assumed to be the same as Mm002.

Comparison of year by location sample groups

AMOVA with 38 (year x location) sample populations yielded weak differentiation among populations on the basis of microsatellites (Table 5, Analysis 3, $p = 0.077$). When comparisons were examined in detail, there were very few significant differences among these sample groups ($p < 0.05$). Most differences that were found involved samples of small sizes. Pangnirtung 1990 narwhals (n=2) differed significantly from those collected in 1996 (n=5). Also, Pond Inlet 1982 narwhals (n=5) differed from those collected in 2000 (n=64). Repulse Bay 1993 (n=2) differed significantly from those collected in 1995 (n=4), 1999 (n=19), and 2000 (n=24). Pairwise comparisons of 38 sample groups involves 703 comparisons and 5 % (n=35) of these are expected to be due to chance at $p < 0.05$.

There was stronger differentiation among (year by location) sample populations on the basis of both N-Type haplotypes (Table 5, Analysis 1, n=41 sample groups, p=0.003) and M-Type haplotypes (Table 5, Analysis 2, n=36 sample groups, p=0.007). There were few differences between years within locations. In the analysis of M-type haplotypes, Igloolik 1995 (n= 7 narwhals, 4 M01 and 3 M05) differed from 1996 (n=1, one M01). Also, Pangnirtung 1996 narwhals (n=3) differed from those sampled in 1990 (n=2) and 2000 (n=1). Analysis of N-Type haplotypes also yielded only three within-population differences, of which two involved very small sample sizes. The only within-population difference that had larger samples sizes was Grise Fiord 1999 (n=10) *versus* Grise Fiord 2000 (n=7), which was differentiated at $p = 0.040$, not significant at a table wide level of α=0.05. Grise Fiord 2000 samples were dominated by M01 (N01), while the 1999 samples

had 5 different M-Type haplotypes. Samples from the other years combined had 6 different M-Type haplotypes of a total of 7 found in all Grise Fiord samples (Table 6).

Because of few within-year differences and small sample sizes, samples for all years within locations were pooled and then analysed (Table 5, Analyses 4 to 10). When sample locations with less than ten narwhals were excluded, only 11 sample groups remained for comparison (Table 5, Analyses 7 to 10). Also, AMOVA leaving out three loci which were missing in more than 5% of samples was performed (Table 5, Analysis 10).

Comparison of location sample groups

In Tables 7 and 8, F_{st} values above the diagonal are a measure of the degree of similarity between sample locations and the values below the diagonal are the probabilities of observing a lower F_{st} due to chance in random sampling from the two populations. The F_{st} values are not related to sample size and thus demonstrate patterns of similarities better than the probabilities.

The AMOVA analysis using 9 microsatellite loci showed no overall significant differentiation among 11 sample populations (p = 0.874, Analysis 6 in Table 5).

The microsatellite loci DlrFCB08, DlrFCB17, and EV37Mm were missing in more than 5% of samples, and were omitted in analyses with reduced loci (Table 5, Analysis 10, details in Table 7). DlrFCB08 and EV37Mm were both loci with relatively low diversity (Table 2). DlrFCB17 had high diversity but had missing values in several sample groups due to analytical problems. The analysis of the remaining 6 microsatellite loci showed patterns of differentiation among narwhals from different communities (p = 0.00674, Analysis 10 in Table 5, Table 7). Most notably, Repulse Bay was significantly differentiated from Broughton Island, Clyde River, Creswell Bay, Grise Fiord and Igloolik (F_{st}s between 0.024 and 0.009, p's between 0.00034 and 0.00101). Also, Igloolik and Grise Fiord were also differentiated from several other locations, but not as strongly as Repulse Bay was. A table-wise α=0.05 would mean that only probabilities of $p < 0.0015$ are significant on this table. This would mean that narwhals sampled from Igloolik and Grise Fiord are not significantly or only weakly differentiated from other locations.

Nevertheless, Igloolik samples resemble high Arctic samples more than those from Repulse Bay (Igloolik *versus* Repulse Bay F_{st} = 0.046, larger than all 9 other F_{st}s, Table 7). Grise Fiord samples mostly resemble Uummannaq and Qaanaaq (F_{st}s < 0, Table 7). A visual examination of microsatellite allele frequencies reveals that both Repulse Bay and Grise Fiord had very similar percentages of common alleles, thus the differentiation observed in these analyses was due to uncommon alleles. Igloolik narwhals, however, had slightly different frequencies of uncommon and common alleles from other locations.

Details of the AMOVA of M-type haplotypes for the 11 locations with samples sizes of n > 10 narwhals is shown in Table 8. AMOVA of N-type haplotypes (not shown) produced a very similar table, but with slightly smaller genetic distances and slightly higher probabilities. Narwhals from Repulse Bay stand out as strongly differentiated from those hunted in other communities. Narwhals hunted in Grise Fiord, Pangnirtung, Pond Inlet, and Qaanaaq are also differentiated from those from some other communities.

Combination and Comparison of mtDNA results in two studies

All haplotype data in this study and in Palsbøll *et al*.'s (1996) study are shown in Table 6.

