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A genetic study of population structure in Atlantic walrus:  
Where do the Canadian walrus fit in?

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## Summary

Genetic analyses comparing samples from 70 walrus from Hudson Bay and Hudson Strait (Canada) with previously analysed samples from W Greenland, NW Greenland, E Greenland, Svalbard and Franz Joseph land indicated (1) the existence of two major complexes of walrus consisting of three sub-populations to the west of Greenland (E Hudson Bay/Hudson Strait, W Greenland, NW Greenland) and two sub-populations to the east of Greenland (E Greenland and Svalbard-Franz Joseph Land); (2) that walrus from the E Hudson Bay/Hudson Strait area are genetically different from W Greenland walrus; (3) that walrus from the E Hudson Bay/Hudson Strait area are more closely related to those wintering in W Greenland than to those occurring nearly all-year round in NW Greenland (the NOW sub-population); (4) that the walrus in E Hudson Bay/Hudson Strait area seem to function as a source for the W Greenland walrus; (5) that walrus from the E Hudson Bay/Hudson Strait area probably have been separated from the NW Greenland walrus for a longer period of time compared to W Greenland walrus; (6) that walrus from East Greenland constitute a separate sub-population with limited connection to the Franz Joseph Land- Svalbard sub-population.

## Introduction

This report presents the preliminary results of a study in which samples from Atlantic walrus (*Odobenus rosmarus rosmarus* L.) from the SE Hudson Bay and Hudson Strait areas (Canada) are compared genetically to samples from W Greenland, NW Greenland, E Greenland, Svalbard and Franz Joseph Land. The study in particular aims at determining to what extent groups of walrus that currently under exploitation in the eastern Canadian Arctic and W and NW Greenland are genetically distinct and therefore can be regarded as different sub-populations.

## Background

The current distribution and movement of Atlantic walrus indicate that 8 sub-populations (or populations) exist. Of these, 5 are distributed along western Greenland and in the eastern parts of Arctic Canada, while the other 3 are distributed in East Greenland, Svalbard-Franz Joseph Land and the Kara-Sea-southern Barents Sea areas (Born et al. 2001, Born et al. 1995).

So far, three studies have concentrated on determination of the genetic relationship among two of the sub-populations to the east of Greenland (i.e. East Greenland and Svalbard-Franz Joseph Land) and two of the sub-populations to the west of Greenland (Central West Greenland and NW Greenland; this latter is also referred to as the North Water sub-population)(Andersen et al. 1998, Andersen & Born 2000, Born et al. 2001).

The studies involved analyses of both restriction fragment length polymorphism (RFLP) of the NADH genes in mtDNA and of 12 nuclear DNA microsatellite markers.

The main results of the three studies indicated that at the mtDNA level no difference was observed amongst the three sub-populations east of Greenland (Andersen et al. 1998), while a significant differentiation was observed between the NW Greenland (North Water) and the West Greenland sub-populations when testing both for differences in haplotype distribution and when the evolutionary distance between haplotypes was accounted for. These results suggested a rather restricted female gene flow between the W and the NW Greenland sub-populations and that they have been separated for many generations (Andersen & Born 2000).

At the nuclear level, the variation at the microsatellite loci grouped the samples from east of Greenland into two significantly different sub-populations, an East Greenland and a Svalbard-Franz Joseph Land sub-population (Andersen et al. 1998). Also the two sub-populations to the west of Greenland were found to differ significantly at the nuclear level, and the hypothesis of the existence of a common sub-population of walrus in the W Greenland area (Attu-Sisimiut) and NW Greenland area was rejected (Andersen & Born 2000). When merging and re-analysing the data in Andersen et al. (1998) and Andersen & Born (2000), four genetically differentiated sub-populations were observed (i.e. NW Greenland, W Greenland, E Greenland and Svalbard-Franz Joseph Land) (Born et al. 2001).

The fact that some of the specific haplotypes that characterise walrus to the east and to the west of Greenland, respectively, were found in the Attu-Sisimiut sample (W Greenland) suggested a genetic connection between the Attu-Sisimiut area and both the NW and the E Greenland walrus. Furthermore, some of the multilocus genotypes (across the 12 DNA microsatellite loci) found in the West Greenland walrus were also seen in few NW and E Greenland walrus. Given that perhaps less than 1000 walrus winter in the Attu-Sisimiut area (Born et al. 1995, Witting and Born submitted), the relatively high genetic variation observed at both the mitochondrial and the nuclear level in walrus from the Attu-Sisimiut area could be explained if (1) there had been a recent mixture of walrus from W and E Greenland, and/or (2) if walrus wintering in the Attu-Sisimiut area are connected with the N Labrador-SE Baffin Island-Hudson Strait-N Hudson Bay sub-population as suggested by Born et al. (1994, 1995). Hypothesis (2) is addressed in the present study, where the genetic variation at the 11 DNA microsatellite (Andersen et al. 1998; Andersen & Born 2000) was analysed in samples of walrus from Hudson Strait (n=36) Hudson Bay (n=34) in Canada.

