Genetic structure of the North Atlantic common minke whale (*Balaenoptera acutorostrata*) at feeding grounds: a microsatellite loci and mtDNA analysis.

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ABSTRACT

The common minke whale (*Balaenoptera acutorostrata*) is widely distributed in the North Atlantic and is frequently observed along the Icelandic, Norwegian and Portugal coasts, in eastern Canada, North Sea and Greenland, and around Jan Mayen and Svalbard islands. Traditionally, the management of the North Atlantic common minke whales has been based on four geographical subdivisions partitioned by the international Whaling Commission, namely the Canadian East coast stock, the West Greenland stock, the Central stock (Iceland) and the Northeastern stock (Norway). These management regions have been primarily established through studies based on catch statistics, biological characteristics and tagging. Lately, genetic studies tend to confirm the established subdivisions.

The primary goal of the present study was to assess the genetic variation of North Atlantic common minke whales collected at different geographical regions using 16 microsatellite loci and mtDNA sequencing. Both genetic markers gave congruent results and did not show significant genetic signals among the samples collected. In addition, two distinct groups of haplotypes were detected and there was a lack of concordance between geographic and phylogenetic position of mtDNA haplotypes. Together these results suggested the presence of two breeding sites based on the two haplotypes groups detected but a lack of genetic structure of the North Atlantic minke whale at feeding grounds.

KEYWORDS: BALAENOPTERA ACUTOROSTRATA, NORTH ATLANTIC OCEAN, GENETICS, MICROSATELLITE LOCI, MTDNA.

INTRODUCTION

The common minke whale (*Balaenoptera acutorostrata*) is widely distributed in the North Atlantic and is frequently observed along the Icelandic, Norwegian and Portugal coasts, in eastern Canada, North Sea and Greenland, and around Jan Mayen and Svalbard islands (Christensen *et al.*, 1990; NAMMCO, 1998; 2003). It has also recently been observed around the British Isles (McLeod *et al.*, 2004). Although their distribution range is wide, they tend to mainly occur in coastal habitat or ice edge areas (Kasamatsu *et al.*, 2000). Like most of the baleen whales, the common minke whale migrate during the spring to their feeding grounds located in boreal, arctic and subarctic areas (high latitude). Although the location of breeding sites remains unknown, it is acknowledged that the breeding of common minke whale usually occurs at lower latitude during winter months, possibly within the Caribbean Sea and around the straits of Gibraltar (Christensen *et al.*, 1990). Therefore, the common minke whale undertake yearly migration from their breeding ground(s) located at lower latitudes to their feeding grounds located at higher latitudes.

Traditionally, the management of the North Atlantic common minke whales has been based on four geographical subdivisions partitioned by the International Whaling Commission (Donovan, 1991), namely the Canadian East coast stock, the West Greenland stock, the Central stock (Iceland) and the Northeastern stock (Norway). These management regions have been primarily established through studies based on catch statistics, biological characteristics and tagging. Lately, genetic studies tend to confirm the established subdivisions. Genetic variation among potential (sub)populations of minke whale have been investigated using isozyme (Daníelsdóttir *et al*., 1992; 1995) and human α-globin 3'HVR (Árnason and Spillaert, 1991). Both types of markers revealed a significant genetic differentiation among samples collected at West Greenland, Icelandic and Norwegian feeding grounds; hence supporting the existence of at least three different populations. A recent study was carried out on a sample of 306 individuals using microsatellite loci and the D-loop in the mtDNA, to determine the population structure of the common minke whale in Greenland, Central, NE Atlantic and North Sea (Andersen *et al.*, 2003). This study confirmed the genetic distinctiveness of four subpopulations: 1) West Greenland, 2) Central North Atlantic-East Greenland-Jan Mayen area, 3) NE Atlantic (Svalbard, The Barents Sea and the North Sea), and 4) North Sea. The authors suggested that the common minke whales within different ecological regions represented genetically distinct subpopulations.

Here we present the results of genetic analyses performed on samples collected at six different geographical locations with temporal replicates. We analyzed the genetic variation of samples at 16 microsatellite loci and the mtDNA.

MATERIALS AND METHODS

The dataset presented here is on conventional genetic analysis of a North Atlantic common minke whale dataset (Table 1) of 16 microsatellite loci (n=536, EV001, EV037, EV094, EV096, GATA028, GATA053, GATA098, GATA417, GT011, GT023, GT195, GT211, GT310, GT509, GT575 and Sam25; see Table 2) and the D-loop of the mtDNA of 565 individuals sampled in six North Atlantic locations; i.e. off coastal area in Norway, Spitsbergen, North Sea, Barents Sea, West Greenland and Iceland. The Icelandic samples, a total of 347 animals caught west and southwest off Iceland came from the commercial catches during 1981-1985 and the catch under scientific permit from 2003-2007. Samples from West Greenland Davis Strait were collected in 1980, 1982 and 1983 and supplied by Finn Larsen, Greenland Fisheries Research Institute, Denmark. Samples collected in Norwegian areas (Barents Sea, Norway coastal, North Sea and Spitsbergen) and Samples collected in

Norwegian areas (Norway, Spitsbergen, North Sea and Barents Sea) were caught during the Norwegian scientific catch.

Table 1. Sampling location, year of sampling, sample acronyms and number of individuals of common minke whales from the North Atlantic scored at 16 microsatellite loci and the mtDNA.

		Acronym	Microsatellite	mtDNA
Iceland	1981	IC1981	33	33
	1982	IC1982	41	41
	1983	IC9183	35	36
	1984-85	IC1984	44	48
	2003	IC2003	36	36
	2004	IC2004	25	25
	2005	IC2005	34	34
	2006	IC2006	58	58
	2007	IC2007	36	36
West Greenland	1980-83	GREEN	37	61
Barents Sea	1992	EB1992	38	38
	1993	EB1993	12	12
Norway coastal	1992	EC1992	19	18
	1993	EC1993	18	19
North Sea	1994	EN1994	7	7
Spitsbergen	1992	ES1992	35	35
	1993	ES1993	28	28
Total			536	565

Microsatellite loci genotyping.

A total of 16 microsatellite markers and one sex marker were used in four multiplex PCR. Multiplex 1 contained GATA098, EV1, ZFYX0582, GT310, EV37, GATA417, GT023, GT211 and GT509. Annealing temperature was 54°C and 32 PCR cycles were performed. Multiplex 2 contained GATA028 and GT575. Annealing temperature was 56°C and 35 PCR cycles were performed. Multiplex 3 contained GT195, EV094, GATA053 and GT011. Annealing temperature was 58°C and 35 PCR cycles were performed. Multiplex 4 contained EV096 and sam25. Annealing temperature was 58°C and 32 PCR cycles were performed. PCR were performed in a total reaction volume of 10 µl. Each reaction consisted of 3 µl of DNA template isolated with 15% Chelex 100 Resin (BioRad, cat.143-2832) (Walsh *et al.*, 1991) and ProteinaseK, 0.2 µl Teg DNA polymerase (3 U / µl, comparable with Taq DNA polymerase), 1.0 µl of 10x buffer, 0.8 µl dNTP (10 mM), 0,04-0,25 (0,3) µl reverse-and forward primers (100 µM) and dH_2O. The amplification cycle consisted of a 4 min denaturation at 94°C followed by 32-35 cycles of 94°C denaturing for 30 s, 54-58°C annealing for 30 s and 72°C extension for 30 s. Cycling was concluded with a 7 min extension at 72°C. Thermal cycling was performed in Peltier Thermal Cycler 225 (MJ Research), configured with a heated lid. Amplified DNA fragments were separated by an ABI 3730 DNA Analyser (Applied Biosystems) and were sized according to the Applied Biosystem GeneScan™ - 500LIZ™ size standard. Alleles were scored manually with the GeneMapper™ Analysis Software version 4.0 (Applied Biosystem).

Sequencing analyzes for mtDNA, D-loop region.

