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ORIGINAL ARTICLE

Multilocus phylogeography and population structure of common eiders breeding in North America and Scandinavia

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ABSTRACT

Aim Glacial refugia during the Pleistocene had major impacts on the levels and spatial apportionment of genetic diversity of species in northern latitude ecosystems. We characterized patterns of population subdivision, and tested hypotheses associated with locations of potential Pleistocene refugia and the relative contribution of these refugia to the post-glacial colonization of North America and Scandinavia by common eiders (*Somateria mollissima*). Specifically, we evaluated localities hypothesized as ice-free areas or glacial refugia for other Arctic vertebrates, including Beringia, the High Arctic Canadian Archipelago, Newfoundland Bank, Spitsbergen Bank and north-west Norway.

Location Alaska, Canada, Norway and Sweden.

Methods Molecular data from 12 microsatellite loci, the mitochondrial DNA (mtDNA) control region, and two nuclear introns were collected and analysed for 15 populations of common eiders (n = 716) breeding throughout North America and Scandinavia. Population genetic structure, historical population fluctuations and gene flow were inferred using F-statistics, analyses of molecular variance, and multilocus coalescent analyses.

Results Significant inter-population variation in allelic and haplotypic frequencies were observed (nuclear DNA F_{ST} = 0.004–0.290; mtDNA Φ_{ST} = 0.051–0.927). Whereas spatial differentiation in nuclear genes was concordant with subspecific designations, geographic proximity was more predictive of inter-population variance in mitochondrial DNA haplotype frequency. Inferences of historical population demography were consistent with restriction of common eiders to four geographic areas during the Last Glacial Maximum: Belcher Islands, Newfoundland Bank, northern Alaska and Svalbard. Three of these areas coincide with previously identified glacial refugia: Newfoundland Bank, Beringia and Spitsbergen Bank. Gene-flow and clustering analyses indicated that the Beringian refugium contributed little to common eider post-glacial colonization of North America, whereas Canadian, Scandinavian and southern Alaskan post-glacial colonization is likely to have occurred in a stepwise fashion from the same glacial refugium.

Main conclusions Concordance of proposed glacial refugia used by common eiders and other Arctic species indicates that Arctic and subarctic refugia were important reservoirs of genetic diversity during the Pleistocene. Furthermore, suture zones identified at MacKenzie River, western Alaska/Aleutians and Scandinavia coincide with those identified for other Arctic vertebrates, suggesting that these regions were strong geographic barriers limiting dispersal from Pleistocene refugia.

Keywords

Arctic, common eider, Pleistocene refugia, population genetic structure, post-glacial colonization, *Somateria mollissima*, suture zones.

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INTRODUCTION

Pleistocene glacial cycles had a major impact on the genetic diversity and distribution of species in northern latitudes (Hewitt, 2004a). During the Pleistocene, climatic conditions were highly variable, with over 20 glacial cycles recorded (Williams *et al.*, 1998). These cycles resulted in major range shifts and fluctuations in population demography as species ranges contracted into both southern and Arctic refugia during glacial maxima, and expanded into ice-free areas during inter-glacial periods (Hewitt, 2004a; Schmitt, 2007). Throughout the Arctic, colder climates and ice sheets displaced many species to lower latitudes and high-latitude, ice-free areas during the Last Glacial Maximum (LGM) (Hewitt, 2004a). Most of northern North America and Europe were covered by the Cordilleran and Laurentide ice sheets and the Fennoscandian ice sheet, respectively (Hewitt, 2001, 2004a). Species that resided in southern temperate refugia expanded north following the recession of glaciers to newly available habitat. Fossil and molecular data, however, suggest that some areas of the Arctic, notably Beringia, were unglaciated. Beringia extended from north-western Canada to the Kolyma River, Russia, and remained largely unglaciated (Abbott & Brochmann, 2003). Beringia has long been hypothesized to have played a role in the diversification of many Arctic biota (Hultén, 1937; Rand, 1954), and evidence for additional high Arctic refugia is mounting, with divergent lineages and high genetic diversity observed in species such as dryads (*Dryas integrifolia*), hares (*Lepus* spp.), lemmings (*Lemmus* spp.) and saxifrages (*Saxifraga oppositifolia*) occupying the high Canadian Arctic and Greenland (Tremblay & Schoen, 1999; Abbott *et al.*, 2000; Fedorov & Stenseth, 2002; Waltari & Cook, 2005).

Population expansion from glacial refugia has left predictable genetic patterns in recently colonized regions. Molecular data coupled with coalescent theory have enabled researchers to investigate distributional and demographic change through evolutionary time, and have aided in the identification of glacial refugia (Lessa *et al.*, 2004; Waltari & Cook, 2005). Ploeger (1968) provided a comprehensive review of proposed ice-free areas during the last Pleistocene glacial period, and postulated their relative importance as potential refugia for Arctic waterfowl (Anatidae) based on current species distributions and ecological requirements. High Arctic refugia proposed by Ploeger (1968) included Beringia, Canadian Arctic Archipelago, northern Greenland, Spitsbergen Bank near Svalbard and north-west Norway. Proposed temperate refugia included Newfoundland Bank, western Greenland, Iceland and western Europe. More recently, molecular data coupled with coalescent theory have substantiated Beringia, Canadian Arctic Archipelago and western Greenland as ice-free refugia for Arctic vertebrates (Holder *et al.*, 1999, 2000; Fedorov & Stenseth, 2002; Fedorov *et al.*, 2003; Flagstad & Røed, 2003; Scribner *et al.*, 2003; Waltari & Cook, 2005). Concordance of demographic patterns among multiple Arctic species could provide insights into the relative importance of proposed glacial refugia as historical reservoirs of genetic diversity within species.

Here we investigate the population genetic structure of common eiders (*Somateria mollissima* Linnaeus, 1758) and their post-glacial colonization of North America and Scandinavia using genotypic data from nuclear microsatellite loci and sequence data from the mitochondrial DNA (mtDNA) control region and two nuclear introns. Common eiders are an Arctic and subarctic nesting seaduck. They have a circumpolar distribution and inhabit coastal marine systems (Goudie *et al.*, 2000). Common eiders show a propensity to nest colonially and form large aggregations in non-breeding months. Populations vary in their degree of migratory behaviour, with some populations remaining resident (Belcher and Aleutian Islands), while others are long-distant migrants (> 2300 km; Goudie *et al.*, 2000). Typically, populations overwinter as far north as open water persists, and facultative movements induced by advancing pack ice or freeze-up have been observed (Goudie *et al.*, 2000). As in other waterfowl, female common eiders are highly philopatric and exhibit breeding-site fidelity, whereas males disperse among populations that share wintering grounds. Common eiders are one of the few Holarctic waterfowl species composed of six to seven distinct subspecies (Goudie *et al.*, 2000). Subspecific designations are based on morphology (Palmer, 1976) and appear to correspond to overwintering areas (Ploeger, 1968; Goudie *et al.*, 2000), suggesting that both sexes display some degree of winter site fidelity (Spurr & Milne, 1976). Common eiders are thus unusual among seaducks and other high-latitude avian species, as they exhibit fine-scale spatial genetic structuring for both mtDNA and nuclear markers (Tiedemann *et al.*, 1999; Sonsthagen *et al.*, 2007, 2009). High levels of structure in mtDNA were observed among colonies in the Baltic Sea, Beaufort Sea and Yukon–Kuskokwim (YK) Delta (Φ_{ST} = 0.135–0.343, F_{ST} = 0.074–0.187). Significant, but lower, levels of structure were detected among Baltic Sea and Beaufort Sea colonies at microsatellite loci (F_{ST} = 0.009–0.029). Furthermore, molecular data indicate that common eider females nest in kin groups, which produces microgeographic genetic structure within populations (McKinnon *et al.*, 2006; Sonsthagen *et al.*, 2010).