## **Materials and methods**

Samples of tongue tissue of a total of 70 Atlantic walruses (*Odobenus rosmarus rosmarus* L.) from eastern Hudson Bay and Hudson Strait (Canada)(Figure 1) were taken by Canadian Inuit during their subsistence catch in the period 1998-2000. DR. W. Doidge (Makivik Cooperation) provided the samples for this study. The samples were frozen at  $-20^{\circ}\text{C}$  until analysed in the laboratory of National Environmental Research Institute (Silkeborg, Denmark).

DNA was extracted using a modified CTAB-buffer method (Milligan 1992) including proteinase K. The 11 microsatellite primers used and their PCR conditions are given in Andersen et al. (1998) and Andersen & Born (2000). For detection of the microsatellite loci, one of the primers was labelled with fluorescent dyes and analysed on an ABI 377 prism sequencer.

The E Greenland sample analysed in Andersen et al. (1998) was supplemented with skin biopsies from 48 different walruses from Young Sound (ca.  $74^{\circ}10' \text{N}$ ) taken in 1999 and 2002. These specimens were not genetically different from the previously analysed E Greenland samples (data not shown) and hence all E Greenland data were pooled.

## Data analyses

The analyses presented here include; (1) Genetic variation estimated as observed and expected heterozygosity and number of alleles per locus (Nei 1987). Tests for goodness of fit to the Hardy-Weinberg expectations were performed in GENEPOP (Raymond & Rousset 1995) based on the hypothesis of heterozygote deficiency and in FSTAT (Goudet 1995). Significant values were computed using Fisher's exact test (Guo & Thomsen 1992); (2) The number of sub-populations represented in the combined sample from all areas was analysed by pooling all, and assuming that they have originated from 2 to 8 population without using prior information of sample origin (STRUCTURE, Pritchard et al. 2000). The degree of population differentiation was analysed by testing for homogeneity of allele frequencies among populations using GENEPOP, and by  $F_{ST}$  and  $R_{ST}$  estimates (Weir & Cockerham 1984, Michalakis & Excoffier 1996). The  $F_{ST}$  and  $R_{ST}$  estimates were permuted 10,000 times and tested using ARLEQUIN (Schneider et al. 1997); (3) The direction and rate of migration over the last generations and migrant ancestries among walruses from the Hudson Bay- Hudson Strait area and from W and NW Greenland was estimated in BAYESASS (Wilson and Rannala 2003) (4) The spatial genetic distance was estimated using the Cavalli-Sforza & Edwards (1967) chord distance,  $D_C$ , after bootstrapping (1000 randomisations) in SEQBOOT and running GENDIST in PHYLIP (Felsenstein 1993); (4) The Neighbor-Joining (NJ) trees based on genetic distance and the pair-wise multilocus  $F_{ST}$  estimates were constructed using the TREEVIEW (Page 1996).The sequential Bonferroni procedure was applied table wide at the 5% significance level (Rice 1989)

## Preliminary results and discussion

First it was analysed whether there was a sub-structure within the 70 samples of Canadian walruses. The total sample was sub-divided according to individual sampling locations into a Hudson Strait sample (n=36) and Eastern Hudson Bay sample (n=34). A test for goodness of fit to the HWE when sub-dividing the samples revealed no *overall* deviation from HWE was observed in any of the two samples or the pooled Canadian sample (Table 1). Hence, the populations structure within the combined Canadian sample was analysed first by testing for homogeneity of the allele frequency distributions and then by  $F_{ST}$  and  $R_{ST}$  estimates between the Hudson Strait and Eastern Hudson Bay samples (Table 2). No significant difference in allele

frequency distributions was observed, nor did the  $F_{ST}$  estimate (or the  $R_{ST}$  estimate, not shown) deviate significantly from 0.

These results indicated that the sample of walruses from Hudson Strait and Eastern Hudson Bay probably belong to the same group of walruses.

Based on this assumption the relationship between the Canadian walruses and the walruses in NW, W, E Greenland, Svalbard and Franz Joseph Land was investigated (Table 3). An *a priori* assumption was that the entire sample of 309 walruses originated from 2 to 8 sub-populations, but no assumptions were made about the origin of the specimens. Bayesian clustering analysis indicated that five genetically distinct sub-populations existed: (1) E Hudson Bay-Hudson Strait, (2) W Greenland, (3) NW Greenland, (4) E Greenland, and (5) Svalbard-Franz Joseph Land (Table 4). Whereas the identification of the four latter groups confirms previous studies (Andersen et al. 1998, Born et al. 2001), the finding that walruses from E Hudson Bay-Hudson Strait differ genetically from walruses in the other areas, including W Greenland, is novel.