Primers MT4-PCR-F (5'-CCTCCCTAAGACTCAAGGAAG-3') and MW-PCR-r (5'-GGTCCTGAAGTAAGAACCAGATG-3') were used to amplify mtDNA fragment. PCR was performed in a total reaction volume of 20 µl. Each reaction consisted of 2 µl of DNA template isolated with 15% Chelex 100 Resin (BioRad, cat.143-2832) (Walsh *et al*., 1991) and ProteinaseK, 0.4 µl Teg DNA polymerase (3 U/µl, comparible with Taq DNA polymerase), 2.0 µl of 10x buffer, 0.4 µl dNTP (10 mM), 0.05 µl of each reverse-and forward primers (100 µM) and 15,1 µl dH_2O. The amplification cycle consisted of a 3 min denaturation at 94°C followed by 35 cycles of 94 °C denaturing for 50 s, 56°C annealing for 50 s and 72°C extension for 90 s. Cycling was concluded with a 7 min extension at 72°C. Thermal cycling was performed in a Peltier Thermal Cycler 225 (MJ Research). PCR fragment was purified by using ExoSAP-IT method according to producer (cat. 78201, usb). ExoSap method was performed in a Peltier Thermal Cycler 225 (MJ Research), 37°C for 25 min and then 80°C for 15 min. Purified PCR product was sequenced with forward or reverse using primers MN312-seq-r (5´-GATCTAATGGAGCGGCCATAAG-´3) and BP15851-seq-F (5´-CATCACACTCCACCATCAG-´3). PCR was performed in a total reaction volume of 10 µl. Each reaction consisted of 5 µl purified PCR product, 0.5 µl Big Dye, 1.5 µl of 5x buffer, 1 µl of either reverse-or forward primers (3,5 µM) and 2,0 µl dH_2O.

Table 2. Characteristics of the 16 microsatellite DNA markers scored for 536 North Atlantic common minke whale individuals.

Locus	Primer sequence (5'→3')	Reference	Size range	No. of alleles
EV01	CCC TGC TCC CCA TTC TC ATA AAC TCT AAT ACA CTT CCT CCA AC	Valsecchi and Amos (1996)	141-175	15
EV037	AGC TTG ATT TGG AAG TCA TGA TAG TZG AGC CGT GAT AAA GTG C	Valsecchi and Amos (1996)	191-213	12
EV094	ATC GTA TTG GTC CTT TTC TGC AAT AGA TAG TGA TGA TGA TTC ACA CC	Valsecchi and Amos (1996)	216-220	3
EV096	AGCTGAAGTTTGAACTAAATTATG CTCTTGACCACTCAATTCTTGC	Andersen *et al*. (2003)	247-269	10
GATA028	AAA GAC TGA GAT CTA TAG TTA CGC TGA TAG ATT AGT CTA GG	Palsboll *et al.* (1997)	155-219	14
GATA053	ATT GGC AGT GGC AGG AGA CCC GAC ACA GAG ATG TAG AAG GAG	Palsbøll *et al.* (1997)	259-263	2
GATA098	TGT ACC CTG GAT GGA TAG ATT TCA CCT TAT TTT GTC TGT CTG	Palsbøll *et al.* (1997)	79-103	7
GATA417	CTG AGA TAG CAG TTA CAT GGG TCT GCT CAG GAA ATT TTC AAG	Palsbøll *et al.* (1997)	205-249	12
GT011	CAT TTT GGG TTG GAT CAT TC GTG GAG ACC AGG GAT ATT GC	Bérubé *et al*. (1998)	123-137	5
GT023	CAT TTC CTA CCC ACC TGT CAT GTT CCC AGG CTC TGCACT CTG	Bérubé *et al.* (2000)	93-115	11
GT195	TGA GAA AGA TGA CTA TGA CTC TGA AGT AAC AGT TAA TAT ACC	Bérubé *et al.* (2000)	163-181	9
GT211	CAT CTG TGC TTC CAC AAG CCC GGC ACA AGT CAG TAA GGT AGG	Bérubé *et al.* (2000)	94-118	13
GT310	TAA CTT GTG GAA GAT GCC AAC GAA TAC TCC CAG TAG TTT CTC	Bérubé *et al.* (2000)	103-125	11
GT509	CAG CTG CAA AAC CTT GAC ATT GTA AAA TGT TTC CAG TGC ATC	Bérubé *et al.* (2000)	185-217	16
GT575	TAT AAG TGA ATA CAA AGA CCC ACC ATC AAC TGG AAG TCT TTC	Bérubé *et al.* (2000)	144-166	12
Sam25	CTG CAA ATG GCA TTA CTT C CCA AAC TTA CCA AAT TGT G	Waldick *et al.* (1999)	218-234	9

The amplification cycle consisted of 35 cycles of 96°C denaturing for 30 s, 50°C annealing for 15 s and 60 °C extension for 4 min. Thermal cycling was performed in a Peltier Thermal

Cycler 225 (MJ Research), configured with a heated lid. For Big Dye terminator removal of the cycle sequencing reaction CleanSeq® from Agencourt, Bioscience Corporation (cat no: 000136) was used according to protocol 000383v027 from producer. Sequencing was performed in ABI 3730 DNA Analyser (Applied Biosystems).

During the laboratory process, careful attention was given to the labelling of individuals to avoid confusion and duplicates. Later on, possible duplicates were manually checked within the genotype matrix and relatedness analyses.

Statistical analyses

Microsatellite loci.

Wright's single-locus *F*-statistics (Wright, 1969) were calculated from allele frequencies at all loci examined for each population according to Weir and Cockerham's method (1984) using FSTAT vers. 2.9.3.2 (Goudet, 1995), and significance of pairwise F_{ST} values was assessed by permuting alleles among samples. The Mean F_{ST} (Weir and Cockerham, 1984) over all loci and samples were calculated. Significance levels were adjusted with Bonferroni correction for multiple tests (Rice, 1989). FSTAT was also used to test for fit to Hardy-Weinberg proportions (HWE); to test for linkage disequilibrium between loci and to compare allelic richness (*r*). In all cases 15,000 permutations were used for significance testing.
As a final means of assessing genetic substructure, we calculated assignment index (AI) values for males and females in our study populations using FSTAT. Assignment indices determine the probability that an individual genotype should occur in the population from which it was sampled (Favre *et al*., 1997). When dispersal is frequent (i.e. the individuals sampled represent a mixture of natal and immigrant animals), the mean AI value for a population should be small and the variance around the mean should be large. Accordingly, in populations with sex-biased dispersal, mean AI should be smaller and variance should be larger for the sex in which dispersal is more common. We also calculated overall level of genetic differentiation as well as pairwise F_{ST} values among samples within sexes.

D-loop region of the mtDNA (control region).

For each sample, gene (H) and nucleotide diversity (π) were calculated using Arlequin vers. 3.0 (Excoffier *et al*., 2005). Shared haplotypes among populations were identified using the same software. Genetic differentiation among populations was assessed taking into account nucleotide differences between haplotypes (Φ_{ST}, Weir and Cockerham, 1984), after correction by the Tamura-Nei formula. Significance was assessed by a permutation procedure (5,000 permutations). Corrected genetic distances accounting for intra-population variability (PiXY-(PiXY + PiY)/2) were also calculated in Arlequin. DnaSP 4.10.4 (Rozas *et al*., 2003) was used to perform tests of neutrality (Tajima's D) and to analyze mismatch distributions (Slatkin and Hudson, 1991) for the inference of demographic history from mtDNA data. Rate of transitions vs. transversions was estimated using the software MEGA4 (Tamura *et al*., 2007). Relationships among mitochondrial haplotypes were depicted in Network4 (Bandelt *et al*., 1999). We selected the Median Joining approach (MJ) implemented by the software Network4 (Bandelt *et al*., 1999), for being one of the most efficient network building methods available to date (Cassens *et al*., 2003). The homoplasy parameter (ε) was set to zero. Two weighting schemes were applied in order to account for differences in substitution rates: (1) equal weight for all classes of changes, and (2) weight of 10 for transitions and 30 for transversions and gaps, as suggested by the authors.