High levels of natal, breeding and winter site fidelity, coupled with fine-scale spatial genetic partitioning, enabled us to investigate patterns of population subdivision and to test hypotheses associated with locations of potential Pleistocene refugia and the relative contribution of these refugia to the post-glacial colonization of North America and Scandinavia by common eiders. Using three types of molecular marker with contrasting modes of inheritance, we evaluated localities that have been hypothesized as ice-free areas or glacial refugia in other Arctic vertebrates, including the southern edge of the Bering Land Bridge, northern Beringia, the High Arctic Canadian Archipelago, Newfoundland Bank, Spitsbergen Bank and north-west Norway.

MATERIALS AND METHODS

Laboratory techniques

Adult common eiders ($n = 716$) were sampled during the breeding season from 15 populations, representing five subspecies, throughout their distribution (Fig. 1; Appendix S1 in Supporting Information; Sonsthagen *et al.*, 2007, 2009): *Somateria mollissima v-nigrum* (Aleutian Islands, YK Delta, Simpson Lagoon, Mikkelsen Bay, Alaska and Kent Peninsula, Canada); *Somateria mollissima borealis* (Baffin Island, Hudson Straits, Southampton Island, Mansel Island, Canada and Svalbard, Norway); *Somateria mollissima sedentaria* (Belcher Islands, Canada); *Somateria mollissima dresseri* (New Brunswick and Nova Scotia, Canada); *Somateria mollissima mollissima* (Tromsø, Norway and Soderskar, Finland). Individuals were classified to subspecies based on morphological characteristics and their geographic origin (Palmer, 1976; Goudie *et al.*, 2000). Sequences or genotypes were obtained from 12 microsatellite loci (Aph08, Aph20, Aph23: Maak *et al.*, 2003; Bca1, Bca11, Hhi3: Buchholz *et al.*, 1998; Sfiμ10: S. Libants and co-workers, Michigan State University, GenBank accession AF180500; Smo4, Smo7, Smo8, Smo10, Smo12: Paulus & Tiedemann, 2003); mtDNA control region (545–563 bp; Sonsthagen *et al.*, 2007; L263rev 5′-CCAAACTGCGCACCTGA CATTCC-3′; L319 5′-TGAATGCTCTAAGAYCCAAACTGC-3′); intron 3 of lamin A (LMNA); and intron 11 of glyceraldehyde-3-phosphate dehydrogenase (GAPDH; McCracken & Sorenson, 2005). Sequence information was collected only for a subset of the individuals from Mikkelsen Bay and Simpson Lagoon (Appendix S2; Sonsthagen *et al.*, 2009).

Genomic DNA was isolated from blood, feather or frozen tissues. Methods for DNA extraction, PCR amplification, electrophoresis and cycle sequencing are described in Sonsthagen *et al.* (2007). For quality control purposes, 10% of samples were re-amplified and genotyped at the 12 microsatellite loci in duplicate. Sequences are deposited in GenBank (EU019602–EU019692, GQ405658–GQ405854, HQ695012–HQ695731).

Analysis of genetic diversity

Allelic phases for LMNA and GAPDH introns were inferred from diploid sequence data using PHASE 2.0 (parameters: 1000 burn-in, 1000 iterations; Stephens *et al.*, 2001), which uses a Bayesian approach to reconstruct haplotypes from genotypic data and allows for recombination and the decay of linkage disequilibrium with distance. The accuracy of haplotypes reconstructed by PHASE has been validated and shown to be greater than that of cloning with large data sets (Harrigan *et al.*, 2008). The PHASE analysis was repeated three times to ensure consistency across runs.

Allelic richness, expected and observed heterozygosities, degree of deviation of observed genotypic frequencies from Hardy–Weinberg equilibrium (HWE), and linkage disequilibrium (LD) for microsatellite and nuclear intron loci were calculated using FSTAT 2.9.3 (Goudet, 1995, 2001). Nucleotide (π) and haplotype (h) diversities for each population were estimated using ARLEQUIN 2.0 (Schneider *et al.*, 2000) for DNA sequences.

Analysis of population genetic structure

Estimates of inter-population variance in allelic and haplotypic frequencies (F_{ST}, R_{ST} and Φ_{ST}) were calculated in ARLEQUIN. Significance levels were adjusted based on Bonferroni correction ($\alpha = 0.05$). Pairwise Φ_{ST} values were calculated using a Tamura & Nei (1993) model with an invariant site parameter,

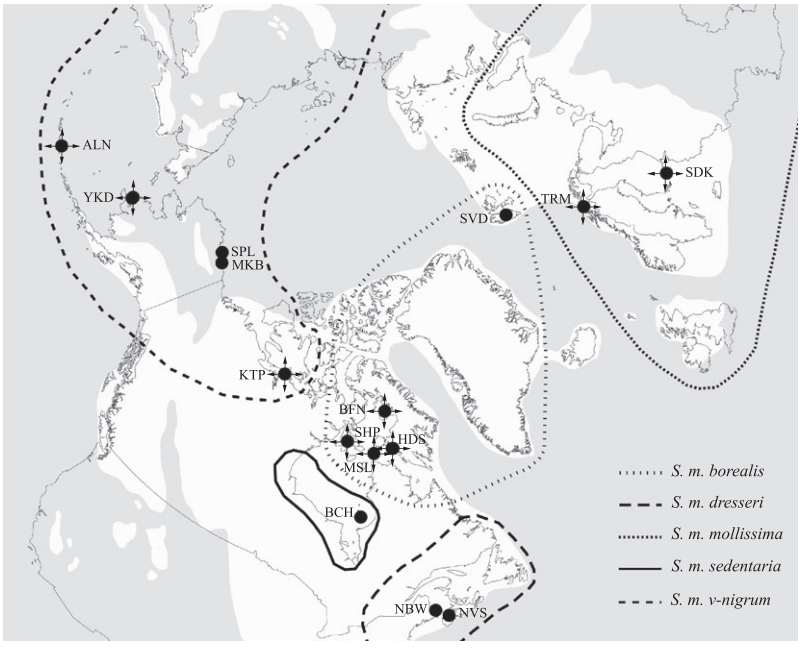

Figure 1 Subspecies distribution and localities of the 15 common eider populations sampled in this study: *Somateria mollissima borealis*, Baffin Island (BFN), Hudson Straits (HDS), Mansel Island (MSL), Southampton Island (SHP) and Svalbard (SVD); *Somateria mollissima dresseri*, New Brunswick (NBW) and Nova Scotia (NVS); *Somateria mollissima mollissima*, Soderskar (SDK) and Tromsø (TRM); *Somateria mollissima sedentaria*, Belcher Islands (BCH); *Somateria mollissima v-nigrum*, Aleutian Islands (ALN), Simpson Lagoon (SPL), Mikkelsen Bay (MKB), Kent Peninsula (KTP) and Yukon–Kuskokwim Delta (YKD). Arrows indicate populations with a positive growth signature based on mitochondrial DNA. The extent of the most recent last glacial ice sheets is illustrated in white; unglaciated regions are in grey (Hewitt, 2004b).

as determined using MODELTEST v. 3.06 (Posada & Crandall, 1998) and Akaike's information criterion (Akaike, 1974). We used Hedrick's (2005) method, implemented in RECODEDATA v. 1.0 (Meirmans, 2006), to calculate the maximum value of F_{ST} obtainable for our suite of microsatellite loci. Haplotype networks for mtDNA and intron genes were reconstructed in NETWORK 4.5.1.6 (Fluxus Technology Ltd, Suffolk, UK, 2009) using the Reduced Median network method (Bandelt *et al.*, 1995).

