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DNA sequence analysis identifies genetically distinguishable populations of harp seals (*Pagophilus groenlandicus*) in the Northwest and Northeast Atlantic

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Abstract Harp seals (*Pagophilus groenlandicus* Erxleben, 1777) comprise three populations based upon whelping areas in the Greenland Sea, White Sea, and Northwest Atlantic. The last comprises two subpopulations, one whelping in the Gulf of St. Lawrence (''Gulf'') and one on the pack ice of the southern Labrador/northern Newfoundland coastal shelf (''Front''). A total of 40 female seals from the four whelping areas were collected during the 1990 and 1992 whelping seasons. DNA sequence variation was examined in a 307 bp region of the mitochondrial cytochrome *b* gene. Eleven variable nucleotide positions defined 13 genotypes: a significant fraction of the genotypic variance ($F_{ST} = 0.12$, or 0.09 as measured by Weir's coancestry coefficient θ) is attributable to differentiation between Northwest and Northeast Atlantic populations. There was no significant differentiation between the two whelping areas in the Northwest Atlantic, or between the Greenland Sea and White Sea. These findings suggest significant reproductive isolation exists between trans-Atlantic breeding populations.

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Introduction

The harp seal (*Pagophilus groenlandicus*) (not *Phoca groenlandica*: for comments on nomenclature see Perry et al. 1995; Carr and Perry 1997) is found only in the North Atlantic where it is the most abundant pinniped (Sergeant 1991). Three separate breeding populations have been recognized based on the geographic locations of whelping areas (see Fig. 1), one on pack ice in the Greenland Sea near Jan Mayen Island, a second on ice in the White Sea and the Gorlo connecting it to the Barents Sea, and a third in the Northwest Atlantic on pack ice along the east coast of Canada. The latter has been separated into two subpopulations, one whelping in the Gulf of St. Lawrence (''Gulf'') and the other off the coast of northeastern Newfoundland and/or southern Labrador (''Front''). Typically, seals form one, two, or three concentrations in each area, but because of current- and wind-driven ice movements, these groups can split, mix, and reform over the course of the whelping period. There is no evidence of site fidelity within a whelping area (Sergeant 1991).

All three populations are harvested commercially, and interest in management of harp seals has increased in recent years due to apparent changes in their abundance and catches. Recent changes in assessment methods have led to markedly higher estimates of pup production in the White Sea, and catch quotas have been increased (Anonymous 1999a). Estimated abundance of the Northwest Atlantic population has increased dramatically since the early 1970s, and the total population was approximately 5 million in 1994 (Shelton et al. 1996; Anonymous 1999d; Stenson et al. 1999). This has raised concerns about the potential impact of seal predation on recovering groundfish stocks in many

