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A GENETIC COMPARISON OF WEST GREENLAND AND BAFFIN ISLAND (CANADA) WALRUSES: MANAGEMENT IMPLICATIONS

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Abstract

Walruses are subject to relatively intense exploitation in West Greenland. However, the demographic identity of the exploited stock and it's connection with walruses in neighbouring areas is not fully known, hampering the determination of sustainable harvest levels. It has been suggested that walruses in West Greenland are connected with walruses at SE Baffin Island (Canada) where they are also hunted for subsistence purposes. To determine the relationship between walruses in these two areas we conducted a genetic analysis including recent samples from West Greenland , the Davis Strait-Baffin Bay region (i.e. Southeast Baffin Island), Hudson Strait in Canada, and Northwest Greenland. Seventeen microsatellite markers were applied to all samples. Samples from West Greenland and Southeast Baffin Island were also analysed using D-loop variation. Walruses in West Greenland and at Southeast Baffin Island did not differ from each other but differed from both Northwest Greenland and East Hudson Strait walruses, genetically. The findings support the notion that there are subunits within the range of walruses in the Hudson Strait-Davis Strait-Baffin Bay region, and indicate that sustainable catch levels in Southeast Baffin Island and in West Greenland must be set in the light of the finding that the same stock is exploited in these two areas.

Key words: Walrus, *Odobenus rosmarus*, stock identity, genetic comparison, DNA analysis, Canada, Greenland

INTRODUCTION

Walrus (*Odobenus rosmarus*) has been exploited by Arctic hunting cultures for millennia (Schledermann 1996). Traditionally, Arctic Inuit in many areas where walruses occur regularly depend on their meat for human consumption and dog food, and their ivory for making hunting implements (Born et al. 1995). The blubber was previously used for oil for heat and light (ibid).

Several life history traits of walruses make them an important resource to the marine hunting cultures in areas where walruses occur. They often occur abundantly in predictable areas such as restricted areas of open water surrounded by ice, polynyas, in winter and hauled out on land in summer. As primarily benthic feeders, they tend to live in shallow waters close to shore (e.g. Fay 1982, Born et al. 1995). However, these traits, coupled with relatively low reproductive rates and long generations (Witting and Born 2005) also make them vulnerable to overexploitation.

The subspecies of Atlantic walrus (*O.r. rosmarus*) living along the shores of Baffin Bay and Davis Strait and adjacent waters was traditionally exploited by Inuit for subsistence purposes (cf. Born et al. 1995) and were also heavily hunted by foreign commercial whalers between during the 19th Century until the 1930s (Ross and McIver 1982, Born et al. 1994, 1995). During the first half of the 20th Century the Inuit living in the Baffin Bay-Davis Strait area adopted modern hunting techniques involving the use of motorized vessels and firearms which not only led to higher catches but also to increased loss in the catch of walruses (Born et al. 1995). For example, in West Greenland south of ca. 70º N where the majority of Greenlanders live (e.g. Born and Böcher 2001), the technological change began in the early 1900s and the landed catch of walrus in West Greenland increased from about 70/year, to a peak around 1940 of more than 600 landed in some years (Born et al. 1994). Catches then declined markedly likely reflecting a decline in the exploited stock far below historical levels (Born et al.1994, 1995, Witting and Born 2005) with walruses abandoning their terrestrial haul-outs in Central West Greenland.

Currently, walruses are hunted in Canada including the Hudson Strait and SE Baffin Island areas, and in West and Northwest Greenland. Exploitation rates in West and Northwest Greenland in particularly are high and thought to be unsustainable (Born et al. 1994, 1995, Anon. 1995, Witting and Born 2005, NAMMCO 2006, COSEWIC 2006). To determine sustainable levels of exploitation in West Greenland, it is crucial to determine the demographical identity of walruses occurring in West Greenland.

We follow Stewart (2008 a) and adopt Secor´s (2005) definition that a stock is a specific part of a population impacted by human activity in a way that affects population productivity, with Ricker´s (1975) caveat to include potential utilization.

Walrus are distributed through the northern reaches of Hudson Bay to SE Baffin Island and to Central West Greenland Fig. 1. Based on information on distribution, migration and genetics, walruses in the Baffin Bay-Davis Strait region are thought to represent at least three separate stocks or sub-populations (Born et al. 1995, Andersen and Born 2000, Born et al. 2001, Andersen et al. in press, Stewart 2008a). One inhabits the waters of northern Hudson Bay and through Hudson Strait to southeast Baffin Island. Another occurs off the central coast of west Greenland. The third inhabits the coastal waters of northwest Greenland and the northern reaches of the Canadian Arctic Archipelago. In central West Greenland walruses occur at two disjunctive, near- shore feeding grounds in the Sisimiut-Aasiaat area ("Store Hellefiske Bank"; ca. 66º 30' and ca. 68º N) and off the west coast of Disko Island (ca. 69º and 70º 30 N) between fall and spring. In May, when sea ice starts melting, walrus leave western Greenland (Born et al. 1994). As they no longer haul out on land during summer in West (or Northwest) Greenland, they must migrate to summering grounds elsewhere. Genetic studies indicate that they have only limited – and mainly male mediated - contact with the population in Northwest Greenland (Andersen and Born 2000, Born et al. 2001,

Andersen et al. in press). Based on miscellaneous observations made in central Davis Strait during spring and early summer it was suggested that walruses migrate in spring ca. 450 km across Davis Strait from West Greenland towards SE Baffin Island (Born et al. 1994) to areas where walruses occur year round and are also hunted (Born et al. 1995, Stewart 2008a). Andersen et al. (in press) compared walruses sampled in West Greenland, Hudson Strait (in the present study called Northeast Hudson Bay) and in NW Greenland. They found that walruses from Hudson Strait differed genetically from walruses from West Greenland but apparently also to a certain extent served as a source for West Greenland walrus. No samples from SE Baffin Island walrus were available.

The aim of the present study was to test the hypothesized connection between West Greenland and Southeast Baffin Islands walruses (Born et al. 1995, Stewart 2008a). Hence, genetic analyses of samples from SE Baffin Island and from West Greenland were performed to test the hypothesis (H_0): Walruses that are being exploited in West Greenland do not differ genetically from those that occur at SE Baffin Island.

METHODS

Sampling in the field and laboratory analyses

Southeast Baffin Island (SEB) is represented by skin biopsies taken in the Hoare Bay area. Most biopsies were taken from unrestrained animals but a few biopsies were taken from chemically immobilized walrus used in satellite tracking studies (Stewart pers.comm). To obtain biopsies, teams of local hunters and scientists travelled by boat or helicopter (2005) to haul-out sites. Walrus herds were approached by stealth on land or slowly by boat to take biopsies from swimming walrus. Care was taken to neither tire the swimming animals nor separate calves from adults. Skin biospies were collected using arrows with a A*B mm (length*external diameter) biopsy tip fired from crossbows (Excalibur X newtons) or Pneudart biopsy darts with 20*5 mm tips fired from CO_2-powered guns. Walrus at seven island haul-out sites in Hoare Bay on SE Baffin Island were sampled in August 2005 and 2007. Eighteen biopsies were sampled in 2005 and 80 in 2007. The NEHB samples (58) (equivalent to the HS sample in Andersen et al. in press) were collected from the subsistence catch in Hudson Strait /Hudson Bay area as explained by Andersen *et al* (in press).The samples from SE Baffin Island were stored in 20% DMSO and saturated $NaCl_2$ solution then frozen at -20^{o}C until analysed.

West Greenland (WGR) samples were collected in 2004 to 2007 by science personnel, local hunters and the staff of the hospital in Sisimiut who collected muscle tissue samples (N=103) from the Greenlanders´ subsistence catch; 4 of these samples were from the Disko Island area and the remainder from the southern wintering ground south of ca. 68º N. The origin of the rest from West Greenland (33) is explained in Andersen et al. (1998). Northwest Greenland (NWGR) muscle samples (N=63) were obtained from walrus killed in the subsistence hunt in 1990 and 1991 (Andersen and Born 2000). The samples were frozen at –20^{o}C until analysed in the laboratory. All NEHB and NWGR samples and the 33 from WGR were previously analyzed by Andersen *et al.* 1998, Andersen and Born 2000, Born et al. 2001, Andersen et al. (in press) using 11 of the 17 microsatellite markers used in the present study (Table 1, Fig. 1).

The samples were analysed at the National Environmental Research Institute (Silkeborg, Denmark), Aarhus University.

DNA was extracted from all samples using a modified CTAB-buffer method (Milligan 1992) including proteinase K. Seventeen microsatellite markers were applied (Table 2) including the 11 had been previously used (Andersen et al. 1998 Andersen and Born 2000, Born et al. 2001, Andersen et al. in press). Another six polymorphic markers used were originally developed for grey

seal, *Halichoerus grypus* (*HG4.1*, *HG8.10*, Allen et al. 1995), Weddell seal, *Leptonycotes weddellii* (*LW20*, *LW15*, Davis et al. 2002), southern elephant seal *Mirounga leonina*, (*M11*, Gemmell et al. 1997) and harbour seal, *Phoca vitulina*, (*PV9*, Goodman 1997). The 17 markers were PCR multiplexed in three separate runs using the QIAGEN Multiplex PCR kit following the manufactures protocol and a 12.5 µl reaction volume and annealing temperature of 57º (QIAGEN). The PCR products were analysed using an ABI PRISM 377 DNA sequencer and subsequently genotyped. D-loop variation was quantified focussing on the samples from SE Baffin Island and the new WGR samples using the primers Odro1025L: 5' - ATGAATCGGAGGACAACC - 3' and CSB-CH: 5' CCACAGTTATGTGTGATCATG – 3 (H00019 in Talbot and Shields 1996) developed for the Pacific walrus, *O. r. divergens* (S.L. Talbot, Alaska Science Centre, Anchorage, Alaska, pers. comm. 2008) and sequencing both strands using MACROGEN Inc. The gender of the walrus from SE Baffin Island (2005, 2007) and West Greenland samples (2004, 2005, 2006, 2007) was determined using the method developed by Fischbach et al. (2008) (Table 1 and 2).