We applied a regression analysis to test for isolation-by-distance and evaluate the relative historical roles of gene flow and drift on broad-scale genetic structure among populations. Isolation-by-distance tests compare pairwise genetic and geographic distances with those expected under a stepping-stone model of population structure (Hutchinson & Templeton, 1999). All three marker types were tested, and the correlation between the logarithm of the geographic distance and Rousset's genetic distance [$F_{ST}/(1 - F_{ST})$; Rousset, 1996] was examined for populations using the program IBD 3.0 (Bohonak, 2002); significance was determined with 500,000 permutations. Geographic distances were estimated as straight-line distances among populations.

We used the Bayesian clustering software STRUCTURE 2.2 (Pritchard *et al.*, 2000) to assign individuals to clusters based on their microsatellite allelic frequencies and to infer the occurrence of population structure without *a priori* knowledge of putative populations. Data were analysed using an admixture model assuming correlated frequencies with a 10,000 burn-in period, 500,000 Markov chain Monte Carlo iterations, and number of possible populations (K) ranging from 1 to 15; the analysis was repeated five times to ensure consistency across runs. We used the method of Evanno *et al.* (2005) and the K that maximized the likelihood given the data to determine the most likely number of clusters.

Analysis of historical demography

We assessed evidence for contemporary and historical fluctuations in population size to determine if populations were located in potential refugia. Population fluctuations were estimated in BOTTLENECK 1.2.02 (Cornuet & Luikart, 1996) for microsatellite loci and LAMARC (Kuhner *et al.*, 1995) for sequence data. Fluctuations in population size inferred from microsatellite data were assessed using a Wilcoxon sign-rank test in BOTTLENECK. To gain insight on the timing of events, the probability distribution was established using 1000 permutations under two models: the stepwise mutation model (SMM) and the two-phase model of mutation (TPM); parameters: 79% SSM, variance 9 (Rousset, 1996). Heterozygote deficiency relative to the number of alleles indicates recent population growth, whereas heterozygote excess indicates a recent population bottleneck (Cornuet & Luikart, 1996). It is important to note that BOTTLENECK compares heterozygote deficiency and excess relative to genetic diversity, not to HWE expectation (Cornuet & Luikart, 1996). LAMARC estimates a population growth parameter, g, incorporating coalescence theory (parameters: 10 short chains with 200 out of 4000 sampled trees, and five long chains with 20,000 out of 400,000 sampled trees). Data were run five times to ensure convergence of parameters across runs. Positive values of g indicate population growth over time; negative values indicate population decline. Because this method incorporates aspects of genealogy, it is sensitive to changes in demography and may have an upward bias (Kuhner *et al.*, 1998). Therefore, we used a conservative estimate of significance based on 99.9% confidence intervals for g to test for significant differences from zero (Waltari & Cook, 2005). Finally, mismatch distributions of mtDNA haplotype data were calculated in ARLEQUIN to gain further insight into historical population demography (Rogers & Harpending, 1992).

Analysis of gene flow

To examine gene flow among eider populations, the number of effective migrants per generation (N_em) and number of effective female migrants per generation (N_fm) among sampled localities was calculated for nuclear microsatellite and intron loci and mtDNA, respectively, in MIGRATE v. 3.0.3 (Beerli & Felsenstein, 1999, 2001). Full models, θ ($4N_e\mu$ or $N_f\mu$) and all pairwise migration parameters were allowed to vary and estimated individually from the data, and were compared with restricted island models for which θ and pairwise migration parameters were equal among populations (symmetrical gene flow). MIGRATE was run using maximum likelihood search parameters; 10 short chains (2000 out of 500,000 sampled trees), five long chains (10,000 out of 2,500,000 sampled trees), and five adaptively heated chains (start temperatures 1, 1.5, 3, 6 and 12; swapping interval = 1). Full models were run five times to ensure the convergence of parameter estimates. Restricted models were run once. Alternative models were evaluated for goodness-of-fit given the data using a log-likelihood ratio test (Beerli & Felsenstein, 2001). Mansel Island was not included in gene-flow estimates because of low sample size.

Contributions of refugial populations

Hierarchical analyses of molecular variance (AMOVA) were conducted in ARLEQUIN to test for significance of geographic partitioning of *a priori* hypothesized genetic units using microsatellite, nuclear intron and mtDNA loci. Populations were grouped to test: (1) the relative contributions of refugia in the post-glacial colonization of common eiders to sampled localities (models A–H), (2) geographic proximity (model I), (3) overwintering locales, which correspond to current subspecific designations (model J), and (4) partitioning among eiders that overwinter in the Atlantic versus Pacific oceans (model K; Table 1). We assumed that groupings that maximized among-group variation values (Φ_{CT}) and were significantly different from random distributions of individuals were the most probable geographic subdivisions.

Table 1 Hierarchical analysis of molecular variance of allelic and haplotypic frequencies to test hypotheses associated with (1) putative source refugia (models A–H); (2) geographic proximity (model I); (3) current subspecific classifications (model J); (4) partitioning among wintering areas in the Atlantic versus Pacific oceans (model K) for common eider (*Somateria mollissima*) populations breeding in North America and Scandinavia.

