Microsatellite DNA and mitochondrial DNA variation in polar bears (*Ursus maritimus*) from the Beaufort and Chukchi seas, Alaska

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Abstract: Radiotelemetry data have shown that polar bears (*Ursus maritimus* Phipps, 1774) occur in separate subpopulations in the Chukchi Sea and the southern Beaufort Sea. However, segregation is not absolute, and there is overlap of ranges of animals in each subpopulation. We used genetic variation at eight microsatellite DNA loci and mitochondrial DNA (mtDNA) to further assess the degree of spatial structure of polar bears from the Chukchi and southern Beaufort seas. Microsatellite allele frequencies and mtDNA haplotype frequencies of bears from the southern Beaufort and Chukchi seas did not differ significantly. Lack of differentiation at both maternally inherited mtDNA and bi-parentally inherited microsatellite loci suggests that gene flow between the two areas is mediated by both sexes. The genetic data indicate that polar bears in the southern Beaufort and Chukchi seas compose one interbreeding population. However, there is considerable fidelity to ranges in each area, particularly by adult females. The combined genetic and movement data suggest that polar bears could be managed as Beaufort Sea and Chukchi Sea subpopulations of a combined southern Beaufort Sea and Chukchi Sea population.

Résumé : Des données de radiotélémétrie montrent que les ours polaires (*Ursus maritimus* Phipps, 1774) de la mer de Chukchi et du sud de la mer de Beaufort forment des sous-populations séparées. La ségrégation n'est pas, cependant, absolue, et il y a un chevauchement d'aires d'animaux de chaque sous-population. Nous utilizons la variation génétique à huit locus microsatellites d'ADN et dans l'ADN mitochondrial (ADNmt) pour préciser le degré de structure spatiale chez les ours polaires de la mer de Chukchi et du sud de la mer de Beaufort. Les fréquences des allèles microsatellites et des haplotypes d'ADNmt chez les ours polaires de la mer de Chukchi et du sud de la mer de Beaufort ne diffèrent pas significativement. Le manque de différenciation tant dans l'ADNmt d'origine maternelle que dans les locus microsatellites hérités des deux parents montre que le flux génétique entre les deux régions est assuré par les deux sexes. Les données génétiques indiquent que les ours polaires du sud de la mer de Beaufort et de la mer de Chukchi forment une seule population reproductive. Il existe, néanmoins, une forte fidélité aux aires vitales dans chaque région, particulièrement chez les femelles adultes. Les données combinées sur la génétique et les déplacements laissent croire que la gestion des ours polaires pourrait bien se faire au niveau des sous-populations de la mer de Beaufort et de la mer de Chukchi au sein d'une population conjointe du sud de la mer de Beaufort et de la mer de Chukchi.

[Traduit par la Rédaction]

Introduction

Polar bears (*Ursus maritimus* Phipps, 1774) in northern Alaska primarily occur in two subpopulations (Fig. 1; Amstrup et al. 2000, 2005). Amstrup et al. (2004, 2005) showed that polar bears occurring between the McKenzie River (Canada) and the Colville River, Alaska, compose a southern Beaufort Sea subpopulation. Similarly, polar bears west of Cape Lisburne, Alaska, represent a Chukchi Sea subpopulation. On an annual basis, more than 90% of the bears in the southern Beaufort Sea subpopulation occur between the Colville River in Alaska and the Mackenzie River in Canada. Similarly, more than 90% of the bears in the Chukchi Sea subpopulation occur west of Cape Lisburne. This high level of fidelity of polar bears to adjacent ranges in the Beaufort and Chukchi seas has led to their management as separate subpopulations, although Amstrup et al. (2005) showed an area of overlap around Barrow (Fig. 1).

Previous analyses suggested there may be some genetic differentiation of bears from the southern Beaufort and Chukchi seas. An analysis of 16 microsatellite loci of 30 bears from each region showed a low level (F_{ST} = 0.01) of differentiation of allele frequencies between the subpopulations in the southern Beaufort and Chukchi seas (Paetkau et al. 1999). An analysis of mitochondrial DNA (mtDNA) restriction fragment length polymorphisms from 10 bears captured in the Chukchi Sea and 15 bears captured in the Beaufort Sea identified three haplotypes, with one predominating (70%–73%) in both areas (Cronin et al. 1991).