Data analysis

Before analysing the genetic data the biopsy samples were checked for incidental resampling of individuals. This was conducted by looking for matching genotypes amongst the 98 samples (collected in 2005 and 2007) taken from live walruses at SE Baffin Island using the Excel Microsatellite Toolkit (Park 2001) applying a minimum number of non-matching alleles of two (to account for genotyping error) required to reject a match. Recaptures were removed from subsequent analyses.

Genetic variation: Microsatellite and D-loop variation

Genetic variation was estimated as expected heterozygosity and allele richness in FSTAT (Goudet 1995). Tests for goodness of fit to the Hardy-Weinberg expectations (HWE) were performed in GENEPOP (Raymond and Rousset 1995) and significant values were computed using Fisher's exact test (Guo and Thompsen 1992). The breeding season in Atlantic walrus is during mainly January-April (Sjare and Stirling 1996, Born 2001, 2003) Most of the samples were collected outside the breeding season when there is some segregation by sex (Born et al. 1995, 1997, Gjertz and Wiig 1994, Stewart 2008a) and the sex ratios among areas was not uniform (Table 1). Females and males may have contributed differently to the amount of genetic variation in our samples. Therefore differences in genetic variation (allele richness) between the two sexes were estimated using a single factor ANOVA test. Tests for linkage disequilibrium between all pairs of loci were conducted for separate samples and analysed in FSTAT (Goudet 1995).

Sequences obtained from the SEB and WGR areas were analyzed using Sequencher version 4.2 (Gene Codes Corp. Ann Arbor, Michigan). Identical haplotypes among the 117 (Table 1) sequences were found using the POPSTR a software package developed by Siegismund (Pers. comm.). Variation in the D-loop was estimated as haplotype diversity (h) and nucleotide diversity (π) (Nei 1978) using ARLEQUIN (Schneider et al. 2000).

Population structure

The number of populations represented in the samples was estimated using a Markov chain Monte Carlo method that cluster individuals to minimise Hardy-Weinberg disequilibrium and gametic phase disequilibrium between loci (STRUCTURE version 2; Pritchard et al. 2000). The results of the tests were based on 1,000,000 iterations and three runs. All samples were pooled and assumed to have originated from one to eight populations without prior information on sample origin. The suggested structure, number of populations, is revealed by the increasing likelihood of the association. The clusters of individuals forming the number of populations with the highest

likelihood were assigned to sampling localities. The criteria used to assign individuals to a population were based on the estimated admixture proportion (q) and the 90% confidence interval (CI) of q from the run including all samples. Individuals with q > 0.568 and between 0.002-1 in 90% CI were assigned to their original sampling area. Individuals rejected from their sampling area had a q < 0.39 and 90% CI between 0-0.98. The remaining individuals in the suggested stocks were assigned according to the highest q, but with a wide, 0-1, 90% CI.

STRUCTURE requires some degree of genetic differentiation so the unbiased F_{ST} statistics (Weir and Cockerham 1984) were applied and performed in FSTAT (Goudet 1995) based on sampling location to analyse the degree of population differentiation. The analysis was performed using the total samples from the different sampling localities, stratified according to sex due to earlier suggestions of female philopatric behaviour.

The population structure of the walruses from SE Baffin Island and West Greenland based on D-loop variation was examined by conventional F-statistics from haplotype frequencies (Weir and Cockerham 1984) and by Φ statistics including a genetic distance between the haplotypes in the different sampling areas (Excoffier et al. 1992). The genetic distance used between the mtDNA sequences was Kimura 2-parameter (Kimura 1980) distance measure with the gamma-distribution correction estimated from the data (Kimura 1980, Jin and Nei 1990). These estimates were all run for 10,000 permutations over individual haplotypes among populations and tested using ARLEQUIN (Schneider et al. 1997) in the total samples from SE Baffin Island and West Greenland, partitioned according to sex.

Migration rates and direction

To estimate recent migration rates and direction between the sampling areas we employed a new Bayesian method based on multilocus genotypes implemented in BIMr (Bayesian Inference of Migration rates) (Faubet and Gaggiotti 2008). Based on information from the gametic disequilibrium that is generated by migration, the model assumes that sampling occurs after reproduction and before migration and infers the individual's population ancestry by assigning alleles to populations of origin. As recommended by the authors, we ran multiple analyses (20) of BIMr and compared their results to ensure that the MCMC chains converged.

Furthermore, we analysed the recent migration rates and directions keeping the sampling areas separate and after pooling the areas according to the results of the STRUCTURE analysis. The two scenarios (separate areas and pooling the areas) were analysed to investigate whether the scenarios reflected differences in the migration rates and directions. The individual and population assignments obtained from the BIMr analysis (keeping the sampling locations separate) (Faubet and Gaggiotti 2008) was plotted using DISTRUCT (Rosenberg 2004).

Detection of first generation migrants

Detection of first generation migrants was conducted using the assignment tests implemented in GENECLASS2 (Piry et al. 2004) that uses the individual's multilocus genotype likelihoods to identify population origin (Paetkau et al. 2004). The partial Bayesian method of Rannala and Mountain (1997) method was used to calculate the individual likelihoods of belonging to a certain population. The method uses allele frequencies to calculate the likelihood of the genotype occurring in the population by assuming the prior probability density to be equal to the allele frequencies of each locus in the population. This method assumes loci to be at Hardy-Weinberg equilibrium, linkage equilibrium, and that the observed allele frequencies are close to the exact frequencies in the population.

To detect first generation migrants in the walrus populations a likelihood computation L=L_home/L_max_not_home was used, describing the likelihood calculated from the home

population (L_home) of the individual compared to the highest likelihood value (L_max) among the population sampled where the home population of the individual was not included (Piry et al. 2004, Paetkau et al. 2004). Levels of significance were determined comparing the assigned individuals' genotypes with a simulated set (10,000) obtained using the allele-frequencies from the different areas (Paetkau et al. 2004). The exclusion probability (at the 5% level) of a population as origin and the probability of an individual to be a migrant are calculated based on the resampling algorithm by Paetkau et al. (2004).

The first-generation migrants detected were identified and their suggested location of origin was compared to the suggested origin obtained from STRUCTURE. The origin obtained from the STRUCTURE results was identified as the location with the highest Q (probability of belonging to the location) for the given individual.

Historical population demography

To determine historical demographic population fluctuations of the SE Baffin Island and West Greenland walrus groups, the neutrality of mutations in the control region was tested using Tajima's *D* test of selective neutrality (Tajima, 1989) and Fu's F_S (Fu 1997). Excess of low frequency mutations relative to expectations under the standard neutral model are indicative of a recent population growth and are detected as significantly negative values of Tajima's *D* and Fu's F_S. Large statistically significant positive values F_S indicate a deficit of rare haplotypes suggesting that the population has experienced a bottleneck.

The distribution of pairwise differences of nucleotide sequences (mismatch distribution) was also examined (Rogers and Harpending 1992). An unimodal distribution of pairwise nucleotide differences suggests the population has expanded recently or experienced a bottleneck because the individual nucleotide difference between the haplotypes for both scenarios shows identical divergence patterns (Slatkin and Hudson 1991, Rogers and Harpending 1992). If the distribution pattern is multimodal or "ragged" the population is expected to be stable or declining slowly (Slatkin and Hudson 1991). The mismatch distributions were tested statistically using test of goodness of fit between observed and expected distributions using the parametric bootstrap (1000) approach in ARLEQUIN. The test statistic used was the sum of square deviations (SSD) between observed and expected distributions, calculating P-values as the proportion of simulations producing a larger SSD than the observed SSD. The raggedness index was calculated to quantify the smoothness of the mismatch distribution and the significance was evaluated in ARLEQUIN similar to SSD. These tests were applied to WGR and SEB locations separately and to pooled locations.

Phylogeny

Phylogenetic relationships among the unique haplotypes were estimated using the software TCS (Clement *et al*. 2000), which is based on the statistical parsimony method of Templeton *et al*. (1992). This method links the haplotypes according to the smaller number of differences (mutations) defined by the 95% criterion and identifies the most probable ancestral haplotype. Gaps were set as the fifth state and the parsimony criterion at 95%.

Furthermore, the phylogenies of the haplotypes were estimated and depicted in a consensus tree of 1000 bootstrap replications constructed on the basis of Kimura 2-parameter distances (Kimura 1980) using SEQBOOT and DNADIST programs in the PHYLIP package (Felsenstein 2004). The consensus tree was constructed using the Neighbour-Joining method in this package.

The sequential Bonferroni procedure was applied using a significance level of 5% whenever multiple tests were performed to give table-wide significance levels (Rice 1989).

