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GENETIC CHARACTERIZATION OF COMMON EIDERS BREEDING IN THE YUKON-KUSKOKWIM DELTA, ALASKA

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Abstract. We assessed population genetic subdivision among four colonies of Common Eiders (*Somateria mollissima v-nigrum*) breeding in the Yukon-Kuskokwim Delta (YKD), Alaska, using microsatellite genotypes and DNA sequences with differing modes of inheritance. Significant, albeit low, levels of genetic differentiation were observed between mainland populations and Kigigak Island for nuclear intron *lamin* A and mitochondrial DNA (mtDNA) control region. Intercolony variation in haplotypic frequencies also was observed at mtDNA. Positive growth signatures assayed from microsatellites, nuclear introns, and mtDNA indicate recent colonization of the YKD, and may explain the low levels of structuring observed. Gene flow estimates based on microsatellites, nuclear introns, and mtDNA suggest asymmetrical gene flow between mainland colonies and Kigigak Island, with more individuals on average dispersing from mainland populations to Kigigak Island than vice versa. The directionality of gene flow observed may be explained by the colonization of the YKD from northern glacial refugia or by YKD metapopulation dynamics.

Key words: Common Eider, gene flow, population genetic structure, Somateria mollissima.

Caracterización Genética de Individuos de *Somateria mollissima* que se Reproducen en el Delta de Yukon-Kuskokwim, Alaska

Resumen. Se evaluó la subdivisión genética poblacional en cuatro colonias de *Somateria mollissima v-nigrum* que se reproducen en el delta del río Yukon-Kuskokwim (DYK), Alaska, mediante el uso de microsatélites y secuencias de ADN, marcadores que presentan patrones de herencia diferentes. Se observaron niveles significativos, aunque bajos, de diferenciación genética entre las poblaciones del continente y la de la isla Kigigak para el intrón nuclear *lamin* A y para la región de control mitocondrial (ADNmt). También se observó variación en las frecuencias de haplotipos de ADNmt entre las colonias. La evidencia de crecimiento positivo obtenida a partir de microsatélites, intrones nucleares y ADNmt indican colonización reciente del DYK y podrían explicar los bajos niveles de estructura poblacional observados. Las estimaciones de flujo génico con base en microsatélites, intrones nucleares y ADNmt sugieren flujo génico asimétrico entre las poblaciones continentales y la población de la Isla Kigigak, con más individuos dispersándose de las poblaciones del continente a la de la isla Kigigak, que viceversa. La dirección del flujo génico observada podría atribuirse a la colonización del DYK desde un refugio glaciar ubicado al norte, o a la dinámica metapoblacional en el DYK.

INTRODUCTION

Natal, breeding, and winter site fidelity can leave varying signatures in molecular markers. For example, in a population in which females exhibit high natal and breeding philopatry and males disperse among populations, spatial genetic structuring is expected at maternally inherited markers, with little or no population subdivision at biparentally inherited markers. Studies that characterize populations using data from only one genome (nuclear or mtDNA) might grossly over- or underestimate levels of spatial genetic structure among populations, depending on the marker type used (Avise 2004). Therefore, researchers examining spatial genetic structure among populations should employ a suite of molecular markers that differ in their mode of inheritance to ask a wider

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range of questions involving species population genetic structure and behavior.

Pacific Common Eiders (*Somateria mollissima v-nigrum*) breed along coastal waters of the Beaufort, Bering, and Chukchi Seas (Goudie et al. 2000). Females of this species exhibit high levels of natal and breeding philopatry (Wakely and Mendall 1976, Swennen 1990, Bustnes and Erikstad 1993, Goudie et al. 2000), which may create genetically distinct breeding populations. Pair formation occurs on the wintering grounds (Spurr and Milne 1976), where several populations of Common Eiders likely intermix. Male Common Eiders accompany females back to breeding sites; therefore, males may exhibit large natal and breeding dispersal distances (0–1270 km; Swennen 1990). Male-biased dispersal among breeding colonies likely homogenizes allelic frequencies of genes within the nuclear genome (Scribner et al. 2001) among populations that share wintering grounds.

