Population structure and space-use of polar bears (*Ursus maritimus*) in Hudson Bay

by

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Abstract

Traditionally, population delineation has been determined using mark-recapture, band returns, and more recently, telemetry, geologgers and genetics. But telemetric and genetic population structure data have rarely been examined concurrently to explore differences and similarities. I define a population as a species global range, which contains local interbreeding subpopulations possessing genetic, spatial and demographic discontinuity. Spatial distribution during the breeding season is likely to structure populations genetically. I investigate the utility of both population genetics and breeding season telemetry data to examine subpopulation structure. Genetic population structure was examined in 414 polar bears (*Ursus maritimus*) caught throughout Hudson Bay using two genetic marker systems, microsatellites and single nucleotide polymorphisms (SNPs). SNPs detected a larger number of biologically meaningful subpopulations, with higher proportions of strongly assigned individuals and more precise estimates of ancestry. SNPs identified four genetic clusters that differ from the subpopulation designations currently used for the region. Spatial structure was assessed by comparing utilization distributions (UDs) during the breeding season from two perspectives: 1) by grouping individuals by the management subpopulation where individuals were caught and 2) by grouping individuals by the genetic cluster they strongly assign to. A combination of high-resolution SNP information and geographic positioning system-satellite telemetry data from 62 female polar bears from three subpopulations of Hudson Bay displayed reduced shared space-use

between grouped UDs based on genetic assignment than those formed by capture location. Combining genetic and telemetric data provides an alternative method for understanding subpopulation delineation.

Preface

This thesis is an original work by Michelle Viengkone. No part of this thesis has been previously published.

Dedication to those by side and in my heart.

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Chapter 1:

Introduction

Defining populations remains a central issue in biological research and conservation management (Berryman 2002; Camus & Lima 2002; Baguette & Stevens 2003; Schaefer 2006). The term population, however, has taken on many definitions, as various components have been deemed more or less important in the scientific community. For example, definitions proposed in the past have emphasized mating (e.g., Arms & Camp 1979) or demographic rates (e.g., Cole 1957) or shared space-use (e.g., Lane 1976) or specified a period of time (e.g., Krebs 1985). Some definitions combine these features to describe a population as "any group of organisms capable of interbreeding for the most part, and co-existing at the same time and in the same place" (Purves & Orians 1983). A universal definition remains unrecognized. I follow the definition of a population as the global range of a species (IUCN 2014), which consists of local interbreeding (Andrewartha & Birch 1984) subpopulations. Subpopulations possess genetic, spatial and demographic discontinuity (Wells & Richmond 1995).

The diversity of methods used to define subpopulations adds complexity to defining subpopulations. These techniques include, but are not limited to, mark-recapture (Lentfer 1983), band recovery (Barrowclough 1978), telemetry (Iverson et al. 1996; Schaefer et al. 2001; Amstrup et al. 2004; Klaver et al. 2008), stable isotopes (Hobson & Wassenaar 2001; Witteveen et al. 2009; Barros et al. 2010), and population genetics (Allen et al. 1995; Paetkau et al. 1999). Individually, none of these methods represents a universal approach to defining subpopulations due to the various strengths and weaknesses each possess. Typically operating independently from one another to describe subpopulations, both temporal and geographic scale have become important

features to defining subpopulations (Lima & Zollner 1996; Johnson et al. 2002; Schaefer 2006).

The issue of subpopulation delineation is challenging for wide-ranging species in remote habitats and in areas where geographic boundaries are lacking or indistinct and events such as mating are difficult to observe. Clear fine-scale structure can be difficult to identify for highly mobile carnivores with low densities and vast distributions, as seen in genetic studies on grey wolf (*Canis lupus*; Roy et al. 1994), wolverine (*Gulo gulo*; Kyle & Strobeck 2001), and cougar (*Puma concolor*; Sinclair et al. 2001). The use of topographical or political boundaries to define subpopulations may be biologically irrelevant to the species (Cegelski et al. 2003), and may mislead management practices.

For the reason above, I advocate an integrative approach to define subpopulations by addressing both genetic and spatial discontinuity during the breeding season. The breeding season represents the period where genetic exchange occurs. For many wide-ranging species, gene flow cannot be observed and the location of breeding areas may be unknown. However, fine-scale structure, and identification of subpopulations, can be investigated and compared to movement patterns from telemetry data during the breeding season and integrated with genetic data. Spatial distribution during the breeding season is likely to structure subpopulations genetically. I investigated how subpopulations are structured using genetic and GPS tracking data of polar bears (*Ursus maritimus*) in Hudson Bay, Canada.

Polar bears are an iconic species of the Arctic and have become closely linked to the effects of climate change (Thiemann et al. 2008; O'Neill et al. 2008; Prowse et al. 2009). The species occupies ice-covered marine habitat of the circumpolar Arctic (DeMaster & Stirling 1981; Stirling et al. 1999), relying on the ice as a platform for hunting prey such as the ringed seal (*Pusa hispida*) (Stirling & Archibald 1977; Smith 1980; Ferguson et al. 2000; Amstrup 2003), mating during the spring (Ramsay & Stirling 1986; Stirling et al. 1993), and

migrating (Schweinsburg & Lee 1982; Garner et al. 1990). Currently 19 subpopulation designations are recognized across the Arctic region (IUCN/SSC PBSG 2009). Boundaries between these subpopulations were based on fidelity to summering areas in conjunction with mark-recapture data, return of harvest tags, radio-collar and satellite telemetry data (Bethke et al. 1996; Taylor et al. 2001). Each subpopulation is managed independently by the political jurisdictions in which they reside (Thiemann et al. 2008).

At the global-scale polar bears are experiencing the effects of climate warming, however not uniformly across their distribution (Stirling & Derocher 1993, 2012; Tynan & DeMaster 1997). In the southernmost extent of their range, polar bears of Hudson Bay are undergoing earlier ice break-up and later freeze-up periods (Stirling & Parkinson 2006), thus, prolonging their fasting and depleting their energy reserves (Stirling et al. 1999; Stirling & Parkinson 2006; Regehr et al. 2007; Towns et al. 2010). By tracking individuals and analysing their telemetry data it is possible to monitor the effects of climate warming on movement behaviour. Using home range size estimates (Ferguson et al. 1999; Amstrup et al. 2000), and its relationship to prey availability (Ferguson et al. 1999; Mauritzen et al. 2003) and sea-ice conditions (Stirling & Øritsland 1995; Ferguson et al. 1999), predictions can be made for the effects from changes to sea-ice extent and type of ice cover to polar bear's distribution and foraging success (Stirling & Derocher 1993; Tynan & DeMaster 1997; Laidre et al. 2008). Although polar bears can travel long-distances, they exhibit site fidelity to onshore and marine areas (Derocher & Stirling 1990; Mauritzen et al. 2001; Stirling et al. 2004) and denning habitat (Derocher & Stirling 1990; Ramsay & Stirling 1990). On ice and onshore space-use are likely to alter with changes to the environment affecting habitat quality. Because polar bears are hunted, subpopulation boundaries are important to their management and should reflect these changes. Perhaps a way to address these changes is to consider a new method of defining subpopulations.

Although information from polar bear genetics was not included in the establishment of subpopulation designations, findings from a circumpolar study broadly supported the 19 subpopulations (Paetkau et al. 1999). The results provided evidence for a relationship between ecological and genetic definitions of subpopulations. The study used microsatellite markers and identified four genetic clusters across the distribution of polar bears. The four genetic clusters defined were the, i) polar basin, ii) Canadian Archipelago, iii) Canadian High Arctic, and iv) Hudson Bay. Paetkau et al. (1999) suggested the presence of landmasses and quality habitat prevents genetic homogeneity across the sea-scape, despite the capacity of bears to travel long distances.

In Chapter 2, I used an emerging genetic marker, single nucleotide polymorphisms (SNPs), to investigate fine-scale structure in polar bears in the Hudson Bay complex. Polar bears in Hudson Bay are currently managed as three subpopulations, Southern Hudson Bay (SH), Western Hudson Bay (WH), and Foxe Basin (FB), in which genetic structure has been examined using microsatellite markers (Crompton et al. 2008, 2014). Errors in the analysis of these studies, however, resulted in uncertainty in interpretation (Crompton et al. 2014). Using more extensive sampling than Paetkau et al. (1999), Crompton et al. (2008, 2014) identified a unique genetic unit within the SH subpopulation. Guided by past population genetic studies on polar bears, the objectives of Chapter 2 were to compare microsatellite and SNP marker performance in detection of fine-scale structure in Hudson Bay and to relate the genetic structure to the current subpopulation designations used for polar bear management.

Despite available year-round telemetry data, the use of on land distributions of polar bears to define subpopulations may not represent breeding behaviour. Therefore, onshore site fidelity may not translate into genetic discontinuity. One way to test my hypothesis is to examine the spring breeding season when fine-scale structure arises. Spring in the polar bear life cycle involves two major events, breeding and feeding on prey such as ringed

seals (*Pusa hispida*) (Ramsay & Stirling 1988; Rosing-Asvid et al. 2002). Females select habitats based on resources such as food, while male distribution is determined by the presence of mates (Stirling et al. 1993). In Chapter 3, I investigated possible mechanisms for the maintenance of fine-scale structure by comparing the results of genetic structure (Chapter 2) with location data collected during the breeding season. Telemetry data was restricted to females because males cannot wear collars (Amstrup et al. 2001). Thus, most of what is known about annual polar bear movement is derived from female GPS data. Space-use during the breeding season is of particular interest because this is the time when genetic exchange occurs. Polar bears exhibit site fidelity (Derocher & Stirling 1990; Ramsay & Stirling 1990; Wiig 1995; Born et al. 1997; Mauritzen et al. 2001), therefore it is likely, given the evidence of genetic structure that fidelity to breeding areas also occurs.

I characterized the location of females during the breeding season using utilization distributions (UDs) (Van Winkle 1975; Ford & Krumme 1979) under two perspectives; 1) using their capture location where collars were deployed and 2) using their genetic assignment (Chapter 2). I compared the two models to examine differences in overlap and used measures from population genetics (F_{ST}) and telemetric analyses to see how genetic and spatial discontinuity relate.

Together these two chapters represent an alternative approach to understanding fine-scale structure and defining subpopulations. Combining the strengths of genetic analyses with telemetric data provides new insights on behavioural patterns during an unobservable, biologically relevant period. The integrative approach may aid population management and conservation of polar bears as their habitat changes and affects their distribution and behaviour occur over time.

Chapter 2:

Comparing two genetic marker systems for assessing polar bear (*Ursus maritimus*) fine-scale structure in Hudson Bay

2.1 Introduction

Populations are a central concept in ecology yet methods vary widely for defining them and thus, inconsistencies in results and conclusions are common (Waples & Gaggiotti 2006). Thus, the challenge of delineating populations persists and increasingly, genetic markers are used to discriminate amongst members of a group and to group individuals into genetic clusters. Genetic techniques have been adopted by evolutionary, ecological, and conservation research streams (Morin et al. 2004; Allendorf et al. 2010). Following suit, I use genetics as a tool to define subpopulations. Specifically subpopulations are interbreeding groups (Andrewartha & Birch 1984) possessing genetic, spatial, and demographic discontinuity (Wells & Richmond 1995), whereas the term population represents a species' global range (IUCN 2014).