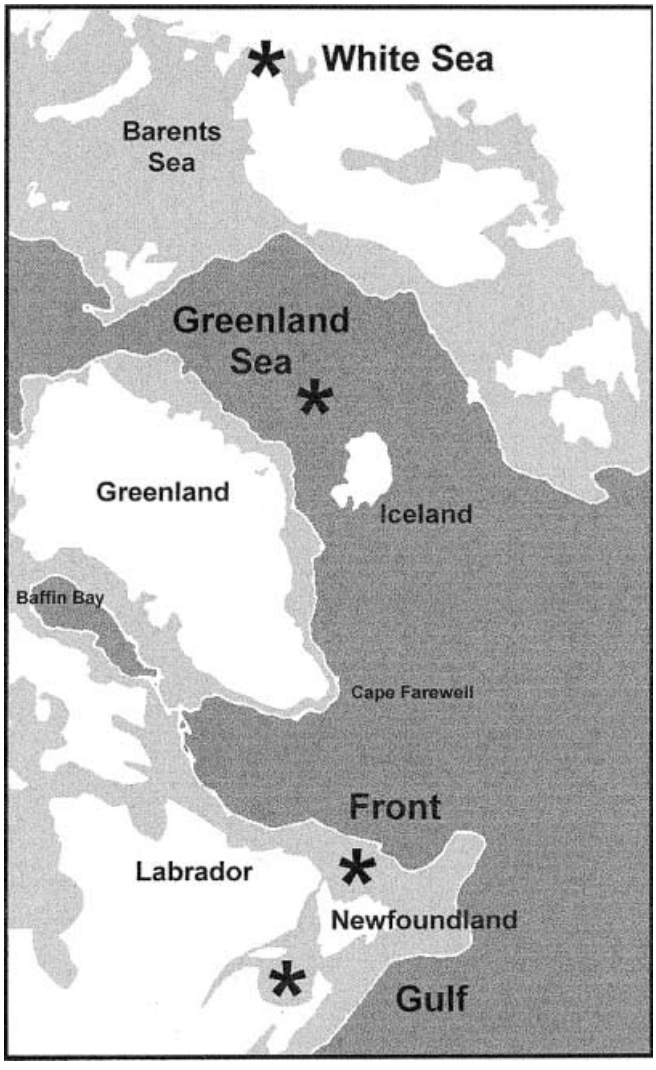

Fig. 1 *Pagophilus groenlandicus*. Whelping areas and the origins of population samples used in this study

areas (NAFO 1998; Anonymous 1999c). In order to develop appropriate management plans for harp seals, it is critical to address the question of reproductive isolation among all breeding populations.

Harp seals undertake migrations between winter whelping grounds and summer feeding areas, and the ranges of adult and immature seals from different populations are known to overlap during the non-breeding season (Sergeant 1991). Harp seals from the Northwest Atlantic population summer in the Canadian Arctic and southeastern Greenland, those from the Greenland Sea population have been recovered between west Greenland and the Barents Sea during the non-breeding season, and those from the White Sea have been recovered primarily from the Barents Sea and occasionally in Greenland waters (Sergeant 1991; Øien and Øritsland 1995; Kapel 1996; Stenson and Sjare 1997). Breeding immediately follows whelping: although limited tagging data suggest site fidelity among breeding adults, and there are no tag returns to indicate that mature adults mix during the breeding season, adult seals tagged in one whelping population have occasionally been found near other breeding areas shortly thereafter (Sergeant 1965, 1973, 1991; Bowen and Sergeant 1983, 1985; Anonymous 1992, 1994; Øien and Øritsland 1995). It is possible that there is genetically effective exchange of reproductively mature adults among breeding areas.

Relationships among the three North Atlantic populations have been examined in studies of cranial measurements (Yablokov and Sergeant 1963) and underwater vocalizations (Perry and Terhune 1999), and in genetic studies of serum transferrins (Møller et al. 1966; Nævdal 1966, 1969, 1971), blood serum proteins (Borisov 1966), allozymes (Meisfjord et al. 1991; Meisfjord and Nævdal 1994), and DNA minisatellites (Meisfjord and Sundt 1996). It has been concluded that populations in the Northwest and Northeast Atlantic are, to some extent, reproductively isolated. No previous genetic study of North Atlantic populations has included separate samples of the Front and Gulf subpopulations taken during the whelping season. In the present study, we examined genetic variation in seals from all four whelping patches by direct comparison of sequences of the mitochondrial DNA (mtDNA) cytochrome *b* gene. Cytochrome *b* has proved a useful molecular marker for the establishment of phylogenetic and population relationships among seal species (Lento et al. 1994; Perry et al. 1995; Carr and Perry 1997) and other marine species (Birt-Friesen et al. 1992; Carr et al. 1995; Vis et al. 1997).

Materials and methods

Tissue samples were obtained during the whelping season from ten female harp seals (*Pagophilus groenlandicus* Erxleben, 1777) at four locations representing three breeding populations: Greenland Sea, White Sea, Front (all March 1990), and Gulf (March 1992) (Fig. 1). Samples from the Front and Gulf were obtained under special permit from the Department of Fisheries and Oceans. DNA was extracted from ~200 mg of muscle by the acid guanidinium/thiocyanate method (Bartlett and Davidson 1992a, b). DNA was amplified by the polymerase chain reaction (PCR) and both strands sequenced using a pair of oligonucleotide primers (L14841 and H15149 of Kocher et al. 1989) that amplify a 359 bp portion of the mtDNA cytochrome *b* gene. Conditions for PCR amplification and dideoxy DNA sequencing are described by Carr and Marshall (1991) and Bartlett and Davidson (1992a, b).