The genetic difference between the Canadian and W Greenland sub-populations was small ( $F_{ST}$  estimate significant (Table 5) but the  $R_{ST}$  estimate non-significant, (0.004,  $p=0.2399$ )), close to the levels observed between Svalbard and Franz-Joseph-Land areas in which walruses likely constitute one sub-population (Wiig et al. 1996, Andersen et al. 1998, Born et al. 2001) (Table 5). However, the Bayesian cluster analyses identified W Greenland as a separate sub-population, while Svalbard and Franz Joseph Land were not separated.

The population structure estimates furthermore suggested a closer genetic relationship between the Canadian and W Greenland walruses than between the Canadian and NW Greenland walruses. This was reflected especially by the  $R_{ST}$  estimate that was lower and insignificant compared to the  $F_{ST}$  estimate between Canada and W Greenland (Table 5), while it was almost twice as high ( $R_{ST}=0.098$ ,  $p<0.0001$ ) as the  $F_{ST}$  estimate and significant between Canadian and NW Greenland walruses.

The significant allele-frequency differences observed between all five sub-populations (Svalbard and Franz Joseph Land considered one) (Table 6) showed that the greatest number of significantly different loci was observed in the comparison of the Canadian walruses with walruses from E Greenland and Svalbard-Franz Joseph Land, respectively. The smallest number of significantly different loci was observed between Svalbard and Franz Joseph Land, and between those two areas and E Greenland. This was not surprising given the distances between the locations and the considerations that Svalbard and Franz Joseph Land belong to the same sub-population. When compared with the W and NW Greenland walruses the Canadian walruses showed identical levels of significantly different number of loci. However, the second allele at the *Igf-1* locus that earlier *only* was observed in the NW Greenland walruses was also observed in the Canadian walruses, and at very much identical frequency (data not shown). This indicated that there probably are some exchanges between the walruses in the two areas, which was analysed looking at the migration direction and rates among the five sub-populations using a Bayesian multilocus genotyping method (Wilson and Rannala 2003).

The results of the migration analysis indicated an asymmetric migration direction (Table 7) - the migration rates into the areas west of Greenland were: from NWGR to W Greenland 0.011; from Hudson Bay/Strait to W Greenland 0.278 and from Hudson Bay/Strait to NW Greenland 0.071 (all S.D.  $<0.05$ , Table 7). The Canadian sub-population functions as a source for the West Greenland sub-population. However, given the estimated population size of ca. 1000 in W Greenland (Witting and Born submitted) the estimated migration rate (Table 7) from Canada to W

Greenland would be 278 individuals/generation which is probably an overestimation, as not all sub-populations in the area have been analysed.

In the areas east of Greenland the analysis indicated that Svalbard could function as a source for the Franz Joseph Land sub-population but further analysis (data not shown) suggested that this may as well be vice-versa probably due to the fact that they belong to the same sub-population. The results also indicated that East Greenland walrus represent a sub-population with little migration from Franz Joseph Land-Svalbard.

The total distribution of the posterior probability of non-immigrants, first-generation and second-generation immigrants from W and NW Greenland, and Hudson Bay/Strait showed a high assignment proportion of non-immigrants in the NW Greenland and Canadian samples (Fig. 2 a, c). The W Greenland sample showed a high proportion of individuals with first- and second-generation immigrant ancestry from Canada (Fig 2 b). Thus migration has been low into the NW Greenland and Canadian sub-populations from the areas examined whereas the W Greenland walrus sub-population has apparently experienced constant migration from Canada. The source and ancestry of individuals sampled in the W Greenland is most likely first or second-generation migrants from Canada (Figure 2). This may reflect male-only migration or a whole seasonal movement of walrus in the west of Greenland since the second-generation immigrants represents offspring of migrants and non-migrants.

To the east of Greenland (Figure 2 d,e,f,g) the assignment proportions indicated that the walrus sampled in 1999-2003 were first generation migrants from walrus sampled in 1989-1993 which was expected as there are descendants. It also suggested that most of the individuals sampled on Franz Joseph Land could be first and second generation migrants from Svalbard, which corroborated with the suggestion that walrus from those two areas constitute the same sub-population and results from satellite studies (Wiig et al. 1996) that showed the travelling of males from Svalbard to Franz Joseph Land.

To illustrate the genetic relationship between the five putative sub-populations/populations (i.e. Hudson-Bay-Hudson Strait, W Greenland, NW Greenland, E Greenland and Svalbard-Franz Joseph Land) (only EGR individuals from 1989-1993 were included) the genetic distance was depicted in a NJ tree on allele frequencies, and a NJ tree obtained from the multilocus pair-wise  $F_{ST}$ -estimates (Figure 3). Both trees divided the walrus into two major clusters according to the geography, i.e. to the east and west of Greenland supporting earlier findings by Andersen et al. (1998) and Born et al. (2001). Furthermore, the  $D_C$  distance illustrated that walrus from Hudson-Bay-Hudson Strait were slightly more closely related to the W Greenland walrus than to the NW Greenland walrus. This relationship was also apparent from the  $F_{ST}$  estimates depicted in Figure 3.