Until recently, most delineation studies used genetic information from microsatellite markers (Vignal et al. 2002; Seddon et al. 2005). The common use of microsatellites to examine genetic structure is largely due to their high level of polymorphism and information content per locus, which can be assessed using the polymerase chain reaction (PCR) (Balloux & Lugon-Moulin 2002; Vignal et al. 2002). In addition to having widespread availability and cross-species utility (Ball et al. 2010), microsatellites have been the mainstay for genetic analysis (Morin et al. 2009). But with the interest in use of very high-densities of genetic markers, single nucleotide polymorphisms (SNPs) are emerging (Vignal et al. 2002; Brumfield et al. 2003; Morin et al. 2004).

The advantages and disadvantages of each genetic marker have been compared at a variety of levels and applications. Evaluation of the power and efficiency of microsatellites markers and SNPs for parentage testing, genetic assignment (Rengmark et al. 2006), estimating population genetic parameters such as genetic divergence, isolation-by-distance and genetic diversity (Ryynanen et al. 2007) have shown that SNPs perform as well as microsatellites. On a genome-wide scale in bighorn sheep (*Ovis canadensis*), SNPs and microsatellites perform similarly in estimating heterozygosity and identity disequilibrium, with improved accuracy of estimates with greater number of loci (Miller et al. 2014). SNPs were effectively used to identify individuals and relationships in Scandinavian wolves (*Canis lupus*) and to monitor genetic diversity and detect gene flow (Seddon et al. 2005). The ability to generate increasingly large marker sets for SNPs suggests they are a good alternative for future population studies (Liu et al. 2005; Rengmark et al. 2006; Ryynanen et al. 2007; Haasl & Payseur 2011).

Some agricultural species have been used to compare fine-scale structure determined by both microsatellite and SNP datasets (e.g., Narum et al. 2008; Coates et al. 2009; Hess et al. 2011). These studies have resulted in conflicting conclusions regarding the ability of SNPs and microsatellites to detect fine-scale structure. For example, Van Inghelandt et al. (2010) found SNPs detect similar genetic structure found using microsatellite markers, while Yang et al. (2011) found contrasting results between the markers for assessing maize genetic structure. Singh et al. (2013) reported that SNPs revealed a different diversity spectrum and fine-scale structure in Indian rice varieties than microsatellites and thus, the issue of hierarchical scale of analysis and the number of markers used may be important to consider. In humans where a large number of SNPs have been screened, it has been noted that a small number of SNPs possess very high information content (Rosenberg et al. 2003; Lao et al. 2006), which suggests SNPs potentially could aid fine-scale structure studies. So far contributions from SNP analyses in addressing ecological or

conservation issues are uncommon because discovery and typing large marker sets is expensive (Vignal et al. 2002). While, microsatellite methods are less expensive and thus predominate in application for many wildlife species (Vignal et al. 2002). However, the ability to automate large-scale genotyping and the increasing cost effectiveness of SNPs are making them more attractive (Morin et al. 2004).

The genetic structure of polar bears (*Ursus maritimus*) is well-understood from analyses using microsatellite markers that reveal genetic differentiation is evident at the circumpolar-scale (Paetkau et al. 1999; Peacock et al. 2015) and regional-scale (Campagna et al. 2013; Crompton et al. 2008, 2014). These past microsatellite-based studies have supported the current subpopulation designations governing polar bear management. Worldwide, there are 19 subpopulations that reflect seasonal fidelity of individuals to geographic areas inferred from analyses using data from mark-recapture studies, harvesting, and female-based radio-telemetry studies (Bethke et al. 1996; Taylor et al. 2001). Polar bears of Hudson Bay, Canada represent the southern extent of their range and are managed as three discrete subpopulations (Southern Hudson Bay (SH), Western Hudson Bay (WH), and Foxe Basin (FB)). The Bay has seasonal ice cover that melts annually, forcing bears ashore for four months (Stirling et al. 2004; Amstrup et al. 2008). During this time, bears exhibit site fidelity to terrestrial areas including denning areas (Derocher & Stirling 1990; Ramsay & Stirling 1990). Studies using Hudson Bay polar bears defined the region as a unique genetic cluster (Paetkau et al. 1999; Peacock et al. 2015), while a more recent regional study (Crompton et al. 2008, 2014), further identified James Bay polar bears, within the SH subpopulation, as genetically distinct and proposed independent monitoring of this group.

With few population genetic studies on polar bears to date, all of which have used microsatellite markers, the objective of my study is to determine and compare genetic structure detected using microsatellite and SNP markers in polar bears sampled at a regional scale in Hudson Bay and compare my

findings to current subpopulation designations. Sex-specific structure is also examined to test whether polar bears exhibit typical mammalian male-biased dispersal patterns.

2.2 Methods

2.2.1 Study area and sampling

The study was conducted in Hudson Bay, Canada. The Bay is a large, shallow inland sea in eastern Canada covered by annual ice (Jones & Anderson 1994). Polar bears are found throughout the Bay and adjoining areas, which are managed as three subpopulations with a close affinity to a fourth subpopulation, Davis Strait (DS). DS was included due to its intermediate genetic relationship to the Hudson Bay complex and the Canadian Archipelago (Paetkau et al. 1999; IUCN/SSC PBSG 2009; Peacock et al. 2015). I sampled bears from Hudson Bay and also included samples from the Labrador coast and southeast of Baffin Island in Davis Strait. Samples from SH and WH were obtained from capture-recapture studies conducted by the Ontario Ministry of Natural Resources and the Canadian Wildlife Service, respectively. FB and DS samples were provided by the Nunavut Department of Environment and the Newfoundland and Labrador Department of Environment and Conservation from capture-recapture, defence of life and property kills, and hunter kills. Capture and handling protocols were consistent with the guidelines of the Canadian Council on Animal Care. Samples were designated to the subpopulation where they were sampled, largely during the ice-free period.

2.2.2 DNA extraction and genotyping

DNA was extracted from tissue samples using DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) following the standard protocol. Individuals were genotyped using a custom-designed (Malenfant et al. 2014, in press), 9K Illumina infinium bead chip (Illumina, San Diego, USA) by Delta Genomics (Edmonton, Canada). SNPs were called using GenomeStudio 2011.1

(Genotyping Module 1.9; Illumina). Individuals with call rates <0.9 were removed. Of 3411 RAD SNPs that were polymorphic, good clustering and had high (>0.9) call rates on the chip, 2603 were retained after removing all X-linked loci and loci with low minimum allele frequencies (<0.01), high rates of missing data (<0.95) and those that were in linkage disequilibrium (LD) as determined using a custom version of PLINK 1.07 (Purcell et al. 2007). All individuals were genotyped at 24 microsatellite loci including CXX20 and CXX110 (Ostrander et al. 1993), G1A, G10B, G1D, G10L (Paetkau & Strobeck 1994), G10C, G10M, G10P, G10X (Paetkau et al. 1995), UarMU05, UarMU10, UarMU23, UarMU26, UarMU50, UarMU51, UarMU59 (Taberlet et al. 1997), G10H, G10J, G10U (Paetkau et al. 1998), MSUT-1, MSUT-2, MSUT-6 and MSUT-8 (Kitahara et al. 2000). Loci were amplified in four multiplexed reactions in a final volume of 10 μL containing 5 μL of 2 X Type-It microsatellite Master Mix (Qiagen, Hilden, Germany), 1 μL of Qiagen Q solution, 1 μL of 10X primer mix (2 μM each primer) and 3 μL of template DNA. Thermocycling was performed using Eppendorf ep thermocyclers using a temperature profile of 95°C for 5 minutes followed by 30 cycles of 95°C for 30 seconds, 50°C for 90 seconds and 72°C for 30 seconds followed by a final extension at 60°C for 45 minutes. Reactions were pooled into three loading mixtures, resolved on an Applied Biosystems 3730 DNA Analyzer and sized relative to Genescan size standards. Genotyping was performed using Genemapper V4.1 (Applied Biosystems, Foster City California).

2.2.3 STRUCTURE analysis and post-processing

I performed five independent STRUCTURE (Pritchard et al. 2000) runs for both the 24 microsatellite marker dataset and the 2603 SNP dataset using an admixture model with correlated allele frequencies while recording the 95% confidence interval (CI) on ancestry values (Q) in each cluster. I assumed one to ten clusters (K) after a burn-in period of 100,000 and 900,000 repetitions of Markov Chain Monte Carlo (MCMC) for the microsatellite dataset and 50,000

and 100,000 respectively for the SNP dataset. I analysed the STRUCTURE output using STRUCTURE HARVESTER version 0.693 (Earl & vonHoldt 2012). Membership plots from STRUCTURE HARVESTER output were created using CLUMPP 1.1.2 (Jakobsson & Rosenberg 2007) and DISTRUCT 1.1 (Rosenberg 2003). In addition to the above SNP analysis, I performed five STRUCTURE runs that included three neighbouring subpopulations, Baffin Bay (BB: N=30), Gulf of Boothia (GB: N=30) and Lancaster Sound (LS: N=31) using the described STRUCTURE settings and post-processing to create membership plots.

Based on STRUCTURE's upper 95% CI estimates of Q across runs, I classified individuals as strongly assigned to a cluster if their mean upper CI overlapped 1 and unassigned if their upper 95% CI of Q did not overlap 1 or overlapped both 1 and 0. Classifying individuals as strongly assigned/unassigned and using capture location data, I created geographical plots for microsatellite and SNPs with ArcMap version 10.1 (ESRI, Redlands, CA, USA). Pie graphs depicting the proportion of individuals sampled in each subpopulation that were strongly assigned/unassigned to each of *K* clusters were generated using Microsoft Excel (2011).

Using the Ln(K) plots from STRUCTURE HARVESTER and my geographic plots of capture locations, I determined the number of clusters (*K*) as the smallest value of *K* that captured the major structure of the dataset while maintaining small differences in likelihoods (Pritchard et al. 2000). Under the assumption that bears do not move extensively after the breeding season, I also referenced maps of strongly assigned individual's capture locations to ensure biological relevance. I applied this technique for both microsatellite and SNP datasets to determine the optimal number of clusters (*K*) for each marker.

I compared the power of the marker systems to estimate genetic structure by comparing F_{ST} and Q values with 95% CI estimates. Weir and Cockerham F_{ST} from microsatellite data was calculated using GENEPOP (version 1.2, Raymond & Rousset 1995), while Hudson's F_{ST} was calculated for SNP data

using jackknifing methods in R (R Core Team 2014). As suggested by Bhatia et al. (2013), Hudson's F_{ST} is better suited for SNPs because the traditional Weir and Cockerham F_{ST} can depend heavily on ascertainment scheme for SNPs. As a result, bias can arise if population sizes or genetic drift are unequal. Pairwise F_{ST} estimates were made for both strong genetic assignments and capture locations (all individuals sampled within a specific subpopulation) levels for both markers.

Sex-specific F_{ST} was assessed by conducting pairwise F_{ST} estimates at only the genetic assignment level and only for SNP data. Under the male-biased dispersal model, I tested whether male polar bears exhibit less structure by performing a one-tailed paired t-test for sex-specific F_{ST} estimates. Using CLUMPP's output for Q values and averaging the lower and upper 95% CI estimates, I created scatterplots depicting an individual's Q and CI values by both markers using Microsoft Excel (2011).