DNA sequences were assembled with the ESEE (Ver. 3.2) program of Cabot and Beckenbach (1989). Genetic heterogeneity within population samples was estimated by the nucleon diversity (h) index for non-selfing populations as calculated by the REAP program of McElroy et al. (1991) and the nucleotide diversity (π) index of Nei and Tajima (1981) from pairwise haplotype divergences (uncorrected *p*-distances) calculated by the Arlequin (Ver. 1.1) program of Schneider et al. (1997). Heterogeneity of genotype distributions among population samples was tested with the Monte-Carlo χ^2 test (5,000 resamplings) (Roff and Bentzen 1989) as implemented in REAP, and by the exact test of population differentiation (Raymond and Rousset 1995) (estimates made with 100,000 Markov chain steps, 1,000 dememorization steps, and a required precision of 0.001) as implemented in Arlequin. The proportion of genetic diversity attributable to subdivision among population samples was estimated by the coancestry coefficient (θ) calculated with the HAPLOID program of Weir (1990); the standard error was estimated by jackknifing over population samples.

F-statistics of genetic structure among populations, based on the distribution of genotype frequencies, were calculated with Arlequin. Minimum-length (parsimony) trees were identified by a branch-and-bound search of unweighted mutational differences among genotypes with the PAUP* (Ver. 4.0) program of Swofford (1998).

Effective population size can be calculated from the nucleotide diversity index (π) as described by Carr et al. 1995 (after Hartl and Clark 1990). Given a nucleotide divergence rate (in humans) for the entire mtDNA molecule of 7.1×10^{-9} per nucleotide site per year per pair of lineages (Nei 1985) corrected by 25% for the slightly higher rate for the portion of the cytochrome *b* molecule examined here (Carr and Hughes 1993), and a generation time in harp seals of approximately 5 years (Bowen et al. 1981), the long-term effective population size (N_e) can be calculated as: $N_e = (\pi)/(7.1 \times 10^{-9})(1.25)(5)$. The variance on this estimate is on the same order as the mean value.

Results

Within the middle 307 bp of the amplified segment, 11 variable positions were identified among 40 seals. Seven of these are at the third positions in their respective codons and are silent; the remaining four are at first positions and result in amino acid substitutions. All except one are transitions. The variable positions define 13 sequence genotypes (Fig. 2). The sequences have been submitted to GenBank and assigned the Accession Numbers AF200479 to AF2004791.

Genotype A was the most common genotype in all population samples (overall frequency 60%, 40% in each of the two Northeast Atlantic populations and 80% in each of the two Northwest Atlantic population samples; Table 1). The remaining genotypes differed from Genotype A by from one to three substitutions: most differed by single substitutions. Some substitutions appear to have occurred in parallel in different genotypes. Analysis of genotype distributions indicated significant heterogeneity among the four population samples (by the Monte-Carlo χ^2 test: $\chi^2 = 46.67$, $df = 36$, $P < 0.007$; by the exact test: $P < 0.02$). A comparison of three population samples representing the three breeding populations [i.e. two Northwest Atlantic population samples (Gulf and Front) pooled versus the Greenland Sea and White Sea population samples] was also significant ($\chi^2 = 38.67$, $df = 26$, $P < 0.002$; by the exact test: $P < 0.0004$), as was a comparison of a pool of the two Northwest Atlantic population samples versus a pool of the two Northeast Atlantic population samples ($\chi^2 = 18.67$, $df = 12$, $P < 0.001$; by the exact test: $P < 0.004$). There were no significant differences between the two Northwest Atlantic population samples ($\chi^2 = 4.00$, $df = 4$, $P > 0.59$), or between the two Northeast Atlantic population samples ($\chi^2 = 10.00$, $df = 8$, $P > 0.23$) [equivalent results were obtained by the exact test (not shown)].

