A genetic comparison of West Greenland and Baffin Island (Canada) walruses: Management implications

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ABSTRACT

Until recently Atlantic walruses (*Odobenus rosmarus rosmarus*) have been subject to relatively intense exploitation in West Greenland. Animals in this stock have also been hunted in Nunavut/Canada. However, the demographic identity of these animals and their connection with walruses in neighbouring areas is poorly resolved, hampering the determination of sustainable harvest levels. It has been suggested that walruses in West Greenland are genetically linked with walruses at SE Baffin Island (Canada) where they are also hunted for subsistence purposes. To determine the relationship(s) between walruses in these areas we conducted a genetic analysis including recent samples from West Greenland, Southeast Baffin Island in western Davis Strait, Hudson Strait in Canada and Northwest Greenland in northern Baffin Bay. Seventeen microsatellite markers were applied to all samples. Walruses in West Greenland and at Southeast Baffin Island did not differ from each other and therefore may be regarded as belonging to the same stock. However, walruses in these two areas differed genetically from both Northwest Greenland and Hudson Strait walruses. These findings support (1) that there are subunits within the range of walruses in the Hudson Strait–Davis Strait–Baffin Bay region and (2) that walruses along East Baffin Island and West Greenland constitute a common population that receive some influx from Hudson Strait. Thus, sustainable catch levels in Southeast Baffin Island (Nunavut) and in West Greenland must be set in light of the finding that they belong to the same stock, which is exploited in these two areas. This requires Canadian–Greenlandic co-management of the West Greenland–Southeast Baffin Island walrus stock.

INTRODUCTION

Walruses (*Odobenus rosmarus*) have been exploited by hunting cultures in the Arctic for millennia (Schledermann 1996). Traditionally, Arctic Inuit in many areas where walruses occur have regularly depended on their meat for human consumption and dog food, their ivory for making hunting implements and, in earlier times, their blubber for oil for heat and light (Born et al. 1995). Several life history traits make the walrus an important resource to marine hunting cultures in areas where this species occurs. Walruses 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. Walruses tend to live in shallow waters close to shore, feeding primarily on benthic organisms (e.g. Fay 1982, Born et al. 1995). These traits, coupled with relatively low reproductive rates and long generation times (Witting and Born 2005 and references therein) make them vulnerable to overexploitation.

Atlantic walruses living along the shores of Baffin Bay, Davis Strait and adjacent waters have been exploited traditionally by Inuit for subsistence purposes (cf. Born et al. 1995). They were also heavily hunted by foreign commercial whalers during the 19th Century, with some hunting of this type continuing up 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 struck and lost rates 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 (Born and Böcher 2001), the technological change began in the early 1900s and the landed catch of walruses in West Greenland increased from about 70/year to a peak around 1940 of more than 600/year (Born et al. 1994). Catches then declined markedly, likely reflecting a decline in the exploited stock far below historical levels, with walruses abandoning their terrestrial haul-outs in Central West Greenland (Born et al.1994, 1995, Witting and Born 2005).

Currently, walruses are hunted in Canada, including in the Hudson Strait and SE Baffin Island areas, and in West and Northwest Greenland. Exploitation rates in West and Northwest Greenland are relatively high and were thought to be unsustainable (Born et al. 1994, 1995, Anon. 1995, NAMMCO 2005, Witting and Born 2005, COSEWIC 2006) before the introduction of quotas in Greenland, which took effect in 2007 (Anon. 2006a,b). To determine sustainable levels of exploitation in West Greenland, it is crucial to determine the demographic identity of walruses occurring in West Greenland.

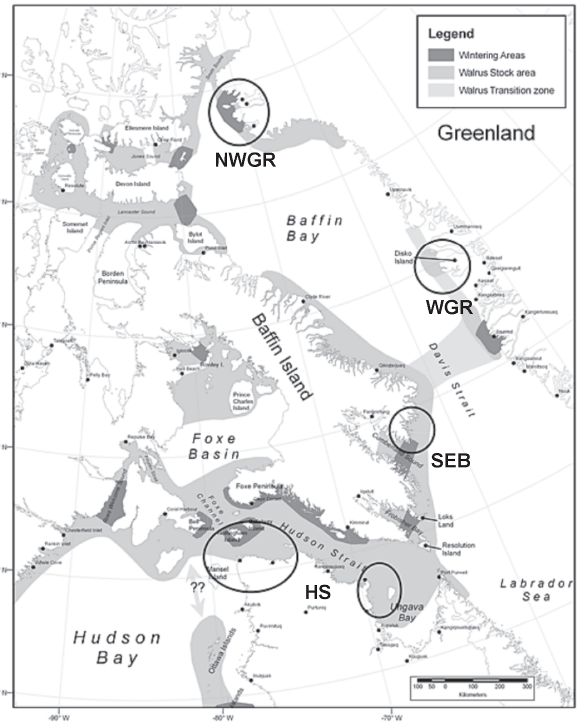

Fig. 1. *Distribution of Atlantic walruses in western Greenland and eastern Canada with indications of putative stocks following Born et al. (1995), Stewart (2008), Andersen et al. (2009). General sampling areas are indicated (NWGR=Northwest Greenland, WGR=West Greenland, SEB=Southeast Baffin Island, HS=Hudson Strait), sample sizes and acronyms see Tables 1 and 2. (Dark grey shaded area=wintering areas, medium grey shaded area=walrus stock area, light grey shaded area=supposed transition zones).*

