Molecular Ecology (1999) **8**, 1571–1584

Genetic structure of the world's polar bear populations

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Abstract

We studied genetic structure in polar bear (*Ursus maritimus*) populations by typing a sample of 473 individuals spanning the species distribution at 16 highly variable microsatellite loci. No genetic discontinuities were found that would be consistent with evolutionarily significant periods of isolation between groups. Direct comparison of movement data and genetic data from the Canadian Arctic revealed a highly significant correlation. Genetic data generally supported existing population (management unit) designations, although there were two cases where genetic data failed to differentiate between pairs of populations previously resolved by movement data. A sharp contrast was found between the minimal genetic structure observed among populations surrounding the polar basin and the presence of several marked genetic discontinuities in the Canadian Arctic. The discontinuities in the Canadian Arctic caused the appearance of four genetic clusters of polar bear populations. These clusters vary in total estimated population size from 100 to over 10 000, and the smallest may merit a relatively conservative management strategy in consideration of its apparent isolation. We suggest that the observed pattern of genetic discontinuities has developed in response to differences in the seasonal distribution and pattern of sea ice habitat and the effects of these differences on the distribution and abundance of seals.

Keywords: microsatellite, polar bear, population structure, sea ice, *Ursus maritimus*

Received 15 January 1999; revision received 11 May 1999; accepted 11 May 1999

Introduction

Polar bears are found on ice-covered waters throughout the circumpolar Arctic (Fig. 1). They prey primarily on ringed seals (*Phoca hispida*), but also on bearded seals (*Erignathus barbatus*) and harp seals (*P. groenlandicus*), which they hunt through breathing holes, in birth lairs, or when hauled out on the ice (Stirling & Archibald 1977; Smith 1980). In the Canadian Arctic the density and productivity of polar bear populations is correlated with ringed seal density which is, in turn, an index of overall marine ecosystem productivity (Stirling & Øritsland 1995). The local distributions of ringed seals and polar bears are also influenced by the type of sea ice habitat (Kingsley *et al*. 1985; Stirling *et al*. 1993). Polar bears and seals are relatively uncommon over areas of thick multiyear ice, particularly in regions such as the polar basin where the water is cold, deep and relatively unproductive biologically. In areas where open water prevails in late summer and autumn, bears move to terrestrial habitats. Most polar bears also have their maternity dens in snow drifts on coastal land areas adjacent to regions where they can hunt in spring (Harington 1968; Uspenski & Kistchinski 1972; Stirling & Andriashek 1992; Wiig 1995; Born *et al*. 1997), although in some areas they also use multiyear ice for denning and as a retreat when the

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§§Sadly, Dr Garner died while this manuscript was being prepared.

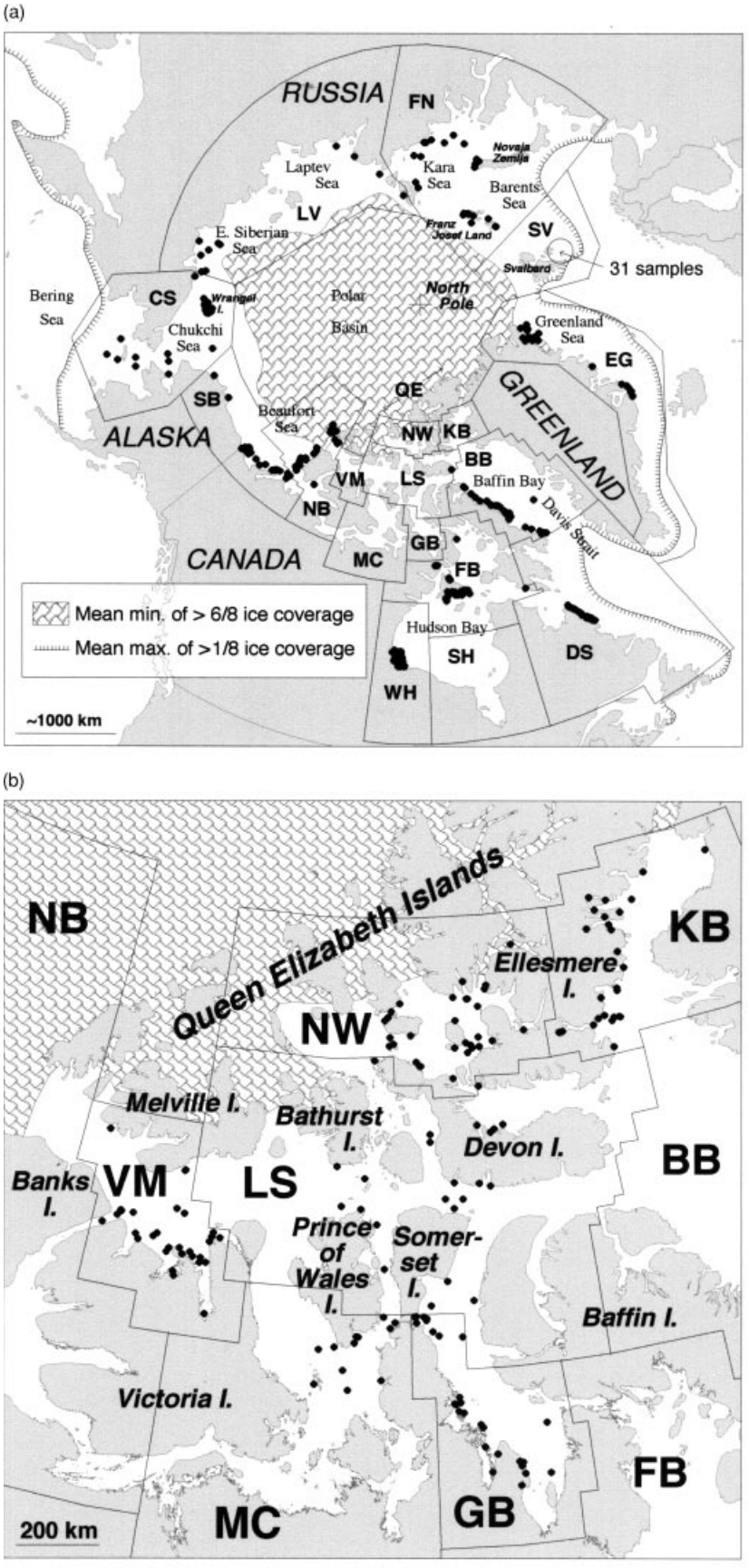

Fig. 1 (a) Current polar bear populations with sampling locations for all populations except those in the Canadian Arctic Archipelago. See Table 1 for abbreviations. (b) Sampling locations in the Canadian Central and High Arctic.

annual ice has melted (Amstrup & Gardner 1994; Messier *et al*. 1994).