## **In conclusion:**

### **The preliminary analyses indicated:**

- (1) The existence of two major complexes of walrus consisting of three sub-populations to the west of Greenland (E Hudson Bay/Hudson Strait, W Greenland, NW Greenland) and two sub-populations to the east of Greenland (E Greenland and Svalbard-Franz Joseph Land).
- (2) That walrus from the E Hudson Bay/Hudson Strait area are genetically different from W Greenland walrus.

- (3) That walrus from the Hudson-Bay-Hudson Strait area are more closely related to those wintering in W Greenland than to those occurring nearly all-year round in NW Greenland (the NOW sub-population).
- (4) That the walrus in E Hudson Bay/Hudson Strait area seem to function as a source for the W Greenland walrus.
- (5) That walrus from the Hudson Area probably have been separated from NW Greenland walrus for a longer period of time compared to W Greenland walrus.
- (6) That walrus from East Greenland constitute a separate sub-population with limited connection to the Franz Joseph Land- Svalbard sub-population.
- (7) Future analyses should include samples from especially N Labrador-SE Baffin Island, as we do not know how the W Greenland walrus are connected to the N Labrador-SE Baffin Island walrus.

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Table 1. Observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosity, number of alleles ( $A$ ), and tests for goodness of fit to the Hardy-Weinberg expectations ( $F_{IS}$ ) performed by testing for heterozygosity deficiency in GENEPOP (Raymond & Rousset 1995) in walrus samples from Hudson Strait and Hudson Bay (Canada), West Greenland (WG) (Attu Sissimiut area), North West Greenland (North Water area), East Greenland, Svalbard and Franz Joseph Land area.