To assess the genetic structuring among subpopulations defined by Andersen *et al*. (2003), we performed an AMOVA with both genetic markers using Arlequin. Samples were then

grouped by location, e.g. West Greenland, North Sea, Central Atlantic (Iceland) and Norway. Pairwsie F_{ST} values were also estimated for these geographical locations.
Estimates of the number of migrants per generation (*Nm*) were calculated in GENETIX (Belkhir *et al*., 2002) e.g. $N\text{m} = (1\text{-}F_{ST})/4*F_{ST}$ for microsatellite loci and $N\text{m} = (1\text{-}F_{ST})/2*F_{ST}$ for the mtDNA (Wright, 1969).

RESULTS

Microsatellite loci.
All microsatellite loci were highly polymorphic. The number of alleles per locus across samples ranged from 2 (GATA053) to 15 (EV01). H_o averaged over loci and all samples ranged from 0.622 to 0.682, while H_e ranged from 0.591 to 0.661 (Appendix 1). Genotypic proportions did not yield any significant departure from HWE at any locus or populations investigated. The genetic variation among and within the samples showed a non-significant F_{ST} of 0.0003 (95% CI: -0.0005-0.0011) and a non-significant F_{IS} of -0.0043 (95% CI: -0.0015-0.0094). Pairwise differentiation between populations did not yield any significant values (Appendix 2).

The AMOVA carried out to assess the regional genetic partition among the four areas defined by Andersen *et al*. (2003) failed to show any significant signal (Table 3).

Table 3. Hierarchical analysis of molecular variance (AMOVA) among samples of *Balaenoptera acutorostrata* grouped in four different geographical regions (West Greenland, Central Atlantic, Norway and North Sea) based on microsatellite genotypes and mtDNA sequencing. None of the values were significant.

Regions	Source of variation	df	Variance components	% variation	Fixation indices
mtDNA	Among groups	3	0.0001	0.00	CT=-0.0001
	Among samples within groups	13	0.0053	1.20	SC=0.0120
	Within samples	548	0.4353	98.80	ST=0.0119
	Total	564	0.4406	100	
Microsatellites	Among groups	3	0.0018	0.04	CT=0.0004
	Among samples within groups	13	0.0041	0.08	SC=0.0008
	Within samples	984	5.2084	99.88	ST=0.0011
	Total	999	5.2143	100	

Tests for sex-biased dispersal performed in FSTAT did not reveal any sex mediated gene flow, as none of the P values were significant (Table 4).

Table 4. Test results for sex-biased dispersal in the common minke whale, based on all samples and 16 microsatellite loci (5,000 randomisation).

	F_{IS}	F_{ST}	Rel.	Mean assignment values	Variance
Female	-0.0081	-0.0004	-0.0009	0.0642	15.083
Male	-0.0000	0.0013	0.0026	-0.0737	15.282
P-values	0.2526	0.8132	0.8124	0.2908	0.4082

The overall F_{ST} within sexes were similar to the overall estimates (sexes grouped) and were not significant. Moreover, pairwise F_{ST} values calculated for each sex did no yield any significant comparisons (data not shown).

D-loop region of the mtDNA.
A total of 37 polymorphic sites were observed among which 4 were transversions (Table 5), 4 were deletion/insertion events (1 deletion/insertion event of A, TA, ATA and TATA) and the rest were transitions.

Table 5. Maximum composite likelihood estimate of the pattern of nucleotide substitution.

	A	**T**	**C**	**G**
A	-	*1.61*	*0.94*	**13.66**
T	*1.64*	-	**11.95**	*0.51*
C	*1.64*	**20.51**	-	*0.51*
G	**44.46**	*1.61*	*0.94*	-

NOTE: Each entry shows the probability of substitution from one base (row) to another base (column) instantaneously. Only entries within a row should be compared. Rates of different transitional substitutions are shown in bold and those of transversionsal substitutions are shown in italics. The nucleotide frequencies are 0.349 (A), 0.343 (T/U), 0.2 (C), and 0.107 (G). The transition/transversion rate ratios are k_1 = 27.056 (purines) and k_2 = 12.703 (pyrimidines). **The overall transition/transversion bias is *R* = 5.413**, where $R = [A*G*k_1 + T*C*k_2]/[(A+G)*(T+C)]$. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated from the dataset (Complete deletion option). There were a total of 348 positions in the final dataset. All calcuations were conducted in MEGA4 (Tamura *et al.*, 2007).

The 37 sites defined a total of 54 different haplotypes where haplotype 1, 2 and 3 are shared and common among all sampling areas. Estimates of nucleotide diversity ranged from 0.0099 for EB1992 to 0.0143 for IC1983, and the haplotypic diversity ranged from 0.7190 for IC2007 to 0.9500 for IC2004 (Table 6).

Neither the pairwise differentiation based on nucleotide differences among haplotypes (Φ_{ST}) nor the corrected genetic distances accounting for intra-population variability (PiXY-(PiXY + PiY)/2) between populations did yield significant values (Appendix 3). Exact test of sample differentiation based on haplotype frequencies yielded 11 significant comparisons out of 136 among which 7 were due to temporal comparisons of Icelandic samples and 4 among Greenlandic and Icelandic samples (Appendix 4).

Table 6. Number of samples (N), gene diversity (H), number of haplotypes (nH), and nucleotide diversity (π) by population with standard deviation (s.d.).

	N	nH	H	s.d.	π	s.d.
IC1981	36	15	0.8968	0.0350	0.0114	0.0065
IC1982	41	19	0.9085	0.0322	0.0117	0.0066
IC1983	38	20	0.9417	0.0206	0.0143	0.0079
IC1984-85	48	20	0.9246	0.0205	0.0129	0.0071
IC2003	36	13	0.7873	0.0646	0.0112	0.0064
IC2004	25	13	0.9500	0.0196	0.0132	0.0074
IC2005	34	16	0.8752	0.0450	0.0120	0.0068
IC2006	58	20	0.9316	0.0136	0.0131	0.0072
IC2007	36	12	0.7190	0.0809	0.0093	0.0054
GREEN	61	18	0.8393	0.0413	0.0108	0.0061
EB1992	38	12	0.8037	0.0582	0.0099	0.0057
EB1993	12	9	0.9394	0.0577	0.0123	0.0073
EC1992	18	10	0.8758	0.0628	0.0124	0.0072
EC1993	22	12	0.9221	0.0354	0.0137	0.0078
EN1994	7	5	0.8571	0.1371	0.0123	0.0079
ES1992	35	11	0.7496	0.0720	0.0100	0.0058
ES1993	28	13	0.9074	0.0342	0.0129	0.0073

The Median Joining network revealed the presence of two different haplotype groups based on haplotype distribution (Figure 1) which did not correspond to any particular geographical areas. The application of differential weights did not alter significantly the phyletic relationships between haplotypes. The weighted network was identical to the unweighted one.

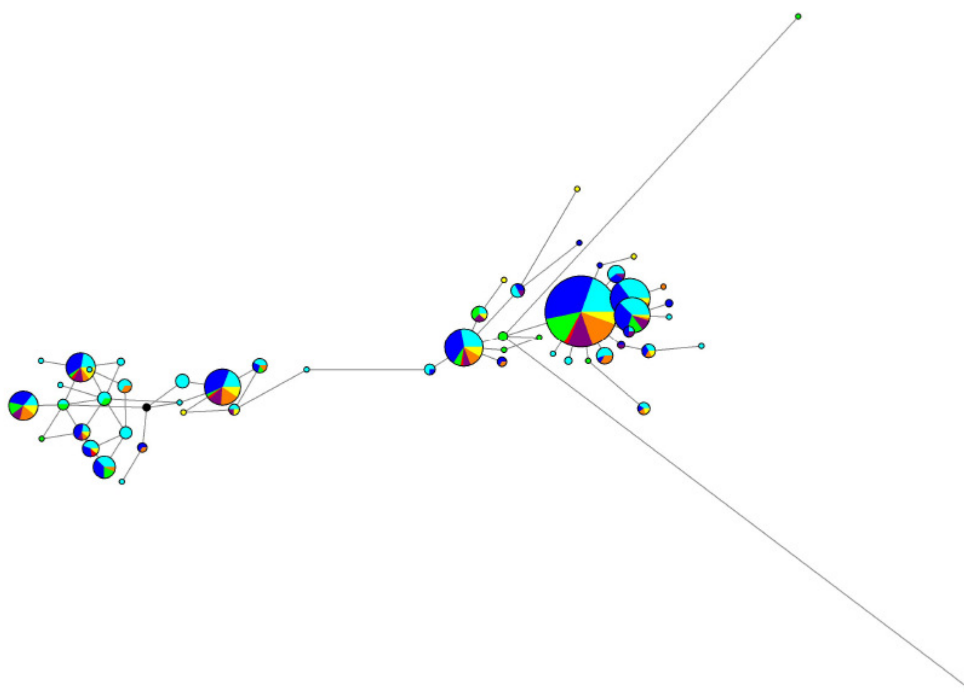

Figure 1. Median joining tree showing relationship among the 54 common minke whale mtDNA haplotypes detected. The tree was constructed using the software Network4. Filling pattern represent the provenance of the samples (Light blue=Iceland 1981 to 1985; dark blue=Iceland 2003 to 2007, yellow=Norway coastal area, Green=Greenland, Red=North Sea, Orange=Spitsbergen; Purple=Barents Sea). Connector length is proportional to the number of substitutions. Small closed circles represent potential intermediate haplotypes that were not sampled.