In the 1960s there was a rapid increase in the number of polar bears being harvested worldwide, and this gave rise to concern about their status (Anonymous 1966). Because of their low reproductive rates, polar bears were thought to be particularly vulnerable to over-harvest (Taylor *et al*. 1987) and the effects of natural or anthropogenic environmental changes (Stirling & Derocher 1993). In 1973, recognizing a need for international coordination of research and management, the five circumpolar nations (Canada, Greenland/Denmark, Norway, USA and USSR) negotiated the Agreement on the Conservation of Polar Bears (Prestrud & Stirling 1994).

A research priority since this time has been to determine whether polar bears are distributed in a panmictic circumpolar population or in multiple discrete populations, and then to determine population size and demographic rates to facilitate estimates of sustainable harvest levels for indigenous people. Initially, population boundaries were based on reconnaissance information and traditional knowledge. Over time they were modified as data became available from aerial surveys, mark–recapture studies and, most recently, satellite telemetry. (Note that telemetry data are restricted to adult females because the muscular necks of male polar bears are shaped in such a way that collars cannot be fitted securely.) Efforts to study population structure have also been made with a variety of other methods including analysis of parasite loads, carbon isotopes, heavy metals, skull morphometrics, and mitochondrial or allozyme genetic markers (e.g. Manning 1971; Allendorf *et al*. 1979; Larsen & Kjos-Hanssen 1983; Larsen *et al*. 1983; Amstrup & Gardner 1991; Born *et al*. 1991; Cronin *et al*. 1991; Shields & Kocher 1991; Dietz *et al*. 1995; Derocher & Stirling 1998). However, while some of these methods have demonstrated regional differences in some characters, only the use of movement data has been successful in delineating populations.

Currently, 19 polar bear populations are recognized (IUCN/SSC Polar Bear Specialist Group 1998; Fig. 1; names are italicized in text). The data on which these population definitions are based range from almost none for *Queen Elizabeth Islands* (which is essentially a geographic catch-all at this time) to systematic coverage with cluster analysis of satellite telemetry data (Bethke *et al*. 1996) for a large part of the Canadian Arctic. (Note that the term 'population' does not imply a high level of independence in this case as there is normally overlap of movements between adjacent populations.)

Although analysis of movement data provides a direct way to identify population boundaries, it may not generate a clear understanding of the long-term rate of gene flow (dispersal and interbreeding) between populations. This is because it is not usually practical to conduct studies that follow enough individuals for a sufficient length of time to address this issue, particularly when considering the entire geographic range of a species such as the polar bear. An alternative approach to studying long-term rates of population interchange is to use highly variable, nuclear, Mendelian genetic markers (e.g. microsatellites). These markers can eliminate the problems of low variability that have been associated with species of large mammals, such as the polar bear, when using allozyme or mitochondrial DNA (mtDNA) markers (Scribner *et al*. 1997; Haig 1998).

Paetkau *et al*. (1995) used eight microsatellite markers in a preliminary survey of four polar bear populations. This work demonstrated that, despite the long-distance movements undertaken by some polar bears, rates of gene flow were insufficient to genetically homogenize populations.

We describe the results of a larger project in which samples from 16 study areas, with collection locations spanning 17 of the world's 19 polar bear populations, were analysed using 16 $(CA)_n$ microsatellite markers. Our goal was to provide a detailed description of how genetic diversity is partitioned across the range of polar bears, and to determine how this genetic partitioning relates to the currently recognized population boundaries. Where possible, we were also interested in identifying the ecological factors, such as habitat type and prey density, that might explain observed genetic discontinuities.

Materials and methods

Sample collection

Our objective was to obtain DNA samples from 30 individuals, excluding known mothers and cubs, from each of the world's polar bear populations. Samples used for DNA extraction were collected between 1986 and 1996, although the vast majority of animals in the study have been captured since 1991. For most populations, sufficient numbers of blood and tissue samples (mostly disks of skin from ear tagging) collected by biologists were available. However, the samples from *E. Greenland*, *Gulf of Boothia* and *M'Clintock Channel* were supplemented with specimens from animals killed by Inuk hunters, and the *Foxe Basin* sample was composed exclusively of such specimens. Samples were not obtained for *S. Hudson Bay* and *Queen Elizabeth Islands*, or for a large region in the middle of *Laptev Sea*. Because of the small number of *Laptev Sea* samples, and given their sampling locations (Fig. 1), these samples were pooled with the neighbouring *Chukchi Sea* and *Franz Josef Land-Novaja Zemlja* (*FN*) samples, eliminating *Laptev Sea* from the analysis. There is a paucity of information about movements in *Laptev Sea* making the boundaries of this population relatively uncertain. This

Table 1 The world's polar bear populations, including estimated population size

Population	Abbr.	Number*	*N*	*A*	H_E
Western Hudson Bay	WH	1200 (+)	33	6.0	0.67
Southern Hudson Bay	SH	1000 (±)	0	—	—
Foxe Basin	FB	2300 (+)	30	6.0	0.66
Davis Strait-Labrador	DS	1400 (±)	30	6.3	0.63
Baffin Bay	BB	2200 (±)	31	6.3	0.68
Kane Basin	KB	200 (+)	30	6.7	0.71
Lancaster Sound	LS	1700 (+)	30	6.9	0.70
Gulf of Boothia	GB	900 (–)	30	6.7	0.72
M'Clintock Channel	MC	700 (–)	15	(5.5)‡	0.68
Viscount Melville Sound	VM	230 (+)	30	6.3	0.66
Norwegian Bay	NW	100 (±)	30	6.2	0.67
Queen Elizabeth Islands	QE	200 (?)	0	—	—
Northern Beaufort Sea	NB	1200 (+)	30	6.8	0.70
Southern Beaufort Sea	SB	1800 (+)	30	6.4	0.69
Chukchi Sea	CS	2000–5000 (?)	30	6.8	0.70
Laptev Sea	LV	800–1200 (?)	0†	—	—
Franz Josef L.-Novaja Z.	FN	2500–3500 (?)	32	6.7	0.66
Svalbard	SV	1700–2200 (?)	31	6.9	0.69
East Greenland	EG	2000–4000 (?)	31	6.8	0.69
Total (mean for *A*, H_E)	19	~25 000	473	6.5	0.68

†Samples from *Laptev Sea* were included in *Chukchi Sea* or *FN*.
*Reliability is indicated as good (+), fair (±), poor (–), or an educated guess (?).
‡Small *N* confounds direct comparison of this value.
Number, IUCN/SSC Polar Bear Specialist Group (1998); *N*, number of individuals analysed in this study; *A*, mean (16 loci) observed number of alleles; H_E expected heterozygosity.

made it easier to justify pooling samples across population boundaries than would be the case if these population boundaries were better characterized. After this adjustment, the sample sizes for all populations except *M'Clintock Channel* were 30–33 (Table 1).