Comparisons of our results and those of Palsbøll *et al*. (1996) are possible if all haplotypes are converted to Mm-Types and if a few additional assumptions and corrections are made. When analysing for M-Types, position 55 was problematic (Footnote 2, Table 4), hence we eliminated it from all haplotypes. We corrected for variable position 262 and 264 in the Mm-Type haplotypes on

the assumption that both studies had the same second-most common haplotype (Footnote 1, Table 4). M-Types could be directly converted to Mm-Types since the Mm-Type region is nested within the M-Type. Converting N-Types to Mm-Types required that we fill in positions 1 to 29, which had not been scored for N-types. This meant that only position 3, different in only haplotype M21 which was observed only once, was not included in the analysis of N-Type haplotypes. On the basis of this observation, N-Types were converted to Mm-Types by assuming that the most common sequence occurred in variable positions 1 to 29.

Seven of our M-Type haplotypes were converted to Mm-Types which had not been observed by Palsbøll *et al*. (1996) (Table 3), yielding a total of eleven Mm-Types in the data set. Three haplotypes, Mm001, Mm002 and Mm005 were observed only in Greenland samples. All eleven Mm-Types were observed in samples from Canada (combination of data from Tables 3 and 6).

Figure 2 is a dendrogram constructed with the Neighbour-Joining Method (Saitou and Nei, 1987) using chord distances (Cavalli-Sforza and Edwards, 1967) for Mm-Type haplotypes among all locations in both studies The frequencies of Mm001, Mm002, Mm005, and Mm004 for each location are noted since their ratios describe branches of the dendrogram. The ratios of N01, N02, N06, and N08, and in fact M01, M06, M05, and M04 are very similar because the most variable part of the sequences is common to all three types of haplotypes.

Locations that have Mm001:Mm002 (N01:N02) ratios close to 3:1 are near the centre of the dendrogram (Fig. 2). These locations are Arctic Bay, Pond Inlet, the “Eastern Canada” mixture (mostly from Pond Inlet, Table 6), the Avanersuaq district, and Disko Bay.

Grise Fiord is at an end branch of the dendrogram and is characterized by a higher fraction of Mm004 (N08, M04). Tables 7 and 8 also showed that Grise Fiord was weakly differentiated from other locations on the basis of both microsatellite and haplotypes. This haplotype also occurred in 1/23 samples in Creswell Bay, and in 1/41 samples from Arctic Bay. Mm012 (N03, M07) occurred more than once in Grise Fiord (3/39 occurrences) and also occurred in Creswell Bay (4/23).

The branch of the dendrogram that terminates with Igloolik has locations with a variable Mm001:Mm002 ratio, but with a notable frequency of Mm005 (N06, M05), the third most-common haplotype. This branch includes Igloolik, three southeast Baffin locations, and Pond Inlet which is also near the centre of the dendrogram.

The branch that terminates with Qaanaaq (Avanersuaq district, our data) has a high Mm001:Mm002 ratio. Uummannaq is also on this branch and the “Eastern Canada” mixture is closer to the centre.

Another branch that terminates with East Greenland has locations with a lower Mm001:Mm002 ratio. The 28 East Greenland samples consist of 28 Mm002, while other locations have a ratio closer to 1:1. These locations include Repulse Bay, and the Upernavik district and Melville Bay in Greenland.

This analysis with Mm-Type haplotypes would not have been sensitive to some differences observed by analysing the N- and M-Types. M08 (N04) occurred at a notable frequency, but because the variable position was past the Mm-Type sequence, it was converted to Mm002, a common haplotype. M08 was observed in 4/63 Repulse Bay narwhals and in 6/91 narwhals from eastern Baffin Island communities. This difference no doubt contributes to the observation that Repulse Bay is significantly differentiated from many other locations (Table 8).

Discussion

With this low degree of genetic differentiation between stocks, the data mainly confirm that several stocks exist. The stronger discrimination expected on the basis of previous knowledge of narwhals and on the study with organochlorine contaminants (de March and Stern 2003) was not observed. Thus it would be impossible to assign stock affiliation to individuals or estimate population parameters with a high degree of confidence.

Early results had already suggested that the ratio of the two most common haplotypes would be the main genetic characteristic that defined stocks (de March 2002b). The study described in this manuscript has a larger sample size than in previous analyses of de March (2002b) and showed that the third- to sixth- most common haplotypes were also important in differentiating putative stocks. These four additional haplotypes were observed in approximately 10 % of all samples.

Analysis for M-Types rather than N-Types contributed only weakly to narwhal stock discrimination. The most common haplotype (N01) was split into several M-Types. Of these, only one of four M-Types was common (M01, 212/216 occurrences of N01), and three were uncommon (M12, 2/216; M13 and M21, one occurrence each). Analysis for an extended mtDNA had been very worthwhile for belugas since several common “old” haplotypes in belugas were split into new haplotypes which were also not uncommon, and these new ones were associated with different geographic areas (de March, unpublished data). With narwhal, the split was not as advantageous.

The most convincing discrimination among locations in this study is Repulse Bay narwhals *versus* most other aggregations from Canada. This confirms previous beliefs about the distinctness of this stock. Samples from Repulse Bay have an Mm001:Mm002 ratio similar to stocks from Upernavik and Melville Bay in Greenland, however microsatellite data shows that Repulse Bay is not similar to stocks in Greenland.