The Common Eider population breeding in the Yukon-Kuskokwim Delta (YKD), Alaska, is composed of partial migrants; some individuals winter along the coast of the YKD, whereas others winter in the nearshore waters of Bristol Bay, 325 km south of the YKD (Petersen and Flint 2002). Numbers of Common Eiders breeding in the YKD have declined >90% in the past 40 years (Stehn et al. 1993). While the reason for this decline is unknown, other populations of eiders wintering in the Bering Sea also have exhibited population declines; these include Common Eiders (Suydam et al. 2000), King Eiders (*S. spectabilis*; Dickson et al. 1997, Suydam et al. 2000), Spectacled Eiders (*S. fischeri*; Stehn et al. 1993, Ely et al. 1994), and Steller's Eiders (*Polysticta stelleri*; Kertell 1991). Satellite telemetry data indicate that birds breeding in the YKD may be relatively isolated from other eiders breeding in Alaska. Only 6% (two of 36) of females studied on the Beaufort Sea, Alaska, used the same wintering area as YKD eiders (Petersen and Flint 2002). Common Eiders breeding on the Aleutian Islands are believed to be residents (Goudie et al. 2000), and, therefore, likely do not intermix with individuals from the YKD. With limited contact with other breeding Common Eider populations, the YKD population may be genetically distinct from other populations in Alaska. However, two females from the Beaufort Sea wintered in the same area as females from the YKD and potentially formed pair bonds with male YKD birds (Petersen and Flint 2002); male dispersal may provide an avenue for sex-biased gene flow between these regions.

Microgeographic population genetic structure has been observed in other populations of Common Eiders. Among European Common Eider (*S. m. mollissima*) breeding colonies in the Baltic Sea (133–1010 km apart), high levels of spatial population genetic structuring were observed for mitochondrial DNA (mtDNA $\Phi_{ST} = 0.262–0.343$, $P < 0.001$), and significant, but lower, levels were found for biparentally inherited microsatellite loci ($F_{ST} = 0.009–0.029$, $P < 0.05$; Tiedemann et al. 1999). Pacific Common Eiders breeding on 12 barrier islands (1–143 km apart) in the Beaufort Sea, Alaska, exhibited spatial structure at mtDNA and nuclear DNA (mtDNA $\Phi_{ST} = 0.135–0.271$, $P < 0.05$; nuclear DNA $\Phi_{ST} = 0.089–0.173$, $P < 0.05$; Sonsthagen 2006; see also McCracken et al. 2006). Population genetic structure observed for maternally inherited mtDNA was attributed to the high levels of natal and breeding philopatry of female Common Eiders. Lower levels of population structure observed at biparentally inherited markers were attributed to nonrandom mating by males on the wintering grounds (i.e., males mate with females from the same locality more often than expected; Tiedemann et al. 1999).

We assessed population genetic structure of Common Eider colonies breeding in the YKD using three types of molecular markers with different modes of inheritance and rates of mutation: biparentally inherited microsatellite genotypes and sequence information from maternally inherited mtDNA control region and two biparentally inherited nuclear introns. Microsatellite and mtDNA loci have been extensively used to examine genetic discordance at fine spatial scales among waterfowl populations (Lanctot et al. 1999, Tiedemann et al. 1999, Scribner et al. 2001, 2003, Pearce et al. 2004, 2005, Sonsthagen 2006). Analyzing markers with varying rates of mutation may provide insight into population demography through evolutionary time, with microsatellite data reflecting more recent processes and mtDNA and nuclear intron data reflecting more historical processes (Hare 2001). We hypothesized that the nuclear markers (micro-