Collection locations are shown in Fig. 1. For most populations the capture locations were close to shore. In some areas the preferred seal-hunting habitat runs parallel to shore, but in other areas the collection locations have more to do with logistic constraints on flying far from shore than the distribution of bears. In some populations samples were collected during the open-water season when all animals are on shore waiting for freeze-up. For many animals, available movement data were not restricted to the collection location of the sample used for DNA extraction, and such data were often used when considering which animals to include in a given population sample.

Laboratory analysis

Except for those specimens where DNA was already available from the preliminary study (Paetkau *et al*. 1995), DNA was extracted using QIAamp columns (Qiagen). The samples collected from hunters were bone disks removed from the mandible, and some of these yielded insufficient DNA to produce complete genotypes and were excluded from the study. Microsatellite analysis was performed using Applied Biosystems' fluorescence-based technology on a 373A automated sequencer. PCR conditions and primers were as described by Paetkau *et al*. (1998) and involved seven reaction mixes that could be combined into two gel lanes per individual for analysis. Genotypes were called using Genotyper software (Applied Biosystems) and designations were checked visually with lanes aligned by scan (in case of errors in band sizing). After genotypes were exported to a database, they were confirmed by calling them again manually using visual reference to adjacent lanes on the gel image.

The 16 microsatellite markers used in this study (see Table 2 for references) included 11 isolated from North American black bears (*Ursus americanus*; a 12th, G10O, was monomorphic in a small number of polar bears tested), three isolated from domestic dogs, and two isolated from brown bears (*U. arctos*, the closest living relative of polar bears; Talbot & Shields 1996). The dog primers were from a set of 12 that were tested for clean amplification and variability.

Statistical analysis

Homogeneity of allele distributions for all pairs of populations was tested using the probability test (Raymond &

Table 2 Comparison of expected heterozygosity (H_E) and observed number of alleles (A) by locus; mean of 16 study areas. The species from which markers were isolated are also shown

Locus	Source Species	H_E	A
G10L*	Black bear	0.36	3.6
G10C†	Black bear	0.51	5.9
G10J‡	Black bear	0.57	2.9
G1A*	Black bear	0.58	5.2
CXX173§	Domestic dog	0.62	5.6
G10U‡	Black bear	0.62	4.7
G1D*	Black bear	0.63	5.0
G10P†	Black bear	0.73	6.5
G10B*	Black bear	0.75	5.9
CXX20§	Domestic dog	0.75	6.6
CXX110§	Domestic dog	0.77	8.2
G10X†	Black bear	0.78	6.9
G10M†	Black bear	0.80	7.0
G10H‡	Black bear	0.80	8.0
MU50¶	Brown bear	0.81	7.3
MU59¶	Brown bear	0.83	8.4

*Paetkau & Strobeck (1994); †Paetkau *et al*. (1995); ‡Paetkau *et al*. (1998); §Ostrander *et al*. (1993); ¶Taberlet *et al*. (1997).

Rousset 1995) or, where possible, exact tests. Tests for each population pair were combined across the 16 loci (Fisher 1970; section 21.1). Each pair of loci was tested for linkage disequilibrium using probability or exact tests, with tests combined across all populations. In each population, every locus was tested for departure from Hardy–Weinberg equilibrium (HW) using the *U*-test (Rousset & Raymond 1995) with the specific alternative hypothesis of heterozygote deficiency. Global tests were also performed across all loci for each population and across all populations for each locus. These tests were all performed using GENEPOP 3.1b.

GENEPOP 3.1b was also used to calculate Weir & Cockerham's (1984) estimate of F_{ST} and to estimate the number of migrants between each pair of populations per generation (Nm). Nm was estimated using the private allele method (Slatkin 1985) and from estimates of F_{ST} [$F_{ST} = 1/(1 + 4Nm)$; Wright (1931)].

The following calculations were made using the calculators at HTTP://www.biology.ualberta.ca/jbrzusto/. The Bowcock *et al*. (1994) allele-sharing distance was calculated between all pairs of individuals, and a neighbour-joining (Saitou & Nei 1987) tree was constructed from the resulting distance matrix and for subsets of the total matrix containing samples from just two populations. Expected frequencies of each individual's 16-locus genotype were calculated for each individual in each population. Bias in this calculation was avoided by removing individuals from allele distributions in which they were included, and absent alleles were given a frequency of 0.01 to avoid zero values. These data were used to perform an assignment test (Paetkau *et al*. 1995) and to calculate the genotype likelihood ratio distance (D_{LR}; Paetkau *et al*. 1997) for each pair of populations. Nei's (1972) standard distance (D_S) was also calculated for each pair of populations.

The Fitch and Drawtree programs in the PHYLIP 3.56 package were used to produce Fitch & Margoliash (1967) trees from genetic distance data. Branches were rotated using MacDraw to aid visual presentation.

Comparison to movement data

The relationship between interpopulation genetic distances and animal movements was studied using data from an ongoing satellite tracking study in the Canadian Arctic (F. Messier and M. K. Taylor unpublished data). We used location data from 135 female bears which had been tracked for a minimum of 330 days and had a minimum of 20 locations each (mean 101 locations per bear). The satellite collars were deployed in seven contiguous populations: *Baffin Bay* (34), *Davis Strait* (11), *Kane Basin* (10), *Lancaster Sound* (53), *N. Beaufort Sea* (8), *Norwegian Bay* (4) and *Viscount Melville Sound* (15). For each of these populations, an index of interpopulation movements was calculated as the percentage of locations observed in another population, averaged across animals. Such calculations were limited to situations where interpopulation movement would require crossing a maximum of two population boundaries because movements across three or more boundaries were not observed. A total of 58 such measures of directional interpopulation movement were calculated, and comparison to genetic distance data was made using the Spearman rank correlation.

Results

We obtained complete genotypes at 16 loci for the 473 polar bears included in the analysis. No two individuals had the same genotype. The 16 markers we used detected considerable variation, with unbiased estimates of expected heterozygosity (H_E; Nei & Roychoudhury 1974) averaging from 0.36 for locus G10L to 0.83 for locus MU59 (Table 2). Given the ease with which the dog markers were developed for use in polar bears, this represents an excellent source of informative markers, although the dog markers tended to amplify less strongly than those isolated from bears. Genotypes are available on request.

Tests of disequilibrium

With 16 study areas and 16 loci, there were 256 tests for HW. The number of tests that returned significant results was no higher than expected due to Type I error if the null hypothesis (no homozygote excess) was true (Table 3).