The mismatch distributions analysis (Figure 2) was consistent with exponential population expansion suggesting that populations of common minke whale are not at equilibrium.

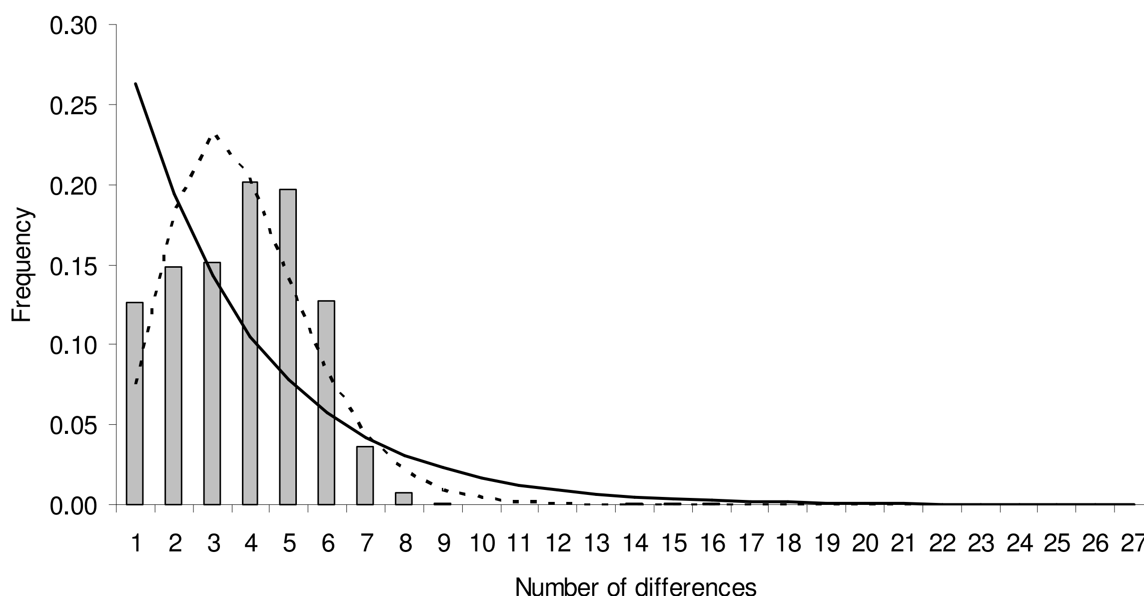

Figure 2. Observed mitochondrial DNA haplotype mismatch distribution (grey bars) and theoretical curves for a historical population expansion (dashed line) and for constant population size (plain line).

In addition, the AMOVA carried out to assess the regional genetic partition among the four areas defined by Andersen *et al*. (2003) did not detect any significant signal (Table 3).

Discussion

The primary goal of the present study was to assess the genetic variation of North Atlantic common minke whales collected at different geographical regions using 16 microsatellite loci and the mtDNA. Both genetic markers gave congruent results and failed to show any significant genetic signals among the samples collected, hence not supporting the actual IWC separation of minke whales into different management units in the North Atlantic. Below we discuss the obtained results and compare them with previous studies carried out within the same geographical regions.

Genetic variability

The genetic diversity of the 16 microsatellite loci assessed as H_O, H_E, A and Ar exhibited a wide range of variation and was generally comparable to what has been observed in other whale species (Andersen *et al.*, 2003; Bérubé *et al.*, 1998; Bérubé *et al.*, 2002; Jorde *et al.*, 2007; Kanda *et al.*, 2007). With regard to other minke whale studies, the observed level of genetic variability was similar to the finding of Andersen *et al*. (2003), although the overall estimates per populations seemed to be slightly higher in the present study.

The variability at the mtDNA was generally comparable to findings on whale species (Kanda *et al.*, 2007), although 6 new haplotypes were discovered with regard to Andersen *et al*. (2003) data.

Genetic differentiation

Both genetic markers gave congruent results with conventional analyses resulting in a lack of genetic differentiation among the samples collected which do not support earlier studies performed on allozyme loci variability (Daníelsdóttir *et al*., 1992; 1995) and human α-globin 3'HVR (Árnason and Spillaert, 1991), and therefore do not support the actual populations subdivision of North Atlantic common minke whale.

Recently, Andersen *et al*. (2003) found significant divergences among four geographical areas and suggested that the observed pattern was linked to ecological regions. Although, some genetic differences could be detected with mtDNA (no geographical pattern detected), the main signal among geographical regions (West Greenland, Central, Northeast Atlantic and North Sea) was detected at microsatellite loci. The observed differences between the former study and the present study at microsatellite loci could be explained by the distribution of the samples analyzed (no Icelandic samples were genotyped in the previous study) as well as the sampling years and the different loci employed. For example, the overall level of genetic variability per samples was higher in the present study than in the study of Andersen *et al*. (2003). The advantage of the present study also relies on a temporal approach which failed to show any differentiation among samples collected with a 20 years interval within Icelandic waters, and a similar level of differentiation among these temporal samples and samples from other areas.

In addition, the present study did not reveal any differences with mtDNA except a haplotype frequency variation in Iceland and a lack of concordance between geographic and phylogenetic position of mtDNA haplotypes. Indeed, two groups of haplotypes were detected with the haplotype network, but none of them corresponded to a particular geographical region, and all regions were represented in each haplotype group. The restriction fragment pattern of mtDNA analysis carried out by Palsbøll (1989) did not show any genetic differentiation among samples collected at feeding grounds in the North Atlantic but suggested the presence of two main groups of genotypes, possibly reflecting the existence of two distinct breeding populations. This pattern was later confirmed by Bakke *et al*. (1996) who revealed a lack of concordance between haplotypes and geographical regions, but suggested the existence of two or more differentiated populations which might co-exist at feeding grounds in the North Atlantic, based on interpretation of a maximum parsimony tree of mtDNA. Therefore, the results obtained with mtDNA during the present study can either reflect a residual ancestral polymorphism or a "recent" isolation of two populations at breeding sites, which roam through large parts of the North Atlantic Ocean during the feeding migration as suggested by Palsbøll (1989) and Bakke *et al*. (1996) results.

Also discordant genetic structure assessed at microsatellite loci and mtDNA are often interpreted as evidence for sex-biased dispersal in marine mammals (Baker *et al.*, 1993; Baker *et al.*, 1994; Lyrholm *et al.*, 1999). Indeed, sex-specific philopatry is a well-known phenomenon in whales species, resulting either in a different pattern of population structure between sexes or between nuclear and mtDNA markers (Baker *et al.*, 1993; Baker *et al.*, 1994; Lyrholm *et al.*, 1999). However, all statistical analyzes performed to detect sex mediated gene flow failed to detect any significant pattern.

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References list

Andersen LW, Born EW, Dietz R, Haug T, Oien N, Bendixen C (2003) Genetic population structure of minke whales *Balaenoptera acutorostrata* from Greenland, the North East Atlantic and the North Sea probably reflects different ecological regions. *Marine Ecology Progress Series* **247**, 263-280.