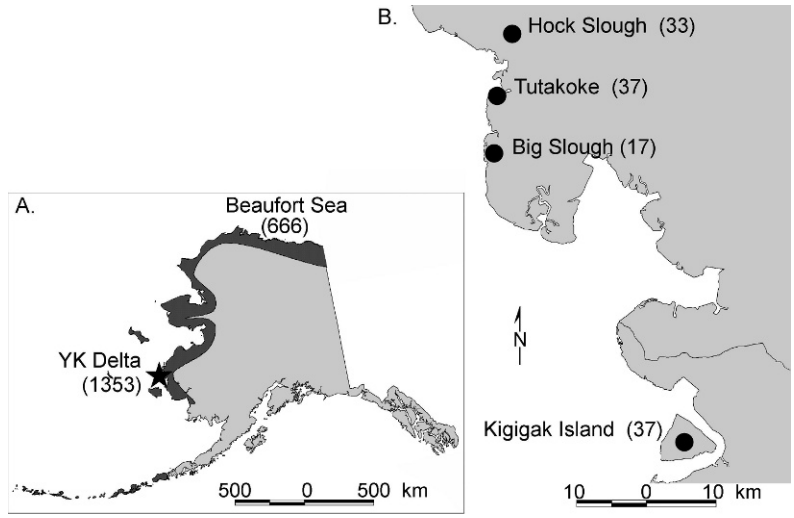

FIGURE 1. (A) Shaded area indicates breeding distribution of Common Eiders in Alaska with labeled locations of Yukon-Kuskokwim Delta (YKD) and Beaufort Sea populations, and estimated number of nests located within each region in parentheses (YKD: Stehn et al. 1993; Beaufort Sea: Noel et al. 2005). Star indicates area enlarged in Figure 1B. (B) Locations of breeding colonies of Common Eiders in the Yukon-Kuskokwim Delta, with sample sizes of females analyzed for this study in parentheses.

satellites and intron sequences) would show little population genetic structure, as Common Eiders breeding in the YKD intermix with other populations of Common Eiders on the wintering grounds. Male-mediated dispersal among YKD colonies could, over time, homogenize allelic frequencies within the nuclear genome. In contrast, we predicted that population subdivision would be observed at maternally inherited mtDNA among YKD colonies because of the philopatric nature of female Common Eiders and the fine-scale spatial genetic differentiation observed for eiders breeding in the Beaufort Sea, Alaska.

METHODS

SAMPLE COLLECTION

Blood samples from adult breeding females ($n = 125$) were collected opportunistically through mark-recapture efforts in the YKD from 1997 to 2002 at four sites: Hock Slough, Tutakoke, Big Slough, and Kigigak Island (8.9–63.4 km apart; Fig. 1B). Samples were stored in blood preservation buffer (Longmire et al. 1988) and archived at -80°C at the Molecular Ecology Laboratory, U.S. Geological Survey, Anchorage, Alaska. Total genomic DNA was extracted using the "salting out" procedure described by Medrano et al. (1990), with modifications described by Sonsthagen et al. (2004). Genomic DNA concentrations were quantified using fluorometry and diluted to 50 ng μL^{-1} working solutions.

MICROSATELLITE GENOTYPING

Initially, twelve individuals were screened at 50 microsatellite loci known to be variable in populations of Common Eiders in Europe and in other waterfowl species, and 14 polymorphic loci with dinucleotide repeat motifs were selected for further analysis: *Aph*02, *Aph*08, *Aph*20, *Aph*23 (Maak et al. 2003); *Bca*1, *Bca*11, *Hhi*3 (Buchholz et al. 1998); *Cm*09 (Maak et al. 2000); *Sfi*μ10 (S. Libants et al., Michigan State University, unpubl. data); and *Smo*4, *Smo*7, *Smo*08, *Smo*10, and *Smo*12 (Paulus and Tiedemann 2003). Fluorescently labeled PCR products were electrophoresed following protocols described by Sonsthagen et al. (2004) for tailed primers (*Aph*02, *Aph*08, *Aph*20, *Aph*23, *Cm*09, *Smo*4, *Smo*7, *Smo*08, *Smo*10, and *Smo*12) and following Pearce et al. (2005) for direct-labeled primers (*Bca*1, *Bca*11, *Hhi*3, and *Sfi*μ10). Ten percent of the samples were reamplified and genotyped in duplicate for the 14 loci for quality control.