Walruses are distributed throughout the northern reaches of Hudson Bay up to SE Baffin Island and over 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 populations (Born et al. 1995, Andersen and Born 2000, Born et al. 2001, Stewart 2008, Andersen et al. 2009). These "populations" or "subpopulations" are denoted as "stocks" by NAMMCO (NAMMCO 2010). One stock (North Hudson Bay–Hudson Strait–North Labrador–Southeast Baffin Island; NAMMCO 2005) inhabits the waters of northern Hudson Bay, through Hudson Strait to southeast Baffin Island (Shafer et al. 2014). Another (Central West Greenland stock; NAMMCO 2005) occurs off the central coast of west Greenland during winter and spring (Born et al. 1994, Heide-Jørgensen et al. 2014).

The third stock inhabits the coastal waters of Northwest Greenland and the northern reaches of the Canadian Arctic Archipelago. This latter stock now denoted as the "Baffin Bay" stock is a subunit of the former North Water population (NAMMCO 2005, 2010). In central West Greenland walruses occur at two, near-shore feeding grounds in the Sisimiut-Aasiaat area ("Store Hellefiske Bank"; between ca. 66º 30' and ca. 68º N) and off the west coast of Disko Island (between ca. 69º and 70º 30′ N) from fall to spring. Around May, when sea ice starts melting, walruses leave western Greenland (Born et al. 1994, Dietz et al. 2014). As they no longer haul out on land in West or Northwest Greenland during summer when ice is virtually absent from the coastal areas, the walruses that have wintered in Greenland clearly must migrate to summering grounds elsewhere (Born et al. 1994).

Genetic studies indicate that they have only limited—and mainly male mediated—contact with the Baffin Bay population in Northwest Greenland (Andersen and Born 2000, Born et al. 2001, Andersen et al. 2009). Based on anecdotal observations made in central Davis Strait during spring and early summer it was suggested that walruses migrate (ca. 450 km) across Davis Strait from West Greenland towards Southeast Baffin Island in spring (Born et al. 1994) to areas where walruses occur year-round and are also hunted (Born et al. 1995, Stewart 2008). Andersen et al. (2009) compared walruses sampled in West Greenland, Hudson Strait and in Northwest Greenland and found that walruses from Hudson Strait differed genetically from walruses from West Greenland but were apparently a source of West Greenland walruses.

The aim of the present study was to test the hypothesized connection between West Greenland and Southeast Baffin Island walruses (Born et al. 1995, Stewart 2008). Hence, genetic analyses of recent samples from Southeast Baffin Island and from West Greenland were performed to test the hypothesis that walruses that are being exploited in West Greenland do not differ genetically from those that occur at Southeast Baffin Island. The hypothesis was addressed by genetic analyses of the migration patterns between Central West Greenland and Southeast Baffin Island, including nearby stocks that are known to be genetically different (i.e. Hudson Strait and Northwest Greenland [Baffin Bay] walruses).

MATERIALS AND METHODS

Sampling in the field and laboratory analyses

Southeast Baffin Island (SEB) was represented by skin biopsies taken in the Hoare Bay area (65° 44′ N, 62° 26′ W). To obtain these biopsies, teams of local hunters and scientists travelled by boat or helicopter to haul-out sites on land or on ice floes. Walrus herds were approached by stealth on land or slowly by boat to take biopsies from swimming walruses. Care was taken not to tire swimming animals or separate calves from adults. Walruses at seven island haul-out sites in Hoare Bay were sampled in August 2005 (n=18) and 2007 (n=80). The samples from SEB were stored in 20% DMSO and saturated $NaCl_2$ solution then frozen at -20°C until analysed. The Hudson Strait (HS) samples (n=58) were collected from the subsistence catch in Hudson Strait/Hudson Bay area as explained in Andersen et al. (2009).