Other suspected stock relationships are weakly confirmed in these results. It is probable that narwhals hunted in Igloolik, all sampled in August, are high Arctic, not Hudson Bay narwhals. The N01:N02 ratio in Igloolik narwhal is more similar to high Arctic narwhals than Hudson Bay narwhals, and N06 was also found, which occurs only in the high Arctic. Genetic distances based on microsatellite loci between Igloolik samples and other locations also suggest that these are high Arctic narwhals. Also, there are hints of other stocks in the Canadian high Arctic, that are best represented by Grise Fiord (N01:N02:N06:N08 is 22:2:0:9) and Broughton Island (N01:N02:N06:N08 is 28:11:6:0).

There may be a higher degree of stock discrimination in the west Greenland sampling locations examined by Palsbøll *et al*. (1996) than were observed in Canadian high Arctic locations. However, our study opens up new questions about Greenland narwhal. Our twelve Qaanaaq samples from the Avanersuaq district had 12/12 Mm001, while samples examined by Palsbøll *et al*. (1996) had 126/173 Mm001 (73%). Our samples were chosen randomly from a large pool of samples available to us, hence sampling 11 of the same haplotype is not highly probable. There may be considerable among -year variation at this sampling location.

The higher haplotype diversity in Canada compared to Greenland may indicate that stocks in Canada are less exploited. It may also indicate that more stocks were sampled in Canada.

All results here are consistent with the stock discrimination demonstrated with organochlorine contaminants (de March and Stern, 2003). In that study we demonstrated that narwhals from Repulse Bay, Pond Inlet, Grise Fiord and Broughton Island may be different stocks. Narwhals from Pangnirtung were most likely from a stock also represented from Broughton Island. Stock discrimination was stronger in the contaminants than in this genetics study, however contaminant profiles still overlapped. It is noteworthy that belugas that summer in Hudson Bay had a similar DDD/PCB ratio to narwhals sampled in Repulse Bay (de March *et al.* in press).

The social behaviour and migration patterns of narwhals are not well understood and cannot presently help interpret these results. While we believe that the same individuals return to the same summering locations, it is not known to what extent different stocks interbreed. The low degree of differentiation for microsatellite loci suggests the possibility that most high Arctic animals interbreed on their wintering grounds or during spring migration. Nevertheless, these are still different maternal "stocks" if the same matriarchal social groups return to the same summering areas over time.

Since there is an inherent belief that more stocks exist, we must ask the question whether or not we have chosen appropriate and a sufficient number of genetic markers. There are several reasons why we believe that a more informative set of markers cannot be found. 1) We used several markers with a high genetic diversity, namely the microsatellite loci. If genetic drift occurs within fairly distinct stocks, these markers should have indicated differentiation. 2) The same microsatellite loci were also used for belugas, where they show a greater degree of differentiation among putative stocks. EV37 and FCB 17 are the most informative microsatellite loci for belugas, and might also be expected to be so for narwhals (Table 2). Also, we used approximately the same number and type of markers for walrus and bowhead, and in these two species we found high genetic diversity and strong differentiation among sample groups. We must conclude that most "stocks" of narwhals that we examined are only weakly differentiated genetically.

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References

Arnason, U., A. Gullberg, and B. Widegren. 1993. Cetacean mitochondrial DNA control region: sequences of all extant baleen whales and two sperm whale species. Molec. Biol. Evol. 10: 960-970.

Born, E. W., M.P. Heide-Jørgensen, M.P. Larsen, and A.R. Martin. 1994. Abundance and stock composition of narwhals (Monodon monoceros) in Inglefield Bredning (NW Greenland). Meddelelser Om Grønland, Bioscience 39:51-68.

Bradstreet, M. S. W. 1982. Occurrence, habitat use, and behaviour of seabirds, marine mammals, and Arctic cod at the Pond Inlet ice edge. Arctic. 3: (1):28-41.

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

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

de March, B.G.E., L.D. Maiers, and M.K. Friesen. 2002a. 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.

de March, B.G.E. 2002b. Nunavut Implementation Fund 1999/2000. Progress Report July 2000.

de March, B.G.E., G.A. Stern, and S. Innes. 2004. The combined use of organochlorine contaminant profiles and molecular genetics for stock discrimination of belugas

(*Delphinapterus leucas*) hunted in three communities on Southeast Baffin Island. Accepted by J. Cetacean Res. Manage.

de March, B.G.E. and G.A. Stern. 2003. Stock separation of narwhal *(Monodon monoceros*) in Canada based on organochlorine contaminants. CSAS (Canadian Scientific Advisory Secretariat) Research Document 2003/079.

DFO (Department of Fisheries and Oceans, Canada). 1998a. Baffin Bay Narwhal. DFO Science: Stock Status Report E5-43. 6 p.

DFO (Department of Fisheries and Oceans, Canada). 1998b. Hudson Bay Narwhal. DFO Science: Stock Status Report E5-44. 5 p.

Dietz, R. and M.P. Heide-Jørgensen. 1995. Movements and swimming speed of narwhals (Monodon monoceros)i nstrumented with satellite transmitters in Melville Bay, Norwest Greenland. Can. J. Zool. 73: 2106-2119.

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.