Φ	μsats – F_{ST}	GAPDH	LMNA	mtDNA
A [**SPL**, **MKB**, KTP] [ALN, YKD, SHP, HDS, **BCH**, BFN] [**NVS**, **NBW**] [**SVD**, SDK, TRM]				
Φ_{CT}	0.041	0.038	0.010	0.259
Φ_{SC}	0.030	0.048	0.065	0.367
Φ_{ST}	0.069	0.085	0.074	0.531
B [**SPL**, **MKB**] [ALN, YKD, KTP, SHP, HDS, **BCH**, BFN] [**NVS**, **NBW**] [**SVD**, SDK, TRM]				
Φ_{CT}	0.037	0.033	0.008	0.273
Φ_{SC}	0.033	0.053	0.067	0.364
Φ_{ST}	0.069	0.085	0.074	0.537
C [**SPL**, **MKB**] [ALN, YKD, KTP, SHP, HDS, **BCH**, BFN] [**NVS**, **NBW**, TRM] [**SVD**, SDK]				
Φ_{CT}	0.029	0.024	−0.002	0.284
Φ_{SC}	0.040	0.060	0.073	0.356
Φ_{ST}	0.067	0.082	0.071	0.540
D [**SPL**, **MKB**] [ALN, YKD, KTP, SHP, HDS, **BCH**, BFN, **NVS**, **NBW**] [**SVD**, SDK, TRM]				
Φ_{CT}	0.037	0.024	0.015	0.264
Φ_{SC}	0.037	0.063	0.064	0.396
Φ_{ST}	0.073	0.085	0.078	0.555
E [**SPL**, **MKB**] [ALN, YKD, KTP, SHP, HDS, **BCH**, BFN] [**NVS**, **NBW**, **SVD**, SDK, TRM]				
Φ_{CT}	0.030	0.027	−0.003	0.279
Φ_{SC}	0.040	0.058	0.074	0.369
Φ_{ST}	0.068	0.084	0.071	0.544
F [**SPL**, **MKB**] [ALN, YKD, KTP, SHP, HDS, **BCH**, BFN, **NVS**, **NBW**, TRM] [**SVD**, SDK]				
Φ_{CT}	0.025	0.011	0.009	0.296
Φ_{SC}	0.047	0.070	0.068	0.393
Φ_{ST}	0.070	0.081	0.076	0.573
G [**SPL**, **MKB**] [ALN, YKD, KTP, SHP, HDS, **BCH**, BFN, **NVS**, **NBW**, **SVD**, SDK, TRM]				
Φ_{CT}	0.017	0.010	−0.003	0.325
Φ_{SC}	0.053	0.072	0.073	0.417
Φ_{ST}	0.069	0.082	0.070	0.606
H [**SPL**, **MKB**, ALN, YKD, KTP] [SHP, HDS, **BCH**, BFN, **SVD**, SDK, TRM] [**NVS**, **NBW**]				
Φ_{CT}	0.027	0.102	0.077	0.209
Φ_{SC}	−0.001	0.008	0.022	0.410
Φ_{ST}	0.026	0.109	0.097	0.534
I [**SPL**, **MKB**, ALN, YKD] [KTP, SHP, HDS, **BCH**, BFN, **NVS**, **NBW**] [**SVD**, SDK, TRM]				
Φ_{CT}	0.059	0.068	0.046	0.179
Φ_{SC}	0.021	0.030	0.041	0.422
Φ_{ST}	0.079	0.095	0.085	0.519
J [**SPL**, **MKB**, ALN, YKD, KTP] [SHP, HDS, **BCH**, BFN, **SVD**] [**NVS**, **NBW**] [SDK, TRM]				
Φ_{CT}	0.078	0.092	0.052	0.166
Φ_{SC}	0.008	0.009	0.035	0.425
Φ_{ST}	0.084	0.100	0.085	0.520
K [**SPL**, **MKB**, ALN, YKD, KTP] [SHP, HDS, **BCH**, BFN, **NVS**, **NBW**, **SVD**, SDK, TRM]				
Φ_{CT}	0.078	0.106	0.062	0.232
Φ_{SC}	0.017	0.015	0.038	0.413
Φ_{ST}	0.094	0.120	0.098	0.549

Populations that exhibited a genetic signature consistent with Pleistocene glacial refugia are in bold text. Population abbreviations are defined in Fig. 1.

All variance measures are significant ($P < 0.01$). Variance measures: among groups (Φ_{CT}); among populations within groups (Φ_{SC}); within populations (Φ_{ST}).

GAPDH, intron 11 of glyceraldehyde-3-phosphate dehydrogenase; LMNA, intron 3 of lamin A; mtDNA, mitochondrial DNA control region.

RESULTS

Genetic diversity

The number of alleles at the 12 microsatellite loci ranged from 3 to 49, with an average of 13.8 alleles per locus. The allelic richness per population ranged from 2.4 to 3.0 (standardized to 3 individuals; Appendix S2). Observed heterozygosity ranged from 44.5% to 57.7% for each population, with an overall heterozygosity of 54.3% (Appendix S2). Comparisons of observed heterozygosity showed higher values in YK Delta, Simpson Lagoon and Mikkelsen Bay, though only Scandinavian populations had significantly lower observed heterozygosity based on non-overlapping 95% confidence intervals.

Seventy alleles were reconstructed for LMNA from 592 individuals in PHASE, and 48 alleles were reconstructed from 474 individuals for GAPDH (Appendices S2 & S3). Observed heterozygosity was 32.1–89.2% and 35.3–96.4% for LMNA and GAPDH, respectively. Haplotype (h) and nucleotide (π) diversities were 0.733–0.901 and 0.005–0.009, respectively, for LMNA, and 0.506–0.897 and 0.004–0.007, respectively, for GAPDH (Appendix S2). Diversity indices (h and π) were similar across populations for LMNA sequences. However, h estimated from GAPDH sequences was higher in YK Delta, Simpson Lagoon and Mikkelsen Bay populations, with Tromsø and Soderskar having lower h than most sampled populations based on 95% confidence intervals.

Sixty-four unique mtDNA haplotypes were identified from 456 individuals. Diversity indices were 0.230–1.000 and 0.001–0.009 for h and π, respectively (Appendix S2). The highest h estimates were observed for *S. m. borealis* populations, and the lowest for Nova Scotia and Soderskar populations. Low π estimates were observed for the Aleutians, Nova Scotia and Soderskar, with Kent Peninsula having the largest π observed.

Spatial genetic structure

Overall estimates of population subdivision were significant for each marker type evaluated (microsatellites, $F_{ST} = 0.060$,

R_{ST} = 0.020; LMNA Φ_{ST} = 0.072; GAPDH Φ_{ST} = 0.075; mtDNA Φ_{ST} = 0.497). The upper limit of F_{ST} for our microsatellite data set was 0.449. Therefore, the overall F_{ST} of 0.060 accounts for 13.4% of the maximum possible level of genetic structure. Moreover, inter-population comparisons showed moderate levels of genetic differentiation for nuclear markers (F_{ST} and R_{ST} or Φ_{ST} = 0.004–0.290; Appendix S4). Significant estimates of inter-population variance in microsatellite and nuclear intron allelic frequency primarily were observed among, but not within, subspecies. Moreover, estimates based on microsatellite data showed that F_{ST} was generally higher than R_{ST}. Out of the 105 pairwise comparisons, 11 comparisons had higher R_{ST} values than F_{ST}, with most of these comparisons (n = 5) between Soderskar and populations in Canada (Appendix S4). This is an indication of deeper, rather than shallow, differences (Rousset, 1996).

In contrast to nuclear loci, comparatively higher levels of inter-population variance in mtDNA haplotypic frequency were observed among most population pairs (Φ_{ST} = 0.051–0.927; Appendix S4). Few significant comparisons were observed among the eiders breeding in different Hudson Bay populations (Baffin Island, Hudson Straits, Southampton Island, Mansel Island and Belcher Islands). Populations that were disproportionately represented by haplotypes located at the tips of the haplotype network (Aleutian Islands, Simpson Lagoon, Mikkelsen Bay and Soderskar; Sonsthagen, 2006) exhibited very high levels of structuring among populations.

A positive correlation between genetic and geographic distances was observed across all marker types (microsatellites, F_{ST} r = 0.822, R_{ST} r = 0.655; LMNA r = 0.706; GAPDH r = 0.790; mtDNA r = 0.533; $P < 0.001$ for all), consistent with a stepwise colonization of Scandinavia and North America.