Árnason A, Spillaert R (1991) A study of variability in minke whale (*Balaenoptera acutorostrata*) in the North Atlantic using a human hypervariable region probe alpha-globin 3'HRV. *Report of the International Whaling Commission* **41**, 439-443.

Baker CS, Perry A, Bannister JL, Weinrich MT, Abernethy RB, Calambokidis J, Lien J, Lambertsen RH, Ramirez JU, Vasquez O, Clapham PJ, Alling A, Obrien SJ, Palumbi SR (1993) Abundant mitochondrial DNA variation and world-wide poulation structure in Humpback whales. *Proceedings of the National Academy of Sciences* **90**, 8239-8243.

Baker CS, Slade RW, Bannister JL, Abernethy RB, Weinrich MT, Lien J, Urban J, Corkeron P, Calmabokidis J, Vasquez O, Palumbi SR (1994) Hierarchical structure of mitochondrial DNA gene flow among humpback whales, world-wide. *Molecular Ecology* **3**, 313-327.

Bakke I, Johansen S, Bakke Ø, El-Gewely MR (1996) Lack of population subdivision among the minke whale (*Balaenoptera acutorostrata*) from Icelandic and Norwegian waters based on mtDNA sequences. *Marine Biology* **125**, 1-9.

Bandelt H-J, Forster P, Rohl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* **16**, 37-48.

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2002). *Genetix, a WindowsTM Based Software for Population Genetic Analyses* Version 4.05. Laboratoire Génome, Populations, Interaction CNRS UMR 5000, Université de Montpellier II, Montpellier, France.

Bérubé M, Aguilar A, Dendanto D, Larsen F, Notarbartolo di Sciara G, Sears R, Sigurjónsson J, Urban-R J and Palsbøll PJ (1998) Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, *Balaenoptera physalus* (Linnaeus 1758): analysis of mitochondrial and nuclear loci. *Molecular Ecology* **7**, 585-599.

Bérubé M, Jorgensen H, McEwing R, Palsbøll PJ (2000) Polymorphic di-nucleotide microsatellite loci isolated from the humpback whale, *Megaptera novaeangliae*. *Molecular Ecology* **9**, 2181-2183.

Bérubé M, Urbán-R J, Dizon AE, Brownell RL, Palsbøll PJ (2002) Genetic identification of a small and highly isolated population of fin whales (*Balaenoptera physalus*) in the Sea of Cortez, Mexico. *Conservation Genetics* **3**, 183-190.

Cassens I, van Waerebeek K, Best PB, Crespo EA, Reyes J, Milinkovitch MC (2003) The phylogeography of dusky dolphins (*Lagenorhynchus obscurus*): a critical examination of network methods and rooting procedures. *Molecular Ecology* **12**, 1781-1792.

Christensen I, Haug T, Wiig O (1990) Morphometric comparison of minke whale *Balaenoptera acutorostrata* from different areas of the North Atlantic. *Marine Mammal Science* **6**, 327-338.

Daníelsdóttir AK, Halldórsson SD, Guðlaugsdóttir S, Árnason A (1995) Genetic variation in northeastern Atlantic minke whales (*Balenoptera acutorostrata*). In: Whales, seals and man, eds Blix AS, Walløe L, Ulltang Ø, pp105-118.

Daníelsdóttir AK, Duke EJ, Árnason A (1992) Genetics variation at enzyme loci in North Atlantic minke whale, *Balaenoptera acutorostrata*. *Biochemical Genetics* **30**, 189-202.

Donovan GP (1991) A review of IWC stock boundaries. *Report of the International Whaling Commission* (special issue 13), 39-68.

Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* **1**, 47-50.

Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London B* **264**, 127-132.

Goudet J (1995) FSTAT (vers. 1.2): a computer program to calculate F-statistics. *Journal of Heredity* **86**, 485-486.

Jorde PE, Schweder T, Bickham JW, Given GH, Suydam R, Hunter D, Stenseth NC (2007) Detecting genetic structure in migrating bowhead whales off the coast of Barrow, Alaska. *Molecular Ecology* **16**, 1993-2004.

Kanda N, Goto M, Kato H, McPhee M, Pastene LA (2007) Population genetic structure of Bryde's whales (*Balaenoptera brydei*) at the inter-oceanic and trans-equatorial levels. *Conservation Genetics* **8**, 853-864.

Kasamatsu F, Ensor P, Joyce GG, Kimura N (2000) Distribution of minke whales in the Bellingshausen and Amundsen Seas (60oW-120oW), with special reference to environmental/physiographic variables. *Fisheries Oceanography* **9**, 214-223.

Lyrholm T, Leimar O, Johanneson B, Gyllensten U (1999) Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings of the Royal of London B* **266**, 347-354.

McLeod K, Fairbains R, Gill A, faribains B, Gordon J, Blair-Myers C, Parsons ECM (2004) Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull Scotland. *Marine Ecology Progress Series* **277**, 263-274.

Palsbøll PJ (1989) Restriction fragment pattern analysis of mitochondrial DNA in minke whales, *Balaenoptera acutorostrata*, from the Davis Strait and the Northeast Atlantic. Chapter of master thesis, University of Copenhagen, Copenhagen.

Palsbøll PJ, Bérubé M, Larsen AH, Jorgensen H (1997) Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. *Molecular Ecology* **6**, 893-895.

Rice WR (1989) Analyzing table of statistical tests. *Evolution* **43**, 223-225.

Rørvik CJ, Jonsgård Å, (1981) Review of balaenopterids in the North Atlantic Ocean. *F.A.O. Fish. Ser. [Mammals in the Seas]* **3**, 269-286.

Rozas J, Sánchez-DelBarrio JC, Messeguer X, Rozas R (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* **19**, 2496-2497.

Slatkin M, Hudson RR (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. *Genetics* **129**, 555-562.

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* **24**, 1596-1599.

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

Waldick RC, Brown MW, White BN (1999) Characterization and isolation of microsatellite loci from endangered North Atlantic right whale. *Molecular Ecology* **8**, 1763-1765

Walsh PS, Metzger DA, Higuchi R (1991) Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques* **10**, 506-513.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. *Evolution* **38**, 1358-1370.

Wright S (1969) Evolution and the genetics of populations. Vol. 2. The theory of gene frequencies. University of Chicago Press, Chicago.

Appendix 1 *Microsatellite loci analysis*. Observed (H_O) and expected (H_E) heterozygosity, number of alleles (A), allelic richness (Ar) in common minke whale samples collected at different feeding areas of the North Atlantic Ocean. "Total" indicates the overall heterozygosity levels for the samples collected as well as the mean number of alleles (Â), the allelic richness (Ar), the F_{IS} and probability values (P). Note that Ar has been calculated without considering the sample EN1994 and is based on 12 individuals.