MTDNA AND NUCLEAR INTRON SEQUENCING

We amplified a 545 base pair (bp) portion of the control region domain I and II (Baker and Marshall 1996) using primer pairs L263 (5′–CCAAATYGCACRYCTGACAYTCCAAGC–3′) and H848 (5′–GCCCCATTATRTAGGAGCTGCGG–3′), approximately corresponding to positions 263 and 848 in the chicken mtDNA genome (Desjardins and Morais 1990). PCR amplifications were carried out in a 50 µL volume; 2–100 ng genomic DNA, 0.5 µM each primer, 1.0 µM dNTPs, 1X PCR buffer (Fisher Scientific, Pittsburgh, Pennsylvania), 2.5 µM $MgCl_2$, and 0.2 units Taq Polymerase (Fisher Scientific). PCR reactions began with 94°C for 7 min followed by 45 cycles of 94°C for 20 sec, 60°C for 20 sec, and 72°C for 1 min, with a 7 min final extension at 72°C. PCR products were gel-purified using a QIAquick Gel Extraction Kit (QIAGEN, Valencia, California), and both strands were sequenced using ABI's BigDye v.3 Terminator Cycle Sequencing Kit diluted four-fold on an ABI 3100 DNA sequencer (Applied Biosystems, Foster City, California). Sequences from opposite strands were reconciled using Sequencher 4.1.2 (Gene Codes Corporation, Ann Arbor, Michigan). Individuals containing double peaks within mtDNA sequence data were resequenced. If polymorphisms were still detected, these individuals were removed (~10%) because of the high number of nuclear pseudogenes present in this species (Tiedemann and Kistowski 1998; SAS, unpubl. data) or heteroplasmy. Sequences are deposited in GenBank (accession numbers EU019593–EU019601).

Six nuclear introns were screened for polymorphism in Common Eiders: beta-fibrinogin (*bf*) intron 7 (BF7F2 5′–GTTAGCATTATGAACTGCAAGTAATTG–3′; BF7R2 5′–TTTCTTGAATCTGTAGTTAACCTGATG–3′; M. D. Sorenson, Boston University, unpubl. data), *lamin* A intron 3 (McCracken and Sorenson 2005), chromosome *Z* chromo-ATPase helicase DNA binding protein (*chd-Z*; McCracken and Sorenson 2005), chromosome *W* chromo-helicase binding protein (*chd*1-*W*; Fridolfsson and Ellegren 1999), glyceraldehyde-3-phosphate dehydrogenase (*gapdh*) intron 11 (McCracken and Sorenson 2005), and ornithine carboxylase (*od*) intron 7 (OD7F 5′–TCGTTCAAGCCATTTCTGATGCC–3′; OD8R 5′–CCAGGRAAGCCACCAATRTC–3′; KGM and M. Sorenson, unpubl. data). The *bf*7, *od*7, *chd-Z* and *chd*1-*W* introns showed very little variation within Common Eiders, with only 1–2 polymorphic sites in ten individuals. Two of the introns, *gapdh* (386–387 bp) and *lamin* A (280 bp) showed high levels of polymorphism and were sequenced using techniques described above with some modifications. PCR amplifications of the introns were carried out in a 50 µL volume; 2–100 ng genomic DNA, 0.5 µM each primer, and 25 µL AmpliTaq Gold PCR Master Mix (Applied Biosystems, Foster City, California). PCR reactions began with 94°C for 7 min followed by 45 cycles each of 94°C for 20 sec, 64°C for 20 sec, and 72°C for 1 min, with a 7 min final extension at 72°C. Only sequences from the forward strand were collected on an ABI 3100 DNA sequencer because the PCR templates were short (280–387 bp) and sequences had a consistent peak height throughout the length of the fragment. Sequences that contained double peaks of approximately equal peak height, indicating the presence of two alleles, were coded with International Union of Pure and Applied Chemistry (IUPAC) degeneracy codes and treated as polymorphisms (Kulikova et al. 2004). Several sequences for *gapdh* contained a single recurring one bp insertion or deletion. To obtain data from the entire fragment for individuals that were heterozygous (~66%) for these alleles, we also sequenced the reverse strand. Sequences are deposited in GenBank (accession numbers EU019602–EU019692).