The two Northwest Atlantic population samples were substantially less variable than those in the Northeast Atlantic. Among the 12 minority genotypes, only four occurred in more than one seal: all of these occurred in the Northeast Atlantic, including the only genotype (other than A) found in more than one sampling location (Genotype F). The haplotype (i.e. nucleon) (h) and nucleotide (π) diversity indices for Northwest Atlantic population samples were less than half those of the Northeast Atlantic population samples (Table 2). The coancestry coefficient (θ) over the four population samples was 0.058 (± 0.024 SD), which indicates that approximately 6% of the genotypic variance was attributable to subdivision among population samples; for this comparison, $F_{ST} = 0.071$, which is significantly nonzero ($P < 0.04$). The coancestry coefficient calculated for a pool of the Northwest Atlantic versus a pool of the Northeast Atlantic population samples ($\theta = 0.093$) indicates that approximately 10% of the variance was attributable to trans-Atlantic subdivision; for the same pooling, $F_{ST} = 0.12$ ($P < 0.006$). Pairwise calculation of the portion of genotypic variance attributable to separation into Front versus Gulf, and Greenland Sea versus White Sea, indicates that neither is significantly different from zero [$F_{ST} = -0.049$ ($P \approx 1.0$) and -0.004 ($P > 0.30$), respectively].

Calculations of N_e for all population samples, and for pools of the samples in the Northwest and in the Northeast Atlantic, are given in Table 2. For the pool of Northwest Atlantic harp seals, $N_e \approx 3.7 \times 10^4$ as compared with a combined census count of ca. 4.5 to 5.0 million individuals in these two areas (Anonymous 1994; Shelton et al. 1996; Stenson et al. 1999), a difference of two orders of magnitude. The most genetically diverse sample (Greenland Sea) has $N_e = 1.37 \times 10^5$, on the same order as the current census estimate of 4.5×10^5 (Anonymous 1999a).

Discussion

Analysis of the distribution of DNA sequence variation in the mtDNA cytochrome *b* gene of *Pagophilus groenlandicus* indicates significant genetic differentiation between samples from the Northwest Atlantic (Front and Gulf samples) and the Northeast Atlantic (Greenland and White Seas), though not between samples within those areas. A substantial portion of the observed genotypic variance is attributable to trans-Atlantic population subdivision. These results confirm previous studies of harp seals, which showed significant genotype heterogeneity at two isozyme loci between the Northwest Atlantic and a pool of Northeast Atlantic population samples (Meisfjord and Nævdal 1994). There was no significant deficiency of heterozygotes in the mixed Northwest Atlantic population sample, nor in pooled Greenland Sea and White Sea samples, as would be expected if these were mixtures taken from genetically isolated populations with distinct allele frequencies (Wahlund Effect). Analysis of minisatellite DNA patterns showed low but essentially uniform band-sharing coefficients within and between the Greenland Sea and White Sea population samples (Meisfjord and Sundt