Heide-Jørgensen, M. P.; H. Lassen; J. Teilmann, and R. A. Davis.1993. An index of the relative abundance of wintering belugas, Delphinapterus leucas and narwhals, Monodon monoceros off West Greenland. Can. J. Fish. Aquat. Sci. 50: 2323-2335.

Heide-Jørgensen, M. P., R. Dietz, K. Laidre, P. Richard, and J. Orr. 2001. Do narwhals from Canada contribute to the harvest in West Greenland? Working Paper Presented to the NAMMCO Working Group on Belugas and Narwhals. 2001 May 9-13 2001, SC/9/BN/9:, 30 p.

IWC (International Whaling Commission). Report from the small cetacean sub-committee. 1999.

Koski, W. R., and R.A. Davis. 1994. Distribution and numbers of narwhals *(Monodon monoceros*) in Baffin Bay and Davis Strait. Meddelelser Om Grønland, Bioscience 39:15-40.

NAMMCO (North Atlantic Marine Mammals Commission) . 2000. NAMMCO Annual Report. 2000:265 p.

Palsbøll, P.J, M.P. Heide-Jørgensen, and R. Dietz. 1996. Population structure and seasonal movements of narwhals, *Monodon monoceros*, determined from mtDNA analysis. Heredity 77: 284-292.

Reeves, R. R. and S. Tracey. Monodon monoceros. Mammalian Species. 1980; 127:1-7.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Richard, P.R. 1991. Abundance and distribution of narwhals (*Monodon monoceros*) in northern Hudson Bay. Can. J. Fish. Aquat. Sci. 48:276-283.)

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

Stewart, D. B.; A. Akeeagok; R. Amarualik; S. Panipakutsuk, and A. Taqtu. 1995. Local knowledge of beluga and narwhal from four communities in Arctic Canada. Can. Tech. Rep. Fish. Aquat. Sci. 2065: viii + 48 p. + appendices on disk.

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

Table 1. Locations, years sampled, sample sizes for different genetic loci, and sex ratios of narwhal in this study.

Location	years	n narwhal	n with Microsatellite loci	n with =>6Mic Loci	n with M-Type haplotypes	n with N-Type haplotypes	F : M
Greenland							
Qaanaaq	1992,96	12	12	12	12	12	3 : 9
Uummannaq	1993,94	13	13	13	11	11	7 : 6
	all years	**13**	**13**	**13**	**11**	**11**	**7 : 6**
Canada							
Grise Fiord	1987	2	2	2	2	2	0 : 0
Grise Fiord	1993	3	0	0	3	3	2 : 1
Grise Fiord	1994	9	9	9	9	9	0 : 0
Grise Fiord	1995	5	5	5	5	5	1 : 4
Grise Fiord	1999	10	10	10	10	10	0 : 10
Grise Fiord	2000	7	7	7	7	7	1 : 6
Grise Fiord	2001	10	10	10	3	3	2 : 7
	all years	**46**	**43**	**43**	**39**	**39**	**6 : 28**
Clyde River	1993	3	0	0	3	3	0 : 2
Clyde River	1994	10	5	5	9	10	0 : 1
Clyde River	1995	12	12	12	9	12	5 : 7
	all years	**25**	**17**	**17**	**21**	**25**	**5 : 10**
Broughton Island	1993	12	0	0	12	12	1 : 11
Broughton Island	1995	10	5	5	6	10	4 : 5
Broughton Island	1996	7	7	7	3	7	2 : 2
Broughton Island	2001	25	25	25	25	25	3 : 16
	all years	**54**	**37**	**37**	**46**	**54**	**10 : 34**
Pangnirtung	1985	2	2	2	2	2	0 : 0
Pangnirtung	1990	2	2	2	1	2	0 : 0
Pangnirtung	1996	5	5	5	3	5	1 : 3
Pangnirtung	2000	1	1	1	1	1	0 : 0
Pangnirtung	2002	3	3	3	2	2	0 : 0
	all years	**13**	**13**	**13**	**9**	**12**	**1 : 3**
Pond Inlet	1982	9	5	5	4	4	4 : 5
Pond Inlet	1992	19	19	19	2	5	11 : 6
Pond Inlet	1994	10	8	8	2	7	5 : 5
Pond Inlet	1999	17	17	16	17	17	4 : 13
Pond Inlet	2000	65	65	64	65	65	29 : 36
	all years	**120**	**114**	**112**	**90**	**98**	**53 : 65**

Table 1. continued.