West Greenland (WGR) samples were collected in the period 2004–2007 by science personnel, local hunters, and the staff of the hospital in the town of Sisimiut, who collected muscle tissue samples (n=103) from the Greenlandic subsistence catches in Central West Greenland; four of these samples were from the Disko Island area and the remainder from the southern wintering ground south of ca. 68º N. The remaining West Greenland samples (n=33) were from the subsistence catch in the latter area (see Andersen et al. 1998 for details). Northwest Greenland (NWGR) muscle samples (n=63) were obtained from walruses killed in the subsistence hunt in 1990 and 1991 (Andersen and Born 2000). The samples were frozen at –20°C until analysed in the laboratory. All tissue sampled from HS and NWGR samples and the 33 from WGR were previously analyzed (see Table 1, Fig. 1; Andersen et al. 1998, Andersen and Born 2000, Born et al. 2001, Andersen et al. 2009).

DNA was extracted from all samples using a modified CTAB-buffer method (Milligan 1992) including proteinase K. Seventeen microsatellite markers were amplified. Eleven were previously used (Andersen et al. 1998, Andersen and Born 2000, Born et al. 2001, Andersen et al. 2009). The other six polymorphic markers that were used in this study were originally developed for grey seals, *Halichoerus grypus (HG4.1, HG8.10*, Allen et al. 1995), Weddell seals, *Leptonycotes weddellii (LW20, LW15*, Davis et al. 2002), southern elephant seals, *Mirounga leonina* (*M11*, Gemmell et al. 1997), and harbour seals, *Phoca vitulina* (*PV9*, Goodman 1997). The 17 markers were PCR multiplexed in three separate runs using the QIAGEN Multiplex PCR kit following the manufacturer's protocol and a 12.5 μl reaction volume and annealing temperature of 57ºC (QIAGEN). The PCR products were analysed using an ABI PRISM 377 DNA sequencer and subsequently genotyped. The gender of the walruses from SE Baffin Island (2005, 2007) and West Greenland samples (2004, 2005, 2006, 2007) were determined using the method developed by Fischbach et al. (2008; Table 1).

Data analysis

Before analysing the genetic data the biopsy samples were checked for incidental re-sampling of individuals. This was done by looking for matching genotypes among the 98 samples (collected in 2005 and 2007) taken from live walruses at Southeast 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.

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

Region (Acronym)	Sex			Sex Ratio (F:M) and χ^2 Probability[1]	Sampling year
	n	F	M		
Northwest Greenland (NWGR)	63	26	37	0.70:1 P >0.05	1990, 1991
West Greenland (WGR)	136	75	52	**1.44:1 P<0.05**	1988, 1989, 1997, 2004-2007
Southeast Baffin Island (Hoare Bay) (SEB)	88	48	36	1.33:1 P >0.05	2005, 2008
HS	58	16	42	**0.38:1 P<0.0005**	1998-2000
Total	345[2]	165	167		

1) χ^2 goodness-of-fit, 1 df
2) sex not determined for 13 individuals
n=number of individuals genotyped for 17 microsatellite markers

Genetic variation

Genetic variation was estimated as expected heterozygosity and allele richness in FSTAT (Goudet 1995). Tests for goodness of fit to 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 possible presence of null-alleles in the microsatellite loci was checked using MICRO-CHECKER 2.2.1 (Van Oosterhout et al. 2004). Most of the samples were collected outside the breeding season (breeding occurs mainly from January–April (Sjare and Stirling 1996, Born 2001, 2003) when there is some segregation of the sexes (Born et al. 1995, 1997, Gjertz and Wiig 1994, Stewart 2008) and the sex ratios among areas were 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 areas and analysed in FSTAT (Goudet 1995).

Population structure

The number of populations represented in the samples was estimated using a Markov Chain Monte Carlo (MCMC) method that clusters individuals to minimise Hardy-Weinberg disequilibrium and gametic phase disequilibrium between loci (STRUCTURE version 2; Pritchard et al. 2000). The analysis was run under the admixture model and the model of correlated allele frequencies between clusters. The results of the tests were based on 1,000,000 iterations and ten 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 an association. The clusters of individuals forming the number of populations with the highest likelihood were assigned to sampling localities.

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

Migration and sex biased dispersal

To estimate recent migration rates and directions between the sampling areas we employed a Bayesian method based on multilocus genotypes implemented in BIMr (Bayesian Inference of Migration rates) in STRUCTURE (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 Faubet and Gaggiotti (2008), we ran multiple analyses (20) with BIMr and compared the results to ensure that the MCMC chains converged. The individual and population assignments obtained from the BIMr analysis (keeping the sampling locations separate; Faubet and Gaggiotti 2008) were plotted using DISTRUCT (Rosenberg 2004). 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) was used to calculate the individual likelihoods of belonging to a certain population.

To detect first generation migrants in the walrus populations the likelihood computation L=L_home/L_max_not_home was used (Paetkau et al. 2004, Piry et al. 2004). Levels of significance were determined by 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 the origin and the probability that an individual is a migrant were calculated based on the re-sampling algorithm of Paetkau et al. (2004). First-generation migrants 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 a given individual.