Delta K was maximized when K equalled 2 (ΔK = 1490.9, Pr|ln L = −24099.7) and the likelihood generated for the microsatellite data was maximized when K equalled 4 (ΔK = 136.0, Pr|ln L = −23921.1), as implemented in STRUCTURE. Individuals overwintering in the Pacific Ocean (*S. m. v-nigrum*) clustered together, with all other individuals grouped into a second cluster, based on the two-population model (Table 2). In the four-population model, individuals grouped loosely by overwintering areas and, as a result, subspecies classification (Table 2). Belcher Island individuals (*S. m. sedentaria*) clustered with birds that overwinter in eastern North America (*S. m. dresseri*), and populations that overwinter in the high latitudes of the Atlantic Ocean (*S. m. mollissima* and *S. m. borealis*) clustered together. Individuals that overwinter in the Pacific Ocean (*S. m. v-nigrum*) were subdivided into two clusters, perhaps driven by the inclusion of the Aleutian Island population, which is resident year-round (Table 2).

Table 2 Proportion of common eider (*Somateria mollissima*) individuals from sampled populations in each of the two and four clusters inferred from 12 microsatellite loci in STRUCTURE (Pritchard *et al.*, 2000), determined by Evanno *et al.* (2005) (K = 2) and the K that maximized the likelihood given the data (K = 4), respectively.

	Inferred clusters (K = 2)		Inferred clusters (K = 4)			
Populations	1	2	1	2	3	4
Somateria mollissima v-nigrum						
Aleutians	0.166	0.834	0.069	0.591	0.211	0.129
YK Delta	0.105	0.895	0.039	0.424	0.442	0.095
Simpson Lagoon	0.089	0.911	0.033	0.385	0.483	0.099
Mikkelsen Bay	0.089	0.911	0.039	0.411	0.470	0.080
Kent Peninsula	0.096	0.904	0.031	0.379	0.476	0.114
Somateria mollissima borealis						
Baffin	0.808	0.192	0.528	0.094	0.111	0.267
Hudson Straits	0.889	0.111	0.536	0.062	0.056	0.346
Southampton	0.891	0.109	0.617	0.068	0.047	0.269
Mansel Island	0.953	0.047	0.757	0.030	0.026	0.188
Svalbard	0.905	0.095	0.677	0.036	0.058	0.228
Somateria mollissima sedentaria						
Belcher	0.909	0.091	0.344	0.051	0.047	0.557
Somateria mollissima dresseri						
New Brunswick	0.850	0.150	0.159	0.072	0.049	0.721
Nova Scotia	0.818	0.182	0.172	0.062	0.058	0.708
Somateria mollissima mollissima						
Tromsø	0.965	0.035	0.867	0.022	0.021	0.090
Soderskar	0.973	0.027	0.916	0.016	0.016	0.052

Cells shaded in dark grey highlight cluster assignment of 50% or more and light grey shaded cells show that 20–49% of the individuals from any given population were assigned to a particular cluster.

Evidence for fluctuations in contemporary and historical population demography

Significant fluctuations in population demography were indicated based on all marker types. Inferences based on microsatellite loci showed that all populations except Mansel Island, Nova Scotia and New Brunswick have excess heterozygote deficiency, suggestive of population growth under the SMM (Table 3). Heterozygote deficiency was also observed under the TPM for three populations: Southampton Island, Tromsø and Soderskar (Table 3). Similarly to the microsatellite SMM results, most populations exhibited significant historical fluctuations in population demography based on nuclear intron sequences, except Mansel Island, Belcher Islands and Soderskar with LMNA, and Baffin Island, Hudson Straits, Svalbard, Tromsø and Soderskar with GAPDH (Table 3).

Historical population growth based on mtDNA sequence data was indicated for populations from the Aleutian Islands, YK Delta, Kent Peninsula, Baffin Island, Hudson Straits, Southampton Island, Mansel Island, Tromsø and Soderskar (Table 3; Fig. 1). Growth estimates for Belcher Islands, New Brunswick, Nova Scotia, Mikkelsen Bay, Simpson Lagoon and Svalbard were not significantly different from zero, consistent with a pattern of populations located in glacial refugia (Lessa *et al.*, 2004). Mismatch distributions failed to reject the sudden expansion model based on Harpending's raggedness index for most populations (Harpending, 1994) or based on the sum of

Table 3 Results of demographic analyses from common eider (*Somateria mollissima*) populations for 12 microsatellite (Msats) loci under the stepwise mutation model (SMM) and two-phased model of mutation (TPM), and sequence data.

	ALN	YKD	SPL	MKB	KTP	BFN	HDS	SHP	MSL	SVD	BLR	NBW	NVS	TRM	SDK
Msats*															
SSM	**HDef**	**HDef**	**HDef**	**HDef**	**HDef**	**HDef**	**HDef**	**HDef**	Eq	**HDef**	**HDef**	Eq	Eq	**HDef**	**HDef**
TPM	Eq	Eq	Eq	Eq	Eq	Eq	Eq	**HDef**	Eq	Eq	Eq	Eq	Eq	**HDef**	**HDef**
LMNA															
g	**327.0**	**550.8**	**800.5**	**589.9**	**442.6**	**2339.5**	**672.9**	**400.5**	373.3	**428.8**	352.3	**1130.7**	**562.2**	**464.0**	437.9
	(61.9)	(31.3)	(46.2)	(88.5)	(102.2)	(355.3)	(198.7)	(64.4)	(287.9)	(84.4)	(272.0)	(34.8)	(38.8)	(63.8)	(208.5)
θ	**0.033**	**0.122**	**0.138**	**0.039**	**0.044**	**0.045†**	**0.008**	**0.019**	0.010	**0.031**	**0.018†**	**0.530**	**0.100**	**0.025**	**0.009**
	(0.003)	(0.007)	(0.012)	(0.005)	(0.010)	(0.022)	(0.001)	(0.002)	(0.008)	(0.005)	(0.008)	(0.052)	(0.010)	(0.003)	(0.002)
GAPDH															
g	**1212.9**	**400.0**	**875.8**	**307.2†**	**1778.2**	53.8	−140.3	**283.5**	**4269.1**	242.9	**770.3**	**749.9**	**842.3**	−69.4	−127.1
	(91.3)	(50.8)	(66.6)	(144.0)	(182.9)	(260.5)	(155.1)	(101.0)	(0.1)	(178)	(208.7)	(161.1)	(178.6)	(171.4)	(156.8)
θ	**0.035**	**0.047**	**0.042**	**0.007**	**0.047**	0.004	**0.003†**	**0.011**	100.0	**0.007**	**0.009**	**0.009**	**0.015**	**0.003†**	**0.003†**
	(0.003)	(0.003)	(0.004)	(0.001)	(0.009)	(0.002)	(0.001)	(0.001)	(157.0)	(0.002)	(0.002)	(0.001)	(0.003)	(0.001)	(0.001)
MtDNA															
g	**3673.2**	**534.1**	133.9	16.8	**303.4**	**1203.8**	**850.7**	**788.0**	**6507.1**	260.9	254.9	132.9	102.1	**518.0†**	**1000.0**
	(272.7)	(71.4)	(123.8)	(86.0)	(65.4)	(230.6)	(132.2)	(161.9)	(298.4)	(137.3)	(257.2)	(120.0)	(247.6)	(174.2)	(2514.1)
θ	**0.012**	**0.023**	**0.007**	**0.007**	**0.021**	**0.017**	**0.050**	**0.034**	8.300	**0.010**	**0.006†**	**0.006**	**0.004**	**0.016**	0.008
	(0.001)	(0.002)	(0.001)	(0.001)	(0.003)	(0.005)	(0.014)	(0.006)	(3.600)	(0.002)	(0.002)	(0.001)	(0.001)	(0.005)	(0.005)

Parameter estimates, exponential growth rate (*g*) and θ ($4N_e\mu$ for nuclear DNA, $2N_f\mu$ for mtDNA) with standard deviation in parentheses. Significant estimates are in bold text. Population abbreviations are defined in Fig. 1.