2.3 Results

Tissue samples from 414 polar bears were collected from across the Hudson Bay region (SH: N=112, WH: N=120, FB: N=119, and DS: N=63), between 1997 and 2012. The dataset was 50.7% male and 49.3% female (N_{Male}=210, N_{Female} =204) with no reported primary relationships amongst individuals.

Fine-scale structure was detected using both the microsatellite and SNP datasets. Microsatellite data supports two genetic clusters defined by a split between northern FB plus DS (hereafter Northern) to the remainder of Hudson Bay (hereafter Western) (Figure 2.1). Based on SNP data, K=3, K=4, and K=5 were supported by nearly equal, yet increasing, likelihoods (Appendix A). In examining these *K*s, specifically K=4, I found evidence of non-convergence in solutions produced by STRUCTURE. One solution was well supported when strongly assigned individuals were mapped by capture location and the other indicated large amounts of admixture. To address the non-convergence, I ran a STRUCTURE analysis to include bears from outside Hudson Bay (i.e. BB,

GB, LS). The analysis resolved the issue of non-convergence (Appendix C, E) and because K=4 represented the smallest value of *K* that captured the majority of the structure in the dataset while maintaining small differences in likelihoods (Pritchard et al. 2000), I proceeded with K=4. The four clusters are: i) a cluster consisting of WH, SH, and southern FB on Southampton Island (hereafter Western), ii) a second cluster with bears of northern FB, on Baffin Island and along the Labrador coast in DS (hereafter Northern), iii) a third cluster composed of bears on Akimiski Island of James Bay (JB) (hereafter Southeast), and iv) a fourth cluster of DS bears on Baffin Island (hereafter Northeast, Figure 2.2).

The two marker systems, using capture locations, and at K=2 for the microsatellite and SNP datasets, had comparable pairwise F_{ST} measures (Table 2.1). Pairwise F_{ST} estimates between capture locations had the greatest differentiation from DS to SH and WH and to a lesser degree from DS to FB. Less differentiation was found between subpopulations of SH, WH and FB. At K=2, both datasets had similar F_{ST} values between the Western and Northern clusters (genetic assignment). However at K=4 and using the SNP dataset, F_{ST} values using genetic clusters exceed those between subpopulations by approximately one order of magnitude (Table 2.1).

Variation between markers was evident when individual Q values and associated estimated CIs were examined at each of K=2 and K=4 for each marker set. SNPs consistently showed smaller CI estimates around estimated Q values (Figures 2.3 and 2.4). At K=2, microsatellite markers had a greater spread in Q values for assigning individuals to the Western cluster, whereas greater consistency in assignment was evident for the Northern cluster (Figure 2.4). At both K=2 and K=4, markers displayed conflicting assignments where an individual was assigned highly by one marker and not by the other. I observed a marked difference in the proportion of strongly assigned individuals for each marker at K=2 (Table 2.1). Conflicting assignments were notable at K=4, where SNPs highly assigned individuals, but microsatellites were unable

to strongly assign individuals to any cluster except the Northeast (Figure 2.4). The small CI ranges demonstrated that SNPs usually assigned individuals to a cluster. Evidence from my marker system comparison and geographical plots (Figure 2.2) suggest SNPs perform well in detecting fine-scale structure and that the genetic clusters identified differ from current subpopulation designations in Hudson Bay.

Using the SNP dataset with individuals defined by genetic assignment, pairwise F_{ST} were significantly lower between males than females. By conducting a one-tailed paired t-test, I found males to be less structured than females ($p=0.042$).

2.4 Discussion

My findings suggest that SNPs are more powerful than microsatellite markers for examining fine-scale population differentiation. The SNP dataset identified four genetic clusters of polar bears within Hudson Bay that differ from past studies that examined global and fine-scale genetic structure in Hudson Bay (Paetkau et al. 1999; Crompton et al. 2008, 2014; Peacock et al. 2015) and to my analysis of a comparative microsatellite dataset. The high-resolution nature of SNP markers identified one previously undocumented genetic cluster within FB, and suggests sex-biased dispersal.

Microsatellite markers had comparable estimates of F_{ST} to SNPs, however differences in Q values and 95% confidence intervals were notable between datasets. Evaluation of microsatellite markers using estimated 95% CI for Q may be unconventional, but is a novel and precise approach to assessing assignment. CI estimates suggest microsatellite markers may not be as precise in estimating cluster membership as previously perceived. A greater number of individuals were strongly assigned to clusters at K=2 using SNPs (Table 2.1, Appendix D), confirming a difference in the relative power of microsatellites and SNPs to strongly assign individuals to clusters. A CI overlap including 1 may be too stringent for microsatellite markers, suggesting the need for further

analyses to determine a comparable threshold to obtain similar levels of strong assignment. Microsatellite marker analysis suggested two genetic clusters, which identified Northern and Western clusters in Hudson Bay. The two marker systems differed in the number of genetic clusters detected. The differences may be due to the vastly larger number of SNP loci, which has also been shown by Rosenberg et al. (2003) and Glover et al. (2010). However, I did not investigate the issue of number of loci relative to power. Conclusions regarding the number of genetic clusters and their geographic locations differ from previous studies (e.g., Paetkau et al. 1999; Crompton et al. 2008, 2014). The differences may be due to the large number of markers I used, larger sample size, and more even sampling. My sampling was continuous and evenly distributed within SH, but was not included in Paetkau et al. (1999). My sampling in northern FB was considerably better than Paetkau et al. (1999) and Crompton et al. (2008), especially given the errors in analyses presented in Crompton et al. (2014). Under the assumption that bears do not move extensively after the breeding season, I included in my approach, individual capture locations in relation to genetic assignments and thus adding biological relevance to support my choice of *K*. The map provides a visual representation of differences in genetic structure relative to current subpopulation designations (Figure 2.1, 2.2). Specifically, I observed a novel genetic cluster in northern Foxe Basin in the FB subpopulation.

The presence of genetic structure in polar bears could be a result of geographic features such as polynyas or landmasses that can act as barriers to gene flow (Paetkau et al. 1999). Or similarly, the structure may be linked to sea-ice habitat, which can influence polar bear movement (Derocher & Stirling 1990; Stirling et al. 2004). Fine-scale structure suggests that polar bears in Hudson Bay are not panmictic. I hypothesize that polar bears of the Hudson Bay complex are assortatively mating while on the sea-ice, giving rise to genetic structure. With evidence of onshore site fidelity for polar bears (Derocher & Stirling 1990; Ramsay & Stirling 1990; Born et al. 1997;

Mauritzen et al. 2001; Lone et al. 2013; Cherry et al. 2013), on-ice fidelity to breeding areas also occur. Gene flow occurs when dispersal is effective (i.e., resulting in genetic exchange Slatkin 1987), and can occur with some randomness to link subpopulations (Waples & Gaggiotti 2006). Paetkau et al. (1999) found circumpolar scale gene flow was uneven across the landscape between polar bear subpopulations. Based on my F_{ST} values, varying levels of gene flow has occurred between clusters within Hudson Bay.

Genetic differentiation was observed between northern and southern FB. South of, and on Southampton Island, members are more similar with those from the Western cluster. North of Southampton Island these FB bears comprise the Northern cluster and share ancestry with individuals along the Labrador coast of DS (Figure 2.2). Outside the breeding season, most of the Northern cluster individuals along the Labrador coast are male. Females of northern ancestry seem to remain in the northern region of FB outside of the spring breeding season (Figure 2.2). The split within FB may be due to sea-ice break-up with the northern portions retaining ice longer (Stewart & Barber 2010) and the physical presence of Southampton Island may separate the bears for part of the year.

Crompton et al. (2008, 2014) found some JB bears were differentiated from the rest of Hudson Bay and my results support this finding. F_{ST} estimates show the greatest differences were between the Southeast and other clusters. This marked difference was also represented by the lack of spread in individual assignments based on the Q value and their CI for this cluster (Figure 2.4). The animals with membership to the Southeast cluster were mostly sampled in James Bay (Akimiski Island). Satellite telemetry data indicate that few animals enter or exit James Bay (Obbard & Middel 2012), suggesting that the genetic differentiation was a product of behavioural and ecological processes. The JB group was genetically distinct, in a small geographic area, similar to Norwegian Bay (Paetkau et al. 1999), and both areas may be more at risk to genetic drift and inbreeding.

Plots comparing Q values (and 95% CIs) by marker type, demonstrate that microsatellite markers display greater admixture and larger confidence intervals than SNPs (Figure 2.3, 2.4). Microsatellite markers, therefore, might be misleading in identifying genetic clusters and preclude understanding of substructure. Because SNPs provide genome-wide content I am confident in their assignments of individuals to clusters and suggest that SNP markers are better suited to examining fine-scale structure.

Females had larger population differentiation estimates in all pairs of clusters in comparison to males except for Western to Northeast (Table 2.1). Overall, F_{ST} estimates were significantly lower in males than females, suggesting sex-based differences of population differentiation. Other studies have suggested male-biased dispersal in ursids using the Y-chromosome structure (Bidon et al. 2014) and female polar bear kin structure in the Barents Sea (Zeyl et al. 2009). These results suggest typical mammalian male-biased dispersal and female philopatry in polar bears.

I detected four genetic clusters using SNPs within Hudson Bay, which differ from the subpopulation designations currently used to manage bears. SNPs are able to detect genetic differences at greater resolution than microsatellites. Microsatellite typing is labour-intensive while SNP typing methods are becoming more cost-effective and automated for non-model organisms (Slate et al. 2009). I suggest that SNPs should be used in population genetics studies because they can identify fine-scale structure and estimate gene flow. Gene flow rates and overall genetic structure are likely to change (or have already changed) as adaptive behaviours develop in response to climate warming. Higher levels of gene flow in response to changes to the environment will make some genetic clusters of polar bears more similar while others may become more isolated and distinct. Additionally, studying fine-scale structure can discover small, isolated populations allowing for the conservation approaches that mitigate potentially detrimental effects that put small populations at risk (i.e., JB). Where polar bear harvest is male-biased, my

findings suggest that continued removal of males could alter the gene flow amongst genetic clusters and management of polar bear subpopulations should account for male-biased dispersal. Conservation management based on genetic, demographic, and biogeographical factors is a robust strategy to address climate change.

Table 2.1 Comparison of pairwise F_{ST} using the microsatellite and SNP datasets at the subpopulation designation and genetic cluster level (K=2) for polar bears in Hudson Bay, Canada. Here the clusters are abbreviated, where W represents Western, N indicating Northern, SE being Southeast and NE being Northeast. K=4 estimates used only the SNP dataset further subdivided by sex. Each analysis indicates the sample size in parentheses.