RESULTS

Sampling

The genetic analysis detected six individuals that were sampled twice and two that were sampled three times in the 2007 SE Baffin sample. A comparison with information from the field showed that four of the resampled individuals had been sampled in the water on the same day and location; one was sampled on the same day but at slightly different locations; and one was sampled on the same day, once on ice and later in the water at the same location. Of the two individuals sampled three times, one was sampled in the water on the same day and location while the other was sampled in the water on two different days and at two different locations. Replicate data were removed before analysing data further leaving the total sample from SE Baffin Island at 88 different individuals**.**

The sex ratios among samples differed significantly (Table 1, $\chi^2 = 10.01$, 3 d.f., $P<0.05$) attributable to the preponderance of males in the NEHB samples (NEHB removed: $\chi^2 = 2.69$, 2 d.f., $P>0.05$). Within areas, sex ratios were significantly different than 1:1, with biases towards females in overall samples from WGR and NEHB and in the D-loop samples from SEB and WGR (Table 1)

Genetic variation

Microsatellites

The expected heterozygosity in the total samples ranged from 0.612 in the NEHB sample to 0.654 in the WGR and SEB samples. Significant deviations from Hardy-Weinberg expectations were observed in the overall HWE tests only in the NWGR sample (Table 2). Separated by sex within regions, there were significant deviations from HWE only among females from NWGR. There were also individual alleles not in HWE: *SGPV9* locus in NWGR males; *Igf-I* locus SEB overall sample; *HGDii* locus in SEB males; and *M11* locus NEHB males (Table 2). , The allele richness observed in males was significantly higher than that in females from the different regions (Single factor ANOVA: $F_{df} = 43.46$, $P = 0.0005$). No linkage disequilibrium was observed between all pairs of loci within the different sampling areas (data not shown).

D-loop variation

A total of 117 individuals from West Greenland and SE Baffin Island were sequenced. The haplotype diversity, h, and nucleotide diversity, π, were 0.87 ±0.022 and 0.009 ±0.005 in the WGR sample and 0.91 ±0.017 and 0.009 ±0.005 in the SEB sample. Twenty segregating sites were observed in the 506-bp fragment representing 24 haplotypes (Table 3). None of the three Pacific walrus haplotypes was found in the Atlantic walruses analysed. Three of the eleven haplotypes observed in the WGR sample were unique to the area while 13 of the 21 haplotypes at SE Baffin Island were unique to SEB. Eight of the 24 haplotypes were shared among the areas and the three most common haplotypes were ODRR2, ODRR5 and ODRR6 (Table 3).

Population structure

STRUCTURE analysis indicated the presence of at least three stocks. NWGR and NEHB were identified while the third population was not clearly identified (Ln probability of data Ln P(D): *k=3, k=1 ln = -16787, k=2 ln= -16706, k=3 ln= -16821, k=4 ln= -16551*). The identified clusters in the 10 runs of *k*=3 all identified NWGR and NEHB but not WGR and SEB (Table 4, Fig. 2a). All 10 runs for *k*=4 to *k*= 8 identified NWGR and NEHB while the others were separated into clusters with no clear patterns. Partition into sex showed the same pattern (data not shown).

All multilocus pairwise F_{ST} estimates based on the total samples showed statistically significant differences except for the WGR and SEB comparisons. When stratified by sex, the female samples in these two areas (WGR and SEB) were significantly different while males were not. The pairwise F_{ST}-estimates over all loci ranged from 0.005 between WGR and SEB to 0.036

between SEB and NWGR (Table 5). When partitioning the samples according to sex the pairwise female samples exhibited a higher level of genetic differentiation compared to the pairwise male samples. Furthermore, the population structure analyses (Haplotype F_{st} and Haplotype Φ_{st} estimates, Table 5) based on the D-loop variation between the SEB and WGR samples did not detect significantly different genetic compositions.

Migration rates and direction

Analyses of migration rates and directions, keeping the sampling areas separate, showed high proportions of non-migrants in NWGR and NEHB, while WGR and SEB had relatively high proportions of migrants (Table 6a). The proportions of migrants from SE Baffin Island in the WGR sample and the proportion of migrants from WGR in the SE Baffin Island sample were similar. While both WGR and SEB also received a similar proportion from NWHB, NEHB received virtually no migrants from any of the other three areas**.** This pattern persisted after pooling the WGR and SE Baffin Island samples (Table 6b). Individual and population assignments obtained from BIMr based on the four sampling areas (Fig. 2b) also indicated that WGR and SEB were closely connected.

Detection of first generation migrants

Based on the results of the population structure analysis, the data from WGR and SEB were pooled (WGR/SEB). Overall, 30 walrus (20 male, 9 female, 1 unknown sex) were identified as first generation migrants, that is they were born someplace other than in the sampling area. Significantly more males were identified as first generation migrants compared to females (Prob(x>=20| p= 0.5, N=29) P = 0.03). In NWGR, six individuals (5 males and 1 female) were identified as putative first generation migrants (Table 7), twice as many as expected by chance (type 1 error, 5% of 63). Three were from WGR/SEB and three from NEHB. In the WGR/SEB sample, 16 individuals were identified as migrants (8 males, 7 females and one unknown sex). Eleven would be observed as migrants due to chance alone (5% of 224). Four were identified as migrants from NWGR and twelve from NEHB. In NEHB eight of the 58 individuals analysed were migrants (7 males and 1 female), all from WGR/SEB. Three would be detected by chance (5% of 58).

In the attempt to identify the true first generation migrants, the individual migrants suggested by GENECLASS 2 were identified in STRUCTURE. Ten of the 30 first generation migrants suggested by GENECLASS 2 were affiliated to another location by STRUCTURE. STRUCTURE identified six as migrants from WGR/SEB and not NEHB while four were identified as migrants from NEHB and not WGR/SEB as suggested by GENECLASS 2 (Table 7).

Historical population demography

Tests of the neutrality of mutations in the control region were non-significant (WGR: Tajima's D = 0.907, P= 0.83, Fu's F_S = 0.465, P= 0.61; SEB: = Tajima's D = -0.043, P=0.54, Fu's F_S = -4.2, P= 0.09; WGR/SEB: Tajima's D = 0.056, P= 0.54, Fu's F_S = -0.439, P= 0.126).

There was therefore no evidence of either recent population growth or a population bottleneck. Conversely, the mismatch distribution generated a pattern that was not statistically different from a unimodal curve (WGR: SSD= 0.041, P= 0.15, Rag. Id. = 0.048, P= 0.38; SEB: Baffin SSD= 0.019, P=0.41, Rag. ID. = 0.023, P=0.67, WGR/SEB: SSD= 0.024, P= 0.293, Rag. Id. = 0.026, P= 0.571) although the observed pattern appeared multimodal (Fig. 3). An unimodal pattern is characteristic of population expansion or a previous bottleneck. The moment estimator of the time to expansion for the pooled WGR/SEB sample was τ = 8.68 (95% CI: 0.89-16.65). The timing of the population expansion in years can be approximated using $\tau = 2$ ut, where u= μk, μ= mutation rate, k= sequence length. Assuming a mutation rate of 0.075 x 10^{-6} substitutions per site

per million years (Slade et al. 1998) and a generation time of 15 years (Andersen et al. in press) the expansion took place c. 7600 (782 – 14700) years ago.

Phylogeny
The phylogenetic relationship illustrated by the statistical parsimony network (TCS) showing the number of mutations relating the 24 haplotypes found in the Atlantic walrus and the three Pacific walrus sequences (Fig. 4a) identified ODRR6 as the ancestral haplotype. The phylogenetic relationship (Fig. 4b) based on Kimura 2-parameter genetic distance (Kimura 1980) separated the Pacific and Atlantic walruses into two clades but within the Atlantic walrus haplotypes, there was no relation between haplotype and geography.

DISCUSSION

Sampling

It was possible that sample selection by biopsy-takers was different than that of walrus hunters (Stewart 2008a) i.e. it could explain the sex-bias observed in the different sampling areas and perhaps distort observed genetic differences. The results, however, indicated both sex differences in samples taken by only one method (hunting) and a lack of differences among samples taken by two methods. We conclude there was no systematic bias resulting from sample method. The unintended resampling of individuals at various locations in the SEB sampling area suggests that the walrus moved among haulouts and the sample was representative of the Hoare Bay area.

Genetic variation

Microsatellites

The levels of genetic variation were similar to those observed in other pinnipeds (H_E = 0.59 to 0.81; Palo et al. 2001, Hoelzel et al. 2001, Davis et al. 2002, Acevedo-Whitehouse et al. 2003). They are also consistent with Andersen et al. (in press) results for a subsample of these (H_E = ranging from 0.59 – 0.66) examined with fewer markers.The significantly greater allele richness among male walrus compared to females in the overall sample might reflect a higher rate of dispersal for males compared to females (which may have a greater tendency toward perennial fidelity to wintering areas during the mating period in February-April) suggesting that the complete male-sample represented both known sampled groups and other hitherto un-sampled and unidentified groups of walruses. A male bias towards greater dispersal has been seen also in satellite telemetry studies in NE Greenland (Born and Knutsen 1992, Born et al. 2005) and at Svalbard (Freitas et al. 2009), in isotopic studies in Canada (Stewart et al. 2003) and previous genetic studies in NW Greenland (Andersen and Born 2000). It may also reflect different selection pressures on males and females, perhaps mediated through a selective hunt where males are replaced by other adult males moving in from nearby groups. In this case, males and females within the population would be responding as different stocks (Stewart 2008b) and the genetic population differences would disappear.

The sample of walruses from NW Greenland analysed in the present study probably consisted of more than one stock/population as implied by the deficit in heterozygotes observed in overall NWGR sample. This has also been suggested by Andersen and Born (2000) due to significant HWE deviation observed in the winter male-sample from NWGR and in the present study in the overall female sample as well analysing more markers (significant deviation was observed in the overall F_{is} (Table 2)). The present study analysed a subset of walrus examined by Andersen and Born (2000)

but included more markers which can be one explanation of the differing results. Significant deviations from HWE at different loci for the two sexes in NWGR, SEB and NEHB, (Table 2) and the significantly greater allele-richness among males overall are consistent with male dispersal behaviour and possible effects of selective hunting.