Location	years	n narwhal	n with Microsatellite loci	n with =>6Mic Loci	n with M-Type haplotypes	n with N-Type haplotypes	F : M
Arctic Bay	1987	10	10	10	6	10	2 : 8
Arctic Bay	1994	4	4	4	2	4	0 : 0
Arctic Bay	1999	27	27	27	27	27	15 : 12
Arctic Bay	2001	7	7	7	0	0	0 : 0
	all years	**48**	**48**	**48**	**35**	**41**	**17 : 20**
Creswell Bay	2000	8	8	8	8	8	8 : 0
Creswell Bay	2001	15	15	15	15	15	8 : 4
	all years	**23**	**23**	**23**	**23**	**23**	**16 : 4**
Resolute Bay	**2002**	**3**	**0**	**0**	**3**	**3**	**0 : 3**
Igloolik	1982	1	0	0	1	1	0 : 0
Igloolik	1994	1	1	1	1	1	0 : 0
Igloolik	1995	8	8	8	8	8	6 : 2
Igloolik	1996	1	1	1	1	1	0 : 1
	all years	**11**	**10**	**10**	**11**	**11**	**6 : 3**
Hall Beach	**1996**	**1**	**1**	**1**	**1**	**1**	**0 : 1**
Coral Harbour	**1995**	**1**	**1**	**1**	**0**	**1**	**0 : 1**
Repulse Bay	1993	2	2	2	0	2	2 : 0
Repulse Bay	1995	4	4	4	4	4	4 : 0
Repulse Bay	1999	21	20	19	21	21	12 : 9
Repulse Bay	2000	24	24	24	24	24	18 : 6
Repulse Bay	2001	12	0	0	12	12	1 : 8
	all years	**63**	**50**	**49**	**61**	**63**	**37 : 23**
Total	**all years**	**421**	**370**	**367**	**350**	**382**	**158 : 201**

Table 2. Alignment of the sequenced 501 nucleotides for narwhal. Variable positions are bolded and marked with an asterisk (*). N-Type haplotypes are defined by the sequence from positions 30 to 376; M-Type haplotypes are defined by the sequence from position 1 to 501.

```
  1
  *
AAGAAGGTTT  ATTGTATAAT  ATCAAACCAT  TACAGTGCTA  CGTCAGTATT  AAAAAAACCT

              2                         3                 4
              *                         *                 *
ATTTCAATAC  ATTTTACTGT  AGCTATTGCA  TACTCGCATA  CACACACGTC  ATAAATCTTA



GTCTTTCCTT  ATAAATATCC  ATATATTCAT  ACTATGTATT  ATTGTGCATT  CATTTATTTT

                                                      5
                                                      *
CCATACGGTC  AGTTAAAGCT  CGTATTAAAT  ATTATTAATT  TTACAAATCA  CATAATATGC

     6                   7 8                   9  10
     *                   * *                   *  *
ATGCTCTTAC  ATATTATATG  TCCCCATTCA  TTTTATTTCC  ATTATATCCT  ATGGCCGCTC

                    11                                    12
                    *                                     *
CATTAGATCA  CGAGCTTAAC  TACCATGCCG  CGTGAAACCA  GCAACCCGCT  TGGCAGGGAT

                          13
                          *
CCCTCTTCTC  GCACCGGGCC  CATATCTCGT  GGGGGTACGT  AATAATGATC  TTTATAAGAC

                   14       15                              16
                   *        *                               *
ATCTGGTTCT  TACTTCAGGA  CCATTTTAAC  TTAAAATCGC  CCACTCGTTC  CTCTTAAATA



AGACATCTCG  ATGGACTAAT  G
```

Table 3. Polymorhic sites in three types of haplotypes. Vertical numbers indicate the position relative to a consensus sequence. Variable position numbers in Palsbøll *et al.* 's (1996)(PJP) study are three positions higher than in ours. Haplotypes (Mm006) to (Mm012) were not observed by PJP, but are haplotypes we found and scored according to the sequence PJP used.

M-Type haplotypes, 501 base pairs,positions 1 to 501

N-Type haplotypes, 347 base pairs, positions 30 to 376

Mm-Type haplotypes, 287 base pairs, positions 1 to 287

Haplotype			Base Position																
Palsbøll *et al.* (1996) Mm-Type	**FWI Short N-Type**	**FWI Extended M-Type**	**3**	**55**	**74**	**99**	**114**	**229**	**246**	**262**	**264**	**281**	**284**	**319**	**351**	**385**	**438**	**445**	**472**
Mm001	N01	M01	**G**	**A**	**T**	**T**	**A**	**C**	**C**	**C**	**C**	**A**	**A**	**A**	**T**	**T**	**G**	**T**	**T**
Mm001	N01	M12	G	A	T	T	A	C	C	C	C	A	A	A	T	T	G	T	**C**
Mm001	N05	M09	G	A	T	T	A	C	C	C	C	A	A	A	T	T	G	**C**	T
Mm001	N10	M14	G	A	T	T	A	C	C	C	C	A	A	A	**C**	T	G	T	T
(Mm007)	N01	M13	G	A	**C**	T	A	C	C	C	C	A	A	A	T	T	G	T	T
(Mm006)	N01	M21	**A**	A	T	T	A	C	C	C	C	A	A	A	T	T	G	T	T
Mm002[1]	N02	M06	G	A	T	T	A	C	C	**T** [1]	C	A	A	A	T	T	G	T	T
Mm003[2]	N02	M06	G	**+A** [2]	T	T	A	C	C	C	**T**	A	A	A	T	T	G	T	T
Mm002	N02	M06	G	A	T	T	A	C	C	C	**T**	A	A	A	T	T	G	T	T
Mm002	N04	M08	G	A	T	T	A	C	C	C	**T**	A	A	A	T	**C**	G	T	T
Mm002	N16	M22	G	A	T	T	A	C	C	C	**T**	A	A	**G**	T	T	G	T	T
Mm004	N08	M04	G	A	T	T	A	**T**	C	C	C	A	A	A	T	T	G	T	T
Mm004	N11	M15	G	A	T	T	A	**T**	C	C	C	A	A	A	**C**	T	G	T	T
Mm005	N06	M05	G	A	T	T	**G**	C	C	C	C	A	A	A	T	T	G	T	T
Mm005	N13	M18	G	A	T	T	**G**	C	C	C	C	A	A	A	T	T	**C**	T	T
(Mm008)	N07	M10	G	A	T	**C**	A	C	C	C	C	A	A	A	T	T	G	T	T
(Mm009)	N12	M17	G	A	T	T	A	C	C	C	C	A	**G**	A	T	T	G	T	T
(Mm010)	N14	M19	G	A	T	T	A	C	C	C	**T**	**G**	A	A	T	T	G	T	T
(Mm011)	N15	M20	G	A	T	T	A	C	**T**	C	C	A	A	A	T	T	G	T	T
(Mm012)	N03	M07	G	A	T	T	A	**T**	C	C	**T**	A	A	A	T	T	G	T	T