*Significant heterozygote deficiency (HDef) indicates population growth; heterozygote excess (Hexc) indicates a population decline; non-significant population estimates indicate population equilibrium (Eq).

†Significant to $P < 0.05$, all others $P < 0.003$.

LMNA, intron 3 of lamin A; GAPDH, intron 11 of glyceraldehyde-3-phosphate dehydrogenase; mtDNA, mitochondrial DNA control region.

squared deviation statistic. Data for YK Delta, Kent Peninsula and New Brunswick deviated from the sudden expansion model, suggestive of a secondary contact zone.

Gene flow

Contemporary gene flow, as represented by microsatellite data, was moderate and there were no strong biases in immigration and emigration rates between population pairs (Table 4; Appendix S5). Number of migrants per generation (N_em) ranged from 0.15 to 2.79 (Table 4; Appendix S5). Larger biases in dispersal between populations were observed for estimates from nuclear intron data, with N_em ranging from 0.00 to 33.28 (Table 4; Appendix S5). Asymmetrical evolutionary dispersal was observed from Aleutian Islands into the YK Delta, Simpson Lagoon into Kent Peninsula, Baffin Island into Belcher Island, Hudson Straits into Tromsø, Southampton into Hudson Straits, Belcher Island and New Brunswick, Soderskar into Svalbard and Tromsø, and Tromsø into Baffin Island (Appendix S5). Differences in the directionality of gene-flow estimates between microsatellite and nuclear introns might be attributed to the deeper coalescence of introns (Hare, 2001). Gene-flow estimates from mtDNA sequence data were low between population pairs, with larger estimates observed among geographically close populations. Number of effective female migrants per generation (N_fm) ranged from 0.00 to 40.17 (Table 4; Appendix S5). Low levels of gene flow were observed among Alaskan populations, except between Simpson Lagoon and Mikkelsen Bay. Gene flow also appears to have occurred from Kent Peninsula into Hudson Straits, Svalbard into Baffin Island and Tromsø, New Brunswick into Hudson Straits, Southampton into Svalbard, and Soderskar into Svalbard.

Across all marker types, fully parameterized models had significantly higher ln likelihoods (ln *L*) than the restricted island model, indicating asymmetric gene flow among populations [msats ln *L* (test) = −10430.2, ln *L* (full) = −9873.6, d.f. = 196, $P < 0.001$; introns ln *L* (test) = −2094.3, ln *L* (full) = −930.6, d.f. = 196, $P < 0.001$; mtDNA ln *L* (test) = −5714.8, ln *L* (full) = 299.7, d.f. = 196, $P < 0.001$].

Contribution of refugial populations

Partitions in the nuclear genome appear concordant with overwintering areas and, therefore, to subspecific designations. Models J (microsatellites), H (LMNA) and K (GAPDH) maximized among-group variance in *a priori* tests of population subdivision (Table 1). In contrast, variance among groups in mtDNA haplotypic frequencies was more consistent with population genetic similarities when northern Alaskan (Simpson Lagoon and Mikkelsen Bay) populations were grouped together exclusively (model G; Table 1), indicating that the Aleutian Islands and YK Delta populations may be more genetically similar to Canadian populations. Among-group variance was also higher when Tromsø was grouped with New Brunswick and Nova Scotia (model C versus model

Table 4 Summary of total number of migrants per generation* (nuclear DNA N_em, mtDNA N_fm) and θ (nuclear DNA N_eμ, mtDNA N_fμ) for each common eider (*Somateria mollissima*) population calculated from 12 microsatellite loci, nuclear introns [intron 11 of glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and intron 3 of lamin A (LMNA)] and mtDNA control region sequence data.

	Microsatellites			Nuclear introns			Mitochondrial DNA		
Location	θ	Immigr.	Emigr.	θ	Immigr.	Emigr.	θ	Immigr.	Emigr.
Aleutians	0.987 (0.926, 1.054)	15.65	13.11	0.008 (0.007, 0.009)	11.27	19.68	0.003 (0.002, 0.004)	0.00	1.48
Yukon–Kuskokwim Delta	0.980 (0.932, 1.033)	15.27	15.02	0.010 (0.008, 0.011)	11.67	24.31	0.007 (0.005, 0.010)	0.00	1.18
Simpson Lagoon	0.948 (0.895, 1.005)	12.04	12.52	0.009 (0.008, 0.010)	21.95	21.96	0.005 (0.004, 0.007)	40.17	22.73
Mikkelsen Bay	0.945 (0.893, 1.002)	10.09	11.03	0.006 (0.005, 0.007)	30.30	26.46	0.003 (0.002, 0.005)	24.07	46.06
Kent Peninsula	0.991 (0.939, 1.047)	16.77	12.09	0.006 (0.005, 0.007)	23.61	8.92	0.004 (0.003, 0.007)	24.67	6.26
Baffin	1.068 (0.99, 1.154)	14.72	15.38	0.008 (0.006, 0.010)	20.56	21.20	0.013 (0.010, 0.018)	17.29	2.80
Hudson Straits	1.081 (1.009, 1.16)	19.59	13.61	0.004 (0.003, 0.005)	12.99	31.28	0.024 (0.013, 0.056)	6.66	37.04
Southampton	0.970 (0.909, 1.037)	18.05	12.72	0.008 (0.008, 0.009)	5.27	33.42	0.005 (0.003, 0.010)	30.32	7.66
Svalbard	0.985 (0.936, 1.037)	11.86	16.56	0.006 (0.005, 0.007)	37.46	13.95	0.012 (0.009, 0.016)	15.71	27.40
Belcher	0.959 (0.906, 1.017)	10.77	18.70	0.010 (0.008, 0.013)	21.27	12.83	0.005 (0.003, 0.013)	8.00	0.00
New Brunswick	0.936 (0.887, 0.989)	13.73	13.94	0.011 (0.009, 0.013)	31.77	24.99	0.003 (0.002, 0.004)	5.54	6.66
Nova Scotia	0.978 (0.927, 1.033)	14.61	13.74	0.008 (0.007, 0.011)	48.95	15.44	0.004 (0.003, 0.005)	1.43	5.54
Tromsø	0.982 (0.933, 1.036)	11.10	16.84	0.008 (0.006, 0.011)	59.62	9.82	0.010 (0.007, 0.016)	10.29	5.20
Soderskar	0.987 (0.926, 1.055)	13.66	12.65	0.005 (0.004, 0.006)	3.85	76.28	0.002 (0.002, 0.032)	0.00	14.14

*Immigration (Immigr.) refers to net number of effective migrations received by the population; emigration (Emigr.) refers to net number of effective migrants dispersing from the population.

B), indicating that Tromsø may be genetically more similar to eastern Canadian than to Scandinavian populations based on mtDNA. Interestingly, model J, which apportioned variance based on overwintering locales and corresponds to current subspecific designations, yielded the lowest among-group variance observed for estimates based on mtDNA (Table 1).