The within-group gene diversity was analysed using FSTAT 2.3.9 (Goudet 1995), following Goudet et al. (2002). F_{IS}, F_{ST}, the mean assignment index (*mAlc*) and variance (*vAlc*) were calculated for the two sexes and tested using a one-tailed t-test after 10,000 randomizations. As residents often have higher mean *Alc* values than immigrants, the sex that disperses most is expected to have the lower *mAlc* value (Goudet et al. 2002). As the more dispersing sex in a sample will include residents as well as immigrants, the variance (*vAlc*) of the assignment index will be higher for the dispersing sex (Goudet et al. 2002). Weir and Cockerham's (1984) unbiased estimator of F_{ST} was used to express the proportion of genetic variance among the populations. It is expected that F_{ST} for the more dispersing sex will be lower than the more philopatric sex (Goudet et al. 2002) while F_{IS} of the more dispersing sex is expected to be higher compared to the more resident sex. The test assumes no-overlapping generations. The differences between the sexes were evaluated statistically after 10,000 permutations performed in FSTAT. The sequential Bonferroni procedure was applied, using a significance level of 5% whenever multiple tests were performed (Rice 1989).

RESULTS

Sampling

Replicate data were removed before analyses, leaving the total sample from SEB of 88 different individuals. The sex ratios among sampling locations differed significantly (Table 1, χ^2=10.01,

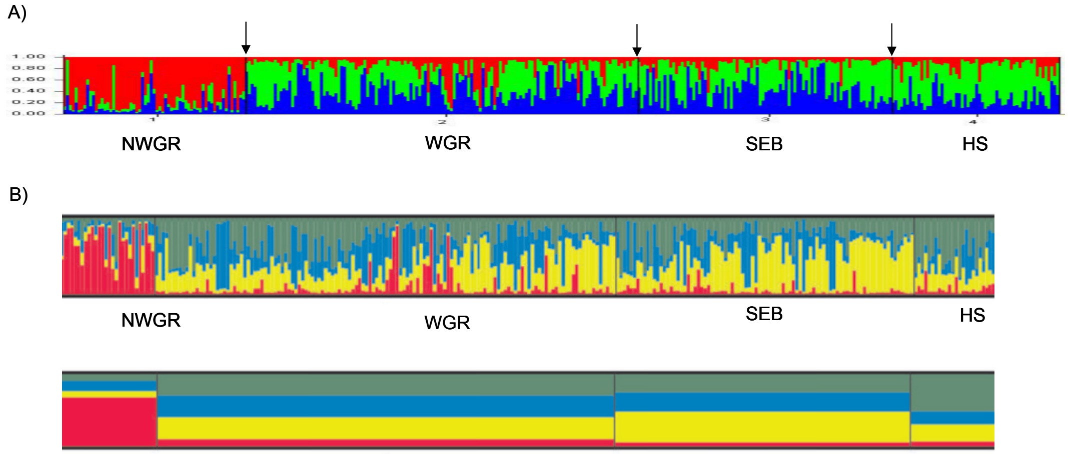

***Fig. 2.** A) Graphical output from the STRUCTURE (Pritchard et al. 2000) for k=3 of walruses sampled in Hudson Strait (HS), Southeast Baffin Island (SEB), West Greenland (WGR) and Northwest Greenland (NWGR). Each vertical line represents an individual and the colour composition displays the probability 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 represent individuals and the colour composition the probability of belonging to each of the four clusters.*

3 df, $P<0.05$), which was attributable to the preponderance of males in the HS samples (HS removed: $\chi^2=2.69$, 2 df, $P>0.05$). Within areas, sex ratios were also significantly different than 1:1, with biases towards females in the total sample from WGR (Table 1).

Genetic variation

The expected heterozygosity ranged from 0.612 in the HS sample to 0.654 in the WGR and SEB samples. Significant deviations from Hardy-Weinberg expectations were observed in the overall HWE test 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 loci that were not in accordance with the Hardy-Weinberg expectations: *SGPV9* locus in NWGR males; *Igf-1* locus SEB overall sample; *HGDii* locus in SEB males; and *M11* locus HS males (data not shown). Indications of null-alleles were found at *ORR23, ORR3, LW20, M11* and *Igf-1*. 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 dis-equilibriums were observed between pairs of loci within the different sampling areas (data not shown).

Table 2. Number of individuals (N), expected (H_E) heterozygosity, allele richness (AR), deviations from HWE (F_{IS}) for the 17 polymorphic microsatellite loci used to study genetic variation in the four areas in the Davis Strait-Baffin Bay region. NWGR = Northwest Greenland, WGR = West Greenland, SEB = SE Baffin Island, HS = Hudson Strait.* **BOLD**: significant deviations from HWE after application of the Bonferroni procedure at $\alpha = 5\%$ level.