These genetic results were preliminary because of small sample sizes compared with the numbers of bears in the

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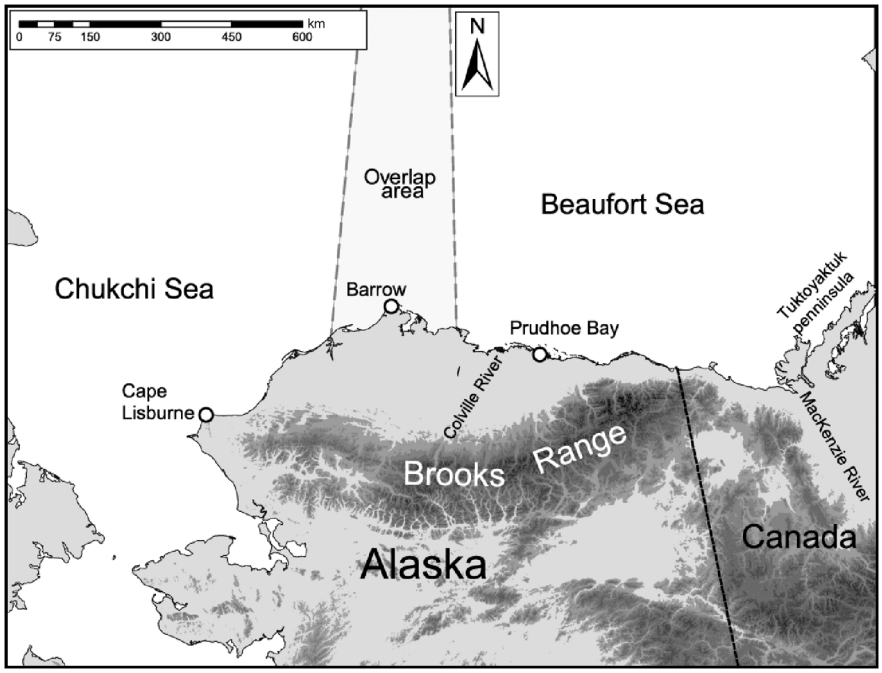
Fig. 1. Map of the geographic area of the southern Beaufort Sea and Chukchi Sea polar bear (*Ursus maritimus*) subpopulations showing place names used in the text. Point Barrow, Alaska, is on the boundary between the Chukchi and Beaufort seas. The subpopulations' area of overlap is shown (Amstrup et al. 2005).



subpopulations. The southern Beaufort Sea subpopulation includes approximately 1800 bears and the Chukchi Sea subpopulation has more than 2000 bears (Lunn et al. 2002). In this paper, we quantify the variations in mtDNA and microsatellite DNA from larger numbers of bears captured in the Chukchi and southern Beaufort seas. mtDNA is maternally inherited and reflects only female-mediated gene flow, while nuclear DNA (e.g., microsatellites) is bi-parentally inherited and provides a measure of gene flow that is mediated by both sexes. Simultaneous analysis of mtDNA and microsatellite DNA provides a more complete picture of the degree of spatial genetic structure than either type of marker alone (Avise 2004). This information is important for an understanding of the population structure of polar bears, and the extent to which movements by both sexes may be reflected in measures of spatial genetic structure. This information may become increasingly useful in conservation and management, as polar bears might face changing habitat conditions coincident with changes in the distribution of sea ice (Stirling and Lunn 1997; Stirling et al. 1999; Ainley et al. 2003; Derocher et al. 2004; Ferguson et al. 2005).

Materials and methods

Blood and tissue samples were collected from bears captured in the southern Beaufort Sea, east of Point Barrow, Alaska, and in the Chukchi Sea, west of Point Barrow, between 1985 and 1995 (Amstrup 2000). Bears were assigned to the southern Beaufort or Chukchi subpopulation depending on the area in which they were captured. We analyzed eight microsatellite loci (*G10C*, *G10L*, *G10P*, *G1A*, *G10B*, *G1D*, *G10X*, *G10M*) with methods described previously (Paetkau et al. 1995). Microsatellite data consisted of two-allele genotypes for each bear for each locus. We used programs Microsatellite Toolkit (Park 2001) and FSTAT (Goudet 1995) to calculate allele frequencies and measures of genetic diversity, which included observed and expected heterozygosities and allelic richness (El Mousadik and Petit 1996). In all analyses, nominal α levels were adjusted for multiple comparisons among the eight microsatellite loci ($P = 0.006$) using Bonferroni corrections (Rice 1989). We used the GENEPOP program (Raymond and Rousset 1995*a*) to test for Hardy–Weinberg equilibrium and linkage among microsatellite loci. To assess population structure of polar bears sampled from the Chukchi and southern Beaufort seas, we conducted tests of heterogeneity of allele frequencies (Raymond and Rousset 1995*b*) with GENEPOP and calculated interpopulation variance of allele frequencies (F_{ST}; Weir and Cockerham 1984) with program FSTAT. We also used the Bayesian clustering method of Pritchard et al. (2000), implemented in program STRUCTURE to assess spatial structure. The STRUCTURE program uses multi-locus genotypes to infer structure and assign individuals to populations based on posterior probabilities. We examined the probability that polar bears originated from K populations (where K is unknown), for K = 1–4, and where no a priori information of population assignment was used. Posterior probabilities were estimated for all K hypothetical populations. Improvement in goodness of fit for each K population was evaluated using a likelihood-ratio test. Results were based on 1 000 000 Markov chain Monte Carlo iterations following a burn-in period of 100 000 iterations and 2 repetitions of each value of K.