	<i>Hg 6.1</i>				<i>ORR7</i>				<i>ORR3</i>				<i>SGPV9</i>				<i>ORR16</i>								
	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$					
<b>Hudson Strait</b>	<b>0.167</b>	<b>0.204</b>	<b>3</b>	<b>0.18</b>	<b>0.833</b>	<b>0.838</b>	<b>11</b>	<b>0.01</b>	<b>0.556</b>	<b>0.696</b>	<b>4</b>	<b>0.20</b>	<b>0.583</b>	<b>0.647</b>	<b>4</b>	<b>0.10</b>	<b>0.778</b>	<b>0.841</b>	<b>8</b>	<b>0.08</b>					
<b>Hudson Bay</b>	<b>0.235</b>	<b>0.349</b>	<b>4</b>	<b>0.33*</b>	<b>0.912</b>	<b>0.899</b>	<b>14</b>	<b>-0.01</b>	<b>0.559</b>	<b>0.619</b>	<b>6</b>	<b>0.10</b>	<b>0.548</b>	<b>0.650</b>	<b>3</b>	<b>0.16</b>	<b>0.824</b>	<b>0.843</b>	<b>8</b>	<b>0.02</b>					
<b>Canada total</b>	<b>0.200</b>	<b>0.275</b>	<b>4</b>	<b>0.27*</b>	<b>0.871</b>	<b>0.873</b>	<b>14</b>	<b>0.002</b>	<b>0.557</b>	<b>0.659</b>	<b>6</b>	<b>0.15</b>	<b>0.567</b>	<b>0.643</b>	<b>4</b>	<b>0.12</b>	<b>0.800</b>	<b>0.841</b>	<b>9</b>	<b>0.05</b>					
WG	0.212	0.197	3	-0.08	0.879	0.556	11	-0.03	0.827	0.767	6	0.05	0.636	0.702	5	0.09	0.818	0.825	10	0.02					
NW Green	0.500	0.523	5	0.04	0.833	0.855	13	0.03	0.750	0.778	8	0.04	0.556	0.694	7	0.20*	0.778	0.801	10	0.03					
E Green	0.429	0.389	3	-0.10	0.679	0.783	8	0.13	0.714	0.720	4	0.01	0.643	0.752	5	0.15	0.750	0.723	7	-0.04					
Svalbard	0.179	0.552	5	0.68*	0.893	0.830	10	-0.08	0.964	0.819	8	-0.18	0.571	0.746	6	0.24	0.714	0.821	7	0.13*					
FJL	0.138	0.167	4	0.17	0.633	0.830	9	0.24	0.867	0.807	7	-0.07	0.733	0.753	6	0.03	0.862	0.859	8	-0.004					
	<i>HGDii</i>				<i>ORR24</i>				<i>ORR23</i>				<i>Igf-I</i>				<i>ORR11</i>				<i>ORR9</i>				N
	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	$H_o$	$H_e$	$A$	$F_{IS}$	
<b>Hudson Strait</b>	<b>0.278</b>	<b>0.302</b>	<b>6</b>	<b>0.08</b>	<b>0.750</b>	<b>0.726</b>	<b>6</b>	<b>-0.03</b>	<b>0.722</b>	<b>0.841</b>	<b>10</b>	<b>0.14</b>	<b>0.143</b>	<b>0.229</b>	<b>2</b>	<b>0.38</b>	<b>0.556</b>	<b>0.529</b>	<b>6</b>	<b>-0.05</b>	<b>0.778</b>	<b>0.687</b>	<b>5</b>	<b>-0.13</b>	<b>36</b>
<b>Hudson Bay</b>	<b>0.441</b>	<b>0.425</b>	<b>6</b>	<b>-0.04</b>	<b>0.882</b>	<b>0.754</b>	<b>7</b>	<b>-0.17</b>	<b>0.882</b>	<b>0.861</b>	<b>11</b>	<b>-0.03</b>	<b>0.294</b>	<b>0.295</b>	<b>2</b>	<b>0.003</b>	<b>0.647</b>	<b>0.582</b>	<b>6</b>	<b>-0.11</b>	<b>0.500</b>	<b>0.688</b>	<b>5</b>	<b>0.27</b>	<b>34</b>
<b>Canada total</b>	<b>0.357</b>	<b>0.362</b>	<b>7</b>	<b>0.01</b>	<b>0.814</b>	<b>0.736</b>	<b>7</b>	<b>-0.11</b>	<b>0.800</b>	<b>0.852</b>	<b>13</b>	<b>0.06</b>	<b>0.217</b>	<b>0.260</b>	<b>2</b>	<b>0.17</b>	<b>0.600</b>	<b>0.554</b>	<b>6</b>	<b>-0.08</b>	<b>0.643</b>	<b>0.689</b>	<b>5</b>	<b>0.07</b>	<b>70</b>
WG	0.242	0.222	4	-0.09	0.636	0.760	6	0.17	0.848	0.861	10	0.01	-	-	1	-	0.758	0.755	7	0.01	0.545	0.758	5	0.26	33
NW Green	0.389	0.382	7	-0.02	0.708	0.750	6	0.06	0.819	0.830	13	0.01	0.250	0.298	2	0.16	0.431	0.532	8	0.19	0.608	0.673	6	-0.07	72
E Green	0.143	0.259	3	0.45*	0.893	0.823	7	-0.08	0.750	0.721	7	-0.04	-	-	1	-	0.500	0.589	5	0.15	0.750	0.732	5	-0.02	28
Svalbard	0.607	0.416	3	0.31*	0.607	0.688	4	0.12	0.789	0.886	14	0.12	-	-	1	-	0.714	0.737	5	0.03	0.679	0.751	5	0.09	28
FJL	0.300	0.411	3	0.27	0.600	0.780	7	0.23	0.733	0.847	11	0.14	-	-	1	-	0.733	0.733	6	-0.001	0.733	0.769	5	0.05	30
	$H_o$ av.	SD	$H_e$ av.	SD	$F_{IS}$ overall																				
<b>Hudson Strait</b>	<b>0.622</b>	<b>0.231</b>	<b>0.622</b>	<b>0.200</b>	<b>0.021</b>																				
<b>Hudson Bay</b>	<b>0.572</b>	<b>0.246</b>	<b>0.584</b>	<b>0.235</b>	<b>0.001</b>																				
<b>Canada total</b>	<b>0.596</b>	<b>0.231</b>	<b>0.603</b>	<b>0.217</b>	<b>0.010</b>																				
WG	0.570	0.281	0.597	0.298	0.046																				
NW Green	0.608	0.189	0.633	0.185	0.040																				
E Green	0.555	0.269	0.570	0.260	0.027																				
Svalbard	0.571	0.291	0.637	0.258	0.103																				
FJL	0.567	0.283	0.612	0.295	0.074																				

\*= significant at the 5% level after application of the sequential Bonferroni procedure



Table 2. Results of the multilocus pairwise test for allele frequency differences between walrus sampled in Hudson Bay and Hudson Strait.  $X^2$  value (df=24) for the allele frequency differences are estimated in GENEPOP (Rousset & Raymon 1995). Result of the pairwise multilocus  $F_{ST}$  test between the two Canadian walrus samples is estimated in FSTAT (Goudet 1995).

Hudson Strait - Hudson Bay	Allele frequencies:	$X^2 = 24.03$ , $p = 0.46$
Hudson Strait - Hudson Bay	Multilocus $F_{ST}$ :	$F_{ST} = -0.0013$

Table 3. Summary of samples used for genetic analysis from eastern Canada, Greenland and Franz Joseph Land. Putative stock numbers from Born *et al.* (1995) and Figure 1.