	Subpop-lations	**SH-WH**	**SH-FB**	**SH-DS**	**WH-FB**	**WH-DS**	**DS-FB**
Micro-satellite loci (n=414)		0.0047	0.0047	0.0187	0.0050	0.0193	0.0107
SNPs (n=414)		0.0045	0.0072	0.0203	0.0058	0.0200	0.0098
	K=2	**W-N**					
Micro-satellite loci (n=220)		0.0351					
SNPs (n=318)		0.0293					
	K=4	**SE-W**	**SE-N**	**SE-NE**	**W-N**	**W-NE**	**N-NE**
SNPs (n=319)		0.1000	0.1084	0.1269	0.0134	0.0351	0.0244
Males (n=157)		0.0593	0.0649	0.0869	0.0129	0.0365	0.0240
Females (n=162)		0.0934	0.1032	0.1206	0.0137	0.0336	0.0243

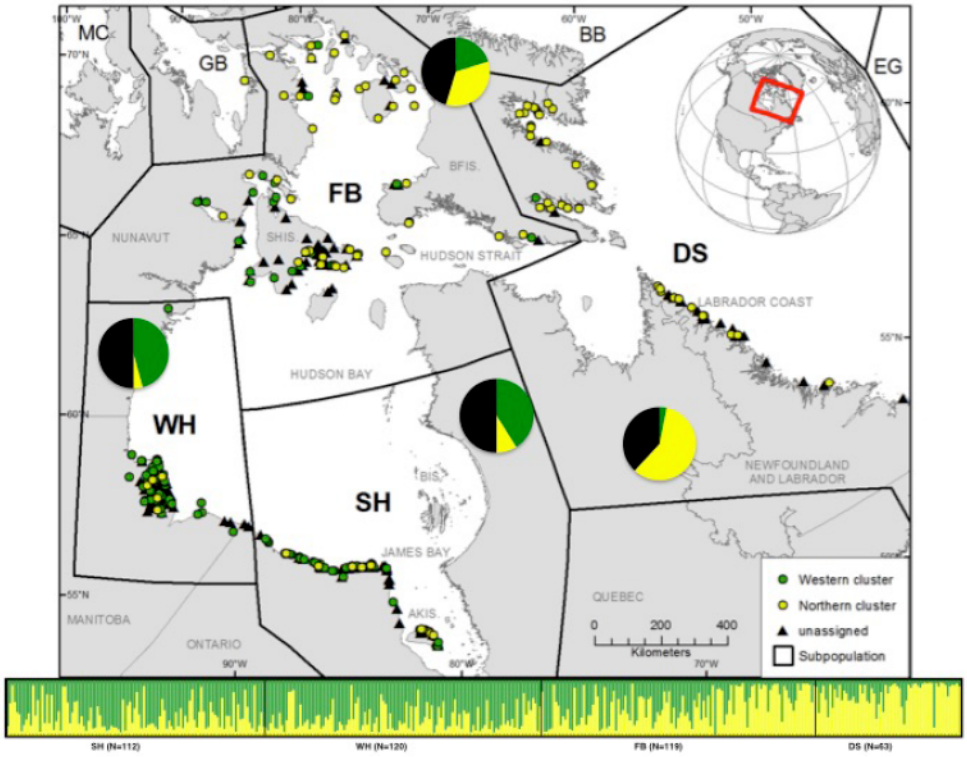


Figure 2.1 Estimated population structure of Hudson Bay polar bears (n=414) using 24 microsatellite markers at K=2 depicted in an admixture (below) and geographical plot (foreground). Admixture plot indicates each individual by a thin vertical line, which is divided into *K* coloured segments that demonstrates an individual's estimated membership in *K* clusters. Black lines separate individuals of different subpopulations (WH=Western Hudson Bay, SH=Southern Hudson Bay, FB=Foxe Basin, DS=Davis Strait). Subpopulations and sample size are labelled below the figure. Symbols for *K* clusters and unassigned individuals are shown in the legend. The geographical plot of Hudson Bay, Canada indicates strongly assigned individuals (Q value upper CI overlaps 1) with their capture location and assignment to one of two clusters (Western and Northern). Overlaid are pie charts showing each subpopulation's proportion of membership to each cluster and unassigned individuals. Neighbouring subpopulations and regional islands have been abbreviated and include MC as M'Clintock Channel, GB as Gulf of Boothia, BB as Baffin Bay, EG as east Greenland, AKIS. as Akimiski Island, BIS. as Belcher Islands, SHIS. as Southampton Island, and BFIS. as Baffin Island.

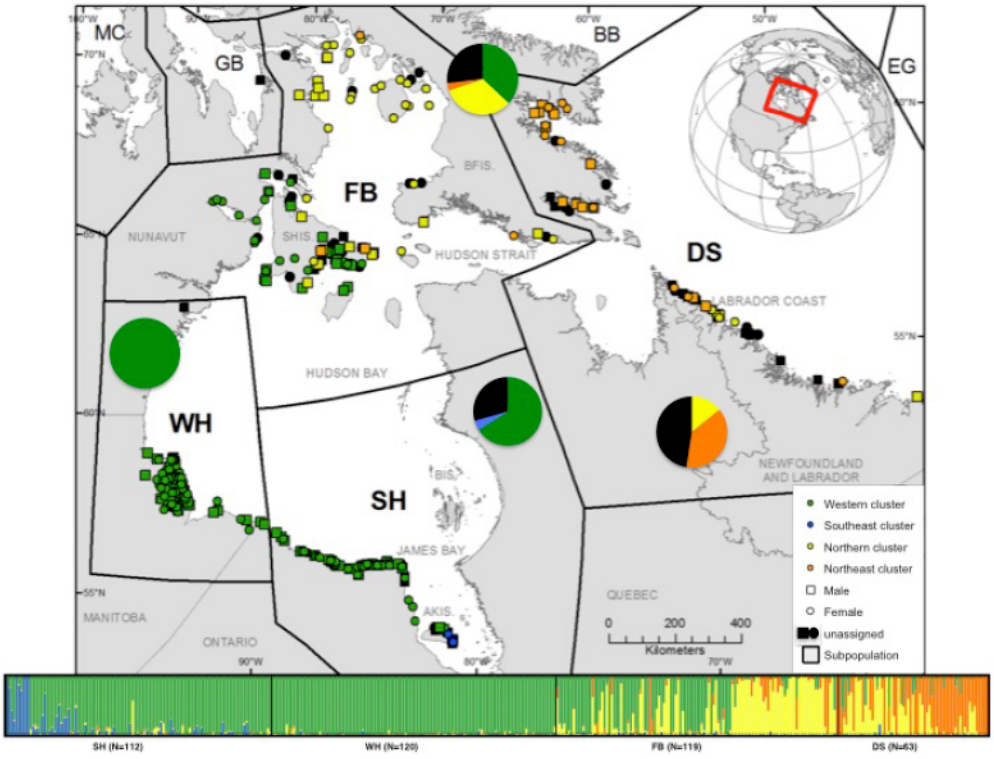


Figure 2.2 Estimated population structure of Hudson Bay polar bears (n=414) using 2603 SNPs at K=4 depicted in an admixture (below) and geographical plot (foreground). Admixture plot indicates each individual by a thin vertical line, which is divided into *K* coloured segments that demonstrates an individual's estimated membership in *K* clusters. Black lines separate individuals of different subpopulations (SH, WH, FB, DS). Subpopulations and sample size are labelled below the figure. Symbols for *K* clusters and unassigned individuals are shown in the legend. The geographical plot of Hudson Bay, Canada indicates strongly assigned individuals (Q value upper CI overlaps 1) with their capture location and assignment to one of four clusters (Western, Southeast, Northern, Northeast). Overlaid are pie charts showing each subpopulation's proportion of membership to each cluster and unassigned individuals. Refer to Figure 2.1 for abbreviation details.

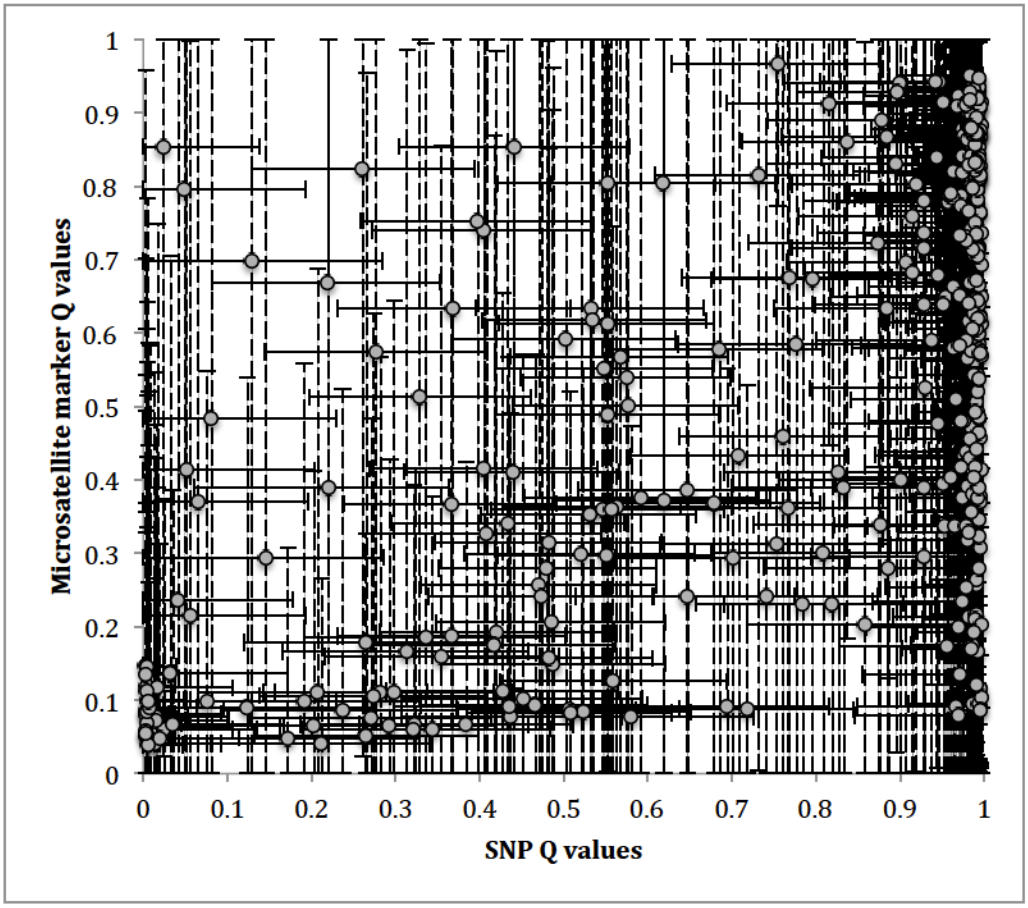


Figure 2.3 Comparison of Q values and 95% confidence intervals for 24 microsatellite markers (dotted, vertical lines) and 2603 SNPs (solid, horizontal lines) of 414 polar bears using a pairwise comparison of cluster at K=2 in Hudson Bay, Canada.