Areas	N	H_E	AR	F_{IS}
NWGR	63	0.652±0.17	7.2±2.9	**0.081***
Females	26	0.666±0.15	4.8±1.5	**0.142***
Males	37	0.646±0.19	6.6±2.7	0.059
WGR	136	0.654±0.19	7.6±2.5	0.015
Females	75	0.645±0.20	4.8±1.5	0.025
Males	52	0.666±0.19	7.2±2.6	0.021
SEB	88	0.654±0.17	7.4±2.7	0.016
Females	48	0.654±0.18	4.8±1.6	0.007
Males	36	0.651±0.17	6.9±2.1	0.062
HS	58	0.612±0.19	6.2±2.9	0.028
Females	16	0.604±0.23	4.3±2.1	0.016
Males	42	0.616±0.18	5.9±2.6	0.048

Population structure

STRUCTURE analysis indicated the presence of at least three populations. NWGR and HS were identified while the third putative population was not clearly identified (Ln probability of data Ln P(D): *k=1 ln=-16787, k=2 ln=-16706, k=3 ln=-16821, k=4 ln=-16551*). Clusters were identified in the 10 runs of *k*=3 for NWGR and HS but not WGR and SEB (Fig. 2A). All 10 runs for *k*=4 to *k*=8 identified NWGR and HS while the others were separated into clusters with no clear patterns. Partitioning the data by sex showed the same pattern (data not shown). Also, due to the significant departures from HWE observed in four loci, STRUCTURE analysis was performed after removing those loci, without any effect, and after removing the loci containing possible null-alleles, also without effect (data not shown). Therefore all loci were retained in subsequent analyses.

Table 3. Pairwise multilocus FST estimates describing the genetic divergence between the four stocks of Atlantic walrus based on 17 microsatellite loci (FSTAT, Goudet 1995). NWGR=Northwest Greenland, WGR=West Greenland, SEB=Southeast Baffin Island, HS=Hudson Strait. **BOLD**: significant after application of the sequential Bonferroni procedure (Rice 1980).

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)	
HS	**0.033**	**0.014**	**0.016**
95%CI	**(0.019-0.047)**	**(0.007-0.023)**	**(0.008-0.026)**

Table 4. 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, HS=Hudson Strait.

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

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

All multilocus pairwise F_{ST} estimates between the four areas showed statistically significant differences except for the WGR vs SEB comparison. The pairwise F_{ST}-estimates over all loci ranged from 0.005 between WGR and SEB to 0.036 between SEB and NWGR (Table 3). When partitioning according to sex the pairwise female samples exhibited a higher level of genetic differentiation than the pairwise male samples.

Migration rates and direction

Analyses of migration rates and directions, with the sampling areas kept separate, showed high proportions of non-migrants in NWGR and HS, while WGR and SEB had relatively high proportions of migrants (Table 4a). The proportions of migrants from SEB in the WGR sample and the proportion of migrants from WGR in the SEB sample were similar. Both WGR and SEB received a similar proportion from NWGR. The proportions of migrants moving from HS to SEB and HS to WG were also about equal to each other and to that between SEB and WG, while HS received virtually no migrants from any of the other three areas. This pattern persisted after pooling the WGR and SEB samples (Table 4b). Individual and population assignments obtained from BIMr based on the four sampling areas (Fig. 2B) also indicated that WGR and SEB were closely connected.

Table 5. Results of tests of sex-biased dispersal (mAlc = mean assignment index, vAlc = variance of the mean assignment index). **BOLD**: significant at the 5% level.

	Females	Males	p-value
F_{IS}	0.038	0.051	0.331
F_{ST}	0.026	0.016	**0.0019***
mAlc	0.283	-0.28	0.186
vAlc	27.27	36.12	**0.022***
N	207	137	

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 walruses (20 male, 9 female, 1 unknown sex) were identified as first generation migrants, i.e. they were born someplace other than in the sampling area. Significantly more males were identified as first generation migrants than 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 (Appendix 1), twice as many as expected by chance (type 1 error, 5% of

63). Three were from WGR/SEB and three from HS. 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 HS. In HS eight of the 58 individuals analysed were migrants (7 males and 1 female); all were from WGR/SEB. Three would be detected by chance (5% of 58).

The migrants suggested by GENECLASS 2 were explored in STRUCTURE. Ten of these 30 first generation migrants were affiliated with another location according to STRUCTURE. STRUCTURE identified six as migrants from WGR/SEB and not HS while four were identified as migrants from HS and not WGR/SEB as suggested by GENECLASS 2 (Appendix 1).