DISCUSSION

Refugial locations, suture zones and post-glacial colonization

Hypothesis testing based on AMOVA, coalescent analyses and spatial patterns observed in the allelic and haplotypic networks suggests that geographic genetic partitions in common eiders were influenced by Pleistocene events associated with glacial refugia. Concordance in allele and haplotype groups among nuclear microsatellites, introns and mtDNA loci suggest that common eiders were subdivided into at least two glacial refugia that existed for extended periods during the Pleistocene. The presence of a distinctive northern group in the nuclear (populations that overwinter in the Pacific Ocean) and mtDNA (northern Alaskan populations) data suggests a historical split into an Arctic refugium north-west of the continental ice sheets and subarctic refugia south of the ice sheets, a pattern identified for mammals by Nadler & Hoffmann (1977). The vicariant event that resulted in the divergence between northern and southern population groups appears to have been maintained through the Pleistocene, as few populations share similar haplotypes with the northern Alaskan populations.

Historical population demographic data estimated from mtDNA growth estimates are consistent with the restriction of common eiders to four glacial refugia during the LGM: Belcher Islands, New Brunswick and Nova Scotia, northern Alaska, and Svalbard. While three of these regions coincide with previously identified glacial refugia – Newfoundland Bank (New Brunswick and Nova Scotia), Beringia (northern Alaska), and Spitsbergen Bank (Svalbard; Ploeger, 1968; Fig. 1; Table 3) – the Belcher Islands were glaciated. Haplotypes currently representing Belcher Island are centrally located within the mtDNA network and therefore ancestral to the other haplotypes (Alsos *et al.*, 2005). As proposed for other Arctic vertebrates (Flagstad & Røed, 2003; Scribner *et al.*, 2003), the Belcher Island population may have derived from populations restricted south of the Laurentide ice sheet. These historical populations may have occupied habitats made available by the ice sheets retreating to their present-day location. Shorter movements from refugia to present-day locations would allow populations to retain genetic diversity because their effective population sizes would not be greatly reduced (Hewitt, 1996), especially if colonization occurred over a long period. Maintenance of genetic diversity while colonizing recently glaciated areas would, therefore, not be expected to produce a genetic signature of population expansion, because this signature assumes low levels of diversity in founder populations (Galbreath & Cook, 2004). Indeed, populations in formerly glaciated regions do not have significantly higher haplotype or lower nucleotide diversity than populations that currently occupy proposed refugial areas, as would be expected in a rapidly expanding population (Avise, 2000). Alternatively, the Belcher Island group may have been established by a founder event involving eiders that became non-migratory. Thus,

historical connections to other populations via common wintering groups may have been lost over comparatively few generations. This pattern, however, was not observed in the other non-migratory population of common eiders that resides in the Aleutian Islands.

The Svalbard refugium appears to have played a more substantial role in the colonization of glaciated areas in Canada and Scandinavia than in North American refugia. Evidence for ice-free areas in northern Norway during the LGM is controversial (Ploeger, 1968). However, eider fossils dating to *c.* 115,000 years ago have been identified from northern Norway (Lauritzen *et al.*, 1996). In addition, Tiedemann *et al.* (2004) examined the post-glacial colonization of Europe by common eiders, and hypothesized that Europe was colonized through range expansion from a single refugium located in southern Norway. This scenario is not inconsistent with our findings, although we are not able to compare our results directly. Our analyses suggest that Tromsø is more genetically similar to Canadian populations (models C and F; Table 1), providing a link between North American and Scandinavian populations. Of the North American refugia, the Newfoundland Bank populations shared haplotypes with most sites sampled, suggesting that this region was a source for colonizers during glacial retreats through both range expansion and long-distance colonization. Belcher Island haplotypes appear more restricted in their geographic range, and this region was not identified as a primary source of colonizers, as the directionality of gene flow was into Belcher Island from Baffin Island and Hudson Bay, suggestive of a northern source.

Despite the importance of Beringia to species' persistence during the Pleistocene (Rand, 1954; MacPherson, 1965), populations occupying northern Alaskan appear to have had minimal interaction with other eider populations (Fig. 2; Table 1; Appendix S5). Limited post-glacial colonization of unglaciated regions by Beringian populations has been observed in other Arctic vertebrates (*Lemmus* spp.; Fedorov *et al.*, 2003). The isolation of the shelf off the northern Alaskan refugium (northern Beringia; Ploeger, 1968) is exemplified by the low gene-flow estimates among other Pacific eider populations. Low dispersal estimates from the Beringian refugium to southern Alaska could be attributed to the longer persistence of the Laurentide ice sheet relative to the Cordilleran ice sheet (Westgate *et al.*, 1987), thus inhibiting colonization of south-west Alaska by common eiders occupying a northern Beringian refugium. In addition, Beringia extended across the current location of the Bering Sea, the Pacific eider's overwintering site, until *c.* 10,000 years ago (Hewitt, 2004b). The presence of the Beringian land mass may have further isolated the northern Alaskan populations from southern Alaska, as common eiders migrate primarily along coastal routes on winter migration and are rarely observed inland (Goudie *et al.*, 2000).

Expansion and subsequent contact of eiders from different refugia after the LGM coincides with contact zones of several other Arctic vertebrates. Two populations, Kent Peninsula and YK Delta, did not fit the sudden expansion model, and may represent a region of contact between Arctic and subarctic haplotype groups. These populations coincide with known

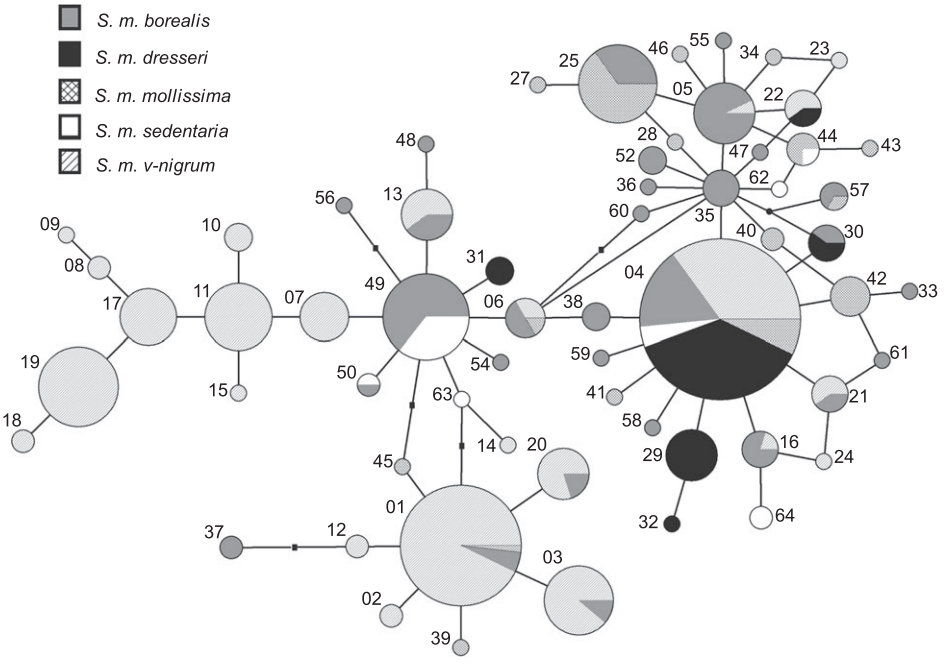

Figure 2 Unrooted 95% parsimony network illustrating relationships of 64 mtDNA control region haplotypes from common eiders (*Somateria mollissima*), with the size of the circle node corresponding to the frequency of each haplotype (numbered). Small black squares indicate intermediate ancestral haplotypes that were not sampled.