Table 3 Observed number of tests returning significant results and number expected due to Type I error if null hypotheses are correct. Values for three significance levels are shown

	Individual HW		Global HW (each)		Linkage disequilibrium		Allele distributions	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
$P < 0.05$	13	12.8	1	0.8	8	6.0	118	6.0
$P < 0.01$	3	2.6	0	0.2	2	1.2	114	1.2
$P < 0.001$	0	0.3	0	0.0	0	0.1	111	0.1

	WH	FB	DS	BB	KB	LS	GB	MC	VM	NW	NB	SB	CS	FN	SV	EG
WH		0.5	1.4	3.9	3.6	3.9	3.5	5.2	4.4	4.3	5.4	5.9	6.6	5.6	5.0	5.9
FB	0.9		1.1	3.3	3.3	3.9	4.1	4.7	4.7	4.9	6.3	6.4	7.8	5.5	5.3	5.8
DS	2.1	1.4		1.6	2.1	2.6	2.4	2.7	3.0	3.4	3.7	4.6	4.9	3.1	3.2	3.8
BB	5.2	4.4	2.6		0.1	0.9	1.3	1.5	1.7	2.5	3.0	3.5	3.9	2.8	2.7	2.7
KB	5.6	4.8	3.6	0.3		1.1	1.5	1.7	1.7	2.2	2.7	3.3	4.0	3.0	2.3	2.2
LS	5.4	5.2	3.9	1.0	1.1		0.7	0.8	0.8	1.7	2.5	3.4	4.5	3.0	2.8	2.6
GB	4.8	5.1	3.6	1.4	2.1	1.0		1.1	1.3	2.6	2.5	2.8	3.8	2.8	3.0	3.1
MC	5.7	5.2	3.2	0.9	1.3	0.5	1.1		0.9	3.7	2.5	3.7	3.9	2.6	2.4	2.7
VM	6.1	6.3	4.3	1.9	2.4	1.7	1.9	0.8		2.2	1.6	2.3	3.6	2.5	2.6	2.5
NW	6.8	7.5	5.8	3.5	2.5	2.4	3.7	3.9	3.5		3.4	4.3	5.4	4.5	4.4	4.1
NB	8.1	8.9	6.5	3.8	3.8	3.9	3.3	2.7	2.6	5.2		0.5	0.9	1.3	1.0	1.3
SB	8.6	9.1	7.4	4.6	4.9	5.8	4.3	4.2	3.7	6.3	0.5		0.9	1.4	1.8	2.1
CS	9.5	10.8	8.2	5.3	6.0	6.8	5.1	5.0	5.5	7.9	0.8	1.0		1.2	1.1	1.9
FN	8.5	8.4	5.3	3.9	4.6	5.1	4.4	3.3	3.7	6.8	1.4	1.8	1.7		0.0	0.4
SV	7.6	7.9	5.3	3.1	3.2	4.1	3.9	2.5	3.5	5.9	1.0	2.2	1.3	0.2		0.4
EG	8.7	8.8	6.5	3.4	3.2	4.2	4.2	3.0	3.8	5.8	1.4	2.6	2.1	0.8	0.3	

Table 4 Genetic distances between study areas: F_{ST} (x 100) below diagonal, D_{LR} above. Rectangles highlight distances within four population clusters (Fig. 3). F_{ST} is a correlation of allele frequencies between populations (Weir & Cockerham 1984) and D_{LR} is the mean genotype log likelihood ratio across individuals from the two populations (Paetkau *et al*. 1997)

We tested for the presence of null alleles (Callen *et al*. 1993; Paetkau & Strobeck 1995) by performing global tests across all populations for each locus, and locus CXX173 returned a probability of 0.024. Again, this result is not significant when the number of tests is considered. These data, and the fact that complete genotypes were obtained for all samples for which adequate DNA was available, suggest that most if not all alleles were successfully amplified.

Global tests of homozygote excess also were performed across all loci for each population as a check for significant genetic structure (nonrandom mating) within populations. *Chukchi Sea* returned a probability of 0.034, but this is also not significant on an experimentwise basis (Table 3). We concluded that the study areas were generally free of significant internal genetic structure.

A problem arose in our tests of nonrandom association of genotypes between loci (linkage disequilibrium) in that 10 of the 1920 tests returned results of 0.00000 causing overall χ^2 values of infinity. These 10 results involved nine different pairs of loci and eight different study areas. If disequilibrium existed between a pair of loci, one would expect to detect it in data from 14 or 15 well-sampled study areas, even if the one (eight cases) or two (one case) study areas returning zero probabilities were ignored. Therefore, we performed the analysis by excluding the 10 problematic tests (the values shown in Table 3), and all nine of the pairs of loci at issue returned overall probabilities in excess of 0.05. Note that eight of the loci used here (including two of the nine problem pairs and the pair that returned the highest overall χ^2 value) were previously tested directly for physical linkage using information from pedigrees (Paetkau *et al*. 1997). No evidence for linkage was found and the data were sufficient to reject strong linkage (recombination frequency < 0.1) in every case. We proceeded with our analysis under the assumption of independence between loci.