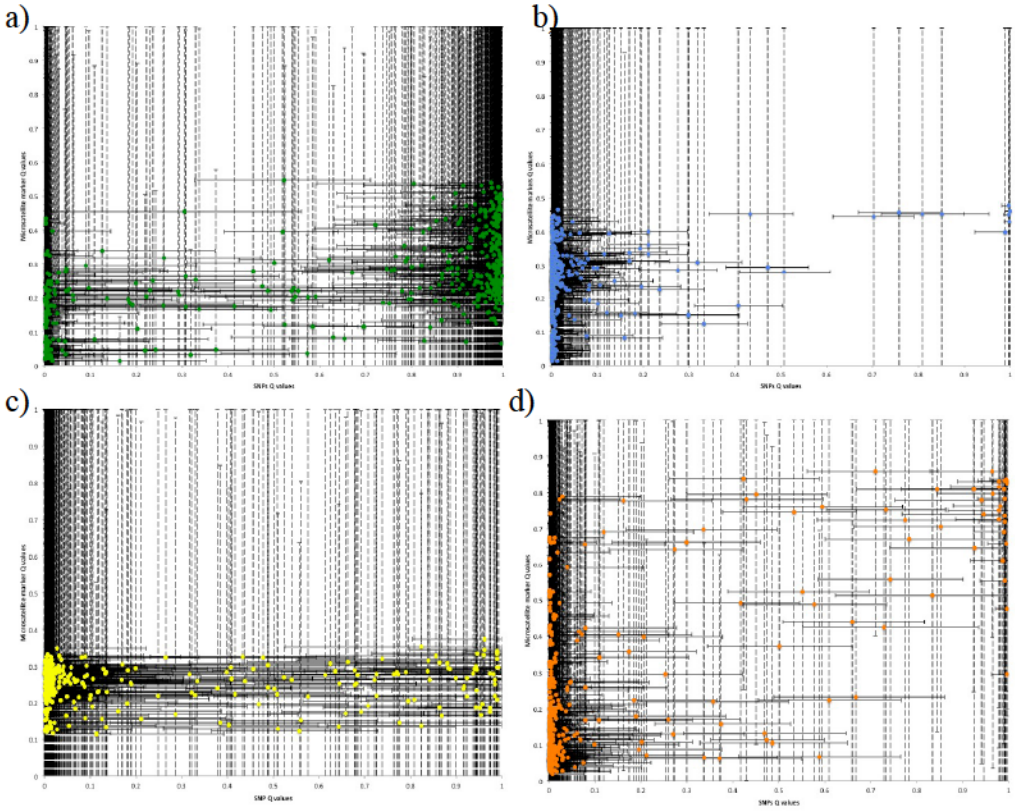


Figure 2.4 Comparison of Q values and 95% confidence intervals for 24 microsatellite markers (dotted, vertical lines) and 2603 SNPs (solid, horizontal lines) of 414 individual polar bears seen at K=4 with a) Western, b) Southeast, c) Northern, and d) Northeast clusters in Hudson Bay, Canada.

Chapter 3:

Understanding how space-use during the breeding season contributes to population structure in polar bears

3.1 Introduction

Effective delineation of populations is confounded by the many definitions for the term "population" (Allee et al. 1949; Andrewartha & Birch 1954; Wells & Richmond 1995; Berryman 2002). As a result, various methods to resolve the number of population units and the boundaries between them have been created. These methods include mark-recapture and band returns (Barrowclough 1978; Lentfer 1983; Kohler & Turner 2001), and more recently; telemetry data (Iverson et al. 1996; Taylor et al. 2001), stable isotopes (Hobson & Wassenaar 2001; Witteveen et al. 2009; Barros et al. 2010), and population genetics (Baker & Palumbi 1997; Hoelzel 1997; Paetkau et al. 1999; Barr et al. 2008).

Although each method has its advantages and shortcomings, each varies in their temporal and spatial scale. Therefore, a combination of two or more methods may be more powerful and informative than any single approach. For example, telemetry data usually provides in-depth tracking of a few individuals annually relative to molecular markers that provide general movement patterns for more individuals over generations (Haig et al. 1998). Some studies have investigated habitat selection and genetic relatedness (Shafer et al. 2014), and migration patterns with genetic assignments derived from the spawning period (Östergren et al. 2012). However, despite the potential gain of integrating telemetry data with genetic information, the combination of both in the same study is uncommon. Telemetric data can

provide year-round insights into space-use, but it is most useful from a population perspective during the breeding season when gene flow may occur. Breeding can involve variable movement behaviour within and between different groups (Bradford & Taylor 1997; Bowne & Bowers 2004; Van Dyck & Baguette 2005), leading to different levels of genetic exchange. Combining telemetric and genetic methods may offer insight into fine-scale structure and provide an alternative perspective to representative designation. In concordance with IUCN (2014), I defined a population as the global range of a species within which many local interbreeding (Andrewartha & Birch 1984) subpopulations are contained. Subpopulations are genetically, spatially and demographically distinct (Wells & Richmond 1995). Spatial distribution during the breeding season is likely to structure subpopulations genetically.

Polar bears (*Ursus maritimus*) are a well-studied species with extensive research on both space-use (Bethke et al. 1996; Amstrup et al. 2000; Taylor et al. 2001; Obbard & Middel 2012) and genetic structure (Paetkau et al. 1995, 1999; Crompton et al. 2008, 2014; Campagna et al. 2013; Peacock et al. 2015, Chapter 2). Although bears are capable of long distance migrations (Ramsay & Andriashek 1986; McCall et al. 2014), there is evidence for genetic heterogeneity (Paetkau et al. 1999). However, they do show fidelity to summer areas in parts of their range (Derocher & Stirling 1990; Ramsay & Stirling 1990; Stirling et al. 2004; Cherry et al. 2013), these areas and spring distribution (Amstrup et al. 2000) have been used as the basis of subpopulation designations. In addition, mark-recapture studies, telemetry data, and return of tags from harvested bears have contributed to the formation of subpopulation designations (Taylor et al. 2001). However, the polar bear breeding season occurs from March to June on the sea-ice (Ramsay & Stirling 1986; Rosing-Asvid et al. 2002; Smith & Aars 2015). Thus, post-breeding summering areas may not reflect genetic structure.

Genetic structure of polar bear populations has been investigated on a worldwide-scale using microsatellite markers (Paetkau et al. 1999; Peacock et

al. 2015), and is in general agreement with established subpopulation boundaries. Paetkau et al. (1999) identified four genetic clusters, one of which includes Hudson Bay with Davis Strait (DS). Regional population structure of Hudson Bay using microsatellite markers found support for the four subpopulations with the exception of James Bay (JB) being genetically unique (Crompton et al. 2008, 2014). However, a higher resolution assessment using single nucleotide polymorphisms (SNPs) detected four genetic clusters in the region (Chapter 2). The genetic clusters described suggest polar bears of Hudson Bay subdivide differently than the current subpopulation designations used for polar bear management.

The main objective of this study was to investigate how combining telemetric data with high-resolution genetic information from SNPs might provide new insights on fine-scale structure. I assessed the breeding season utilization distributions (UD) of adult female polar bears collared during 2005-2013 under two perspectives: 1) by subpopulation assignments based on capture location (capture location), and 2) genetic clusters derived from Chapter 2 (genetic assignment). I used an integrated approach to address polar bear fine-scale structure by taking advantage of the temporal scale of DNA with SNPs and the movement patterns derived from satellite telemetry.

3.2 Methods

3.2.1 Study area and study population

Hudson Bay, Canada is a shallow inland sea that spans approximately 10^6 km^2 (Jones & Anderson 1994) and has an annual freezing and thawing cycle. The Bay is completely ice covered from late December until the end of April; it is not until May to mid August that the ice starts to break-up with the last remaining ice floes along the Ontario coast (Markham 1984; Barber & Massom 2007; Hochheim & Barber 2010).

Three core subpopulations are recognized in Hudson Bay also known as the Hudson Bay complex; Southern Hudson Bay (SH), Western Hudson Bay

(WH), and Foxe Basin (FB) (IUCN/SSC PBSG 2009; Peacock et al. 2010). These subpopulations remain separated during the ice-free season which occurs when the sea-ice melts in summer (Peacock et al. 2010; Obbard & Middel 2012), however their on-ice distributions overlap (Peacock et al. 2010).

3.2.2 Capture and handling

Bears were caught onshore during late summer and autumn by remote injection using immobilizing darts fired by researchers in a helicopter (Stirling et al. 1989). Females, usually accompanied by offspring, were handled to deploy GPS radio-collars (Telonics Inc., Mesa, AZ) programmed to provide six locations/day via ARGOS satellites (Service Argos Inc., Landover, MD). Collars had an automatic release mechanism (CR-2a, Telonics Inc., Mesa, AZ) and were deployed in 2005 to 2013 to provide data for up to two years. Males were not collared because their neck circumference is larger than their head. DNA samples were obtained from blood, tissue, and hair samples. Some samples from FB were obtained from subsistence hunters from Nunavut and were provided by the Nunavut Department of Environment. Capture and handling protocols were approved by the University of Alberta Animal Care and Use Committee for Biosciences, the Environment Canada Prairie and Northern Region Animal Care committee, the Animal Care Committee of Ontario Ministry of Natural Resources following the guidelines described by the American Society of Mammalogists and the Canadian Council of Animal Care.

3.2.3 Location data screening and utilization distributions

I used data from satellite-collared bears across Hudson Bay that also had SNP genotypes (see below). Telemetry data was restricted to the core breeding season (February 1 to May 31). I used the first location acquired each day and set the threshold for including individuals in analyses at ≥10 locations/month and ≥40 total over four months to obtain reasonable UD estimates (Seaman et

al. 1999). Kernel density analysis was used to estimate UD at 50% (core area) and 95% (broader-use area) (Worton 1989; Fieberg 2007; Laver & Kelly 2008) for pooled individuals based on 1) capture location reflecting the subpopulation an individual was caught and collared and 2) the genetic assignment that refers to the genetic cluster an individual strongly assigned to (Q value upper confidence interval=1; Chapter 2). UDs and volume of intersection index (VI) were calculated using KS package (Duong 2008) for KDE in the R statistical computing software (R Core Team 2014) and plug-in methods to determine a smoothing factor. Following Fieberg & Kochanny (2005), VI is a measure of UD overlap ranging from 0 (no overlap) to 1 (complete overlap) and was calculated for pooled individuals for both capture location and genetic assignment.

3.2.4 Capture location versus genetic assignment

Based on sampling between 1997-2012, previously defined SNP-based genetic clusters (Chapter 2); Western, Northern, and Southeast clusters were applied to females with corresponding location data. The Western cluster consisted of a mix of individuals from SH (excluding James Bay), WH and the southern portion of FB. The Northern cluster was composed of individuals from northern FB and the Labrador coast of DS. Lastly, the Southeast cluster was exclusively SH bears in James Bay (JB, Chapter 2). Based on these genetic assignments, I created UDs ($n_{Western}$= 53, $n_{Northern}$=6, $n_{Southeast}$=3) and calculated VI values. Similarly, I created UDs and calculated VI values based on capture locations; SH, WH, and FB (n_{SH}=18, n_{WH}=35, n_{FB}=9). For capture location and genetic assignment UDs created, I used pairwise VI values to calculate mean VI within and between groups of strongly assigned individuals (Table 3.2).

3.2.5 Statistical analyses

I used R (R Core Team 2014) and a script developed by Robinson et al. (2010) to calculate mean pairwise VI values as input for an ANOVA analysis by

capture location and genetic assignment categories. I created a set of dummy variables to represent the within and across assignment groups for each category and I examined the mean pairwise VI and associated standard error to assess the performance of these classifications.

Using derived female-based F_{ST} values (Chapter 2) I assessed the relationship between population differentiation (F_{ST}) and overlap (VI) present using both groupings (i.e., capture location and genetic assignment).

3.3 Results

GPS satellite collars were deployed on 62 polar bears with SNP genetic data (n_{SH}=18 with $n_{Western}$=15, $n_{Southeast}$=3, n_{WH}=35 with $n_{Western}$=35, and n_{FB}=9 with $n_{Western}$=3, $n_{Northern}$=6). Each bear had a mean of 103 locations (standard error=1.7) across the breeding season. I used 6410 GPS locations to calculate UDs and VIs.