D-Loop

The haplotype variation observed was high with low to moderate nucleotide diversity, similar to the level observed in other pinnipeds that have experienced declines or are declining as the Guadalupe fur seals (*Arctocephalus townsendi*) (prebottleneck H= 0.997, π = 5.5%; postbottleneck H= 0.798, π = 2.5%, Weber et al. 2004) and the Pacific harbour seals (*Phoca vitulina*) (H= 0.975, π = 1.47%, Westlake and O'Corry-Crowe 2002) but higher compared to the northern elephant seals (*Mirounga angustirostris*) (H= 0.406, π = 0.68% Weber et al. 2000). Both the Guadelupe fur seal and northern elephant seal have been subjected to commercial hunting, reducing the numbers and genetic diversity at the mtDNA level (Hubbs and Norris 1971, Hoelzel et al. 1993). The diversity found in the Atlantic walrus reflects that the haplotypes are phylogenetically closely related but do not imply that the WGR/SEB walrus stock/population has been through a bottleneck (see later). Although equivocal, it cannot be ruled out that West Greenland - SE Baffin Island walrus populations have been reduced as no prehunting samples are available.

There was no indication of genetic separation between SE Baffin Island and West Greenland haplotypes. The number of haplotypes observed only in the SEB sample might indicate the presence of more than one stock represented in the sample. Alternatively, the population might be large as population size and genetic variation is expected to be positively correlated.

Population structure

STRUCTURE analysis indicated that SE Baffin Island and West Greenland walruses are part of a common genetic stock (Fig. 2). The identification of a fourth cluster, with no apparent explanatory variable like season, sex or year, might indicate more than one group of walruses in the total sample of SE Baffin Island and West Greenland. However, the present sample did not allow for the genetic and demographic implications of this finding to be pursued further - and further sampling is needed. Meanwhile, the overall genetic differentiation was low and close to the limit of what STRUCTURE requires in order being able to identify immigrants (Väha and Primmer 2006).

The F_{ST}-statistics based on the 17 microsatellite markers (Table 5) indicated walruses sampled in NW Greenland and in NE Hudson Bay were genetically differentiated. The genetic difference observed between NEHB and WGR and SEB was low, consistent with earlier indications (Andersen and Born 2000, Born and Andersen 2001, Andersen et al. in press) of a relatively close connection among walruses in these three areas. The very close relationship between WGR and SEB suggests that these to areas constitute a part of a single population which supports earlier suggestions (cf. Born et al. 1994, 1995). The apparent higher differentiations observed between female samples compared to male samples can perhaps be explained by female philopatry as mentioned earlier.

Plotting the individual assignments obtained from BIMr analysis and their probability of belonging to one or the other populations (Fig. 2b) was visually identical to the plot obtained from STRUCTURE.

Migration rates and direction

Keeping the sampling areas separate despite the observed lack of significant genetic differences between SEB and WGR the estimated gene flow or proportion of migrants observed in the two sampling areas showed very high migration rates between SEB and WGR, which again implies that they belong to the same walrus stock (Table 6). Both WGR and SEB received similar and substantial proportions of migrants from NEHB which received virtually none from WGR, SEB or the combined WGR/SEB. Andersen et al. (in press) reported a similar pattern based on 11 markers, and interpreted it as an indirect indication that NEHB must also function as a source for SEB walrus.This apparent asymmetrical migration does not necessarily mean that animals do not move from WGR/SEB to NEHB, but only that they rarely mate with NEHB walruses. There might be additional stock / population structure between NEHB and SEB.

These results generally confirm the suggestions made by Dunbar (1956). From the dates when walruses appeared at various locations, Dunbar (1956) suggested that walruses in Hudson Bay, Hudson Strait and at Frobisher Bay/Iqaluit on SE Baffin Island might comprise one large population. He suggested that the population moves into Hudson Strait in the spring and out again in late fall, wintering perhaps in the neighbourhood of the eastern ice edge in the Davis Strait, where they may well join the walruses occurring off Central West Greenland, as has been implied previously by Freuchen and Salomonsen (1961) Mansfield (1973), Born et al. (1994).

Detection of migrants

The detection of more first generation migrants than expected by chance ("true" non-resident individuals) in the NEHB sample from the WGR/SEB alone and from WGR/SEB to NEHB supports that there is a close connection between walruses in these areas.

As mentioned earlier at least three clusters were identified by STRUCTURE. A fourth cluster was indicated but this could not be affiliated to a specific locality apart from a mixture of individuals from SE Baffin Island, W Greenland and NEHB. This might explain some of the discrepancies between the results obtained using the two different identification methods (partial Bayesian method, GENECLASS2 and Bayesian based, STRUCTURE). STRUCTURE had difficulties identifying migrants from WGR/SEB and NEHB while migrants from NWGR were identified in all locations (Table 7). This could probably be attributed to the low F_{ST} estimate observed between WGR/SEB and NEHB. The level of F_{ST} will strongly affect the percentage of correctly assigned individuals. The more genetically different the populations the higher percentages of individuals correctly assigned (Berry et al. 2004, Manel et al. 2002).

The apparent discrepancy between the migration direction indicated by BIMr and GENECLASS2 may be due to differences in the methods used. The first generation migrants have not yet contributed to the gene-pool in the receiving area estimated by GENECLASS 2 whereas the migrants estimated in BIMr have participated in the reproduction and contributed to genetic composition of the stock. Both methods implies a connection between the NEHB stock and the WGR/SEB stock.

Historical population demography

Analysis of mismatch distribution and neutrality test (Tajima´s *D* and Fu's F_S) indicated population expansion although Tajima´s *D* and Fu's F_S were non-significant. Despite the statistical problems related to the use of mismatch distribution analysis for detection of population growth (Ramos-Onsins and Rozas 2002), the very crude estimate for the time for expansion suggested that the population growth happened c. 7600 (782 – 14,700) years ago. This suggested that the population growth was not a recent phenomenon. It indicated that the expansion occurred in relation to the retraction of the ice-edge after the last Ice Age c. 12,000 years ago and supported the

hypothesis proposed by Born et al. (2001) and Andersen et al. (in press) that the walruses in the areas to the west of Greenland belonged to the same ancestral population.

Phylogeny

The two sub-species of walrus, Pacific and Atlantic walrus, were clearly separated genetically using both approaches (Fig. 4a,b) confirming earlier findings that they are genetically separate sub-species (Cronin et al. 1994).

Management implications

The genetic data examined did not reject the hypothesis that walrus in WGR and in SEB form a part of a single genetic stock, supporting earlier suggestions (e.g. Dunbar 1956, Freuchen and Salomonsen 1961, Mansfield 1973, Born et al. 1994) that there is a connection between walruses on SE Baffin Island and in West Greenland. It was therefore concluded that walruses exploited from fall to spring in the central areas of West Greenland belong to the same stock or stocks distributed along SE Baffin Island. The putative West Greenland walrus stock (Born et al. 1995, NAMMCO 1996, Stewart 2008a) is a part of the North Hudson Bay-Hudson Strait-North Labrador-South-eastern Baffin Island stock (Born et al. 1995, NAMMCO 1995; HBDS, Hudson Bay-Davis Strait in Stewart 2008a). Apparently, this HBDS stock has further sub-structure in that NE Hudson Bay walruses differ from SE Baffin Island-West Greenland animals. While STRUCTURE separated WGR/SEB from NEHB, the migration analyses indicated that the catch at SE Baffin Island and in West Greenland may be supplied by walruses from NEHB, reinforcing the concept of further sub-structure.

However, Greenland and Canada manage this common resource separately and under different management schemes. Until 2007 the catch of walruses in West Greenland was regulated by a system limiting the hunting season and hunting methods (Born et al. 1994, 1995) with no quota system, therefore no upper limit to the numbers taken. However, in Greenland quotas for the catch of walrus were introduced in 2006 (Anon. 2006a) taking effect in Central West Greenland from the spring of 2007 (Anon. 2006b). In contrast, in Canada the catch of walruses has been regulated for decades by either personal limits (four walrus per hunter) or community quotas (COSEWIC 2006).

During 1993-2006, the reported landed catch of walrus in West Greenland averaged 136/year (sd=53.4, range=64-240, N=14 years) (Department of Fisheries, Hunting and Agriculture, in litt. 2008). This does not include losses which are unknown but believed to be substantial in some cases (Born et al. 1995). Total allowable catches quotas for the West Greenland walrus stock in 2007, 2008 and 2009 were 80, 65, 50 animals (Anon. 2006b) respectively. Walruses occur along SE Baffin Island during the entire year where they are hunted mainly during the period May-November (Stewart 2008a). The reported catch of walruses on SE Baffin Island in the communities Iqaluit, Qikiqtarjuaq, Pangnirtung and Clyde River that likely harvest from the Baffin Island-West Greenland group of walruses was reported to be 32/year (sd=19.4, range=2-71, N=20 years) during 1989-2008 (COSEWIC 2006: table 2, and Stewart unpublished data). This is likely a minimum because in some years reports about catches were not reported.

Aerial surveys conducted during late March – mid April 2006 and 2008 resulted in estimates (corrected for animals submerged and visibility bias) of the number of walruses wintering in Central West Greenland of around 3000 (Heide-Jørgensen et al. unpublished). The 2006 and 2008 estimates are not statistically significant different from a previous corrected estimate of ca. 1000 animals (cv=0.48) for this area in 1990-1991 (Witting and Born 2005, NAMMCO 2006)..