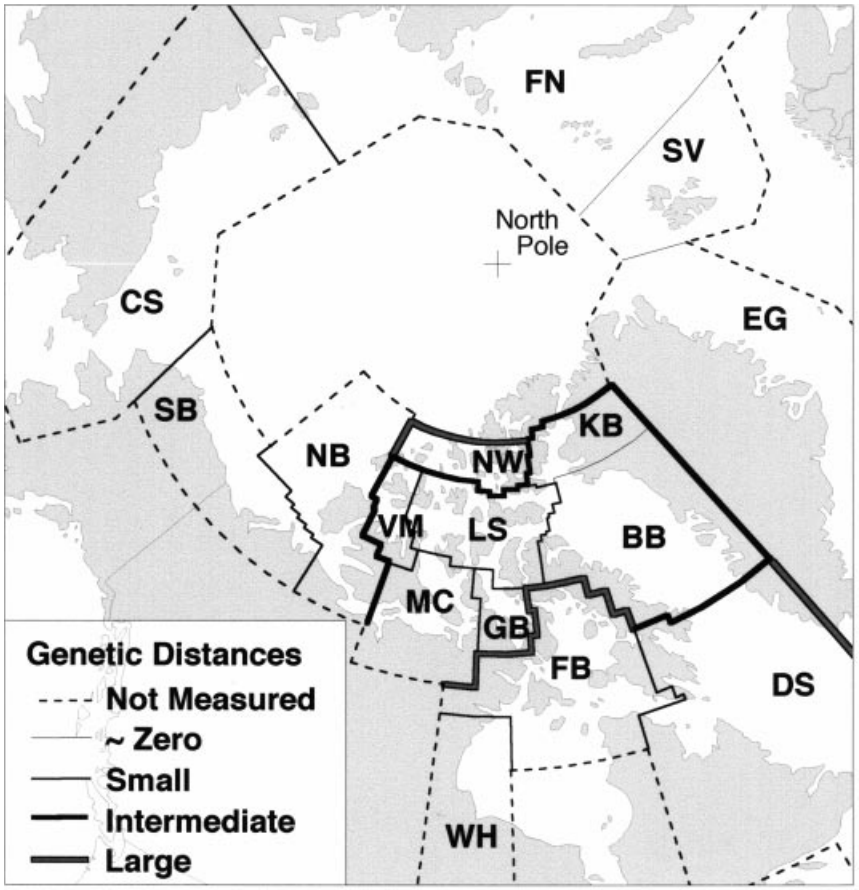

Fig. 2 A map-based view of genetic distances between adjacent populations (categories defined in the text). The borders of *Norwegian Bay* and the populations touching Greenland were adjusted to allow more data to be shown (see Fig. 1 for actual boundaries). *Laptev Sea* was eliminated and the *FN* and *Chukchi Sea* population boundaries were extended to reflect the way in which samples were grouped into study areas. The coding of the northern borders of *Norwegian Bay* and *Kane Basin* reflect genetic distances to all polar basin populations except that the distances from *Kane Basin* to *S. Beaufort Sea*, *Chukchi Sea* and *FN* were actually large, not intermediate as shown.

Relationships between study areas

Of 120 pairs of populations in the current study, 118 had allele distributions that differed at the 5% level, and 111 of those differed at the 0.1% level (Table 3). The two pairs of study areas for which no significant differentiation was found were *Baffin Bay/Kane Basin* and *FN/Svalbard*. Population pairs with low levels of differentiation ($0.05 > P > 0.001$) were: *E. Greenland/FN* and *E. Greenland/Svalbard*, *N. Beaufort Sea/S. Beaufort Sea*, *W. Hudson Bay/Foxe Basin*, and *M'Clintock Channel* and each of its conterminous neighbours except *N. Beaufort Sea* (the results involving *M'Clintock Channel* are misleading as small sample size will have reduced the power of the test).

Three measures of genetic distance were used to quantify the relationships between study areas: D_{LR} (Paetkau *et al*. 1997; Table 4); D_S (Nei 1972; data not shown); F_{ST} (Weir & Cockerham 1984; Table 4). These measures are not calculated on a locus-by-locus basis, and therefore estimates of standard error were not available. The high correlation between distance measures ($r = 0.98$ for all pairs of distance measures), particularly given how much they differ in their calculation, indicates that the values are not dominated by variance. Previous work in brown bears using eight of the loci used in this study also found a strong relationship between genetic and geographic distances, supporting the contention that genetic distance data can provide a strong reflection of biological relationships. However, even with zero variance and perfect correlation, the possibility would remain that some other variable was confounding the biological meaning of these statistics. For example, low intrapopulation genetic diversity might cause exaggerated genetic distances (Paetkau *et al*. 1997), although this specific variable is not likely to be an issue here because diversity is similar across polar bear populations (Table 1).

D_S differs from D_{LR} and F_{ST} in that it cannot be negative. This means that D_S will be biased upwards when genetic distance values approach zero. This problem was apparent from the data set where D_S approached a value of 0.03 as D_{LR} and F_{ST} approached zero. As this could have a large impact on our data, where many of the distances are small, D_S was de-emphasized in the remainder of the analysis.

Several approaches were tried to provide an accessible presentation of the distance data. Distances between neighbouring populations were portrayed on a map (Fig. 2) by assigning genetic distances to four arbitrary

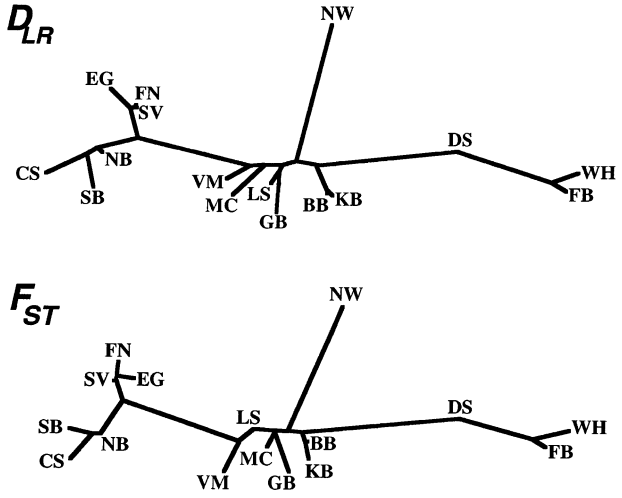

Fig. 3 Fitch and Margoliash trees of genetic distances between study areas. While this method permits visualization of population clusters, the relationships between populations are not bifurcating and hierarchical as implied by the figures.

categories: zero distance ($D_{LR} < 0.5$, $F_{ST} < 0.004$); small distance ($D_{LR} = 0.5 - 1.4$, $F_{ST} = 0.004 - 0.019$); intermediate distance ($D_{LR} = 1.5 - 2.9$, $F_{ST} = 0.02 - 0.04$); large distance (anything larger). The concordance between D_{LR} and F_{ST} is illustrated by the fact that all pairs of conterminous populations could be placed unambiguously into one of these categories.

The genetic distances observed between conterminous populations surrounding the polar basin were small at most, whereas neighbouring populations in the Canadian Arctic sometimes had intermediate or even large genetic distances. The low level of genetic structure found around the perimeter of the polar basin, and the fact that no significant evidence of disequilibrium was found in the *Chukchi Sea* or *FN* samples, argue that our decision to pool the *Laptev Sea* samples with neighbouring population samples was reasonable.

It is common to use a clustering analysis to present data from a matrix of genetic distances. As bifurcating trees may oversimplify the patterns of relationships between study areas, which may take all manner of forms including rings, it would be preferable to use a multidimensional approach. We attempted to do this using nonmetric multidimensional scaling, but this approach was undermined by extremely poor 'goodness of fit' (stress > 0.55) between the distances on the plot and the values in Table 4. Therefore, we settled for Fitch and Margoliash trees (Fig. 3), which provided a better reflection of the data. These trees identified four geographic clusters of populations.

An assignment test (Paetkau *et al*. 1995) was also used to study relationships between study areas (Table 5). We found that 42% of animals were assigned to the population in which they were sampled, and 82% of animals were assigned to the correct cluster of populations identified by genetic distances (Fig. 3). When sets of eight loci were used the mean rate of correct assignment dropped to 32%, and with sets of four loci the mean rate of correct assignment was only 22%.