Using genetic assignments (Chapter 2), my analysis showed variation in breeding season space-use area of 95% UDs for the Western cluster (434,312 km^2), Southeast cluster (24,086 km^2) and Northern cluster (164,630 km^2) (Figure 3.2a). The Western cluster's UD spread into the SH subpopulation. The Northern cluster's UD was concentrated in northern FB and extended eastward into DS. The Southeast cluster's UD was contained within James Bay. All pairwise comparisons of VI between the three genetic clusters were 0 (Table 3.1).

In comparison, the capture location approach demonstrated generally greater UD areas ($area_{WH}$=307,867 km^2, $area_{SH}$=416,492 km^2, $area_{FB}$=422,572 km^2, Figure 3.2b). Using capture locations, the UDs were concentrated in two areas, 1) in the northern part of FB existing of only bears sampled in FB, 2) in the western-central part of Hudson Bay including James Bay. In the latter area, UDs of bears sampled in WH, SH, and FB overlap however; in James Bay only the SH UD was present (Figure 3.2).

I examined the mean pairwise VI values within and across capture location and genetic cluster subpopulations. I found that within genetic clusters, mean pairwise VI was greater than between genetic clusters (Table 3.2). The relationship under the capture locations showed greater mean pairwise VI within each subpopulation, than between subpopulations. Overall mean pairwise VI between respective assignments was greater for capture location approach. I found that the mean pairwise VI values were significantly different across both categories (ANOVA, $p<2.2x10^{-16}$). From my pairwise VI comparisons of within and across both capture location and genetic cluster, I found significant difference between all pairs (Table 3.3). These p-values were obtained from Bonferroni *post hoc* tests. Mean pairwise VI within groups (capture location=$1.17x10^{-1}$, genetic assignment=$1.03x10^{-1}$) was greater than across groups (capture location: $4.42x10^{-2}$, genetic assignment: $2.81x10^{-7}$). Standard error surrounding means were small and did not overlap in value with one another across comparisons. The mean pairwise VI was zero in the across genetic cluster category.

When I considered the measure of differentiation, female F_{ST} established in Chapter 2 and VI values obtained here, I found that, as predicted, greater F_{ST} values were associated with lower VI. Specifically, under the genetic assignments I found high F_{ST} values between genetic clusters, but zero to low mean VI. Contrasting, the capture locations exhibit generally greater VI to F_{ST}.

3.4 Discussion

Effective wildlife management relies on the accurate delineation of subpopulations. Therefore how a subpopulation is defined is of utmost importance. I advocate that delineation is best described by integrating genetic and spatial data to maximize distinct units. I proposed defining a subpopulation as a local gene pool that contains members of shared ancestry, which remain spatially segregated from other subpopulations during the breeding season. My study indicated that genetically similar female polar bears share breeding areas

that were spatially distinct from adjacent subpopulations. My approach supports the designatable unit framework for polar bear conservation proposed by Thiemann et al. (2008).

Other polar bear population delineation studies have considered telemetric and genetic methods independently. For telemetric studies, the focus has been examining regional distribution patterns and the application of cluster analyses to delineate spatial structure (Bethke et al. 1996; Taylor et al. 2001; Mauritzen et al. 2002) and genetic analyses broadly supported the telemetric analyses (Paetkau et al. 1999). Studies integrating genetic and telemetric data are uncommon (but see D'Amelio et al. 2008; Östergren et al. 2012). Both studies emphasized the importance of breeding season telemetry on population processes.

I detected genetic and spatial discontinuity in polar bears that differs from how polar bears are managed in Hudson Bay. My use of a high-resolution genetic marker set and temporal specificity to assess tracking data provide insights applicable for the long-term conservation for polar bears. Variable levels of gene flow were present among the genetic clusters in Hudson Bay (Chapter 2). From genetic methods and the space-use of female polar bears, I found that when female space-use was categorized by genetic cluster assignment, the genetic clusters result in spatially distinct areas during the breeding season. Thus, the detected genetic structure (Chapter 2) was supported by space-use patterns. Polar bears are generally solitary, non-territorial carnivores with most age and sex classes using similar habitats (Ramsay & Stirling 1986). Because the mating season for polar bears coincides with a period of food abundance (i.e., seal pupping), male distribution is linked to the distribution of females (Ramsay & Stirling 1986; Gehrt & Fritzell 1998; Carnes et al. 2011). This aligns with the fine-scale structure detected in Chapter 2, since genetic structure only occurs when members of the same genetic cluster mate.

The polar bear mating system has been described as female defence polygyny (Derocher et al. 2010) and male dispersal would be predicted for such a mating system (Balloux et al. 1998). In other ursids, males tend to have larger home ranges and subadult dispersal is common (Rogers 1987; Dahle & Swenson 2002; Zedrosser et al. 2007; Edwards & Derocher 2015). Dispersal may allow genetic exchange between subpopulations and colonization of new habitats, but only if dispersal leads to reproduction (Broquet & Petit 2009; Östergren et al. 2012). My genetic analysis indicated the presence of some level gene flow, and my analysis of F_{ST} values suggested males are responsible for genetic exchange between clusters (Chapter 2). Chapter 2 served as indirect means to understand the male component of the system and suggested males move from their genetic cluster outside the breeding season. However my overall understanding would be improved with the inclusion of male space-use patterns during the breeding season.

Similar to small home range seen in some other areas (Mauritzen et al. 2001; Amstrup et al. 2004; Lone et al. 2013), the Southeast cluster appears to have a similar space-use strategy. The small home ranges coupled with geographic isolation in James Bay, may foster genetic distinctiveness. Bears of FB in the Northern cluster were genetically differentiated from the southern regions (Chapter 2) and these Northern cluster bears had space-use patterns that differed from bears further south within their subpopulation. The Northern cluster used the ice north of Southampton Island and east into Hudson Strait. FB bears on Southampton Island were genetically more similar to the Western cluster.

Lack of overlap in female space-use areas when genetic cluster assignments were applied suggests that a combination of site fidelity, habitat quality, prey availability, physical barriers (e.g., landmasses, polynas), learned movement patterns, or fidelity to maternity denning areas may have affected polar bear movements (Ramsay & Stirling 1990; Paetkau et al. 1999; Mauritzen et al. 2001). However, under the capture location approach, females

of SH, WH, and FB showed greater overlap on the western coast and central portions of Hudson Bay. Thus indicating under this perspective, bears were neither genetically or spatially distinct. Evidence for spatial segregation within SH and FB, that corresponded to the Southeast and Northern cluster, suggests that the capture location model does not account for this discontinuity.

I tested whether or not the mean pairwise VI of my categories was equal using an ANOVA analysis, finding they were significantly different across classification. When I conducted a pairwise comparison, all pairs were significantly different (Table 3.3). It was evident that mean pairwise VI across genetic cluster was significantly lower than across capture location. Thus, providing support for genetic assignment being a better classification because it identified no overlap in habitat use. Although no significant difference was found between within capture location and genetic cluster assignment (Table 3.3), this was likely due to sample sizes for representing the genetic cluster.

In comparing the level of population differentiation (F_{ST}, Chapter 2) and overlap (VI) by capture location and genetic cluster assignment, I found an inverse relationship with a greater genetic distances (higher F_{ST}) corresponding to less space-use being shared as seen for genetic cluster assignments. Whereas, capture location assignment linked to lower levels of differentiation and low- to mid-level overlap. The two perspectives suggest two different relationships in this comparison, however, based on the UDs and ANOVA analysis I considered the genetic cluster assignment perspective as a reliable approach.

In summary, I advocate reconsideration of how subpopulations are defined and delineated for management and conservation purposes. For polar bears in Hudson Bay, combining genetic and telemetric data recognizes the biological significance of on-ice breeding site fidelity for the identification meaningful subpopulations. Consideration of the differences in genetic ancestry and space-use has implications for harvest quotas, conservation of

genetic diversity, gene flow, and the subpopulation designations that they are governed by.

As climate continues to warm, behaviours such as movement patterns are likely to change (Parmesan & Yohe 2003) along with subpopulation boundaries (Derocher et al. 2004). Identification of designatable units that are genetically, geographically, and ecologically separable is an approach used for conservation planning in Canada (Amiel et al. 2008; Thiemann et al. 2008; Seip & Jones 2013). Thus, my approach will be valuable for monitoring and the long-term conservation of polar bears and other highly mobile species.

Table 3.1 Estimated volume of intersection (VI) values based on a) capture location assignment (top quadrant), b) genetic cluster assignment (bottom quadrant) of female polar bear telemetry data during the breeding season for the years 2005-2013. Here, WH refers to Western Hudson Bay, SH is South Hudson Bay, and FB is Foxe Basin.

Capture / **Genetic**	**WH**	**SH**	**FB**
Western cluster	0.99	0.34	0.18
Southeast cluster	0	0.99	0.22
Northern cluster	0	0	0.99

	Western cluster	**Southeast cluster**	**Northern cluster**
WH	0.99		
SH		0.99	
FB			0.99

Table 3.2 Mean pairwise volume of intersection (VI) within and between respective subpopulations under capture and genetic cluster assignment for female polar bears during the breeding season for the years 2005-2013. Refer to Table 3.1 for abbreviations.

Capture / **Genetic**	**WH**	**SH**	**FB**	
Western cluster	0.1343 / 0.1046	0.0566	0.0348	**WH**
Southeast cluster	0	0.0804 / 0.0505	0.0153	**SH**
Northern cluster	0	0	0.0141 / 0.0189	**FB**
	Western cluster	**Southeast cluster**	**Northern cluster**	

Table 3.3 P-values from Bonferroni *post-hoc* tests of the pairwise comparisons of mean pairwise volume of intersection (VI) within and across capture location and within and across genetic cluster assignment.