[1] Since both our study and PJP's (1996) study are assumed to have the same two most common haplotypes, an adjustment was made near position 262 to facilitate alignments. This aligns Mm002 and N02, the second-most common haplotypes in the two studies.

[2] We deleted position 55 (58 in PJP's (1996)) study from all comparisons. The reference sequence often has a string of 7 A's from position 52-57, and samples often had an additional "A" at position 55. We attributed this A addition to a function of the Taq enzyme in the PCR process, not a true polymorphisim. Thus the haplotype "Mm003" in PJP (1996) is used as an "Mm002" in comparisons of the two studies. This was confirmed by resequencing the same sample and obtaining different results in the number of A's in this portion of the sequence.

Table 4. Details of nine microsatellite loci based on all individuals (382 narwhal, > 1300 belugas) analysed in genetic studies.

			Narwhal				Beluga			
Microsatellite Locus	*Annealing Temperature*	*Reference*	*n Alleles*	*Range of Sizes*	*Major Modes*	*Observed Heterozygosity*	*n Alleles*	*Range of Sizes*	*Major Modes*	*Observed Heterozygosity*
DlrFCB1[1]	64	Buchanan *et al.* 1996	7	109-123	113+115	0.62	9	107-127	117	0.73
DlrFCB3	61	"	33	137-215	147,151,191	0.91	25	141-207	141,157,165	0.85
DlrFCB4	63	"	7	151-171	159+161	0.57	14	155-183	159,163	0.69
DlrFCB5	61	"	11	114-140	124+126,134	0.71	10	106-132	108,124	0.60
DlrFCB8	63	"	9	171-187	(179+181)	0.67	9	163-185	171,177	0.73
DlrFCB10	61	"	9	171-187	171,179	0.64	10	171-189	183	0.79
DlrFCB14	61	"	11	293-319	303,307	0.70	9	289-329	309	0.61
DlrFCB17	64	"	33	153-221	(155+157), 195	0.79	24	139-205	(167+169),177	0.84
EV37Mn	59	Valsecchi and Amos 1996	9	176-212	176,188	0.65	15	177-215	195,(205-209)	0.84

[1] Dlr refers to *Delphinapterus leucas* repeat, FCB to Fiona C. Buchanan

[2] Mn refers to *Megaptera novaeangliae* , EV to Elena Valsecchi

Table 5. Summary of AMOVA (Analysis of Molecular Variance). Analysis number 10 does not utilize loci DlrFCB8, DlrFCB17, and EV37Mn.

	Analysis	n sample groups	Loci in Analysis	Fixation Index (overall F_{st})	p of smaller F_{st}
Year by Location Sample Groups	1	41	M-Type haplotypes	0.04979	0.00302
	2	36	N-Type haplotypes	0.04365	0.00706
	3	38	Nine microsatellite loci	0.00424	0.07661
Location Comparisons	4	13	M-Type haplotypes	0.05711	0.00000
	5	14	N-Type haplotypes	0.04282	0.00000
	6	13	Nine microsatellite loci	-0.00216	0.87399
Location Comparisons, Sample sizes < 10 omitted	7, Table 7	11	M-Type haplotypes	0.06210	0.00101
	8	11	N-Type haplotypes	0.04933	0.00000
	9	11	Nine microsatellite loci	-0.00264	0.95600
	10, Table 8	11	Six microsatellite loci	0.00674	0.00100

Table 6. Listing and comparisons of haplotype frequencies in this study and in those of Palsbøll *et al.* (1996) marked"PJP". A dash "-" indicates that readings were not possible in a study, while "0" is a count of zero. "M-Types" are subsets of "N-Types". "Mm-Types" from Palsbøll *et al.* (1996) can be equated with "N-Types" (explanations Table 3 and text). Totals for Mm001, Mm002, Mm005, and Mm004 are associated with locations in Figure 2.