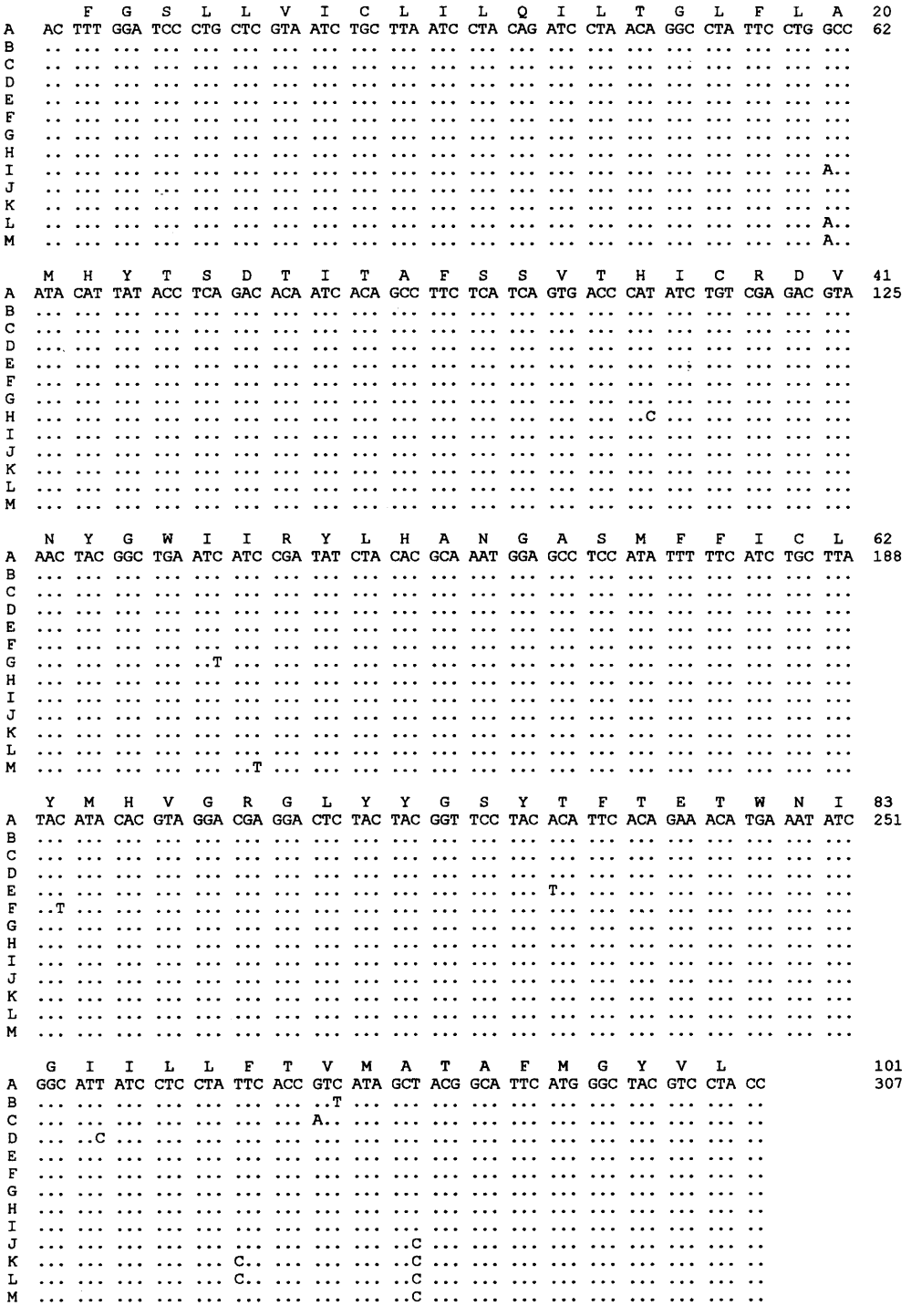

Fig. 2 *Pagophilus groenlandicus*. Variation in DNA sequences within a 307 bp region of the mtDNA cytochrome *b* gene. In each of the 13 genotypes, each nucleotide is identical to that in Genotype A except where indicated. The top line gives the inferred amino acid sequence according to the IUB single-letter code. Numbers adjacent to the first and second lines indicate position numbers in the protein and nucleotide sequences, respectively

1996). Meisfjord and Sundt (1996) concluded that the total stock of harp seals could be divided into reproductively isolated Northwest and Northeast Atlantic components, and that there was no detectable genetic differentiation between the Greenland Sea and White Sea populations. On the assumption that these populations were in fact distinct stocks, they suggested that this was a shortcoming of the method rather than an indication of homogeneity (Meisfjord and Sundt 1996). We suggest instead that the allozyme, DNA minisatellite, and DNA sequence data are all consistent with an alternative hypothesis, that neither the two Northeast Atlantic nor the two Northwest Atlantic harp seal breeding areas are reproductively isolated from one another. However, larger sample sizes are needed to state unequivocally that there is no genetic differentiation attributable to stock structure within populations in the Northwest and Northeast Atlantic (cf. Bentzen 1998; Carr and Crutcher 1998).

