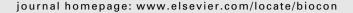


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Population genetic structure in polar bears (Ursus maritimus) from Hudson Bay, Canada: Implications of future climate change

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ABSTRACT

The primary habitat for polar bears is sea ice, yet unlike most of the high Arctic, Hudson Bay undergoes a summer ice-free period that forces all bears ashore until ice forms again in fall. Polar bear populations in the greater Hudson Bay region have been placed in four management units based primarily on data from tag returns from harvested animals, capture–recapture studies, and conventional and satellite telemetry. Our results indicate that there is a high level of gene flow among management units observed using 26 microsatellite loci and analysis of genetic profiles of 377 polar bears. However, individual-based Bayesian analysis identified population genetic structuring into three clusters and significant $F_{\rm ST}$ differentiation. Specifically, our data suggest differentiation of polar bears sampled from islands in James Bay. These results were in spite of the extensive dispersal capabilities of polar bears that could homogenize the population. Mapping of high-ancestry individuals suggests that two of the three clusters have foci in southern Hudson Bay and may be a result of predictable annual freeze-thaw patterns that are maintaining breeding 'groups'. Predicted changes in the distribution and duration of sea ice in Hudson Bay suggest that gene flow among these clusters may be reduced in the future.

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1. Introduction

Polar bears (*Ursus maritimus*) are distributed throughout the circumpolar Arctic and are closely linked to the distribution, density, and productivity of their primary prey, ringed seals (*Pusa hispida*) (Stirling and Øritsland, 1995; Ferguson et al., 2000; Amstrup et al., 2001; Amstrup, 2003). Polar bears are

adapted to the marine environment and live out much of their life on sea ice (Stirling et al., 1999; Amstrup, 2003). However, along the southern margin of their range the sea ice melts completely each summer (Etkin, 1991; Wang et al., 1994), transforming the bears' primary habitat into open water and forcing the bears ashore. In southern Hudson Bay, polar bears spend up to four or five months on-shore

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waiting for ice to reform (Stirling et al., 2004). The pattern of ice formation and thaw is predictable based on winds, tides, and prevailing currents in Hudson Bay though the timing varies among years (Stirling et al., 1977; Etkin, 1991; Stirling et al., 2004). In recent years there has been a significant trend towards earlier spring break-up; as much as three weeks earlier than in the 1970s in both western Hudson Bay (Stirling et al., 1999; Stirling et al., 2004) and eastern and southern Hudson Bay (Gough et al., 2004; Gagnon and Gough, 2005). Many studies that examine the effects of climate change on distributions consider habitat to be homogeneous and fail to take into account the inter-play between landscape characteristics and population structure (Opdam and Wascher, 2004). Here we examine the genetic structure of polar bears in Hudson Bay and consider the influence of sea ice patterns on distribution.

Current polar bear management units, although influenced by jurisdictional boundaries, were defined using tag returns of hunter-harvested animals, capture-recapture, and data from radio and satellite telemetry studies (Taylor and Lee, 1995; Bethke et al., 1996; Taylor et al., 2001). These management units, used to monitor the legal harvest of polar bears, are thought to correspond to demographically discrete sub-populations; although it is recognized that polar bears can and do move between units. For example, Stirling et al. (1977) reported a yearling male being tagged near Churchill, Manitoba and subsequently harvested at Ivujivik, Québec a straight-line movement of about 1000 km in nine months and transit from the Western Hudson Bay management unit to the Foxe Basin management unit. Thus it is not surprising that levels of genetic differentiation among management units are generally low and all polar bears are considered as one population (Paetkau et al., 1995; Paetkau et al., 1999; Cronin et al., 2006).

Telemetry data are primarily obtained from adult females as the neck diameter of adult males exceeds that of their head, causing collars to fall off. Young animals are also not generally fitted with collars for fear of injury as they grow (Amstrup et al., 2001). Such female-specific data yield valuable information regarding denning ecology (Ramsay and Stirling, 1990; Lunn et al., 2004) and individual-specific movement and distribution patterns on the sea ice (Amstrup et al., 2000). However, sub-population delineation may be biased because of this reliance on movement data from adult females as the distribution of adult males and sub-adults is less well known during much of the year. Of course, this female bias may be justified since a pattern of female philopatry and male dispersal is common in mammals (Greenwood, 1980). However, delineating core regions primarily based on adult female movements limits the estimation of sub-adult dispersal and male-mediated gene flow. Creating management and harvest plans then may become difficult as critical areas may be missed. This discrepancy between units defined using direct (field) methods and those based on indirect (genetic) methods can lead to estimates of migration that do not reflect long-term levels of gene flow (Slatkin, 1987) leading to poor management schemes.

Genetic data have been used extensively to resolve population structure in mammals (e.g., Forbes and Hogg, 1999;

Hellborg et al., 2002). Often these studies pool opportunistically collected samples (e.g., from harvested animals) from different seasons and multiple years, strategies that may mask season-specific population structure (Latch and Rhodes, 2006). Alternatively, samples can be collected from a single season when the distribution of animals may not be representative of the overall population structure. The breeding season for polar bears occurs from March through May when the bears are on the ice (Ramsay and Stirling, 1990; Rosing-Asvid et al., 2002). However, in Hudson Bay, given the logistical and cost constraints it is necessary for biologists working in this region to sample polar bears while they are on-shore. This presents a situation where genetic structure may be seasonally masked or cryptic, as it is unknown whether the spatial arrangement of polar bears onshore corresponds to the spatial arrangement during the breeding season. Cryptic structure has been identified when discrete genetic subdivisions are identified that do not correspond to current knowledge of the species' distribution (Sacks et al., 2005) - we are extending this definition to masked genetic structure at the population level. Recent statistical advances can identify cryptic population structure using clustering methods that do not make a priori assumptions regarding population membership (Rueness et al., 2003; Sacks et al., 2005).

We tested three alternate hypotheses regarding the population structure of polar bears in Hudson Bay using genetic data: (1) polar bears in Hudson Bay consist of one panmictic population; (2) on-shore spatial structure is concordant with breeding structure (i.e., current management units each represent a genetic unit); and (3) there is cryptic population structure which is independent of summer site-fidelity (i.e., population structure that does not correspond to current management units).

The null hypothesis of panmixia is suggested by the known, high mobility of polar bears that would tend to promote gene flow and eliminate genetic structure (Lentfer, 1983; Amstrup et al., 2000; Taylor et al., 2001). Previous genetic work indicated high levels of gene flow among polar bear subpopulations across the Canadian and Alaskan Arctic (Paetkau et al., 1995; Paetkau et al., 1999; Cronin et al., 2006); although polar bears from southern Hudson Bay and James Bay were not included in these analyses.

In spite of high levels of gene flow, previous genetic analyses detected some genetic structuring in polar bears in support of current management unit boundaries (Paetkau et al., 1995; Paetkau et al., 1999) leading to our second hypothesis that there may be a correspondence between on-shore and on-ice spatial arrangements. Evidence in support of this hypothesis comes from the observed philopatric behaviour of polar bears. Philopatry to summering areas has been identified in polar bears that experience reductions in summer ice cover such as in the southern Beaufort Sea (Amstrup et al., 2000), western Hudson Bay (Stirling et al., 1977; Derocher and Stirling, 1990), Baffin Bay (Ferguson et al., 1997), and southern Hudson Bay (Stirling et al., 2004). For example, Stirling et al. (2004) found that the mean distance between consecutive annual captures was 46 and 62 km for adult female and male polar bears, respectively, in the Western Hudson Bay population. If on-shore fidelity exists, concordant

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