N-Type and Mm-Type haplotypes	**N01**					Mm001	**N02**		Mm002	**N06**		Mm005	N08	Mm004	N04		N03	N05	N14	N07	N10	N11	N12	N13	N15	N16	
M-Type haplotypes and remaining N-Types	M01	M12	M13	M21	other N01	Mm001	M06	other N02	Mm002	M05	other N06	Mm005	M04	Mm004	M08	other N04	M07	M09	M19	M10	M14	M15	M17	M18	M20	M22	Total
Grise Fiord	21	0	1	0	0	-	2	0	-	0	0	-	9	-	1	1	3	0	0	0	0	1	0	0	0	0	39
Pond Inlet	61	0	0	0	4	-	16	3	-	5	1	-	4	-	1	0	0	2	0	0	0	0	0	0	1	0	98
Arctic Bay	24	1	0	0	4	-	6	1	-	0	0	-	1	-	1	1	1	1	0	0	0	0	0	0	0	0	41
Broughton Island	22	0	0	0	6	-	9	2	-	8	0	-	0	-	3	0	0	0	2	0	0	0	1	1	0	0	54
Pangnirtung	4	0	0	0	2	-	0	1	-	4	0	-	0	-	1	0	0	0	0	0	0	0	0	0	0	0	12
Clyde River	13	0	0	0	3	-	2	0	-	1	1	-	1	-	2	0	1	0	0	1	0	0	0	0	0	0	25
Eastern Canada (PJP)	-	-	-	-	-	22	-	-	4	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	28
(19 Pond Inlet + 5 Arctic Bay + 2 Grise Fiord + 1 Broughton Island + 2 Pangnirtung)																											
Creswell Bay	12	0	0	1	0	-	4	0	-	0	0	-	1	-	1	0	4	0	0	0	0	0	0	0	0	0	23
Resolute Bay	2	0	0	0	0	-	1	0	-	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	3
Igloolik	7	0	0	0	0	-	0	0	-	4	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	11
Hall Beach	1	0	0		0	-	0	0	-	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1
Repulse Bay	25	1	0	0	2	-	26	0	-	0	0	-	0	-	4	0	4	0	0	0	0	0	0	0	0	1	63
Coral Harbour	0	0	0	0	1	-	0	0	-	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1
Qaanaaq	11	0	0	0	0	-	0	0	-	0	0	-	0	-	0	0	0	0	0	0	1	0	0	0	0	0	12
Avanersuaq district (PJP)	-	-	-	-	-	125	-	-	45	-	-	3	-	0	-	-	-	-	-	-	-	-	-	-	-	-	173
Melville Bay (PJP)	-	-	-	-	-	9	-	-	11	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	20
Uummannaq district	8	0	0	0	0	-	2	0	-	0	0	-	0	-	1	0	0	0	0	0	0	0	0	0	0	0	11
Uummannaq district (PJP)	-	-	-	-	-	81	-	-	7	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	88
Upernavik district (PJP)	-	-	-	-	-	16	-	-	15	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	31
															-	-											
Disko Bay (PJP)	-	-	-	-	-	39	-	-	11	-	-	1	-	0	-	-	-	-	-	-	-	-	-	-	-	-	51
															-	-											
Eastern Greenland (PJP)	-	-	-	-	-	0	-	-	28	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	28

Table 7. AMOVA with 6 microsatellite loci. F_{st} values are above the diagonal and probabilities of a lower F_{st} values are below the diagonal. Sample locations are arranged as in the Table 8 (AMOVA for haplotypes) to emphasize similarities and differences in that table. *** indicates p <= 0.001, ** 0.001 > p <= 0.01, * 0.01 > p <= 0.05.

	Uummannaq	Clyde River	Igloolik	Broughton Island	Pangnirtung	Creswell Bay	Pond Inlet	Qaanaaq	Arctic Bay	Grise Fiord	Repulse Bay
Uummannaq		0.025	0.041	< 0	0.007	0.001	0.008	0.005	< 0	< 0	0.009
Clyde River	*		0.031	0.011	0.003	0.001	0.002	< 0	0.010	0.019	0.024
Igloolik	*	*		0.019	0.032	0.019	0.017	0.002	0.030	0.035	0.046
Broughton Island	0.754	0.067	*		< 0	0.004	< 0	< 0	< 0	0.003	0.016
Pangnirtung	0.343	0.421	*	0.852		0.012	0.001	< 0	< 0	0.003	0.024
Creswell Bay	0.493	0.481	0.078	0.220	0.149		0.005	< 0	< 0	0.012	0.020
Pond Inlet	0.132	0.338	*	0.529	0.397	0.140		< 0	< 0	0.009	0.013
Qaanaaq	0.344	0.868	0.360	0.989	0.950	0.768	0.891		< 0	< 0	0.015
Arctic Bay	0.581	0.090	**	0.674	0.504	0.611	0.518	0.520		0.003	0.006
Grise Fiord	0.558	*	**	0.217	0.348	*	**	0.633	0.189		0.014
Repulse Bay	0.119	**	***	**	*	**	***	0.056	0.058	**	

Table 8. AMOVA for M-Type haplotypes. F_{st} values are above the diagonal and probabilities of a lower F_{st} below the diagonal. Sample locations are arranged to emphasize differences and similarities. *** indicates p <= 0.001, ** 0.001 > p <= 0.01, * 0.01 > p <= 0.05.