There is no current estimate of abundance of walruses at SE Baffin Island (cf. Born et al. 1995, NAMMCO 2006). Richard and Campbell (1988) assigned the number "1000+" to the area of SE Baffin Island from Gabriel Strait north to Clyde Inlet, as a guess at the population size at the time. However, aircraft and boat-based surveys during August, 2005, 2006 and 2007 along SE Baffin Island between Pangnirtung and Qikiqtarjuaq indicate the presence of 1000+ walruses on various terrestrial haul-outs. If corrected for walruses that were not present at the haul-outs an estimated 2000-4000 walruses are found along SE Baffin Island during summer (Stewart et al. unpublished).

Currently, the management of the populations of Atlantic walruses shared by Canada and Greenland is not formally coordinated although transboundary stocks deserve coordinated management. An important part of such management is identification of stocks or management units. The present study is a contribution to identification of meaningful management units. Both the stock affiliations of walrus between NEHB and our sampling area on SEB and the abundance of walrus should be examined.

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Table 1. Summary of samples from Northeast Hudson Bay, Southeast Baffin Island, West Greenland and Northwest Greenland used for genetic analyses. Bold= significant at the 5% level.

Region (Acronym)	N	F	M	Sex Ratio and χ^2 Probability F:M[3]	Sampling year
Northwest Greenland (NWGR)	63	26	37	0.70:1 P >0.05	1990, 1991
West Greenland (WGR)	136 45[2]	75 30[2]	52 13[2]	**1.44:1 P<0.05** **2.31:1 P <0.025**	1988, 1989, 1997, 2004-2007
Southeast Baffin Island (Hoare Bay) (SEB)	88 (98) 72[2]	48 44[2]	36 27[2]	1.33:1 P >0.05 **1.63:1 P<0.05**	2005, 2008
Northeast Hudson Bay	58	16	42	**0.38:1 P<0.0005**	1998-2000
Total	345[1]	207	137		

[1)] 3 individuals not sexed

N= number of individuals genotyped for 17 microsatellite markers

[2] Numbers of individuals with D-loop information

Number in parentheses ()= actual number of biopsies taken

[3)] χ^2 goodness-of-fit, 1 d.f

Table 2. The expected (H_E) heterozygosity, allele richness (AR), deviations from HWE (F_{IS}) and number of individuals (N) for the 17 polymorphic microsatellite loci used to study genetic variation in the four samples of walruses in the Davis Strait-Baffin Bay region. NWGR = Northwest Greenland, WGR = West Greenland, SEB = SE Baffin Island, NEHB = Northeast Hudson Bay.* (bold) significant deviations from HWE after application of the Bonferroni procedure at α = 5% level.

	HG6.1	*Orr16*	*Orr23*	*Orr24*	*Orr9*	*HGDii*	*Igf-I*	*Orr11*	*Orr3*	*Orr7*	*SPGV9*	*Hg4.2*	*LW20*	*M11*	*HG8.10*	*PV9*	*LW15*	Overall/ sdv.
NWGR																		
H_E	0.503	0.8	0.835	0.749	0.688	0.326	0.301	0.534	0.778	0.862	0.697	0.655	0.49	0.771	0.692	0.724	0.685	0 .652±0.166
AR	3.98	9.35	12.3	5.69	5.69	6.14	2	7.55	7.63	12.37	6.93	10.03	3.74	7.71	6.65	4.98	9.63	7.2±2.87
F_{IS}	0.021	0.048	0.031	0.088	-0.084	0.025	0.104	0.167	0.082	0.024	0.203	0.103	0.097	0.187	0.123	0.154	0.01	**0.081***
N	63	63	63	63	63	63	63	63	63	63	63	63	61	59	61	62	59	
Females																		
H_E	0.631	0.832	0.789	0.738	0.655	0.345	0.34	0.617	0.788	0.868	0.659	0.718	0.497	0.79	0.685	0.72	0.643	0.666±0.151
AR	3.57	6.33	6.99	4.62	3.97	3.6	1.99	4.85	4.91	7.33	4.14	6.3	2.89	5.69	4.35	4.54	5.81	4.82±1.45
F_{IS}	0.024	0.167	0.172	0.062	-0.234	0.107	-0.018	0.19	0.171	0.069	0.067	0.251	0.303	0.209	0.27	0.278	0.253	**0.142***
N	26	26	26	26	26	26	26	26	26	26	26	26	26	24	24	25	25	
Males																		
H_E	0.387	0.776	0.857	0.758	0.71	0.316	0.276	0.475	0.761	0.86	0.729	0.616	0.463	0.779	0.699	0.728	0.794	0.646±0.189
AR	3.87	8.59	11.44	4.87	5.85	4.86	2	6.83	7.85	11.66	6.86	7.83	3.91	5.99	5.85	4.87	9.94	6.65±2.67
F_{IS}	-0.049	-0.045	-0.072	0.108	0.011	-0.027	0.217	0.146	0.005	-0.006	**0.296***	-0.01	0.135	0.193	0.033	0.072	0.074	0.059
N	37	37	37	37	37	37	37	37	37	37	37	37	35	35	37	37	34	
WGR																		
H_E	0.354	0.786	0.867	0.706	0.737	0.3	0.196	0.756	0.765	0.867	0.695	0.663	0.54	0.735	0.668	0.77	0.717	0.654±0.194
AR	4.65	10.06	11.81	7.56	6.47	5.55	3.53	8.21	8.11	11.94	6.44	9.7	4.37	9.27	5.2	8.31	7.96	7.6±2.49
F_{IS}	-0.059	-0.039	0.05	0.055	0.003	0.018	0.174	0.017	0.108	-0.011	0.055	-0.098	0.17	0.107	-0.142	0	-0.054	0.015
N	136	136	136	135	136	136	136	136	129	130	134	136	134	125	135	135	135	

	HG6.1	*Orr16*	*Orr23*	*Orr24*	*Orr9*	*HGDii*	*Igf-I*	*Orr11*	*Orr3*	*Orr7*	*SPGV9*	*Hg4.2*	*LW20*	*M11*	*HG8.10*	*PV9*	*LW15*	Overall/ sdv.
Females																		
H_E	0.355	0.788	0.86	0.689	0.749	0.275	0.186	0.759	0.76	0.861	0.69	0.678	0.463	0.709	0.656	0.753	0.728	0.645±0.2
AR	3.11	6.31	7.64	4.56	5.27	2.85	2.23	5.33	5.5	7.68	4.41	5.2	3.11	4.58	3.63	4.88	5.41	4.81±1.54
F_{IS}	-0.016	-0.033	0.023	-0.007	-0.015	0.08	0.139	-0.002	0.129	-0.05	0.08	-0.101	0.212	0.162	-0.071	0.067	-0.007	0.025
N	75	75	75	75	75	75	75	75	71	73	74	75	74	69	74	74	75	
Males																		

H_E	0.326	0.772	0.875	0.751	0.757	0.311	0.227	0.738	0.782	0.873	0.697	0.624	0.608	0.777	0.674	0.788	0.743	0.666±0.195
AR	3.56	8.75	11.42	7.73	5.85	5.17	2.95	7.03	8.15	11.11	4.83	9.71	4.49	10.26	5.21	8.41	8.21	7.23±2.61
F_{IS}	-0.122	-0.046	0.099	0.138	-0.016	0.195	0.238	0.035	0.131	0.061	0.172	-0.079	0.096	0.041	-0.113	-0.073	0.024	0.021
N	52	52	52	52	52	52	52	52	50	50	52	52	51	47	52	52	51	
SEB																		
H_E	0.327	0.776	0.888	0.679	0.785	0.463	0.263	0.755	0.675	0.855	0.7	0.648	0.508	0.72	0.636	0.708	0.74	0.654±0.172
AR	4.63	8.93	12.75	7.2	6.74	5.96	3	7.73	9.72	12.16	5.48	7.85	4.03	9.69	5.76	6.04	8.01	7.39±2.67
F_{IS}	0.014	0.048	0.068	0.029	-0.158	0.165	**0.482***	-0.127	0.038	0.072	-0.12	0.035	0.072	0.1	0.036	-0.059	-0.056	0.016
N	87	88	87	88	88	88	87	87	77	87	88	88	87	88	88	88	87	
Females																		
H_E	0.312	0.758	0.891	0.692	0.783	0.425	0.247	0.775	0.698	0.857	0.718	0.65	0.504	0.739	0.629	0.682	0.758	0.654±0.181
AR	2.65	5.62	8.79	4.17	5.33	3.82	2.5	5.65	5.47	7.51	4.22	4.62	3.11	5.23	3.59	3.8	5.37	4.79±1.64
F_{IS}	-0.091	0.094	0.065	-0.053	-0.197	0.215	0.409	-0.182	0.011	0.052	0.014	0.007	0.113	0.098	0.073	-0.191	0.011	0.007
N	47	48	48	48	48	48	48	48	42	48	48	48	47	48	48	48	48	
Males																		
H_E	0.358	0.788	0.867	0.692	0.789	0.537	0.251	0.73	0.65	0.834	0.699	0.66	0.457	0.696	0.632	0.744	0.686	0.651±0.165
AR	4.78	7.77	10.82	6.86	6.88	5.99	2.99	6.98	8	10.9	5.77	7.77	4.78	8.64	4.88	5.88	6.91	6.86±2.07
F_{IS}	0.145	-0.023	0.077	0.077	-0.092	**0.431***	0.557	-0.104	0.087	0.11	0.126	0.074	-0.094	0.082	-0.011	0.067	-0.041	0.062
N	36	36	35	36	36	36	36	36	32	35	36	36	36	36	36	36	35	
	HG6.1	*Orr16*	*Orr23*	*Orr24*	*Orr9*	*HGDii*	*Igf-I*	*Orr11*	*Orr3*	*Orr7*	*SPGV9*	*Hg4.2*	*LW20*	*M11*	*HG8.10*	*PV9*	*LW15*	Overall/ sdv.
NEHB																		
H_E	0.282	0.843	0.857	0.726	0.685	0.361	0.269	0.557	0.675	0.847	0.654	0.611	0.371	0.69	0.687	0.739	0.552	0.612±0.19
AR	2.95	8.55	12.1	6.73	4.95	6.63	2	5.95	5.55	12.49	3.8	9.44	4.41	5.77	4.77	4.78	5	6.23±2.91
F_{IS}	0.205	0.039	0.075	-0.069	-0.032	-0.002	0.217	-0.082	0.132	-0.038	0.099	0.069	-0.01	0.146	-0.118	-0.004	0.034	0.028
N	58	58	58	58	58	58	58	58	58	58	56	58	56	56	56	58	45	
Females																		
H_E	0.354	0.86	0.883	0.75	0.733	0.181	0.286	0.502	0.694	0.908	0.683	0.592	0.271	0.79	0.683	0.706	0.389	0.604±0.23
AR	2	6.44	8.4	4.94	4.53	2.69	1.99	4.25	3.9	9.37	3	4.86	1.99	4.81	3	3.94	3	4.3±2.12
F_{IS}	0.118	0.056	0.009	0	0.063	-0.034	-0.167	-0.12	0.099	0.106	-0.098	0.155	-0.154	0.05	-0.006	-0.15	0.143	0.016
N	16	16	16	16	16	16	15	16	16	16	16	16	16	16	16	16	9	
Males																		
H_E	0.254	0.832	0.851	0.723	0.671	0.423	0.266	0.58	0.677	0.827	0.634	0.621	0.391	0.72	0.693	0.729	0.575	0.616±0.183
AR	2.95	8.51	11.17	6.51	4.75	5.84	2	5.75	5.52	11.21	3.8	8.99	3.6	5.76	4.76	4.76	4.88	5.93±2.64
F_{IS}	0.251	0.027	0.105	-0.087	-0.064	-0.013	0.373	-0.067	0.155	-0.094	0.172	0.042	-0.022	**0.41***	-0.155	0.02	0.034	0.048
N	42	42	42	42	42	42	42	42	42	42	40	42	40	40	40	42	36	