Region	Putative Stock	N	Abbreviation in text	Source
Foxe Basin <sup>1</sup>	1	-	-	
Eastern Hudson Bay	2	34	HBHS	New material 1998-2000
Hudson Strait	3	36		
West Greenland	4	33	WGR	a
Northwest Greenland	5	72	NWGR	a
East Greenland	6	76	EGR	a, new material 1999-2000
Svalbard	7	28	SVA	a
Franz Joseph Land	8	30	FJL	a
Total		309		

<sup>1</sup>Foxe Basin subpopulation recognized by Born *et al.* (1995) but not included in the present study

a) Born *et al.* 2001

Table 4. Identification of the five sub-populations of Atlantic walrus based on the highest log-likelihood estimate suggested by STRUCTURE (Pritchard *et al.* 2000) without using prior population information. The number of individuals assigned to the five suggested sub-populations is given and the populations identified (Suggested populations).

Suggested populations	NWGR	WGR	CAN	EGR-tot	FJL	SVA
1) North West Greenland	50	1	0	0	4	1
2) West Greenland	12	26	11	0	1	3
3) Canada (E Hudson Bay, Hudson Strait)	7	5	57	2	2	4
4) East Greenland	0	1	0	72	2	1
5) Franz Joseph Land- Svalbard	3	0	2	2	21	19
N	72	33	70	76	30	28

Table 5. Results of the pair-wise multilocus  $F_{ST}$  tests for genetic differences between the five putative sub-populations of Atlantic walrus from the Canadian area ( E Hudson Bay and Hudson Strait),NW Greenland, W Greenland, Et Greenland and the Svalbard-Franz Joseph Land area. Figures in brackets gives the 95%CI. All tests performed in FSTAT after 10000 permutations (Goudet 1995)

	NWGR	WGR	HBHS	EGR	FJL
West Greenland	<b>0.0352</b> (0.021-0.052)				
E Hudson Bay/Hudson Strait	<b>0.0483</b> (0.028-0.066)	<b>0.0218</b> (0.019-0.068)			
E Greenland	<b>0.0685</b> (0.039-0.112)	<b>0.0482</b> (0.027-0.068)	<b>0.0693</b> (0.048-0.094)		
Franz Joseph Land	<b>0.0464</b> (0.030-0.065)	<b>0.0270</b> (0.012-0.042)	<b>0.0379</b> (0.023-0.056)	<b>0.0373</b> (0.020-0.054)	
Svalbard	<b>0.0604</b> (0.037-0.086)	<b>0.0405</b> (0.019-0.068)	<b>0.0408</b> (0.022-0.064)	<b>0.0538</b> (0.048-0.094)	<b>0.0242</b> (-0.005-0.063)

Table 6. Results of the genetic differences based on the number of loci with significant different allele frequencies after sequential Bonferroni corrections. Figures are the number of loci with significant different allele distributions observed between the areas in question.

	NW Greenland	W Greenland	Hudson Bay and Strait	E Greenland	FJL
West Greenland	9				
E Hudson Bay and Hudson Strait (Canada)	10	10			
E Greenland	10	9	12		
Franz Joseph Land (FJL)	10	8	12	5	
Svalbard	10	9	11	6	3

Table 7. Means of the posterior distribution of migration rates (m) into three sub-populations of Atlantic walrus west of Greenland. The sub-populations where individuals migrated from are given in columns while populations where individuals were **sampled** are given in rows.

	NWGR	WGR	CAN	EGR-tot	FJL	SVA
North West Greenland	<b>0.908</b>	0.003	0.071	0.010	0.002	0.006
West Greenland	0.011	<b>0.678</b>	<b>0.278</b>	0.021	0.005	0.007
E Hudson Bay/Hudson Strait	0.001	0.002	<b>0.993</b>	0.001	0.001	0.002
East Greenland	0.002	0.001	0.002	<b>0.993</b>	0.001	0.001
Franz Joseph Land	0.010	0.005	0.011	0.033	<b>0.677</b>	<b>0.263</b>
Svalbard	0.008	0.004	0.026	0.007	0.004	<b>0.951</b>