	Uummannaq	Clyde River	Igloolik	Broughton Island	Pangnirtung	Creswell Bay	Pond Inlet	Qaanaaq	Arctic Bay	Grise Fiord	Repulse Bay
Uummannaq		< 0	0.086	0.015	0.151	< 0	< 0	0.045	< 0	0.033	0.073
Clyde River	0.847		0.037	0.007	0.076	< 0	< 0	0.064	< 0	0.002	0.086
Igloolik	0.123	0.179		0.022	< 0	0.090	0.072	0.196	0.095	0.096	0.195
Broughton Island	0.246	0.290	0.233		0.017	0.017	0.036	0.149	0.038	0.059	0.049
Pangnirtung	0.095	0.092	0.510	0.287		0.108	0.151	0.327	0.169	0.121	0.189
Creswell Bay	0.418	0.602	0.058	0.184	*		0.028	0.137	0.009	0.012	0.039
Pond Inlet	0.890	0.505	0.050	*	*	0.103		0.057	< 0	0.053	0.104
Qaanaaq	0.203	0.093	0.057	**	*	*	0.079		0.051	0.124	0.256
Arctic Bay	1.000	0.738	*	*	*	0.254	0.896	0.117		0.041	0.090
Grise Fiord	0.193	0.333	*	*	*	0.233	*	*	*		0.124
Repulse Bay	0.094	*	**	*	**	0.088	***	***	**	***	

Figure 1. Locations in this manuscript and in de March and Stern (2003).

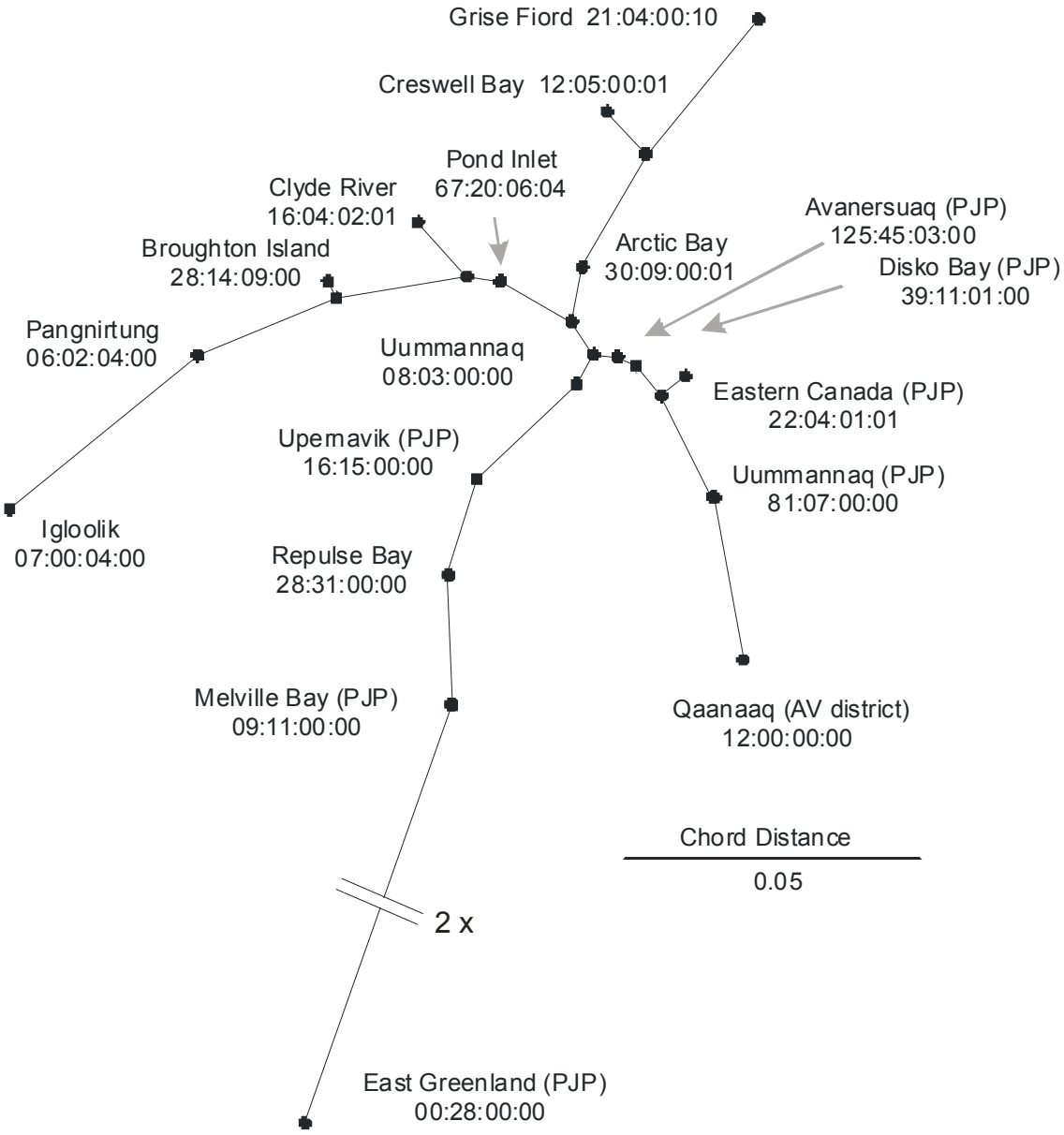

Figure 2. Neighbour-Joining tree based on Chord Distances for all hapolotypes converted to Mm-Types. Locations from Palsboll *et al.*'s (1996) study are identified by (PJP). The frequencies of Mm001, Mm002, Mm005, and Mm004 are given for each location.