Levels of DNA sequence variation were substantially less in the Northwest versus the Northeast Atlantic

Table 1 *Pagophilus groenlandicus*. Distribution of mtDNA genotypes among four breeding populations in the North Atlantic and adjacent areas

Location	mtDNA genotype:													
	(*n*)	A	B	C	D	E	F	G	H	I	J	K	L	M
Northwest Atlantic Gulf	(10)	8	0	1	0	0	0	0	0	0	0	1	0	0
Northwest Atlantic Front	(10)	8	0	0	0	0	0	0	1	1	0	0	0	0
Greenland Sea	(10)	4	2	0	0	0	1	1	0	0	0	0	1	1
White Sea	(10)	4	0	0	1	2	1	0	0	0	2	0	0	0

Table 2 *Pagophilus groenlandicus*. Haplotype (h) and nucleotide (π) diversity indices and effective population sizes (N_e) for population samples from four breeding populations in the North Atlantic and adjacent areas, and for pools of population samples from the Northwest and from the Northeast Atlantic

Location	h	π	N_e
Single samples			
Northwest Atlantic Front	0.3778	0.00195	44×10^3
Northwest Atlantic Gulf	0.3778	0.00130	30×10^3
Greenland Sea	0.8444	0.00608	137×10^3
White Sea	0.8222	0.00362	82×10^3
Pooled samples			
Front + Gulf	0.3684	0.00163	37×10^3
Greenland Sea + White Sea	0.8316	0.00487	110×10^3

population samples, and imply effective population numbers substantially smaller than current census counts (Table 2). The low N_e of the Northwest Atlantic population(s) might be due to a relatively ancient event, such as a founder event accompanying trans-atlantic dispersal. In contrast, historical evidence indicates that the size of the Greenland Sea population has been greatly reduced in recent times. This population has been harvested since the 1700s, and annual catch rates in excess of 450,000 individuals (equal to the current census number) are recorded from the 1920s (Sergeant 1976). Thus, although the higher N_e of this population is closer to the current census count, it may actually indicate that the historical population count has been much higher. Disparities between census counts and effective population numbers in harp seals require further study.

The identification of genetically distinguishable components of harp seals in the North Atlantic may contribute to a better estimate of the impact of increased hunting in the North Atlantic, and also may provide a basis for modified management practices. Currently, the Northwest Atlantic, Greenland Sea, and White Sea stocks are treated as separate for management purposes (Anonymous 1999a). Allowable catches are based upon abundance estimates derived primarily from pup production surveys in each of the whelping concentrations. The Greenland harvest, which has tripled in recent years, includes seals from all three populations but primarily from the Northwest Atlantic and Greenland Sea populations (Øien and Øritsland 1995; Kapel 1996). Catches in this harvest are assigned to source populations based upon assumptions about area of capture (Anonymous 1998). Given the markedly different sizes of these populations [5.0×10^6 in the Northwest Atlantic (Anonymous 1999d; Stenson et al. 1999) versus 4.5×10^5 in the Greenland Sea (Anonymous 1999a)], the consequences of errors in this assumption could be significant. In the Northwest Atlantic, the Front and Gulf components are assessed together, but the total allowable catch is allocated to each area based upon a traditional division reflecting historical trends in their relative pup production (Anonymous 1999b). Recently, however, there have been calls for differential management plans in the two areas, and questions have also been raised about the potential impact of seal predation on various fish stocks (Anonymous 1999c). As well, because estimates of the genetically effective population size of the harp seal population in the Northwest Atlantic are substantially smaller than census estimates, it is possible that culls or harvests of this population may have a disproportionately large impact on any existing genetic structure. A better understanding of the genetic relationships within and between the two components of the Northwest Atlantic harp seal population, based on more extensive sampling and analysis, is required before any proposals for differential management can be considered.

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