Analyses of mtDNA were as described by Cronin et al. (1991), including isolation of genomic DNA, restriction enzyme digestion, agarose gel electrophoresis, Southern blotting, and hybridization to a radioactively labeled mtDNA

Table 1. Microsatellite allele frequencies, allelic richness (AR), observed heterozygosity (H_o), expected heterozygosity (H_e), and F_{ST} in polar bears (*Ursus maritimus*) captured in the southern Beaufort Sea and Chukchi Sea of northern Alaska, USA. Sample sizes were 116 bears for the Beaufort Sea samples and 127 bears for the Chukchi Sea samples.

Locus and allele	Beaufort Sea	Chukchi Sea
G10C		
101	0.017	0.043
103	0.737	0.732
105	0.194	0.161
107	0.013	0.012
109	0.013	0.035
111	0.009	0
113	0.013	0.012
115	0.004	0.004
AR/H_o/H_e	8.0/0.45/0.42	6.9/0.44/0.44
F_{ST}	–0.001	
G1A		
188	0	0.012
190	0.461	0.465
192	0.103	0.154
194	0.138	0.146
196	0.203	0.157
198	0.047	0.028
200	0.047	0.039
AR/H_o/H_e	6.0/0.73/0.72	7.0/0.78/0.72
F_{ST}	0.000	
G10M		
200	0.065	0.063
206	0.026	0.008
208	0.297	0.272
210	0.289	0.378
212	0.086	0.114
214	0.19	0.142
216	0.043	0.02
218	0.004	0.004
AR/H_o/H_e	8.0/0.73/0.78	7.9/0.74/0.75
F_{ST}	0.004	
G10B		
142	0.164	0.22
150	0.069	0.071
152	0.039	0.051
154	0.461	0.421
156	0.159	0.154
158	0.103	0.083
162	0.004	0
AR/H_o/H_e	7.0/0.72/0.72	6.0/0.72/0.74
F_{ST}	0.000	
G10P		
145	0.478	0.492
147	0.022	0.055
149	0.052	0.035
151	0.043	0.039
153	0.207	0.244
155	0.134	0.114
157	0.034	0.012
159	0.009	0.004
161	0.022	0.004
AR/H_o/H_e	9.0/0.73/0.71	8.4/0.69/0.68
F_{ST}	–0.001	
G1D		
180	0.034	0.008
182	0.552	0.543
184	0.246	0.276
186	0.056	0.083
188	0.047	0.039
190	0.065	0.043
192	0	0.008
AR/H_o/H_e	6.0/0.64/0.63	6.9/0.61/0.62
F_{ST}	–0.002	
G10X		
133	0.125	0.118
135	0.116	0.098
137	0.121	0.075
139	0	0.004
141	0.138	0.169
143	0.362	0.398
145	0.056	0.051
147	0.082	0.087
AR/H_o/H_e	7.0/0.82/0.80	7.9/0.79/0.78
F_{ST}	–0.001	
G10L		
145	0.772	0.768
147	0.147	0.173
149	0.034	0.051
151	0.047	0.008
AR/H_o/H_e	4.0/0.39/0.38	4.0/0.35/0.38
F_{ST}	–0.001	
Over all 8 loci		
AR/H_o/H_e	6.9/0.65/0.64	6.9/0.64/0.64
F_{ST}	–0.0002	

probe. We identified mtDNA haplotypes of polar bears from the Beaufort and Chukchi seas with 2 (*Hin*dIII and *Cla*I) of the 11 restriction enzymes previously used to assess mtDNA variation. Each enzyme results in a mtDNA fragment pattern, and the patterns for the two enzymes compose a haplotype for each bear. The haplotypes have a low level of DNA sequence divergence (0.003–0.006 substitutions/nucleotide). A test for variance in haplotype frequency among subpopulations was conducted using a molecular analysis of variance (AMOVA) to calculate ϕ_{ST} using program Arlequin version 2.0 (Schneider et al. 2000). We also compared the numbers of each haplotype in the Beaufort and Chukchi seas for males and females separately with χ^2 contingency tests.