Sex biased dispersal

The results of the test for sex-biased dispersal (Table 5) indicated significant male-dispersal; the component of FST contributed by males was significantly lower than the F_{ST} component contributed by females. Furthermore, the variance of the mean assignment index, *vAIc* , was significantly higher for males as well, reflecting the mixture of native and immigrant males. The negative mean assignment index for males was indicative of individuals having a lower assignment probability or higher probability of being an immigrant (cf. Mossman and Waser 1999). Finally, the fixation index, F_{IS} , was numerically somewhat higher, although not statistically significant, for males.

DISCUSSION

Sampling

It is possible that sample selection by biopsy-takers is different than that of walrus hunters (Stewart 2008). This could explain the sex-bias observed in the different sampling areas and could also distort the interpretation of genetic differences. However, the results indicated 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 sampling method. The unintended re-sampling of individuals at various locations in the SEB sampling area suggests that walruses moved among haulouts and the sample was representative of the Hoare Bay area.

Genetic variation

The levels of genetic variation were similar to those observed in walruses (0.53–0.61, Shafer et al. 2014) and 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) elsewhere. They are also consistent with results in Andersen et al. (2009), which included a subsample of the animals in this study (H_E = ranging from 0.59–0.66) that had been examined with fewer markers. The significantly greater allele richness among male walruses compared to females in the overall sample might reflect a higher rate of dispersal for males compared to females. Females may have a greater tendency to show perennial fidelity to wintering areas during the mating period in January-April (Sjare and Stirling 1996). This suggests 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 also been seen in satellite telemetry studies in the Davis Strait and southern Baffin Bay (Dietz et al. 2014), as well as in Northeast Greenland (Born and Knutsen 1992, Born et al. 2005). This is likewise the case in isotopic studies from Canada (Stewart et al. 2003) and previous genetic studies in Northwest Greenland (Andersen and Born 2000). It may also reflect different selection pressures on males and females, perhaps mediated through a selective hunt where shot males are replaced by other adult males moving in from nearby groups. In this case, males and females within the population would respond as different populations (Stewart 2008) and the genetic population differences would disappear.

The sample of walruses from Northwest Greenland analysed in the present study probably came from more than one population, as implied by the deficit in heterozygotes observed in the overall NWGR sample. This was previously suggested by Andersen and Born (2000) based on significant HWE deviation observed in the winter male-sample from NWGR and is also reflected in the present overall female sample analysed with more markers (significant deviation was observed in the overall F_{IS} [Table 2]). The present study analysed a subset of walruses 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 HS (Table 2) and the significantly greater allele-richness among males overall are consistent with male dispersal behaviour (see below) and possible effects of selective hunting.

Population structure

STRUCTURE analysis indicated that SEB and WGR walruses are part of a common genetic population (Fig. 2). This information is in accordance with the migrations documented via satellite-tagged walruses that have been shown to migrate from Store Hellefiske Banke to SEB shores and is also consistent with the resighting of a rototag in WGR deployed in SEB (Dietz et al. 2014). The identification of a fourth cluster, with no apparent explanatory variable (e.g. season, sex or year) might indicate more than one group of walruses in the total sample of SEB and WGR. Walruses do winter in both areas (Born et al. 1995, DFO 2002, Stewart 2008) and those that remain in Canada may comprise a fourth group that was included in a mixed summer sample. However, the present sample did not allow for further exploration of the genetic and demographic implications of this finding, more sampling would be needed. Meanwhile, the overall genetic differentiation was low and close to the limit of what STRUCTURE requires to be able to identify immigrants (Vähä and Primmer 2006).

The F_{ST}-statistics based on the 17 microsatellite markers (Table 3) indicated walruses sampled in NWGR and in HS were genetically different. However, the genetic difference observed between HS and WGR and SEB was low, consistent with earlier indications of a relatively close connection among walruses in these three areas (Andersen and Born 2000, Born et al. 2001, Andersen et al. 2009). The very close relationship between WGR and SEB suggests that animals in these two areas belong to a single population (also see Born et al. 1994, 1995). The higher level of differentiation observed between females can be explained by female philopatry, and is also consistent with male-biased dispersal (see below).

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, again implying they belong to the same population (Table 4). Both WGR and SEB received similarly high proportions of migrants from HS which received virtually none from WGR, SEB or the combined WGR/SEB subgroup. Andersen et al. (2009) reported a similar pattern based on 11 markers and interpreted it as an indirect indication that HS must also function as a source for SEB walruses. This apparent asymmetrical migration does not necessarily mean that animals do not move from WGR/SEB to HS, but only that they rarely mate with HS walruses. However, there might be additional population structure between HS and SEB. The results of the current study generally confirm Dunbar's (1956) suggestions (based on the appearance of walruses at various locations) that walruses in Hudson Bay, Hudson Strait and at Frobisher Bay 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, perhaps wintering in the ice at the eastern edge in the Davis Strait, where they may well join walruses that spend much of their time off Central West Greenland. Our study indicates that walruses in Central WGR and along SEB belong to the same stock. A direct connection between walruses in these two areas was shown in a recent study using satellite telemetry (Dietz et al. 2014). Of 23 walruses equipped with satellite transmitters in West Greenland during spring 2005–2008, five (4 F and 1 M) migrated from their wintering grounds in Central WGR to SEB. The migration of females from WGR occurred between 7–29 April and that of the adult male occurred the 15th of May. Hence, it is very likely that the migration of these individuals happened after the breeding season. Dietz et al. (2014) recently demonstrated a two-way migration between WGR and SEB (one male, among seven walruses tagged on SEB in 2007, was shot in Central WGR in 2008), but none of the tagged animals moved into Hudson Strait.