Location	Years	Acronym	EV01				EV037				EV094				EV096				GATA028				GATA053			
			H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar
Iceland	1981	IC1981	0.788	0.840	11	7.90	0.576	0.548	7	5.44	0.242	0.298	2	2.00	0.667	0.692	9	6.41	0.813	0.790	9	6.89	0.303	0.257	2	1.99
	1982	IC1982	0.805	0.797	9	6.53	0.610	0.626	8	5.49	0.366	0.381	2	2.00	0.805	0.708	8	5.98	0.775	0.776	8	6.35	0.098	0.093	2	1.76
	1983	IC1983	0.857	0.831	9	7.40	0.629	0.685	7	5.55	0.219	0.285	2	2.00	0.686	0.772	9	6.69	0.829	0.825	9	7.70	0.143	0.133	2	1.89
	1984-85	IC1984	0.796	0.812	10	6.86	0.591	0.597	12	5.31	0.286	0.245	2	1.99	0.791	0.735	7	6.05	0.886	0.806	9	6.86	0.136	0.127	2	1.86
	2003	IC2003	0.889	0.825	9	7.25	0.667	0.618	6	5.10	0.278	0.278	2	2.00	0.667	0.725	7	5.82	0.861	0.809	8	6.92	0.111	0.105	2	1.81
	2004	IC2004	0.840	0.830	10	8.39	0.600	0.538	7	5.48	0.480	0.374	2	2.48	0.680	0.711	7	5.63	0.792	0.785	9	7.14	0.240	0.211	2	1.99
	2005	IC2005	0.882	0.840	9	7.58	0.677	0.683	8	5.97	0.294	0.360	2	2.00	0.588	0.685	8	5.82	0.912	0.845	9	7.61	0.118	0.111	2	1.83
	2006	IC2006	0.741	0.825	10	7.05	0.638	0.623	8	6.01	0.345	0.311	3	2.20	0.862	0.771	9	6.48	0.810	0.819	9	7.24	0.241	0.212	2	1.97
	2007	IC2007	0.833	0.828	11	8.40	0.611	0.624	7	5.22	0.278	0.282	3	2.33	0.667	0.667	9	6.00	0.889	0.841	11	8.30	0.167	0.153	2	1.92
West Greenland	1980-83	GREEN	0.806	0.819	10	6.85	0.676	0.631	7	4.88	0.353	0.291	2	2.00	0.667	0.715	7	5.66	0.829	0.804	11	7.42	0.054	0.053	2	1.55
Barents Sea	1992	EB1992	0.790	0.801	10	7.01	0.632	0.652	8	6.03	0.395	0.347	2	2.00	0.684	0.747	8	6.26	0.921	0.802	9	7.09	0.105	0.145	2	1.91
	1993	EB1993	0.917	0.816	6	6.00	0.583	0.465	5	5.00	0.167	0.153	2	2.00	0.917	0.726	7	7.00	0.917	0.792	8	8.00	0.000	0.000	1	1.00
Norway coastal	1992	EC1992	0.842	0.751	7	6.24	0.684	0.722	7	5.89	0.263	0.301	2	2.00	0.842	0.708	6	5.68	0.684	0.798	8	7.44	0.105	0.100	2	1.87
	1993	EC1993	0.833	0.813	8	6.97	0.500	0.457	5	4.68	0.500	0.424	2	2.00	0.611	0.577	6	4.90	0.706	0.789	6	5.90	0.222	0.198	2	1.99
North Sea	1994	EN1994	0.714	0.684	4		0.571	0.684	4		0.286	0.245	2		1.000	0.674	5		0.857	0.857	8		0.143	0.337	2	
Spitsbergen	1992	ES1992	0.914	0.840	8	6.98	0.657	0.716	7	5.52	0.400	0.325	3	2.34	0.771	0.741	8	6.03	0.849	0.829	12	8.44	0.114	0.108	2	1.82
	1993	ES1993	0.750	0.760	7	5.99	0.643	0.611	6	5.22	0.250	0.223	3	2.40	0.679	0.747	8	6.25	0.714	0.767	8	6.30	0.107	0.101	2	1.82

Location	Years	Acronym	GATA098				GATA417				GT011				GT023				GT195				GT211			
			H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar
Iceland	1981	IC1981	0.788	0.696	6	4.86	0.636	0.794	10	7.64	0.424	0.405	3	2.36	0.697	0.747	6	4.72	0.406	0.429	4	3.52	0.909	0.784	7	5.85
	1982	IC1982	0.683	0.695	6	4.94	0.829	0.819	10	7.69	0.366	0.442	2	2.00	0.781	0.757	7	5.67	0.415	0.350	4	3.11	0.878	0.785	7	5.75
	1983	IC1983	0.647	0.694	6	4.77	0.886	0.832	11	8.46	0.286	0.408	2	2.00	0.857	0.768	9	6.37	0.457	0.458	4	3.67	0.725	0.707	6	5.05
	1984-85	IC1984	0.796	0.719	6	5.18	0.886	0.824	10	7.73	0.341	0.386	2	2.00	0.750	0.789	9	6.36	0.296	0.332	4	3.25	0.727	0.729	6	5.36
	2003	IC2003	0.778	0.747	5	4.80	0.917	0.856	10	8.34	0.417	0.413	2	2.00	0.667	0.688	7	5.17	0.500	0.446	4	3.62	0.778	0.756	5	4.91
	2004	IC2004	0.720	0.734	7	5.82	0.880	0.855	9	7.93	0.400	0.403	2	2.00	0.760	0.755	8	6.30	0.440	0.400	4	3.66	0.720	0.762	8	5.89
	2005	IC2005	0.647	0.676	5	4.61	0.853	0.835	10	7.84	0.471	0.466	4	2.71	0.706	0.706	7	5.56	0.382	0.403	4	3.18	0.647	0.772	7	5.44
	2006	IC2006	0.793	0.744	6	5.11	0.862	0.844	10	7.58	0.328	0.370	3	2.21	0.759	0.744	8	5.39	0.397	0.394	5	3.78	0.862	0.755	9	5.65
	2007	IC2007	0.833	0.723	6	5.15	0.889	0.836	10	8.00	0.361	0.389	2	2.00	0.667	0.721	9	5.48	0.528	0.477	4	3.63	0.861	0.784	9	6.42
West Greenland	1980-83	GREEN	0.676	0.709	7	4.93	0.853	0.836	10	7.90	0.355	0.367	2	2.00	0.757	0.770	9	6.31	0.541	0.459	5	4.02	0.865	0.813	9	6.63
Barents Sea	1992	EB1992	0.737	0.724	6	4.82	0.947	0.836	9	7.29	0.474	0.411	2	2.00	0.737	0.748	8	6.29	0.263	0.238	4	2.91	0.816	0.763	7	4.95
	1993	EB1993	0.667	0.712	5	5.00	0.833	0.809	8	8.00	0.583	0.497	3	3.00	0.917	0.840	9	9.00	0.250	0.219	2	2.00	0.667	0.806	6	6.00
Norway coastal	1992	EC1992	0.895	0.718	6	5.26	0.895	0.805	7	6.74	0.316	0.465	2	2.00	0.842	0.770	7	6.33	0.579	0.490	5	4.22	0.737	0.799	9	7.63
	1993	EC1993	0.611	0.704	5	4.86	0.833	0.826	10	8.68	0.611	0.461	2	2.00	0.722	0.727	8	6.64	0.278	0.338	4	3.76	0.889	0.790	6	5.64
North Sea	1994	EN1994	0.429	0.531	4		0.857	0.827	8		0.286	0.245	2		0.857	0.735	5		0.286	0.255	3		0.714	0.735	6	
Spitsbergen	1992	ES1992	0.771	0.762	7	5.60	0.857	0.838	10	8.23	0.457	0.423	3	2.57	0.914	0.780	7	6.09	0.514	0.479	5	4.08	0.857	0.791	7	5.83
	1993	ES1993	0.679	0.698	7	5.21	0.893	0.847	9	7.98	0.464	0.469	2	2.00	0.750	0.760	7	5.63	0.429	0.365	4	3.55	0.714	0.772	7	5.53