Table 2. Mitochondrial DNA (mtDNA) haplotype frequencies and allelic richness (AR) of polar bears captured in the southern Beaufort Sea and Chukchi Sea of northern Alaska.

	Beaufort Sea (N = 51)	Chukchi Sea (N = 47)
mtDNA		
PB1	0.7647	0.7872
PB2	0.2157	0.1489
PB3	0.0196	0.0638
AR	3.0	3.0

Results

Genotypes were obtained at eight microsatellite DNA loci for 116 bears captured in the southern Beaufort Sea and 127 bears captured in the Chukchi Sea (Table 1). We observed 4–9 alleles at the eight microsatellite loci, with an average of 6.9 alleles per locus in the southern Beaufort Sea and 7.0 alleles per locus in the Chukchi Sea. Allelic richness was 6.9 alleles per locus in both areas. Overall observed heterozygosity was 0.652 in the southern Beaufort samples and 0.639 in the Chukchi samples, and overall expected heterozygosity was 0.641 in the southern Beaufort samples and 0.637 in the Chukchi samples. Samples from both areas were in Hardy–Weinberg equilibrium at each locus ($P > 0.06$) and at all loci combined ($P > 0.3334$). Hardy–Weinberg equilibrium also was apparent at each locus ($P > 0.1193$) and at all loci combined ($P > 0.5115$) when all of the Chukchi and Beaufort sea samples were pooled into one group. We found no significant associations of loci ($P > 0.0646$), suggesting that the microsatellite loci are not linked (Paetkau et al. 1999).

Microsatellite allele frequencies in the Chukchi and southern Beaufort sea samples were not significantly different. The eight-locus F_{ST} value was not significantly different from zero (F_{ST} = –0.0002) and the tests of heterogeneity showed that the allele frequencies did not differ significantly (P = 0.0827) between the southern Beaufort and Chukchi samples over the eight loci combined (Table 1). Results of the Bayesian analysis without a priori assignment of individuals to populations indicated that the number of genetic populations most consistent with the data was K = 1.

We obtained mtDNA restriction fragment patterns for the *Hin*dIII and *Cla*I restriction enzymes for 51 bears from the southern Beaufort Sea and 47 bears from the Chukchi Sea. Three mtDNA haplotypes were identified in polar bears from the Beaufort and Chukchi seas (Table 2), as in previous analyses (Cronin et al. 1991). Haplotype PB1 predominated in both areas (76%–79%), haplotype PB2 was the second most abundant in both areas (15%–22%), and haplotype PB3 was the least common in both areas (2%–6%). mtDNA haplotype frequencies did not differ significantly between the southern Beaufort and Chukchi seas (ϕ_{st} = –0.006). Of the 51 bears from the southern Beaufort Sea for which mtDNA haplotypes were determined and the sex was known, 12 were males and 30 were females. The sex was not known for nine of the southern Beaufort Sea bears. Of the 47 bears from the Chukchi sea for which mtDNA haplotypes were determined, 6 were males and 41 were females. mtDNA haplotype frequencies did not differ significantly between the Beaufort and Chukchi seas for males (P = 0.6775) or females (P = 0.2294).

Discussion

The frequencies of microsatellite alleles and mtDNA haplotypes of polar bears captured in the Chukchi Sea and southern Beaufort Sea were not significantly different, and the microsatellite genotypes of the combined samples from the two areas were consistent with expected Hardy–Weinberg proportions (i.e., no Wahlund effect). This suggests that there is no genetic subdivision, and bears from the Chukchi Sea and southern Beaufort Sea can be considered to be one interbreeding population. This result corroborates previous studies, based upon smaller sample sizes, that suggested little genetic differentiation between bears from the southern Beaufort and Chukchi seas (Cronin et al. 1991; Scribner et al. 1997; Paetkau et al. 1999).