Detection of migrants

The detection of more first-generation migrants than expected by chance ("true" non-resident individuals) in HS from WGR/SEB supports the suggestion that there is a close connection between walruses in these areas. Three clusters were identified by STRUCTURE (see above). A fourth cluster was indicated but could not be affiliated to a specific locality apart from a mixture of individuals from SEB, WGR and HS. 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 analysis failed to identify migrants from WGR/SEB and HS while migrants from NWGR were identified in all locations (Appendix 1). This might be due to the low F_{ST} estimate observed between WGR/SEB and HS. The level of F_{ST} will strongly affect the percentage of correctly assigned individuals. The more genetically different the populations the higher the percentages of individuals correctly assigned (Manel et al. 2002, Berry et al. 2004).

The apparent discrepancy between the migration direction indicated by BIMr and GENECLASS2 might be due to differences in the methods used. 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 reproduction and hence have contributed to the genetic composition of their new population. Both methods imply a connection between the HS population and the WGR/SEB population.

Sex-biased dispersal

Male-biased dispersal patterns in mammals are related to the expectation that dispersal is more costly for females due to marked differences in parental investment within polygynous species (Greenwood 1980). Females therefore focus on good breeding areas characterized by familiarity and food availability, while males focus on access to females (Greenwood 1980). The genetic consequences of this male-biased dispersal pattern and female philopatry were reflected in the present study of Atlantic walruses. As expected, the marker data revealed a significant male-dispersal which was reflected by: 1) significantly higher number of alleles (allele richness) in the total male sample compared to the female sample; 2) a significant higher proportion of the detected first generation migrants were males; 3) the significantly higher F_{ST} component from the females in the population structure total F_{ST} value and; 4) the significantly higher *vAlc* for males, indicative of male-dispersal. Sex-bias in favour of male dispersal has been noted among walruses in Foxe Basin (Outridge and Stewart 1999, Stewart et al. 2003). Male-biased dispersal has also been reported from other marine mammals such as Steller sea lions (*Eumetopias jubatus*; Trujillo et al. 2004), southern elephant seal (*Mirounga leonina*; Fabiani et al. 2006), harbour seals (*Phoca vitulina*; Herreman et al. 2009), bottlenose dolphins (*Tursiops aduncus*; Möller and Beheregaray 2004) and sperm whales (*Physeter macrocephalus*; Engelhaupt et al. 2009). However, suggestions of male-biased dispersal were never reflected by all three different tests used to explore this issue in the present study. Natal female philopatry in the Atlantic walrus might drive the population structure although female walruses are capable of moving over long distances. The knowledge of availability of food resources close to the natal breeding areas and probably also the social structure of the walrus urge females to return to the same site(s) for reproduction.

Management implications

The genetic analyses in this study did not reject the hypothesis that walruses occurring in WGR and SEB are both part of a single genetic population, supporting earlier suggestions (e.g. Dunbar 1956, Freuchen and Salomonsen 1961, Mansfield 1973, Born et al. 1994, Dietz et al. 2014) that there is a connection between walruses in these two areas. The study therefore concludes that walruses exploited from fall to spring in WGR belong to the same stock that is distributed along SEB in summer. The putative WGR walrus stock (Born et al. 1995, NAMMCO 1995, Stewart 2008) is part of the North Hudson Bay–Hudson Strait–North Labrador–Southeastern Baffin Island "complex" (Born et al. 1995, NAMMCO 1995; HBDS, Hudson Bay–Davis Strait in Stewart 2008). Apparently, this HBDS population has further sub-structure in that HS walruses do differ from SEB–WGR animals. While STRUCTURE separated WGR/SEB from HS, the migration analyses indicated that the catch at SEB and WGR might be supplied by walruses from HS. Furthermore, a pronounced male-mediated dispersal was observed between the populations, suggesting that there is a high probability that the male component of a population constitute a mixture from various populations. Resolution of this substructure may be found through more extensive sampling in the Hudson Strait region and along Baffin Island. Until then, for the purposes of management advice, it is convenient to consider the WGR/SEB walrus as a single management unit.