Table 3. Polymorphic sites defining the observed haplotypes and their frequencies amongst the walruses sampled in West Greenland (WGR) and SE Baffin Island (SEB).

ODRR= Atlantic walrus, ODR= Pacific walrus

Bp No.	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	Haplotype frequencies	
	4	7	7	7	8	8	8	8	8	9	4	4	4	5	6	7	8	9	0	0	1	2	2	3	3	3	4	7	2	3	5	7		
Haplotype	9	0	7	8	9	0	1	2	3	4	1	2	3	5	2	2	2	0	3	1	5	3	5	6	2	3	5	1	8	6	9	8	0	WGR	SEB
ODRR1	T	T	T	T	-	-	-	-	-	C	T	T	A	T	T	T	T	C	A	A	T	A	T	T	G	T	A	G	A	G	C	C	A	0.022	0.056
ODRR2	.	.	.	.	T	T	T	T	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	0.178	0.167
ODRR3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	0.067	0.028
ODRR4	C	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.067	0.014
ODRR5	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.222	0.143
ODRR6	.	.	.	.	T	T	T	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	0.156	0.181
ODRR7	.	.	.	.	T	T	T	.	.	.	.	.	G	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	0.178	0.069
ODRR8	C	C	.	-	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.044	
ODRR9	.	.	.	.	T	T	T	T	T	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	0.022	0.014
ODRR10	.	.	.	-	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.022	
ODRR11	.	.	.	.	T	T	T	.	C	.	.	.	G	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	0.022	
ODRR12	.	.	.	.	T	T	T	T	.	.	.	.	G	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.		0.014
ODRR13	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.		0.056
ODRR14	.	.	.	.	T	T	T	C	C	.	.	.	G	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	T	T	.		0.014
ODRR15	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.		0.042
ODRR16	.	.	.	.	.	.	.	.	.	-	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		0.028
ODRR17	C	.	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		0.028
ODRR18	.	.	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		0.014
ODRR19	.	C	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.		0.028
ODRR20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.		0.014
ODRR21	.	.	.	.	T	T	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	T	T	.		0.014
ODRR22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	T	.	.		0.028
ODRR23	.	C	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.		0.014
ODRR24	.	C	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		0.028
ODR1	.	.	.	.	T	T	T	.	C	.	.	.	G	.	C	C	.	T	G	.	.	G	C	C	A	C	.	A	G	A	T	.	G		
ODR2	.	.	.	.	T	T	.	.	.	-	.	C	.	.	.	C	C	T	G	.	.	G	C	.	A	.	G	A	G	A	T	.	G		
ODR3	.	.	.	.	T	T	T	C	C	.	.	C	G	.	.	C	.	T	G	G	.	G	C	.	A	.	G	A	G	A	T	.	G		

Table 4. Mean posterior probabilities of belonging to one of the three identified clusters

(Fig. 2). Numbers in parentheses and bold are the number of individuals assigned to one of the clusters with the highest probability (q) and 90% CI (0.002-1).
Numbers in parentheses bold and italics are individuals with highest q but broad 90% CI (0-1).
NWGR = Northwest Greenland, WGR = West Greenland, SEB = Southeast Baffin Island, NEHB = Northeast Hudson Bay

	Clusters			
Sampling areas	1	2	3	All or 2 clusters
NWGR	**0.723 (45, *12*)**	0.126 (1,*1*)	0.152 (2, *2*)	
WGR	0.171 (4, *9*)	0.413 (7, *53*)	0.416 (19, *36*)	8
SEB	0.118 (*2*)	0.451 (13,*23*)	0.431 (7, *39*)	4
NEHB	0.156 (*2*)	**0.574 (8, *37*)**	0.269 (1, *6*)	4

Table 5. Pairwise multilocus F_{ST} estimates describing the genetic divergence between the four stocks of Atlantic walrus based on 17 microsatellite loci (FSTAT, Goudet 1995, ARLEQUIN, Scneider et al. 2000). *Italics*= not significant after application of the sequential Bonferroni procedure (Rice 1980). NWGR = Northwest Greenland, WGR = West Greenland, SEB = Southeast Baffin Island, NEHB = Northeast Hudson Bay

Total

	NWGR	WGR	SEB
WGR	0.031		
95%CI	(0.016-0.047)		
SEB	0.036	*0.005*	
95%CI	(0.02-0.051)	*(0.001-0.009)*	
NEHB	0.033	0.014	0.016
95%CI	(0.019-0.047)	(0.007-0.023)	(0.008-0.026)

Haplotype F_{st} : WGR-SEB = *0.002, p= 0.33***,** Haplotype Φ_{st}: WGR-SEB = *0.003, p= 0.27*

Females

	NWGR	WGR	SEB

WGR	0.044		
95%CI	(0.022-0.067)		
SEB	0.05	0.007	
95%CI	(0.027-0.072)	(0.002-0.012)	
NEHB	0.039	0.02	0.028
95%CI	(0.018-0.06)	(0.005-0.038)	(0.009-0.05)

Haplotype F_{st} : WGR-SEB = *-0.001, p= 0.45*, Haplotype Φ_{st}: WGR-SEB = *-0.002, p= 0.36*

Males

	NWGR	WGR	SEB
WGR	0.02		
95%CI	(0.008-0.032)		
SEB	0.025	*0.005*	
95%CI	(0.01-0.04)	*(-0.001-0.010)*	
NEHB	0.024	0.012	0.013
95%CI	(0.011-0.037)	(0.005-0.019)	(0.003-0.021)

Haplotype F_{st} : WGR-SEB = *-0.009, p= 0.62*, Haplotype Φ_{st}: WGR-SEB = *0.008, p= 0.28*

Table 6. Recent migration rates and directions between the four walrus areas based on the estimates of means a) keeping the areas separate and b) after pooling West Greenland (WGR) and Southeast Baffin Island (SEB). Figures in parentheses = highest posterior density intervals (HPDI) (BIMr, Faubet and Gaggiotti 2008). NWGR = Northwest Greenland, NEHB = Northeast Hudson Bay.

a)	From			
Into	NWGR	WGR	SEB	NEHB
NWGR	**0.74**	0.106	0.027	0.127
	(0.492-0.962)	(0.002-0.343)	(0.0004-0.174)	(0.0007-0.386)
WGR	0.012	**0.451**	**0.258**	**0.278**
	(0.0002-0.114)	(0.266-0.625)	(0.098-0.507)	(0.062-0.475)
SEB	0.009	**0.281**	**0.459**	**0.251**
	(4.25E-07-0.083)	(0.049-0.644)	(0.177-0.659)	(0.057-0.503)
NEHB	6.34E-07	6.29E-07	6.28E-07	**1**
	(4.17E-07-4.09E-05)	(2.19E-11- 4.54E-05)	(6E-11-4.87E-05)	(1-1)

b)	From		
Into	NWGR	WGR+SEB	NEHB
NWGR	**0.73**	0.053	0.214
	(0.479-0.909)	(1.86E-04 - 0.338)	(0.003-0.442)
WGR+SEB	0.011	**0.543**	**0.446**
	(4.25E-07- 0.083)	(0.416-0.67)	(0.302 - 0.564)
NEHB	0.0003	0.0004	**0.999**
	(1.62E-12-0.05)	(0.001 - 0.101)	(0.894 - 0.995)

Table 7. Detection of first generation migrants using assignment test of GENECLASS2 (Piry et al. 2004) and STRUCTURE (Pritchard et al. 2000). Probability = the probability of the individual belonging genetically to sampling location. Assigned location = the location from which the individual most likely originates according to GENECLASS 2. Q= probability of belonging to the suggested location mentioned according to STRUCTURE. It could also be described as the possibility that the individual is a migrant from the location mentioned. NWGR= Northwest Greenland, WGR/SEB= West Greenland + Southeast Baffin Island, NEHB= Northeast Hudson Bay.