The two methods of estimating *Nm* between study areas gave extremely discordant results. For example, estimated

Table 5 Results of the assignment test. Each row contains the samples from one study area and the columns indicate the populations to which these samples were 'assigned' (in which their genotypes had the highest likelihood of occurring)

	WH	FB	DS	BB	KB	LS	GB	MC	VM	NW	NB	SB	CS	FN	SV	EG	Total
WH	**21**	6	5											1			33
FB	9	**16**	3	1	1												30
DS	1	5	**13**	4	2		2	1			1			1			30
BB			3	**13**	7	2	1	2					1	1		1	31
KB		1		9	**9**	2		2		4	1	1				1	30
LS			2	1	2	**10**	2	5	4	3				1			30
GB	1		1	4	2	3	**10**	3	3	2		1					30
MC			2			1	2	**7**	3								15
VM	1		2	1		4	2	1	**14**	1	4						30
NW	1	1		2	1	3	2		2	**17**				1			30
NB					1			1	1	1	**11**	6	6	1	1	1	30
SB							2		2		6	**11**	3	5		1	30
CS											1	7	**15**	4	1	2	30
FN	1			1				1	2		3	3	1	**8**	9	3	32
SV						1	1		2		1		1	5	**11**	9	31
EG					2				2	1	2	1	3	5	4	**11**	31

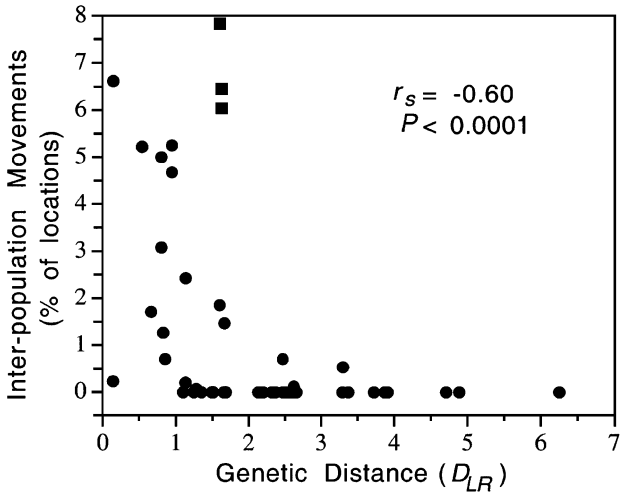

Fig. 4 Relationship between genetic distance and an index of interpopulation movements (see the Materials and methods) based on satellite tracking data from the Canadian Arctic Archipelago (F. Messier and M. K. Taylor unpublished data). The three points indicated by squares probably reflect exaggerated estimates of interpopulation movements due to an over-representation of animals caught near population boundaries (these samples were still included in the statistical analysis).

Nm between *E. Greenland* and *Svalbard* was 89 using the F_{ST}-based approach and 4.4 using the private-allele method. The index of interpopulation movement based on satellite tracking data was strongly correlated with the genetic distance between populations, with D_{LR} showing a stronger relationship ($r_s = -0.60$, $P < 0.0001$; Fig. 4) than F_{ST} ($r_s = -0.47$, $P < 0.001$).

Allele-sharing distances (Bowcock *et al*. 1994) calculated between all pairs of individuals failed to produce meaningful geographic clusters (data not shown).

Discussion

Evolutionary significant units (ESUs)

Genetic studies have the potential to identify groups within a species that have undergone significant independent evolution (subspecies or ESUs). The greatest degree of genetic differentiation we observed in polar bears was between *Chukchi Sea* and *Foxe Basin* (Table 4). To place our data in context, it is useful to compare them to microsatellite data that are available from several other large members of the Carnivora. Using a subset of the markers used in the current study, surveys have been conducted on brown bears and North American black bears (Paetkau *et al*. 1997). Although the black and brown bear data covered only a fraction of the total distributions of those species, the distances observed between widely separated study areas in continuous parts of the North American distributions were considerably larger ($D_S = 0.46$ and 0.57, respectively) than that observed between *Chukchi Sea* and *Foxe Basin* in this study ($D_S = 0.33$). In brown bears, pairs of Arctic study areas separated by approximately 1300 km in a continuous distribution had genetic distances similar to the *Chukchi Sea–Foxe Basin* distance. Similarly, the *Chukchi Sea–Foxe Basin* distance was at the small end of values observed between North American populations of grey wolves ($D_S = 0.13–0.67$; Roy *et al*. 1994). The relatively small genetic distances observed in polar bears and the lack of dramatic genetic or population discontinuities (Durner & Amstrup 1995; Taylor & Lee 1995) across the range lead us to conclude that polar bears belong to a single ESU at this time. While it might be tempting to conclude that polar bear populations do not differ significantly in terms of adaptive genetic traits, such conclusions could be ill founded because differentiation in adaptive traits can occur between populations showing little genetic structuring at neutral genetic loci (e.g. Karhu *et al*. 1996).

Management units (MUs)

Just as the identification of ESUs is important from a broad-scale conservation perspective, identification of MUs is important from a local management perspective. Moritz (1994) suggested that MUs could be identified genetically as regions with significantly different allele frequency distributions. From a demographic perspective, MUs could be considered as regions where the local population dynamics will be driven primarily by birth and death, not immigration and emigration (Taylor & Lee 1995). In this sense, the goal of the manager is to prevent local declines by ensuring that anthropogenic sources of mortality are not excessive. This is particularly relevant to polar bears where local population declines would represent the loss of an important cultural and economic resource for many northern aboriginal communities, and where recovery could be slow.

Using the genetic definition, two pairs of polar bear populations failed to qualify for MU status based on our data: *Kane Basin/Baffin Bay* and *Svalbard/FN*. These population pairs also represent two of the three pairs that fell into the smallest of the genetic distance categories used to generate Fig. 2 (the 3rd pair being *East Greenland/Svalbard*). The failure to detect significant differentiation between these two pairs of populations with 16 highly variable genetic markers stands in stark contrast to data from brown bears, where significant differences were detected between two samples of 25 brown bears centred less than 50 km apart, and this with only eight loci (Paetkau *et al*. 1998). Thus, the lack of significant differentiation in these cases is not due to lack of resolving power, it is due to a remarkable degree of genetic homogeneity.

Satellite tracking and mark–recapture data are available from both regions where pairs of populations failed to meet the genetic criterion for MU identification. The separation of *Svalbard* and *FN* was initially supported by telemetry data that showed a high degree of seasonal fidelity for females captured in *Svalbard* (Wiig 1995). However, recent data with more broadly based sampling (A. E. Derocher, G. W. Garner and Ø. Wiig unpublished data) indicate that cross-border movements in the Barents Sea are common (involving 19 of 47 females followed by satellite telemetry for greater than 1 year), and that substantial overlap may occur during the spring breeding season. In this light, the genetic data and movement data from *Svalbard* and *FN* are consistent, with both indicating a high degree of overlap between these populations.

The concordance between genetic data and movement data is less clear for *Kane Basin* and *Baffin Bay*, where there appears to be less cross-border movement (e.g. involving 4 of 44 females followed by satellite telemetry for greater than one year; F. Messier and M. K. Taylor unpublished). A particular limitation with using genetic data to identify MUs is that results may not be accurate for populations that are not at equilibrium. It is likely that there is an ongoing over-harvest in *Kane Basin*. Such an over-harvest could cause a source–sink relationship between *Baffin Bay* and *Kane Basin* that would not be apparent from following the movements of adult animals. This would explain the lack of genetic differentiation between these populations, but emphasizes the point that a lack of genetic differentiation cannot be taken as proof of population homogeneity. In short, our genetic data provide perspectives on the discreteness of polar bear populations, but we do not believe that they should be used on their own for drawing new population boundaries.