Greenland and Canada manage the shared WGR/SEB walrus resource separately, under different management schemes. Until the recent introduction of quotas, the catch of walruses in West Greenland was regulated by a system that limited the duration of the hunting season and hunting methods (Born et al. 1994, 1995); there was no limit to the numbers taken. However, quotas for the catch of walruses were formulated in 2006 in Greenland (Anon. 2006a), taking effect in Central West Greenland in the spring of 2007 (Anon. 2006b). While the catch of walruses in Canada has been regulated for decades by either personal limits (four walruses per hunter) or community quotas (DFO 2002, Stewart 2002, COSEWIC 2006), the Nunavut Wildlife Management Board, the managing authority, is considering advice on stock-specific allowable harvest levels (DFO 2013).

During 1993–2006, the reported landed catch of walruses in West Greenland averaged 136/year (sd =53.4, range=64–240, N=14 years; Department of Fisheries, Hunting and Agriculture, Nuuk, Greenland, in litt. 2008). This does not include losses, which are unknown but believed to be substantial in some years (Born et al. 1995). Quotas for the Central West Greenland walrus stock in 2007, 2008 and 2009 were 80, 65, and 50 animals (Anon. 2006b), respectively.

Walruses occur along SE Baffin Island during the entire year (DFO 2002) where they are hunted mainly during the period May–November (Stewart 2008). 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 were reported to be 32/year (sd=19.4, range=2–71, N=20 years) during 1989–2008 (COSEWIC 2006: Table 2, and DFO unpublished data). This is likely a minimum because in some years catches were not reported.

Aerial surveys in West Greenland indicated the presence of ca. 2300 to ca. 3000 walruses on the West Greenland walrus wintering banks in 2006 and 2008 (Heide-Jørgensen et al. 2014). Boat surveys along parts of the joint stock's coastal feeding grounds on Southeast Baffin Island indicated that 2,100–2,500 walruses summered in Hoare Bay in 2007 (Stewart et al. 2014). Modeling based on recent estimates of abundance indicates that about 3900 walrus occupy the West Greenland–Southeast Baffin Island area (Witting and Born 2014).

Wiig et al. (2014) summarize current management schemes for Atlantic walruses including stocks shared by Canada and Greenland (i.e. Baffin Bay and putative WGR/SEB stocks). At the moment there is formally no bilateral Canada–Greenland agreement or management authority that deals with assessment and advice on sustainable quotas for stocks shared by the two jurisdictions. Greenland has expressed that it regards NAMMCO as the suitable forum for management of walruses (NAMMCO 2010:111) and this organization has established a NAMMCO Scientific Committee Working Group on Walrus, chaired by Greenland. This working group has met twice (2005 and 2009) to assess the status of all stocks of Atlantic walruses (Wiig et al. 2014). Although Canada is not a member of NAMMCO, Canadian scientists have presented data to these meetings and participated in the discussions. Based on recent estimates of abundance the scientific working group at its 2009 meeting offered advice on sustainable takes for the various stocks including the West Greenland–SE Baffin Island stock (NAMMCO 2009, this study, Dietz et al. 2014).

Despite the fact that there is no formal agreement between Canada and Greenland currently on the management of shared stocks, Greenland has decided to *de facto* base its walrus quotas on the advice regarding total removals offered by the NAMMCO Scientific Committee (cf. NAMMCO 2009). This implies that estimates of abundance at West Greenland and Southeast Baffin Island, landed catches reported from these two areas and estimates of non-reported losses from the shared stocks, and a management scheme that would allow the stock to increase (NAMMCO 2010) were all elements taken into consideration when Greenland unilaterally set national quotas for the 2010–2012 hunting seasons. The Greenland quota issued for the catch of walruses in western Greenland from the West Greenland–Southeast Baffin Island group for the three years 2010–2012 was 61/year (GINR 2011). This represents a substantial reduction in the exploitation of walruses in Greenland since 2006 and is in accordance with the NAMMCO recommendation that a total (Canada and Greenland combined) annual removal (catch and losses) of less than 89 would allow for a 70% probability that the stock will increase.

In Canada, Potential Biological Removal (PBR) is applied to marine mammal stocks deemed to be data deficient (Hammill and Stenson 2007). Recent PBR estimates for walrus harvested by communities close to the SEB hunting areas were accompanied by many caveats, but indicated current reported harvest levels in Canada were in the range of PBR estimates, but with the Greenland harvest, would not be (Stewart and Hamilton 2013). Clearly, a formalized agreement between Canada (and the various jurisdictions within Canada that share walruses with Greenland) and Greenland is warranted to ensure sound management of shared stocks.

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Appendix 1. 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 the specified sampling location. Assigned location = the location from which the individual most likely originated according to GENECLASS 2. Q= probability of belonging to the suggested location 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, HS= Hudson Strait.

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