suture zones: MacKenzie River (e.g. *Dicrostonyx* spp., Fedorov & Stenseth, 2002; *Lemmus* spp., Fedorov *et al.*, 2003; *Lagopus mutus*, Holder *et al.*, 1999, 2000) and western Alaska/Aleutians (e.g. *Calidris alpina*, Wenink *et al.*, 1996; *L. mutus*, Holder *et al.*, 1999, 2000). In addition, shared haplotypes from Canadian and Scandinavian refugia suggest that Tromsø may have been a contact zone for common eiders. Northern Scandinavia has been identified as a contact zone for other vertebrates (*Microtus agrestis*, Jaarola & Searle, 2002; *Microtus oeconomus*, Brunhoff *et al.*, 2003; *Lemmus* spp., Fedorov *et al.*, 2003). Concordance of contact zones in other Arctic vertebrates in the MacKenzie River, western Alaska and Scandinavian ice cap suggests that these regions represented strong geographic barriers limiting dispersal from Pleistocene refugia and, in the case of Alaska, from Beringia.

Population subdivision

Common eider populations exhibit spatial variance in allelic and haplotypic frequencies across all marker types assayed in this study. Low to moderate levels of spatial genetic structuring observed for nuclear markers are consistent with common eider biology and subspecific designations. Pair formation occurs in coastal waters during non-breeding months, where admixture of several breeding populations occurs. Populations representing subspecies winter in different locations (Ploeger, 1968; Goudie *et al.*, 2000), which may maintain subspecies limits. Limited genetic subdivision observed among populations that share wintering grounds is consistent with observations that males are dispersing among populations (Ploeger, 1968; Tiedemann & Noer, 1998; Petersen & Flint, 2002), contributing to similarities in allelic frequencies in the nuclear genome. Maintenance of differences in wintering locations for eiders suggests some degree of winter site fidelity (Robertson & Cooke, 1999), which has probably been maintained through evolutionary time, allowing for the accumulation of genetic differences among populations representing different subspecies.

Pacific eider populations appear to be differentiated from populations representing the other subspecies, as genetic partitions were observed among *S. m. v-nigrum* and other subspecies at nuclear loci and between northern Alaskan populations and all other populations based on mtDNA. The vicariance between Atlantic and Pacific wintering eiders provides further evidence for the importance of Beringia and the Pacific Basin as a reservoir of genetic variation and speciation for Arctic species (Rand, 1954; MacPherson, 1965; Livezey, 1995). Genetic partitioning among Canadian and Scandinavian subspecies, however, was not as well resolved. Admixture among populations representing Canadian and Scandinavian subspecies may have resulted from the colonization by the same glacial refugia and/or contemporary gene flow among populations. Vagrancy in common eider migration has been reported (Goudie *et al.*, 2000), with *S. m. v-nigrum* individuals collected in Minnesota (Dickerman & Lee, 1961). In addition, an *S. m. borealis* male was collected from Point Barrow, Alaska during autumn migration (7 August 1994, UAM6631). Furthermore, in areas where subspecies distributions overlap, individuals may winter in areas that are geographically closer and intermix with members of other subspecies, rather than migrating further to winter with populations of the same subspecies (Tiedemann *et al.*, 2004). Occasional male dispersal among populations that do not normally share wintering grounds may provide enough gene flow among wintering areas to limit the accumulation of genetic differences among subspecies and populations.

High spatial genetic structure assayed for mtDNA control region support banding data, which clearly indicate that female common eiders exhibit natal and breeding philopatry throughout their range (Goudie *et al.*, 2000). However, in contrast to microgeographic population subdivision assayed between northern Alaskan populations (*c.* 90 km apart) and between eastern Canada populations (*c.* 200 km apart), few significant inter-population comparisons were observed among Hudson Bay populations (*S. m. borealis* and *S. m. sedentaria*). Female dispersal among Hudson Bay populations would be expected to minimize variation in mtDNA haplotypic frequencies. Researchers have hypothesized that, given the availability of suitable habitat, first-time female breeders may breed near their wintering grounds rather than returning to natal sites (Tiedemann *et al.*, 2004). However, high levels of inter-female relatedness have been documented among Southampton Island females of all ages that arrive concurrently at nesting sites (McKinnon *et al.*, 2006), suggesting a high degree of philopatry and retention of female kin associations throughout the year. Alternatively, Hudson Bay populations may have been colonized recently from the same glacial refugium. Given significant positive growth rates observed at nuclear and mtDNA markers, except for Belcher Islands, Hudson Bay populations may not have had sufficient time for genetic partitions to evolve among populations.

Alternatively, the comparatively higher levels of population subdivision observed in mtDNA, relative to nuclear DNA, could be attributed to lineage sorting. MtDNA has a lower effective population size relative to nuclear DNA (Avise, 2004). Therefore, when mutation rate and selection are held constant, genetic drift has a larger effect on mtDNA than nuclear DNA (Avise, 2004), translating to higher estimates of population subdivision (Φ_{ST} relative to F_{ST}). Over half of the pairwise inter-population comparisons (62%, $n = 65/105$) had lower than expected F_{ST} values at microsatellite loci, after accounting for differences in the effective population size between genomes (Zink & Barrowclough, 2008) and maximum possible F_{ST} value. In these instances, male-mediated gene flow and incomplete lineage sorting may be playing a role in the lower F_{ST} estimates observed for nuclear microsatellite loci. The effects of lineage sorting and sex-biased differences in philopatry on spatial genetic subdivision, however, are not mutually exclusive, and both factors may have played a role in the degree of population structure observed. Given differences in the degree of philopatry in common eiders between the sexes and congruence in results between microsatellite and nuclear

intron loci, we suggest that differences in estimates of population subdivision are more attributable to male dispersal and high philopatry in females, than to lineage sorting for sampled populations.

CONCLUSIONS

Concordance of proposed glacial refugia occupied by common eiders with other Arctic species indicate that Arctic and subarctic refugia north-west and south-east of the ice-sheets, respectively, were important reservoirs of genetic diversity during the Pleistocene. Despite the importance of the Beringian refugium during the Pleistocene as a reservoir of genetic diversity for Arctic taxa, the presence of a strong barrier to dispersal was maintained through evolutionary time, limiting post-glacial colonization to the rest of North America.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Localities and years sampled of common eider populations assayed in this study.

Appendix S2 Indices of genetic diversity for common eider populations assayed from microsatellite loci, nuclear gene introns and mitochondrial DNA control region.

Appendix S3 PHASE results for nuclear gene introns sequenced from common eiders.

Appendix S4 Inter-population comparisons of genetic differentiation estimated among common eider populations.

Appendix S5 Pairwise gene-flow estimates among common eider populations.

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BIOSKETCH

This manuscript represents a portion of Sarah A. Sonsthagen's PhD research at the University of Alaska Fairbanks. Currently, she is studying population genetics and microevolutionary processes, focusing on Arctic avian species, at the US Geological Survey.

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