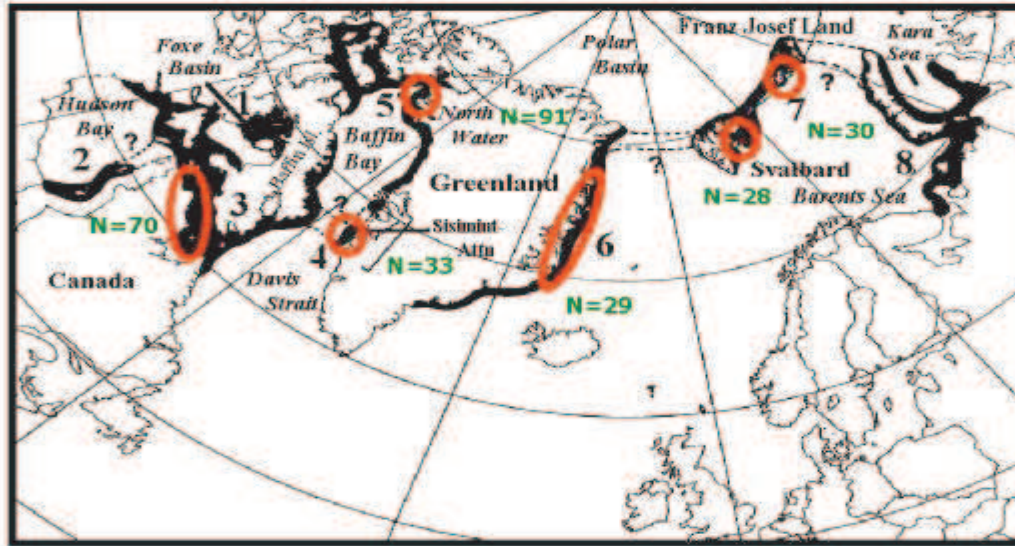


Figure. 1. Map showing the putative sub-populations of Atlantic walrus based on current distribution and information on movement (Born et al. 1995, Born et al. 2001): 1 Foxe Basin, 2 southern and eastern Hudson Bay, 3 northern Hudson Bay-Hudson Strait-southeastern Baffin-Northern Labrador, 4 W Greenland, 5 NW Greenland(North Water Baffin Bay-eastern Canadian Arctic), 6 East Greenland, 7 Svalbard-Franz Josef Land, and 8 Kara Sea-southern Barents Sea-Novaya Zemlya. *Question marks* indicate potential connections between populations based on animal movement information (cf. Born et al. 1995, Born et al. 2001)

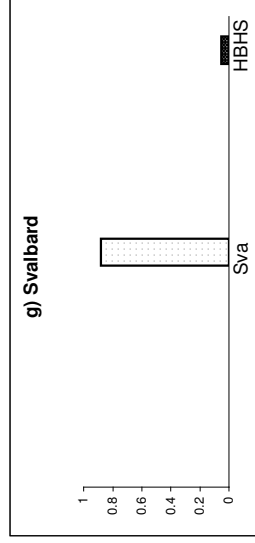
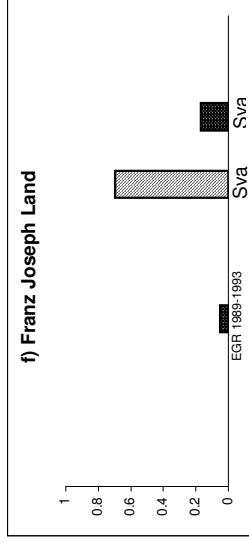
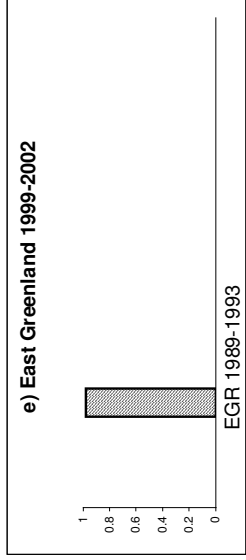
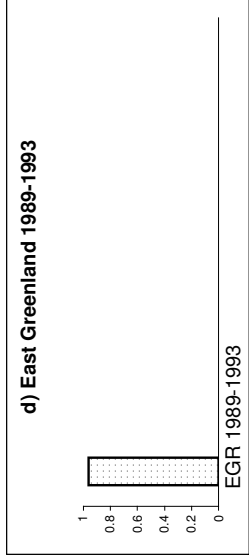
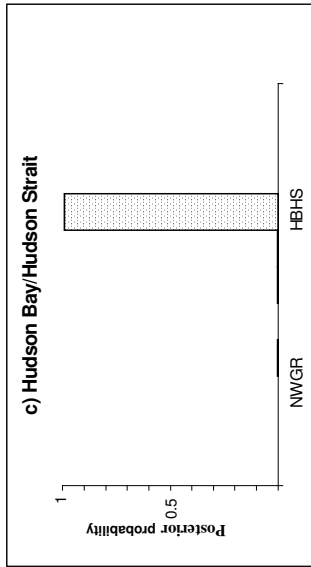
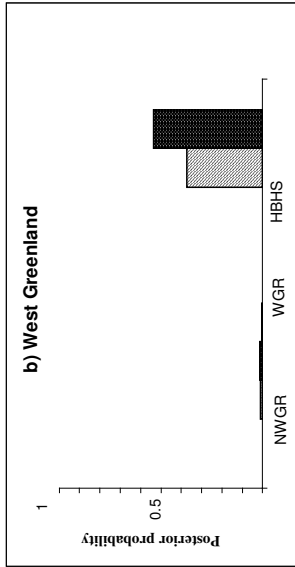
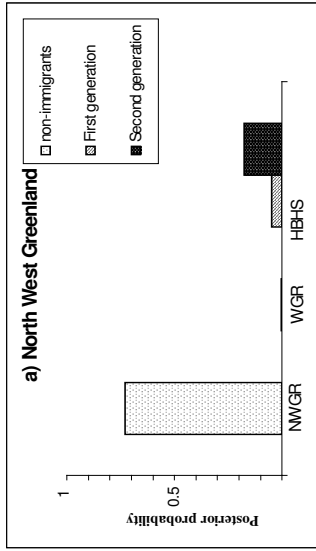
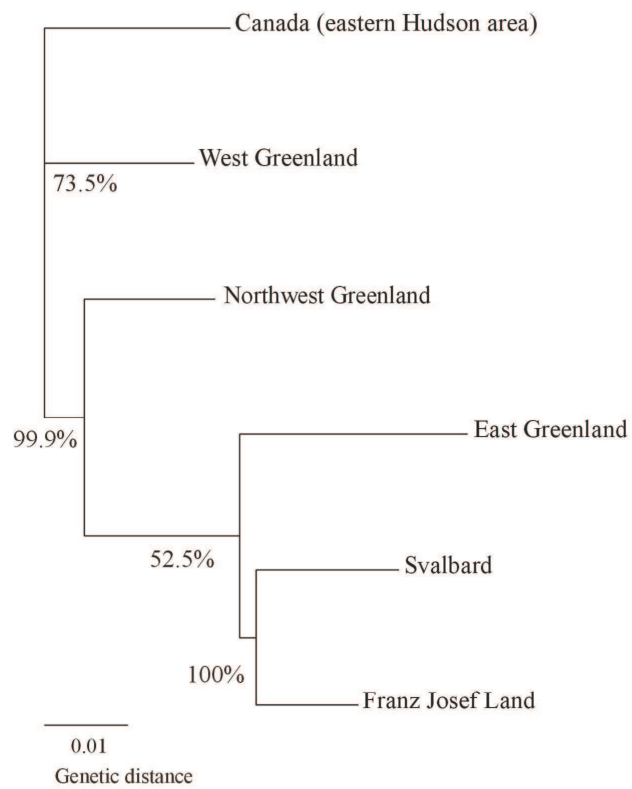