Indv.	Sex	Sampling location	Assigned location	Log Ratio	Resident probability	STRUCTURE, Q NWGR	WGR/SEB	NEHB
th234	m	NWGR	WGR/SEB	4.485	0.0005		0.812	
th696	f	NWGR	NEHB	3.224	0.0030			0.415
th613	m	NWGR	WGR/SEB	2.101	0.0108		0.589	
th714	m	NWGR	NEHB	2.182	0.0110		0.686	
th609	m	NWGR	NEHB	1.990	0.0137		0.639	
th4890	m	NWGR	WGR/SEB	1.780	0.0174			0.803
att6	f	WGR/SEB	NWGR	2.841	0.0018	0.853		
att19	m	WGR/SEB	NWGR	2.081	0.0075	0.914		
bf002	m	WGR/SEB	NEHB	2.013	0.0078			0.752
bf005	f	WGR/SEB	NEHB	1.749	0.0127			0.523
att5	f	WGR/SEB	NEHB	1.695	0.0134		0.893	
att18	m	WGR/SEB	NWGR	1.489	0.0168	0.852		
bf009	m	WGR/SEB	NEHB	1.453	0.0182			0.906
att973	m	WGR/SEB	NEHB	1.347	0.0218			0.867
bf016	?	WGR/SEB	NEHB	1.052	0.0276			0.802
att12	f	WGR/SEB	NEHB	1.048	0.0321		0.557	
bf07014	m	WGR/SEB	NEHB	1.014	0.0358		0.895	
att587	m	WGR/SEB	NEHB	0.956	0.0359			0.891
att586	m	WGR/SEB	NEHB	0.863	0.0430			0.900
att200515	f	WGR/SEB	NEHB	0.701	0.0444			0.709
att496	f	WGR/SEB	NWGR	0.765	0.0475	0.924		
bf07024	f	WGR/SEB	NEHB	0.705	0.0499		0.895	
ca365	m	NEHB	WGR/SEB	3.809	0.0006		0.460	
ca1071	m	NEHB	WGR/SEB	3.673	0.0018			0.699
ca1037	m	NEHB	WGR/SEB	2.467	0.0060		0.753	
ca1412	m	NEHB	WGR/SEB	2.427	0.0074			0.659
ca1056	m	NEHB	WGR/SEB	2.159	0.0097		0.596	
ca1407	m	NEHB	WGR/SEB	1.558	0.0226			0.718
ca1038	m	NEHB	WGR/SEB	1.157	0.0357		0.850	
ca1072	f	NEHB	WGR/SEB	0.997	0.0399		0.422	

Figure 1. Map showing the distribution of Atlantic walruses in western Greenland and Canada with indications of putative stock following Born et al. (1995), Andersen et al. 2009 (in press) with indications of sites where samples used for genetic studies were collected.

Figure 2. a) Graphical output from the STRUCTURE (Pritchard et al. 2000) for *k* =3 of walruses sampled in Northeast Hudson Bay (NEHB), Southeast Baffin Island (SEB), West Greenland (WGR) and Northwest Greenland (NWGR). Each vertical line represents an individual and the colour composition displays the probability of belonging to each of the three clusters defined by STRUCTURE. b) Graphical output from the BIMr analysis (Faubet and Gaggiotti 2008) based on individual assignment (top) and on population assignment (bottom) keeping the sampling areas

separate. The vertical lines in represents an individual and the colour composition the probability of belonging to each of the four clusters

Figure 3 Mismatch distributions of pairwise nucleotide differences for the pooled WGR/SEB walruses.

Figure 4 . a) Parsimony network showing the haplotype relationship among the 24 observed Atlantic walrus haplotypes and the 3 Pacific walrus haplotypes based on the 506 bp sequences. The small circles show the minimum number of steps separating the haplotypes. No circle indicates one step. The size of the ovals is equivalent to the frequency of the haplotype in the whole sample.
b) Haplotype relationship based on genetic distance (Kimura 2P) among the haplotypes observed in the West Greenland and Southeast E Baffin Island samples.

Figure 1

30°

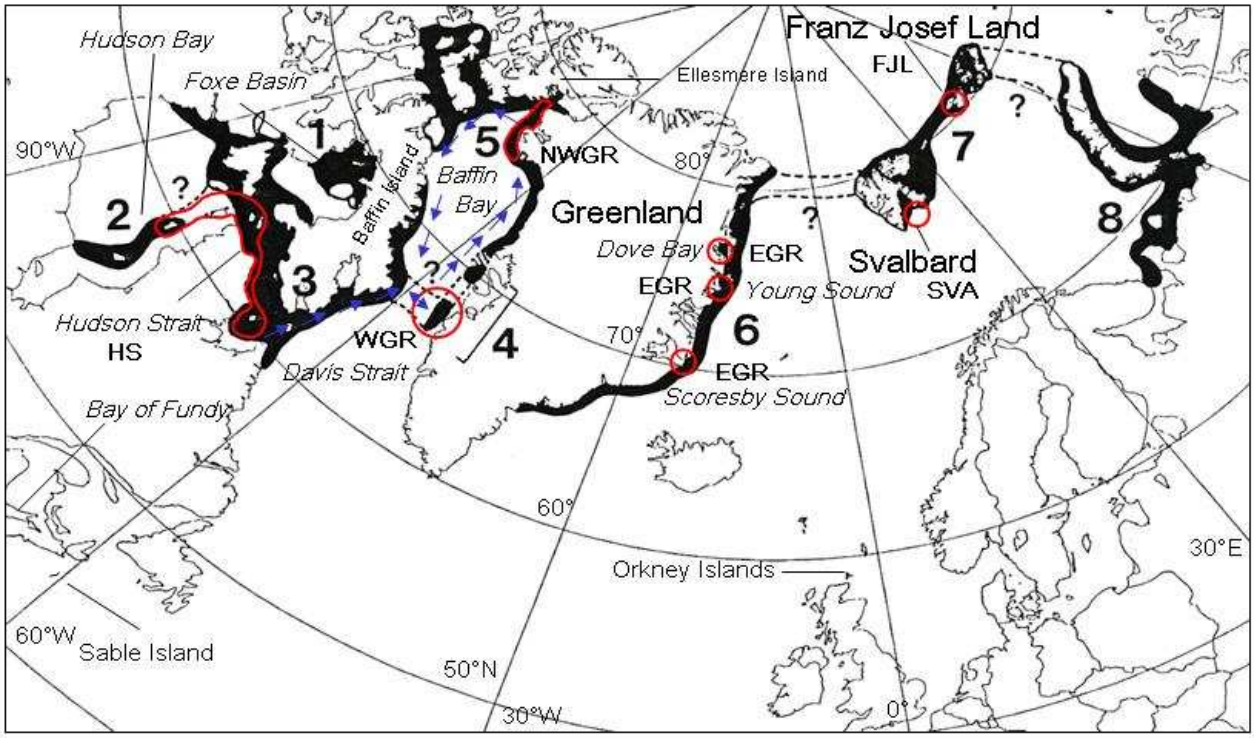
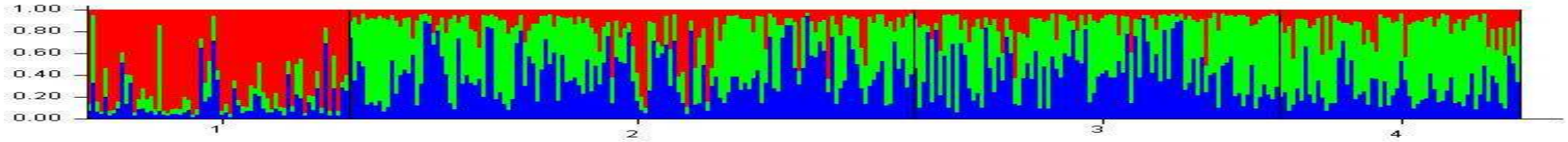

Hudson Bay
Foxe Basin
90°W
1
2
?
3
Hudson Strait
HS
Bay of Fundy
Baffin Island
5
NWGR
Baffin
Bay
WGR
4
Davis Strait
Ellesmere Island
80°
Greenland
Dove Bay
EGR
EGR
Young Sound
70°
6
EGR
Scoresby Sound
Franz Josef Land
FJL
7
Svalbard
SVA
8
60°
Orkney Islands
30°E
60°W
Sable Island
50°N
30°W
0°

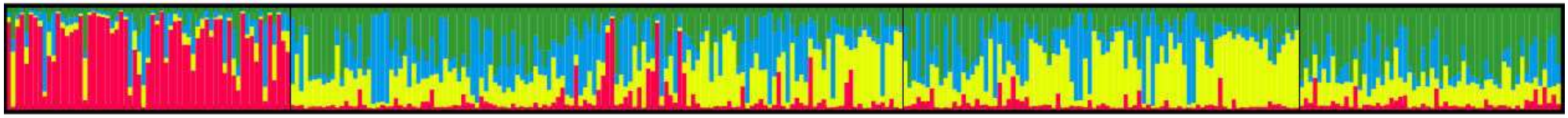
Figure 2

a)



NWGR WGR SEB NEHB

b)