There are three geographic scales of interest regarding the population genetic structure of polar bears: adjacent subpopulations, subpopulations across the north polar basin, and subpopulations across the worldwide distribution of polar bears. At the scale of geographically adjacent subpopulations, our data indicate no genetic differentiation between bears from the southern Beaufort and Chukchi seas. There is more differentiation of microsatellite allele frequencies across the larger geographic scale of the north polar basin. The average pairwise F_{ST} (0.013) for 16 microsatellite loci among polar bears from six Arctic locations across the north polar basin (including the northern and southern Beaufort seas, the Chukchi Sea, the Siberian Arctic, Svalbard archipelago, and eastern Greenland; Paetkau et al. 1999) was higher than our F_{ST} (–0.0002) between the adjacent Beaufort and Chukchi sea subpopulations. On the worldwide geographic scale, there is considerable genetic differentiation among polar bears in four major geographic regions: the north polar basin; the Norwegian Bay area of northern Canada; the Canadian Arctic archipelago; and areas in Canada and Greenland south of the Canadian Arctic archipelago, including Hudson Bay, Davis Strait, and the Foxe Basin (Paetkau et al. 1999). Average pairwise F_{ST} between these regions was higher (0.050) than the average pairwise F_{ST} within these regions (0.013). These patterns of genetic differentiation are thought to be due primarily to differences in the seasonal distribution of sea-ice habitat between the high Arctic land masses (Paetkau et al. 1999). Across the north polar basin, including the Chukchi and Beaufort seas, sea ice is continuous and there are no barriers to movement of polar bears. In contrast, differing patterns of distribution of ice and land masses may constitute barriers to gene flow among the four regions that show a higher degree of genetic differentiation.

Our data show that polar bears are not genetically differentiated between the Chukchi and Beaufort seas, despite movement data showing high range fidelity. The combined genetic and field data indicate the potential for discordance between direct (animal movements) and indirect (molecular genetic) measures of gene flow (Slatkin 1987). Genetic homogeneity may result from relatively low level of continuous gene flow, episodic gene flow, or recent common ancestry of currently segregated subpopulations. The range overlap and movements of polar bears between the Beaufort and Chukchi seas suggests that there is probably enough continuous gene flow to maintain genetic homogeneity over

these areas. Lack of genetic differentiation as revealed by both maternally inherited mtDNA and bi-parentally inherited microsatellite DNA suggests that gene flow between the Chukchi and southern Beaufort seas is mediated by both sexes. This is consistent with radiotelemetry and tag-recovery data showing that male and female polar bears have similar range sizes and movement patterns in these areas (Amstrup et al. 2000, 2001).

The discrepancy between genetic and movement data may also be due to collection of movement data primarily from adult female bears, which exhibit high fidelity to ranges. Therefore, the radiotelemetry data would not record dispersal and gene flow between subpopulations. However, some of the adults sampled for genetic analysis may have immigrated as subadults prior to being captured and radio-collared. The genetic analysis would thus include adults born in the subpopulation and adults that immigrated into the subpopulation as subadults, and thus reflect gene flow over time. Subadult bears might disperse more than adult females, as Taylor et al. (2001) found that subadult polar bears of both sexes travel more widely than adults, although they usually return to near their natal area by the time they reach sexual maturity. Additional research is needed to understand the movements of adult and subadult polar bears and the resulting gene flow in the Beaufort and Chukchi seas.

In the context of management and conservation, our results suggest that problems associated with small, isolated subpopulations are not manifested in polar bears in the southern Beaufort Sea and Chukchi Sea. It appears that immigration and emigration between the southern Beaufort and Chukchi seas facilitate gene flow and maintain genetic diversity. These data also suggest that reductions in numbers of bears in one area could be compensated by immigration from the adjacent area, and the bears in our study areas could be considered to be one population. However, factors other than genetics need to be considered in identifying units for management (Cronin 1993, 2006). For example adult females have high fidelity to ranges, and are critical from a management standpoint because of the importance of production and recruitment of new bears (Taylor et al. 1987). Therefore, it is appropriate to manage polar bears in the Beaufort and Chukchi seas as separate subpopulations despite the genetic homogeneity. Other factors that differ between the bear ranges in the southern Beaufort Sea and Chukchi Sea, such as seasonal movements of sea ice, also suggest that they should be treated as separate management units (Amstrup et al. 2000). Considering the combined genetic and movement data, it is appropriate to consider the polar bears from the southern Beaufort Sea and Chukchi Sea as subpopulations of a combined southern Beaufort and Chukchi population.

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