Higher level structure

Although the majority of the polar bear populations covered by our study met the definition of MU's *sensu* Moritz (1994), the degree of genetic isolation between neighbouring populations varied widely. When these data are viewed on a map (Fig. 2), or subjected to a cluster analysis (Fig. 3), four population clusters are apparent. The recognition of this higher-level population structure is important because the consequences of local decline in small, isolated populations would be more severe and long lasting than for other populations.

By far the smallest of the population clusters in both geographic and demographic terms is the one consisting only of *Norwegian Bay*, which is estimated to contain just 100 animals (Table 1). This population showed a considerably larger degree of genetic differentiation from all other populations than the next most isolated population (*Davis Strait*). Assuming that the genetic data reflect actual rates of movement, a more conservative management strategy is merited to account for the extra risk this isolation presents.

A complication with the genetic data is that the small size of the *Norwegian Bay* population might cause exaggerated genetic distances due to elevated rates of genetic drift in this population. However, this effect will be offset by the fact that individual immigrants into this population will represent a larger proportion of the population and so will have a larger impact. Simulated data suggest that the latter effect actually more than corrects for the former effect (A. Estoup and D. Paetkau unpublished data). This means that fewer immigrants into *Norwegian Bay* would be required to maintain the observed genetic distance than would be the case if *Norwegian Bay* had a population size similar to the other polar bear population clusters that we identified, and supports our contention that *Norwegian Bay* is particularly isolated demographically.

The closest cluster to *Norwegian Bay* in geographic and genetic terms contains all the remaining populations in the Canadian Arctic Archipelago (*Viscount Melville Sound*, *M'Clintock Channel*, *Lancaster Sound*, *Gulf of Boothia*) and the two populations between the archipelago and Greenland (*Baffin Bay*, *Kane Basin*). Within this cluster, the most genetically distinct populations (*Viscount Melville Sound* and *Kane Basin*) showed genetic distances similar to the smallest distances between members of this cluster and populations outside it (*Lancaster Sound–Norwegian Bay* or *Baffin Bay–Davis Strait*).

The third cluster consists of the three southernmost populations included in this survey (*W. Hudson Bay*, *Foxe Basin*, *Davis Strait*). We assume that it would also include the unsampled *S. Hudson Bay* population (Fig. 1), an assumption based on mark–recapture and satellite-tracking studies which suggest that the degree of isolation between *S. Hudson Bay* and *W. Hudson Bay* is no greater than the degree of isolation between *Foxe Basin* and *W. Hudson Bay* (Stirling & Derocher 1993; Taylor & Lee 1995; I. Stirling unpublished), the latter pair being separated by a small genetic distance. The genetic data suggest that most gene flow between the southern Canadian cluster and the one to the north occurs around eastern Baffin Island, and not via Fury and Hecla Strait, the direct maritime connection between *Foxe Basin* and *Gulf of Boothia*.

The last cluster, covering a geographic area that exceeds the combined area covered by the other three clusters, comprises the populations distributed around the perimeter of the polar basin (hereinafter called polar basin populations). Despite the huge area covered by this group, the largest genetic distances within it were similar to the smallest distances between a member of this cluster and a conterminous population outside it (*N. Beaufort Sea Sea–Viscount Melville Sound*).

The polar basin is encircled by a band of leads and

polynyas, first termed 'the Arctic ring of Life' by Uspenski (1977 in Stirling 1988), that creates a semicontinuous zone of polar bear habitat. Our sampling of the polar basin populations had two gaps in it: we had no samples from *Queen Elizabeth Islands* and our *Laptev Sea* samples were limited to the extreme western and eastern parts of that population prompting us to consider them with the samples from neighbouring populations. Nonetheless, the genetic data suggest that there is gene flow across these unsampled areas; the genetic distances across the region are small in magnitude and the lowest degree of genetic differentiation between populations separated by either sampling gap is between the populations located immediately on either side of those gaps. Furthermore, the movements of three individuals from the Beaufort Sea (*S. Beaufort Sea* and *N. Beaufort Sea*) to *E. Greenland* (Durner & Amstrup 1995; I. Stirling unpublished) demonstrate that a connection exists across one of these gaps, although such movements are rare (for example, only one of 155 females equipped with satellite collars in *S. Beaufort Sea* made this movement; Durner & Amstrup 1995). We suggest that complete sampling of *Queen Elizabeth Islands* and *Laptev Sea* would demonstrate that the pattern of genetic relationships among the polar basin populations is circular, as the geographic relationship is.

Migration rates

Although genetic distance measures provide insight into the relative rates of gene flow between populations, it is not obvious what they mean in terms of the actual movements of animals. A traditional approach to bridging this gap is to estimate *Nm* from allele distribution data. We tried two different models for estimating *Nm* and obtained dramatically different results. Given this discordance, and given that polar bear populations do not conform to an island model, mutational dynamics of microsatellites are complex and poorly understood, generations in polar bears are not discrete, polar bear populations may not be at mutation-drift equilibrium and that this approach does not distinguish between dispersal and interbreeding, we do not believe that these data add significantly to the existing knowledge of polar bear movements. However, it is worth noting that the *Nm* values suggested by these statistics are in excess of 1, even for the most distinct of conterminous populations.

An emerging approach to the genetic study of dispersal is to use individual genotypes as the units of comparison (Waser & Strobeck 1998). Two ways to do this are to calculate genetic distances between pairs of individuals (e.g. Bowcock *et al*. 1994), which has the advantage of obviating the need for a priori assumptions about population boundaries, and calculating the expected frequency (likelihood) of each individual's genotype in each study area (Paetkau *et al*. 1995), which has the advantage of using more of the information present in the genotype.

Our attempt to use allele sharing was unsuccessful. This stands in contrast to work done on brown bears with the same loci we used (Paetkau *et al*. 1998), but the degree of genetic structure was much greater in that study. We used genotype likelihoods to perform the assignment test (Paetkau *et al*. 1995; Table 5) and found that 16-locus genotypes were generally sufficient to determine which region animals were from. While these data suggest that movement is limited between the four population clusters identified in Fig. 3, the power of this approach to identify where animals were born needs to be tested before more specific conclusions can be drawn. We hope to return to this subject in detail as methods become better developed.