	Within capture location	Across capture location	Within genetic cluster
Across capture location	$<2 \times 10^{-16}$		
Within genetic cluster	0.015	$<2 \times 10^{-16}$	
Across genetic cluster	$<2 \times 10^{-16}$	3.2×10^{-13}	$<2 \times 10^{-16}$

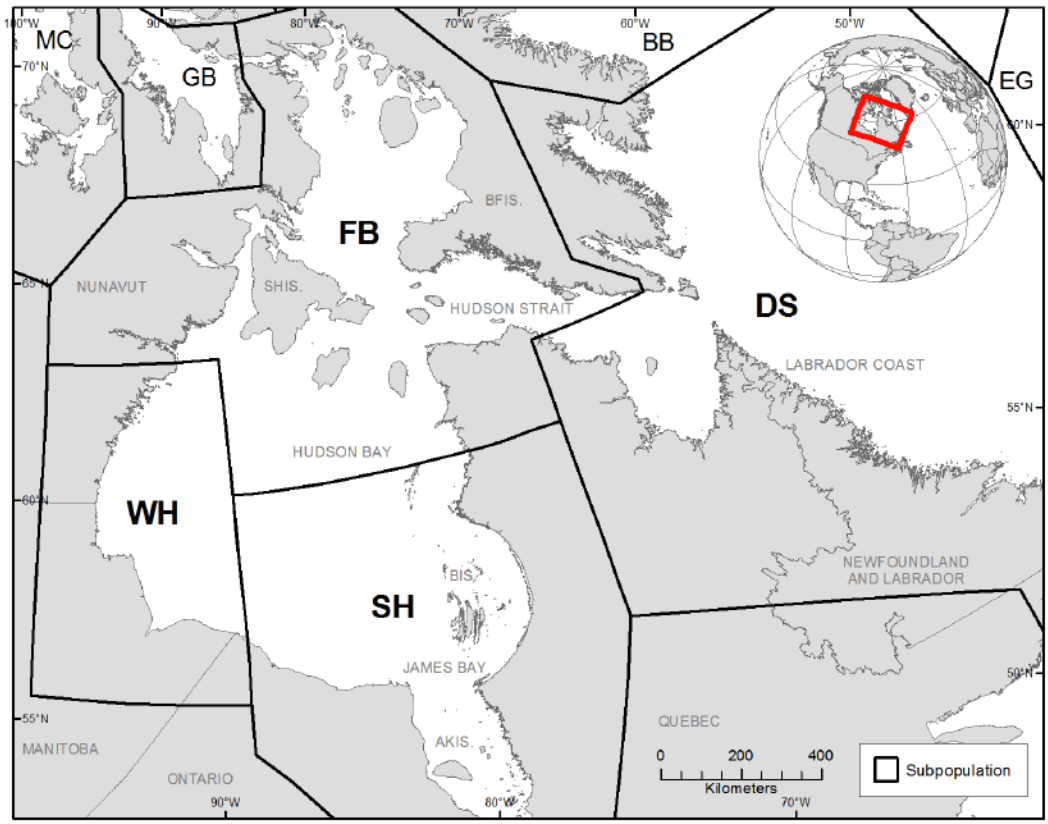
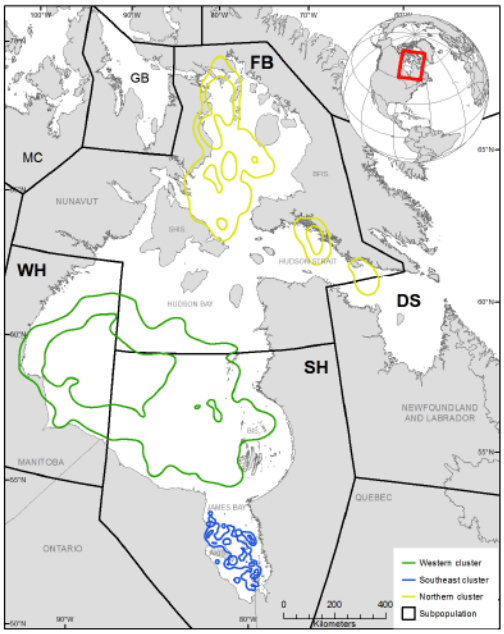


Figure 3.1 Hudson Bay study area depicting the current subpopulation designations in bold, Western Hudson Bay (WH), Southern Hudson Bay (SH), Foxe Basin (FB), and Davis Strait (DS) with neighbouring subpopulations M'Clintock Channel (MC), Gulf of Boothia (GB), Baffin Bay (BB), and east Greenland (EG). Regional islands are abbreviated and include, AKIS. as Akimiski Island, BIS. as Belcher Islands, SHIS. as Southampton Island and BFIS. as Baffin Island.

a)



b)

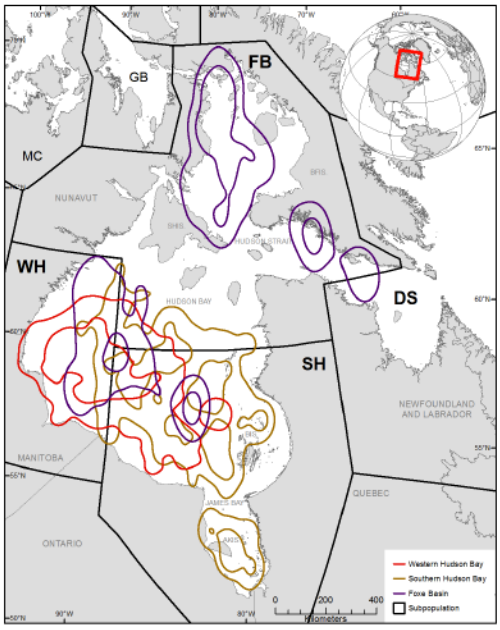


Figure 3.2 Utilization distributions of breeding season (February 1–May 31) home ranges of 62 female polar bears shown under a) genetic assignments b) capture locations in Hudson Bay. General space-use is represented by 95% contours and core areas are presented by 50% contours. Abbreviations follow Figure 3.1.

Chapter 4:

Synthesis

The focus of my thesis was to investigate an alternative approach to delineating subpopulations using a new and promising genetic marker known as SNPs and incorporating detailed tracking information from telemetry. Often *a priori*, topographical features of the habitat or political jurisdictions are used for defining subpopulations and their boundaries (Cegelski et al. 2003). However, these may not be biologically meaningful for wide-ranging species and requires evaluation of its representation of the subpopulation. To evaluate, I use the polar bears (*Ursus maritimus*) in Hudson Bay, Canada as a model system to assess fine-scale structure and used the derived genetic clusters as *a posteriori* subpopulations for examining space-use on ice during the breeding season. I defined a population as the global range of a species (IUCN 2014), which consists of many local interbreeding (Andrewartha & Birch 1984) subpopulations possessing genetic, spatial and demographic discontinuity (Wells & Richmond 1995). Spatial distribution during the breeding season is likely to structure subpopulations genetically. With the integrative approach, I was able to determine that genetic structure relates to spatial discontinuity, which contrast to the subpopulations in use for the polar bears in Hudson Bay. The findings provided by this thesis illustrate how subpopulation delineation can be approached in a more meaningful and representative way.

In my assessment of fine-scale structure, I compared two genetic marker systems (Chapter 2). Both makers identified fine-scale structure, however I found that SNPs were superior to the microsatellites because SNPs i) exhibit a greater number of strongly assigned individuals to a cluster, ii) identify a greater number of meaningful genetic clusters, and iii) demonstrate greater precision in their assignments as seen by smaller confidence interval estimates

of ancestry. For nearly two decades, microsatellites have been the primary molecular tool of choice (Glover et al. 2010), mainly due to their high level of polymorphism, ease of use and relatively low cost (Vignal et al. 2002; Selkoe & Toonen 2006). The dominance of microsatellites is evident in past polar bear genetic research (Paetkau et al. 1995, 1999; Crompton et al. 2008, 2014; Campagna et al. 2013; Peacock et al. 2015). However, with increasing progress of molecular techniques to produce SNP data (Vignal et al. 2002), expense and ease of application of SNPs for non-model organisms is becoming more common (Slate et al. 2009). With the advances in the accessibility of SNPs, my results support the potential role of SNPs as a reliable genetic marker system in conservation to identify fine-scale structure and estimate gene flow. The application of SNPs has been demonstrated (e.g., Seddon et al. 2005; Glover et al. 2010; vonHoldt et al. 2011) and advocated as a wide-spread tool (e.g., Vignal et al. 2002; Brumfield et al. 2003; Morin et al. 2004; Allendorf et al. 2010; Helyar et al. 2011). To add to the literature, I demonstrated an effective method for identifying strongly assigned individuals through the examination of confidence interval estimates using SNPs. Most microsatellite based studies examining hierarchical structure have used a Q value of 0.70 to 0.80 to assign individuals strongly to a cluster (e.g., Bergl & Vigilant 2006; Crompton et al. 2008, 2014; Warnock et al. 2010), whereas the limited number of SNP-based studies report using a Q value of 0.65-0.80 (Emanuelli et al. 2013; Singh et al. 2014). The effective performance of SNPs in assigning individuals suggests confidence interval estimates should overlap with 1, however further work needs to find a similar threshold for microsatellites.

SNPs detected four genetic clusters in Hudson Bay, which differ from the current subpopulation designations. Recall these designations reflect seasonal fidelity of individuals to geographical areas inferred from a combination of mark-recapture studies, harvest returns, radio-collar and satellite telemetry data (Bethke et al. 1996; Taylor et al. 2001). Similar to Crompton et al. (2008, 2014), I found that some individuals sampled in James Bay were genetically

unique. Isolation and inbreeding has been noted for polar bears in Norwegian Bay (Paetkau et al. 1999), also in Weddell seal (*Leptonychotes weddellii*) colony at White Island (Davis et al. 2008) and Atlantic cod (*Gadus morhua*) sampled in Norway (Knutsen et al. 2003). The Southeast cluster (SE) may require additional monitoring as the effects of climate warming may further isolate bears in the James Bay area. Derocher & Stirling (2004) suggested that subpopulation boundaries are likely to change with climate warming. Gene flow rates and overall fine-scale structure as detected here are likely to change (or have already changed) as adaptive behaviours take effect. Higher levels of gene flow in response to changes to the environment will make some genetic clusters of polar bears more similar while others may become more isolated and distinct (e.g., SE). The value of studying higher-level structure can serve to document climate induced changes as it provides retrospective genetic structure and contribute to establishing conservation approaches against the potential devastating and long-lasting effects that can put small, isolated populations at risk.

In my analysis of sex-based dispersal, I found that males have a reduced genetic differentiation relative to females thus suggesting higher rates of male movement between clusters outside the breeding season. Although male-biased dispersal in polar bears has been suggested, it has yet to be quantified and tested until now. My support for male-biased dispersal has implications for harvest quotas as male polar bears are targeted (Taylor et al. 2005) and represent a contributor to genetic structure.

In Chapter 3, I examined female movement during the breeding season by grouping individuals in two ways; 1) by capture location and 2) by genetic assignment. Genetically similar females shared similar space-use patterns, suggesting polar bears exhibit site fidelity on ice during breeding in addition to ashore and to denning areas. Also the detected fine-scale structure is maintained by assortative mating. Although these findings are expected, they have not been supported empirically. Beyond the characterization of Baffin

Bay and east Greenland male and female movement during the breeding season, Laidre et al. (2008) did not examine the behaviour or fidelity of these polar bears. Based on the lack of overlap between genetic cluster UDs, results from my ANOVA analysis, and greater population differentiation being associated with less overlap, I have provided further evidence that my approach described spatial and genetic structure of bears of Hudson Bay differently than how they are managed.

The discrepancy between current management and the results of my study is associated with how polar bear subpopulations are defined. In a sense, the current subpopulations represent what Harwood (2009) described as "externally imposed classifications", in the case of polar bears their membership to a subpopulation relates to their summer distribution. However, I demonstrated that these subpopulation designations do not reflect the on-ice distribution of polar bears and instead are misleading. The issue of wide-ranging species lacking clear subpopulation boundaries is familiar amongst research of grey wolf (*Canis lupus*; Roy et al. 1994), wolverine (*Gulo gulo*; Kyle & Strobeck 2001) and cougar (*Puma concolor*; Sinclair et al. 2001). To mitigate the reoccurring problem, biologists and managers should reconsider how subpopulations are defined and the power of the integrative approach described here. By examining and defining polar bear subpopulations in Hudson Bay by their genetic and spatial structure during a time that most directly impacts population processes, I was able to demonstrate a differential philopatry with summering areas. I showed how *a priori* established subpopulation boundaries can conceal fine-scale structure.