NWGR WGR SEB NEHB

Figure 3

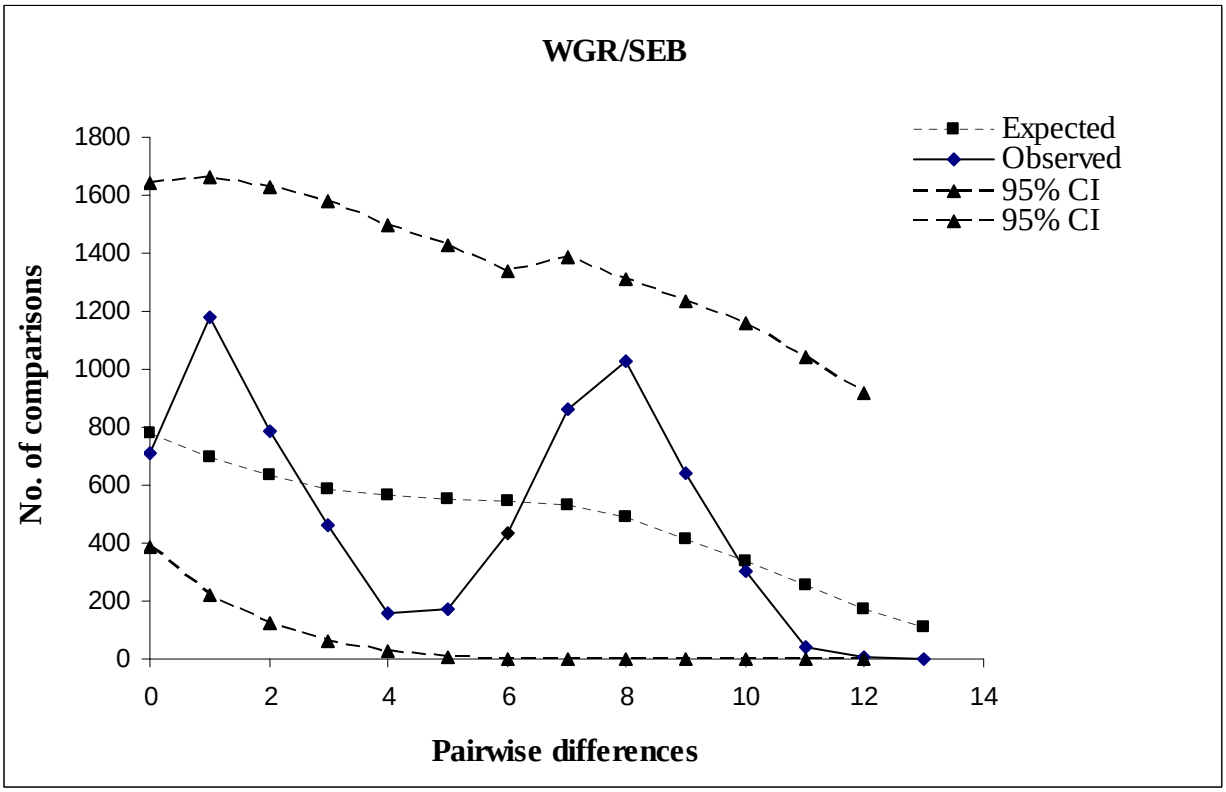
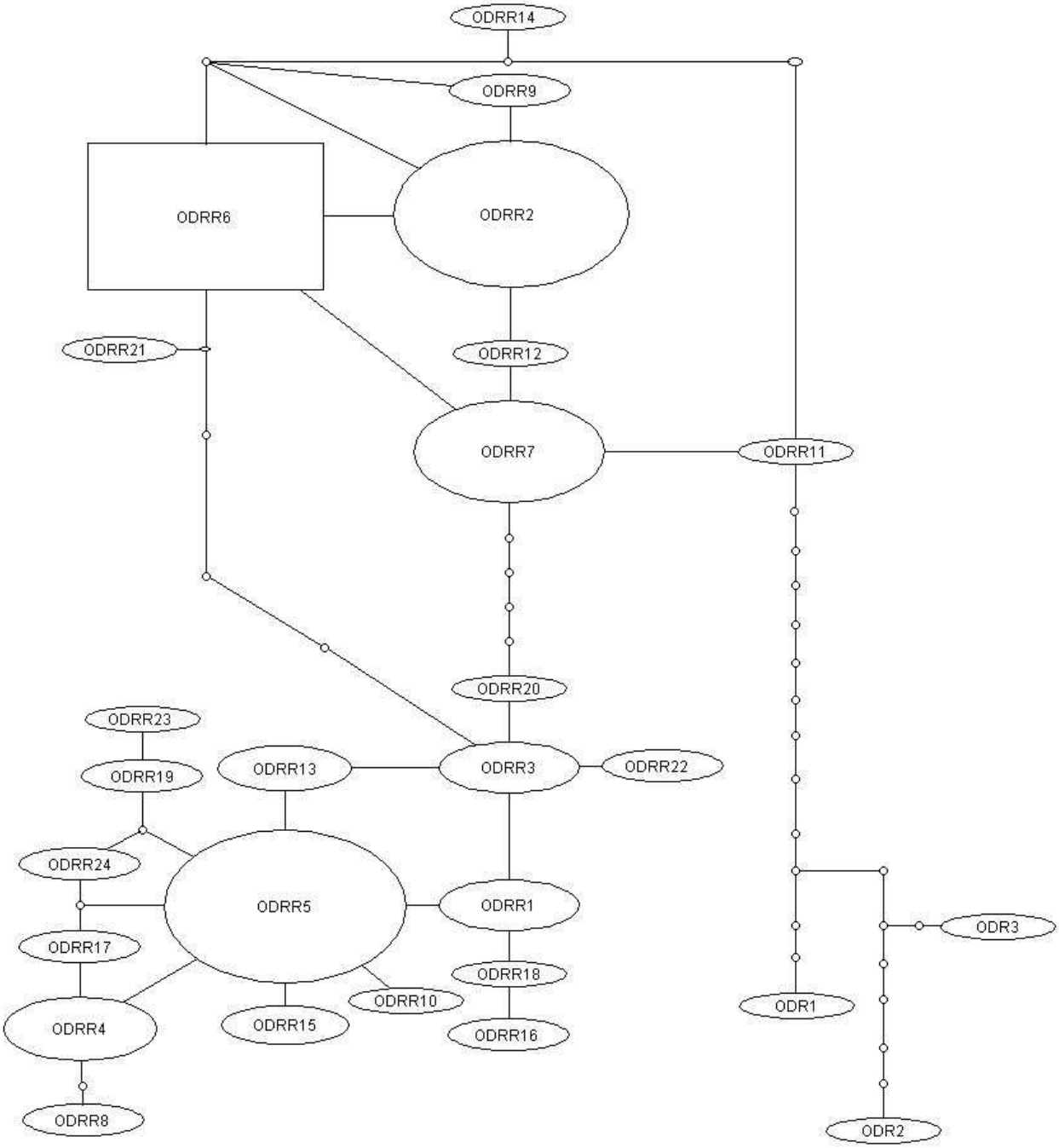
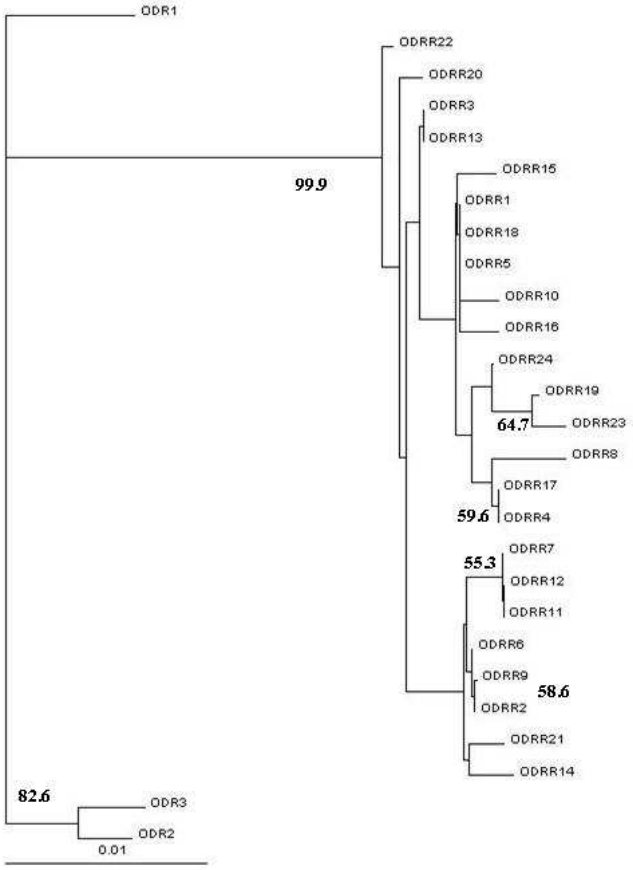


Figure 4

a)


ODRR14
ODRR9
ODRR6
ODRR2
ODRR21
ODRR12
ODRR7
ODRR11
ODRR20
ODRR23
ODRR19
ODRR13
ODRR3
ODRR22
ODRR24
ODRR5
ODRR1
ODR3
ODRR17
ODRR18
ODRR10
ODR1
ODRR4
ODRR15
ODRR16
ODRR8
ODR2

b)


ODR1
ODRR22
ODRR20
ODRR3
ODRR13
99.9
ODRR15
ODRR1
ODRR18
ODRR5
ODRR10
ODRR16
ODRR24
ODRR19
64.7
ODRR23
ODRR8
ODRR17
59.6
ODRR4
ODRR7
55.3
ODRR12
ODRR11
ODRR6
ODRR9
58.6
ODRR2
ODRR21
ODRR14
82.6
ODR3
ODR2
0.01