We also made a direct comparison between movement data and genetic distances in the Canadian Arctic (Fig. 4). The strong correlation we found suggests that the genetic data do reflect contemporary polar bear movement patterns. This analysis also identified a genetic distance threshold ($D_{LR} = 3.5$, $F_{ST} = 0.05$) above which we observed no inter-population movements. We believe that such direct comparisons are useful both as a method to evaluate the impact of deviations from mutation-drift equilibrium on genetic distance data and as a way to calibrate genetic distance data so that they can be interpreted in terms of actual rates of movement. Our analysis of movement data had some important limitations, including small sample size, age and sex bias, and disregard for the season in which movements occurred, but we expect these limitations to decrease as more data are collected and hope to see more detailed comparisons of genetic and movement data in the future.

Impact of landscape features

Our genetic data demonstrate that gene flow between polar bear populations is not equal across all landscapes. Looking across the entire range of polar bears, there is a marked contrast between the relatively low degree of genetic structure observed among polar basin populations and the discontinuities observed in the Canadian Arctic Archipelago; discontinuities which define the four population clusters we identified (Figs 2 and 3).

Garner *et al*. (1994) suggested that there were fundamental differences in ecology and seasonal movements between the populations in the Beaufort, Chukchi and Bearing Seas (*N. Beaufort Sea*, *S. Beaufort Sea* and *Chukchi Sea*) and the archipelagic populations of the Canadian Central and High Arctic. This view is supported by movement data from satellite tracking studies (Amstrup 1986; Born *et al*. 1997; A. E. Derocher and Ø. Wiig unpublished data; Garner *et al*. 1990; F. Messier and M. K. Taylor unpublished data; Wiig 1995). In polar basin populations,

reported mean home-range sizes varied from 72 263 km² (*E. Greenland*) to 244 463 km² (*Chukchi Sea*) whereas in the Canadian Central and High Arctic mean home-range sizes were between 12 162 km² (*Kane Basin*) and 82 827 km² (*Lancaster Sound*).

Important as regional differences in the scale of movements may be, the more interesting task is to determine what the underlying causes of those differences are. Essentially, we are faced with the challenge of explaining why an animal with a proven capacity to move long distances through difficult terrain should have strikingly different movement patterns in different parts of its range. We suggest that many of the observed genetic patterns could be explained by the hypothesis that polar bears are unwilling, although certainly not unable, to move even relatively short distances through areas with poor hunting opportunities.

Aerial surveys have been used to study ice conditions and seal distribution and abundance in the Canadian High Arctic (Kingsley *et al*. 1985) and the Beaufort Sea (Stirling *et al*. 1993). While seals preferred active, annual (< 1-year-old) ice of high cover in both areas, the different ice types were distributed continuously and linearly (parallel to shore) in the Beaufort Sea, but patchily in the Canadian Arctic. Ferguson *et al*. (1998) studied the relationship between polar bear movements and sea ice distribution in the Canadian Arctic and found that the irregularity (fractal dimension) of sea ice distribution was negatively correlated with size of seasonal ranges and positively correlated with fractal dimension (tortuosity) of bear movements. They explained the relatively smaller size of seasonal ranges in the Canadian Arctic Archipelago as being due to increased fractal dimension of sea ice caused by the patchy distribution of land masses in this region. Taken together, these analyses can be used to support the argument that patchiness in the distribution of ice types causes patchiness in seal distributions which, in turn, reduces the scale of polar bear movements.

An examination of the locations of the strongest genetic discontinuities in our data set (Fig. 2) suggests some habitat types that may particularly deter polar bear gene flow. The first of these is land, which is obviously not seal-hunting habitat. For example, the large genetic distances between *Foxe Basin* and *Baffin Bay* argue against direct gene flow across Baffin Island (Fig. 1). Many of the population boundaries associated with the largest genetic discontinuities run along land masses.

While population boundaries comprised mostly of land may generally be associated with low gene flow, the type of sea ice habitat in the intervening channels may also be important. Most notably, the high concentrations of multiyear ice that are found to the north of *Kane Basin*, in the northern and western parts of *Norwegian Bay*, and in *Viscount Melville Sound* (Fig. 1) may explain most of the genetic discontinuity that separates polar basin populations from the rest (Fig. 2). Multiyear ice is associated with the lowest densities of ringed seals reported to date in the Canadian High Arctic (Kingsley *et al*. 1985).

Another interesting observation is that the maritime connections between *Norwegian Bay* and the populations to the south and east are through narrow passages spanned by polynyas (Stirling 1997). Cleator & Stirling (1990) demonstrated that, over a period of years, there was an inverse relationship between the abundance of bearded seals and walruses at Dundas Polynya (between Bathurst Island and Devon Island). Low densities of ringed seals were also observed near the polynyas between *Norwegian Bay* and *Lancaster Sound* (Kingsley *et al*. 1985), and Stirling (1997) suggested that an inverse relationship between the abundance of walruses and the abundance of ringed and bearded seals might be characteristic of such small polynyas. These observations generate a hypothesis that a walrus–seal–polar bear mechanism might be operating to enhance the isolation of *Norwegian Bay*.

The factors discussed above are neither certain nor likely to be exhaustive. Other factors that may play roles in some areas include the distribution of humans, the location of and fidelity to maternity denning areas and areas used during the open-water season, and seasonal variation in the type, extent and distribution of sea ice, particularly as it affects bears during the breeding season.

Although our explanations of the ecological variables underlying the observed genetic patterns remain qualified at this time, this study has produced several substantial results. The first is that we found a strong relationship between ecological and genetic definitions of MUs. This affirms the potential for using genetics in this capacity, although the need for comparative movement data remains. We also identified four striking clusters of populations, a pattern of higher level structure that had not previously been recognized. Of particular interest was the relatively high degree of genetic structure found among populations in the archipelagic environment of the Canadian Central and High Arctic as compared to populations in geophysically simpler environments. The process of understanding this contrast, which we have begun here, will undoubtedly take us well into the future.

Acknowledgements

This research was supported by: NSERC; Parks Canada; Canadian Wildlife Service; Polar Continental Shelf Project; Department of Indian and Northern Affairs (Canada); University of Saskatchewan; Nunavut Wildlife Management Board; Inuvialuit Wildlife Management Advisory Council; Department of Resources, Wildlife and Economic Development (NWT); Shikar Safari Club International; Aage V. Jensen Foundation; Commission for Scientific Research in Greenland. John Brzustowski wrote the web-based computer programs that we used. David Paetkau was

supported by NSERC and the Alberta Heritage Trust Fund. Craig Moritz provided the space, physical and otherwise, that made the preparation of this manuscript possible.

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This project was one of a number of population genetic studies on bears undertaken by David Paetkau during his tenure as a student in Curtis Strobeck's laboratory, a place where similar projects are in progress on a number of North American mammals. The other authors were biologists who have devoted substantial portions of their careers to studying polar bear ecology, and who have had long-standing interests in identifying, quantifying and understanding discontinuities in the polar bear distribution.