In the long-term, the use of mating season telemetry data of SNP genotyped individuals can provide the basis for assessing how subpopulations are adapting to climate warming. Hudson Bay represents the southernmost extent of the polar bear's range and is already experiencing earlier break-up and later freeze-up conditions (Stirling & Parkinson 2006). Adaptive behavioural changes could result in altered levels of gene flow between genetic

clusters such as homogenization or induce genetic drift. However with baseline knowledge about the genetic diversity, effective monitoring is possible.

In areas such as Canada, where harvest is practiced (Freeman & Wenzel 2006), my approach should improve demographic estimates and in turn would affect harvest quotas. Males are targeted in polar bear harvest (Taylor et al. 2005) and their removal may affect fine-scale structure by deteriorating it. Subpopulations may become less genetically distinct as males whom contribute to the genetic structure are removed from the gene pool. Thus, the number of bears taken from a particular subpopulation should avoid the overexploitation of a genetic stock as practiced in fisheries harvest regulations (Östergren et al. 2012). To adjust the management framework to align with the described definition of subpopulations, it is necessary to initiate rigorous sampling and collaring of polar bears across their distribution. Currently, insufficient data due to unequal and infrequent sampling is problematic.

A more comprehensive study could have been achieved with the inclusion of male movement. Tracking males by radio collar has been made difficult due to their conical shaped head, however a few studies have successfully tracked males with subcutaneously implanted transmitters (Amstrup et al. 2001) and satellite transmitters attached to the ear (Laidre et al. 2008). Female movement has been described to be representative of both sexes, however my genetic work suggests males move more than females outside the breeding season. Further studies of male movement patterns would provide insights to improve subpopulation delineation.

Despite hesitation to incorporate genetics into population criteria (Taylor & Dizon 1999), I encourage of the role of genetics in ecology as others have done so (Manel et al. 2003, 2005; Pearse & Crandall 2004; Palsboll et al. 2007). As I have depicted with my results, I support the use of genetics specifically for subpopulation delineation. I have demonstrated the potential genetics has in *a posteriori* based approach when accompanied with telemetry data.

My studies illustrated the powerful and complementary techniques of genetic and telemetry data to better understand fine-scale structure and delineation. I advocate this new approach to be implemented in future studies of subpopulations because it resolves individuals into simple units based on their genetic ancestry and breeding season space-use pattern. It takes into account a biologically relevant time period to better understand the relationships between individuals that remain unclear and unobserved. Indirectly my approach lends to identifying key areas of habitat use that are ecologically important to the subpopulation. I suggest collaboration between scientific groups and implementation of study designs that include genetics and telemetry for defining study populations. The identification of genetic clusters in the context of phenotypic and biogeographical characteristics will aid in the creation of a biologically-sound conservation approach as suggested by Thiemann et al. (2008). As a strategy, it has the adaptability and robustness to reflect the needs of the subpopulation of concern and as climate changes.

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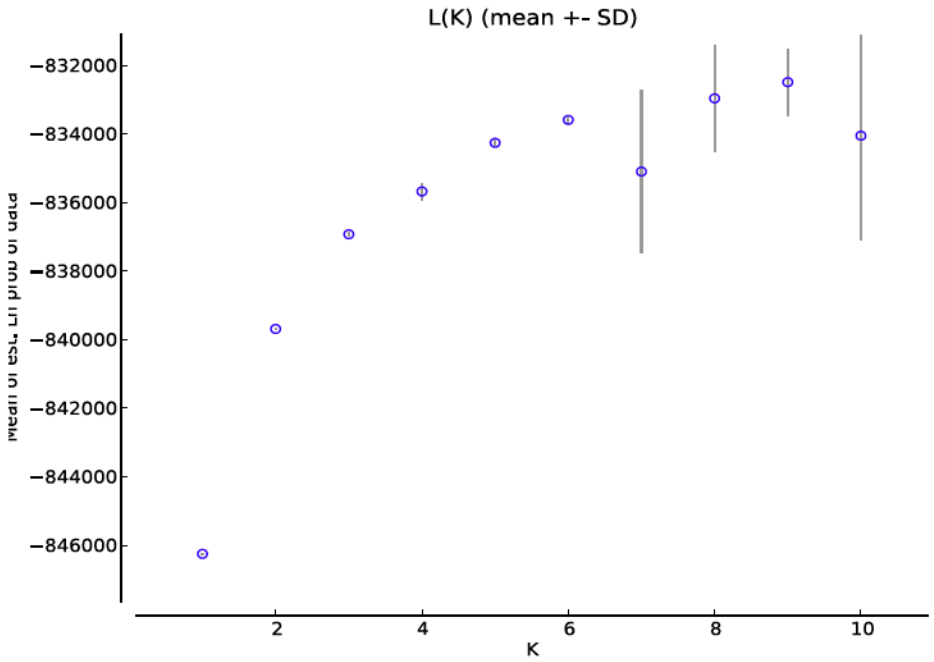
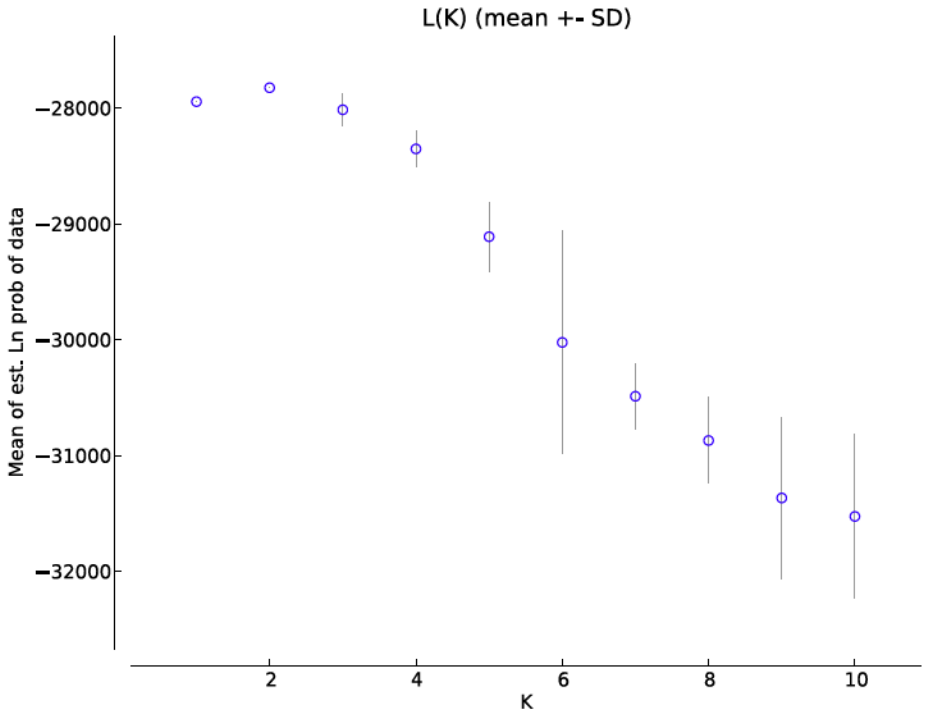
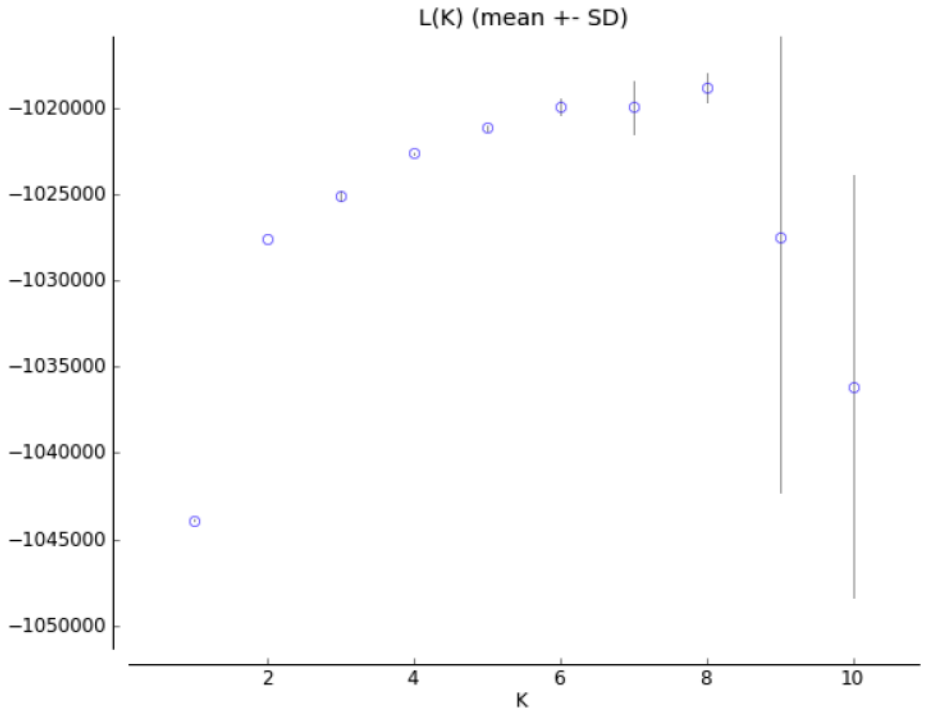
Appendices



Appendix A. Mean Ln(K) probability plot for SNP-based (n=2603) STRUCTURE analysis for Hudson Bay complex (n=414) examining K1 to 10 for five repetitions.

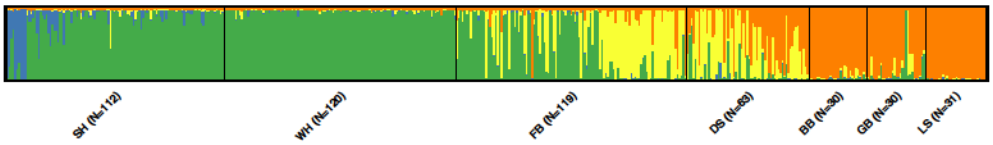


Appendix B. Mean Ln(K) probability plot for microsatellite-based (n=24) STRUCTURE analysis for Hudson Bay complex (n=414) examining K1 to 10 for five repetitions.



Appendix C. Mean Ln(K) probability plot for SNP-based (n=2603) STRUCTURE analysis for Hudson Bay complex (n=414) and neighbouring subpopulations (BB=30, GB=30, LS=31) examining K1 to 10 for five repetitions.

Appendix D. Estimated population structure of Hudson Bay polar bears (n=414) using 2603 SNPs at K=2 depicted in a membership plot. Admixture plot indicates each individual by a thin vertical line, which is divided into *K* coloured segment that demonstrates an individual's estimated membership in *K* clusters. Black lines separate individuals of different subpopulations (Southern Hudson Bay: SH, Western Hudson Bay: WH, Foxe Basin: FB, Davis Strait: DS). Subpopulations and sample size are labelled below the figure.



Appendix E. Estimated population structure of Hudson Bay polar bears (n=505) using 2603 SNPs at K=4 depicted in a membership plot. Admixture plot indicates each individual by a thin vertical line, which is divided into *K* coloured segment that demonstrates an individual's estimated membership in *K* clusters. Black lines separate individuals of different subpopulations (Southern Hudson Bay: SH, Western Hudson Bay: WH, Foxe Basin: FB, Davis Strait: DS, Baffin Bay: BB, Gulf of Boothia: GB, Lancaster Sound: LS). Subpopulations and sample size are labelled below the figure.