Location	Years	Acronym	GT310				GT509				GT575				Sam25				Total					
			H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	A	Ar	H_O	H_E	Â	Ar	F_{IS}	P
Iceland	1981	IC1981	0.636	0.686	6	4.66	0.875	0.803	9	6.95	0.849	0.783	8	7.00	0.727	0.734	7	6.00	0.646	0.643	6.63	5.26	0.011	0.301
	1982	IC1982	0.585	0.689	6	4.69	0.805	0.804	9	6.61	0.732	0.721	9	6.63	0.659	0.638	8	5.81	0.637	0.630	6.56	5.06	0.001	0.518
	1983	IC1983	0.743	0.697	7	5.35	0.771	0.787	8	6.49	0.829	0.806	8	6.76	0.800	0.724	6	5.81	0.649	0.651	6.56	5.34	0.018	0.852
	1984-85	IC1984	0.636	0.691	7	4.90	0.818	0.796	9	6.69	0.568	0.661	8	6.26	0.651	0.613	6	4.76	0.622	0.616	6.50	5.09	0.002	0.450
	2003	IC2003	0.694	0.697	5	4.77	0.778	0.809	9	7.14	0.806	0.775	9	6.78	0.667	0.713	8	6.19	0.655	0.641	6.13	5.16	-0.007	0.836
	2004	IC2004	0.640	0.584	5	4.34	0.840	0.798	10	7.56	0.760	0.777	7	5.89	0.600	0.631	5	4.20	0.650	0.634	6.44	5.29	-0.004	0.417
	2005	IC2005	0.618	0.707	6	5.23	0.824	0.798	10	7.37	0.794	0.774	10	7.41	0.706	0.717	6	5.26	0.632	0.649	6.75	5.34	0.040	0.776
	2006	IC2006	0.759	0.693	8	5.40	0.810	0.821	13	7.33	0.810	0.768	8	6.79	0.707	0.728	9	6.20	0.670	0.651	7.50	5.40	-0.020	0.506
	2007	IC2007	0.778	0.637	6	5.15	0.861	0.807	10	6.76	0.889	0.784	8	7.03	0.694	0.684	7	5.77	0.675	0.640	7.13	5.47	-0.042	0.999
West Greenland	1980-83	GREEN	0.622	0.637	6	4.74	0.781	0.822	10	7.66	0.703	0.745	8	6.69	0.750	0.723	7	5.40	0.625	0.637	7.00	5.29	0.005	0.164
Barents Sea	1992	EB1992	0.579	0.650	5	4.36	0.737	0.811	9	6.91	0.658	0.797	7	6.16	0.658	0.711	8	6.03	0.633	0.636	6.50	5.13	0.018	0.339
	1993	EB1993	0.667	0.667	6	6.00	0.667	0.729	7	7.00	0.583	0.587	5	5.00	0.667	0.653	6	6.00	0.625	0.592	5.34	5.38	-0.013	0.827
Norway coastal	1992	EC1992	0.579	0.627	5	4.25	0.895	0.790	6	5.62	0.737	0.687	6	5.56	0.579	0.591	6	5.36	0.655	0.633	5.69	5.13	-0.008	0.914
	1993	EC1993	0.722	0.711	6	5.46	0.722	0.836	10	8.68	0.889	0.755	7	6.62	0.889	0.739	7	5.97	0.659	0.634	5.89	5.30	-0.010	0.727
North Sea	1994	EN1994	0.714	0.541	4		0.857	0.755	6		0.571	0.684	5		0.571	0.678	5		0.607	0.591	4.56		0.050	0.763
Spitsbergen	1992	ES1992	0.714	0.700	5	4.76	0.743	0.825	11	7.98	0.868	0.738	8	6.49	0.686	0.682	7	5.89	0.682	0.661	6.88	5.54	0.005	0.941
	1993	ES1993	0.464	0.603	6	4.58	0.893	0.808	9	7.27	0.821	0.750	7	6.42	0.750	0.691	6	5.45	0.625	0.623	6.13	5.10	-0.016	0.961

Appendix 2 *Microsatellite loci analyses*. Pairwise F_{ST} comparisons among common minke whales samples from six locations (above diagonal). None of the comparisons were significant (Indicative adjusted nominal level (5%) for multiple comparisons is: P = 0.000549). The number of migrants Nm was calculated according to Wright (1969), Nm = (1-F_{ST})/4*F_{ST} and is indicated below the diagonal.

	IC1981	IC1982	IC1983	IC1984	IC2003	IC2004	IC2005	IC2006	IC2007	GREEN	EB1992	EB1993	EC1992	EC1993	EN1994	ES19992	ES1993
IC1981	0	-0.0002	0.0012	-0.0016	-0.0005	0.0033	-0.0022	0.0023	-0.0012	0.0020	0.0046	0.0099	0.0001	-0.0042	0.0112	0.0029	-0.0002
IC1982	∞	0	0.0059	-0.0010	0.0024	0.0079	0.0025	0.0018	0.0019	0.0033	0.0009	0.0064	-0.0050	0.0045	0.0081	0.0013	-0.0007
IC1983	211.24	42.23	0	-0.0001	-0.0011	0.0005	-0.0038	-0.0013	-0.0042	-0.0013	0.0008	0.0076	-0.0031	0.0031	0.0043	-0.0028	-0.0013
IC1984	∞	∞	∞	0	-0.0001	0.0055	-0.0010	0.0002	-0.0002	0.0016	0.0023	0.0002	-0.0058	0.0054	0.0075	0.0001	-0.0022
IC2003	∞	104.81	∞	∞	0	0.0029	-0.0026	-0.0005	-0.0027	0.0018	-0.0018	0.0061	-0.0033	0.0016	0.0047	-0.0053	-0.0030
IC2004	75.11	31.6	549.37	44.92	86.76	0	0.0014	-0.0016	-0.0024	0.0003	-0.0021	0.0088	0.0004	-0.0008	0.0039	0.0034	-0.0044
IC2005	∞	98.33	∞	∞	∞	175.54	0	0.0007	-0.0049	-0.0007	-0.0008	0.0021	-0.0018	-0.0047	0.0074	-0.0022	-0.0008
IC2006	107.76	137.26	∞	1122.84	∞	∞	351.32	0	-0.0020	0.0001	-0.0014	0.0055	-0.0003	0.0055	0.0000	-0.0006	-0.0023
IC2007	∞	134.36	∞	∞	∞	∞	∞	∞	0	0.0000	0.0004	0.0067	-0.0036	0.0040	0.0027	-0.0020	-0.0042
GREEN	128.22	74.79	∞	158.5	137.11	794.01	∞	1992.4	6077.36	0	0.0023	0.0029	-0.0014	0.0015	0.0074	-0.0003	-0.0016
EB1992	54.06	266.13	328.7	108.45	∞	∞	∞	∞	715.9	110.36	0	0.0045	-0.0045	0.0010	0.0051	-0.0012	-0.0060
EB1993	25.14	39.15	32.85	1615.52	40.5	28.17	119.9	45.65	36.97	85.16	55.48	0	-0.0015	0.0148	0.0191	0.0026	0.0010
EC1992	2437.66	∞	∞	∞	∞	575.03	∞	∞	∞	∞	∞	∞	0	0.0080	-0.0004	-0.0056	-0.0103
EC1993	∞	55.55	80.98	45.67	156.94	∞	∞	45.41	62.16	165.86	258.92	16.61	30.93	0	0.0167	0.0044	0.0034
EN1994	22.03	30.54	57.97	32.96	52.96	63.37	33.52	29986.4	92.61	33.47	49.22	12.87	∞	14.74	0	0.0045	0.0048
ES1992	87.46	199.07	∞	5112.37	∞	73.83	∞	∞	∞	∞	∞	95.65	∞	56.69	55.33	0	-0.0019
ES1993	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	253.63	∞	73.91	51.55	∞	0

Appendix 3 *Mitochondrial (mtDNA) data analyses*. Above diagonal: Pairwise Φ_{ST} comparisons taking into account nucleotide differences between haplotypes (Weir and Cockerham, 1984) after correction by the Tamura-Nei formula among common minke whales samples from six locations. Below diagonal: Corrected genetic distances accounting for intra-population variability (PiXY-(PiXY + PiY)/2). In both cases, none of the comparisons were significant.