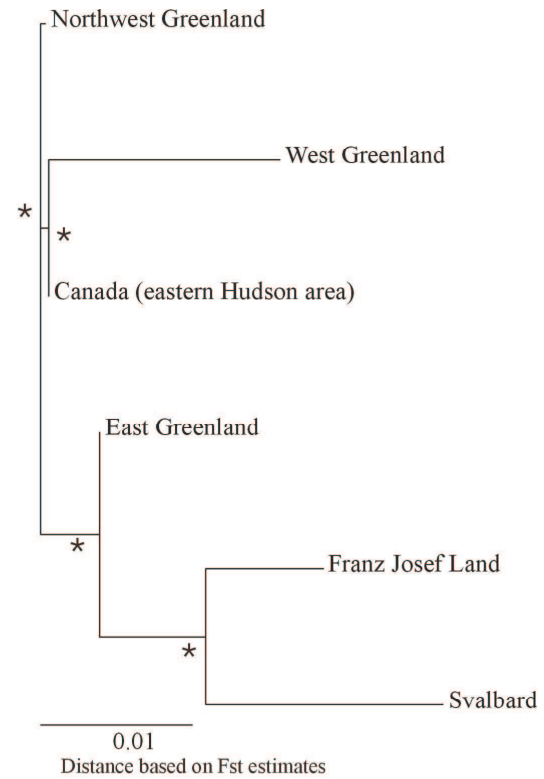
Figure 2. Posterior probability of non-immigrants, first- and second-generation immigrants observed in the five samples of walruses from North West Greenland, West Greenland, Hudson Bay/Strait, East Greenland and FJL-SVA (Wilson and Rannala 2003).

immigrants observed in the five samples of walruses from North West Greenland, Rannala 2003).



Neighbor-Joining tree based on Cavalli-Sforza & Edward's (1967) chord distance obtained from allele frequencies and bootstrapping 1000 times. Numbers at the nodes indicates the number of times the groups clustered together out of the 1000 trees

a)



Neighbor-Joining tree based on multilocus pairwise  $F_{ST}$ -estimates. \* indicates that pairwise  $F_{ST}$  (see table 3) is significantly different from 0 at the 5% level and after sequential Bonferroni correction.

b)

Figure 3. Neighbor-Joining trees based on Cavalli-Sforza & Edward's (1967) chord distance obtained from allele frequencies a) and on  $F_{ST}$  estimates b).