	IC1981	IC1982	IC1983	IC1984	IC2003	IC2004	IC2005	IC2006	IC2007	GREEN	EB1992	EB1993	EC1992	EC1993	EN1994	ES19992	ES1993
IC1981	0	-0.0069	-0.0118	-0.0103	-0.0183	-0.0267	-0.0155	-0.0076	-0.0001	0.0062	-0.0075	-0.0390	-0.0068	-0.0104	-0.0738	-0.0038	-0.0066
IC1982	-0.0199	0	-0.0028	-0.0058	-0.0141	-0.0050	-0.0204	0.0003	0.0052	-0.0123	-0.0062	-0.0220	-0.0146	0.0014	-0.0569	0.0047	0.0025
IC1983	-0.0386	-0.0111	0	-0.0055	-0.0139	-0.0215	-0.0108	-0.0088	-0.0059	0.0048	-0.0011	-0.0293	-0.0143	-0.0153	-0.0749	-0.0042	-0.0080
IC1984	-0.0301	-0.0176	-0.0215	0	-0.0100	-0.0149	-0.0127	-0.0082	0.0010	0.0081	-0.0103	-0.0382	-0.0086	-0.0082	-0.0523	-0.0071	-0.0169
IC2003	-0.0502	-0.0385	-0.0447	-0.0276	0	-0.0182	-0.0234	-0.0103	-0.0105	-0.0084	-0.0098	-0.0369	-0.0226	-0.0122	-0.0755	-0.0087	-0.0116
IC2004	-0.0829	-0.0188	-0.0742	-0.0495	-0.0570	0	-0.0190	-0.0173	0.0033	0.0054	-0.0054	-0.0445	-0.0157	-0.0262	-0.0815	-0.0067	-0.0147
IC2005	-0.0449	-0.0594	-0.0361	-0.0386	-0.0647	-0.0608	0	-0.0085	-0.0029	-0.0109	-0.0109	-0.0318	-0.0198	-0.0111	-0.0670	-0.0051	-0.0086
IC2006	-0.0212	0.0026	-0.0338	-0.0271	-0.0277	-0.0572	-0.0249	0	0.0132	0.0134	0.0081	-0.0398	-0.0161	-0.0265	-0.0680	0.0079	-0.0160
IC2007	-0.0011	0.0147	-0.0178	0.0070	-0.0250	0.0015	-0.0081	0.0450	0	0.0025	-0.0163	-0.0130	-0.0047	0.0308	-0.0434	-0.0215	0.0037
GREEN	0.0127	-0.0339	0.0057	0.0209	-0.0221	0.0031	-0.0321	0.0385	0.0070	0	-0.0026	-0.0068	-0.0113	0.0241	-0.0446	0.0025	0.0181
EB1992	-0.0207	-0.0159	-0.0046	-0.0273	-0.0246	-0.0215	-0.0299	0.0287	-0.0367	-0.0062	0	-0.0283	-0.0097	0.0211	-0.0429	-0.0224	-0.0015
EB1993	-0.1148	-0.0677	-0.0815	-0.1121	-0.1095	-0.1324	-0.0946	-0.1167	-0.0558	-0.0391	-0.0895	0	-0.0522	-0.0524	-0.1007	-0.0238	-0.0494
EC1992	-0.0175	-0.0390	-0.0339	-0.0171	-0.0611	-0.0436	-0.0537	-0.0396	-0.0194	-0.0352	-0.0297	-0.1473	0	-0.0219	-0.0817	-0.0073	-0.0242
EC1993	-0.0428	-0.0073	-0.0559	-0.0346	-0.0505	-0.0928	-0.0446	-0.0961	0.0663	0.0425	0.0432	-0.1628	-0.0688	0	-0.0872	0.0249	-0.0210
EN1994	-0.1957	-0.1520	-0.1989	-0.1324	-0.1996	-0.2183	-0.1781	-0.1782	-0.1342	-0.1329	-0.1278	-0.2665	-0.2144	-0.2403	0	-0.0410	-0.0645
ES1992	-0.0103	0.0137	-0.0126	-0.0169	-0.0216	-0.0243	-0.0139	0.0294	-0.0480	0.0062	-0.0523	-0.0783	-0.0237	0.0558	-0.1241	0	-0.0039
ES1993	-0.0215	0.0054	-0.0266	-0.0554	-0.0365	-0.0485	-0.0280	-0.0524	0.0053	0.0407	-0.0087	-0.1466	-0.0680	-0.0755	-0.1699	-0.0144	0

Appendix 4 *Mitochondrial (mtDNA) data analyses*. Above diagonal: Number of migrants (*Nm*) calculated according to Wright (1969), $Nm = (1-\Phi_{ST})/2*\Phi_{ST}$. Below diagonal: Exact test *P*-values of samples differentiation based on haplotype frequencies. Bold values indicated *P*-values which were significant prior to correction for multiple tests.

	IC1981	IC1982	IC1983	IC1984	IC2003	IC2004	IC2005	IC2006	IC2007	GREEN	EB1992	EB1993	EC1992	EC1993	EN1994	ES19992	ES1993
IC1981	0	∞	∞	∞	23.65	∞	∞	1583.66	13.05	64.83	544.94	∞	∞	∞	∞	17.66	∞
IC1982	0.4520	0	∞	220.57	44.39	81.14	∞	35.56	15.78	364.58	95.37	∞	∞	62.00	∞	20.80	813.55
IC1983	0.9360	0.7068	0	∞	10.87	∞	406.72	∞	8.07	29.67	25.82	∞	42.71	∞	3625.50	10.38	427.82
IC1984	0.6851	0.5148	0.7663	0	11.33	∞	43.51	∞	6.31	16.87	18.86	∞	25.48	∞	123.28	10.14	899.86
IC2003	0.1261	0.2993	**0.0147**	0.1361	0	8.33	∞	8.82	∞	108.69	∞	∞	∞	12.44	∞	∞	50.65
IC2004	0.8848	0.2267	0.9838	0.8080	**0.0056**	0	50.55	∞	5.52	15.57	15.76	∞	29.87	∞	80.58	8.19	164.56
IC2005	0.8407	0.8369	0.8264	0.3419	0.4567	0.4145	0	21.51	42.43	∞	∞	∞	∞	43.33	∞	51.88	∞
IC2006	0.4845	0.0679	0.3637	0.6965	**0.0353**	0.7528	**0.0457**	0	5.34	12.20	12.89	∞	24.75	∞	96.38	7.94	∞
IC2007	0.3439	0.2957	0.3111	**0.0119**	0.3980	**0.0249**	0.6958	**0.0238**	0	137.12	∞	19.66	43.77	6.79	∞	∞	12.22
GREEN	**0.0208**	0.1338	0.0688	**0.0111**	0.1045	**0.0171**	0.1161	**0.0004**	0.6169	0	∞	∞	2723.48	16.58	∞	∞	28.92
EB1992	0.7246	0.4037	0.5663	0.4399	0.2597	0.2196	0.6691	0.2283	0.9434	0.6107	0	∞	∞	24.89	∞	∞	48.91
EB1993	0.7521	0.4453	0.8032	0.6295	0.3453	0.8939	0.4423	0.8012	0.2185	0.2646	0.5259	0	∞	∞	∞	305.65	∞
EC1992	0.4037	0.4203	0.3860	0.2555	0.6751	0.2537	0.4680	0.3041	0.2554	0.0977	0.2530	0.8290	0	70.65	∞	2651.34	∞
EC1993	0.6983	0.1838	0.8591	0.4760	0.0711	0.8323	0.2087	0.8162	0.0855	0.0737	0.3554	0.9908	0.3656	0	∞	9.95	∞
EN1994	0.9708	0.8558	0.8528	0.7963	0.9413	0.7722	0.8329	0.8731	0.4727	0.3564	0.5859	1.0000	1.0000	0.9340	0	∞	∞
ES1992	0.1988	0.1858	0.1529	0.1588	0.6090	0.1203	0.3449	0.1908	0.8348	0.5448	0.9302	0.3639	0.3412	0.0803	0.4931	0	25.68
ES1993	0.4968	0.1689	0.4803	0.4503	0.3094	0.2582	0.3053	0.6315	0.1114	0.0124	0.1925	0.8753	0.6510	0.7279	0.8999	0.2993	0

Appendix 5

Microsatellite analysis. Above diagonal: Pairwise F_{ST} comparisons among North Atlantic minke whale geographical samples. Below diagonal: F_{ST} P values. None of the comparisons were significant (Indicative adjusted nominal level (5%) for multiple comparisons is: $P = 0.008$).

	ICELAND	NORWAY	NORTH SEA	GREENLAND
ICELAND	0	0.0002	0.0056	-0.0013
NORWAY	0.2896	0	0.0074	-0.0016
NORTH SEA	0.1978	0.1520	0	0.0094
GREENLAND	0.7844	0.8159	0.1405	0

Mitochondrial (mtDNA) data analyses. Above diagonal: Pairwise Φ_{ST} comparisons among North Atlantic minke whale samples from five geographical locations (above diagonal) based on mtDNA. Below diagonal: Corrected genetic distances accounting for intra-population variability (PiXY-(PiXY + PiY)/2). None of the comparisons were significant after Bonferroni correction.

	ICELAND	NORWAY	NORTH SEA	GREENLAND
ICELAND	0	0.004	-0.027	0.008
NORWAY	0.004	0	-0.039	0.007
NORTH SEA	-0.021	-0.032	0	-0.025
GREENLAND	0.008	0.006	-0.022	0