STATISTICAL ANALYSES

Estimation of genetic diversity. Allelic phases of nuclear introns *lamin* A and *gapdh* were inferred from diploid sequence data using PHASE 2.0 (Stephens et al. 2001). PHASE uses a Bayesian approach to reconstruct haplotypes from population genotypic data and allows for recombination and the decay of linkage disequilibrium with distance. The PHASE analysis (1000 iterations with a 1000 burn-in period) was repeated three times to ensure consistency across runs.

We calculated allelic frequencies, inbreeding coefficient (F_{IS}), and expected and observed heterozygosities for each microsatellite locus, mtDNA, and the two nuclear introns in GENEPOP 3.1 (Raymond and Rousset 1995) and FSTAT 2.9.3 (Goudet 1995, 2001). Hardy-

Weinberg equilibrium and linkage disequilibrium were tested in GENEPOP (Markov chain parameters: dememorization number 1000, number of batches 100, and number of iterations per batch 10 000), adjusting for multiple comparisons using Bonferroni corrections (α = 0.05).

Estimation of population demography. Evidence for historical fluctuations in population demography was evaluated for 14 microsatellite loci using BOTTLENECK 1.2.02 (Cornuet and Luikart 1996) and for sequence data using FLUCTUATE 1.4 (Kuhner et al. 1995). BOTTLENECK compares the number of alleles and gene diversity at polymorphic loci under the infinite allele model (IAM; Maruyama and Fuerst 1985), stepwise mutation model (SMM; Ohta and Kimura 1973), and two-phased model of mutation (TPM; Di Rienzo et al. 1994). Parameters for the TPM were set at 79% SMM with a variance of 9% (Piry et al. 1999, Garza and Williamson 2001), with 1000 simulations performed for each population. Significance was assessed using a Wilcoxon sign-rank test, which determines if the average of standardized differences between observed and expected heterozygosities is significantly different from zero (Cornuet and Luikart 1996). Significant heterozygote deficiency values relative to the number of alleles indicate recent population growth, whereas heterozygote excess relative to the number of alleles indicates a recent population bottleneck (Cornuet and Luikart 1996, Luikart 1997). It is important to note that heterozygote deficiency and excess calculated in BOTTLENECK differ from values calculated in other population genetic programs. As mentioned previously, BOTTLENECK compares heterozygote deficiency and excess relative to genetic diversity, not to Hardy-Weinberg equilibrium expectation (Cornuet and Luikart 1996). FLUCTUATE was run using maximum likelihood search parameters: ten short chains (200 trees used out of 4000 sampled) and three long chains (20 000 trees used out of 400 000 sampled). Nuclear intron alleles were treated as one common pool for each of the populations and data were analyzed three times to ensure convergence of parameters across runs. Sequence data were tested for selective neutrality and historical fluctuations in population demography using Fu's *Fs* (Fu 1997) and Tajima's *D* (Tajima 1989) in ARLEQUIN. For critical significance, alpha values of 0.05 require a *P*-value below 0.02 for Fu's *Fs* (Fu 1997). Unrooted phylogenetic trees for each gene were constructed in TCS 1.21 (Clement et al. 2000), which estimates genealogies using 95% statistical parsimony probabilities (Templeton et al. 1992). *Lamin* A and *gapdh* intron sequences were analyzed in NETWORK 4.1.0.8 (Fluxus Technology Ltd. 2004) using the Median Joining network (Bandelt et al. 1999), to illustrate possible reticulations in the gene trees because of homoplasy or recombination.

Estimation of population subdivision. To assess levels of population subdivision among sampled sites, pairwise F_{ST}, R_{ST}, Φ_{ST}, global *F*-statistics, and *R*-statistics were calculated in FSTAT version 2.9.3 (Goudet 1995, 2001) or ARLEQUIN 2.0 (Schneider et al. 2000), adjusting for multiple comparisons using Bonferroni corrections (α = 0.05) or permutations (3000) in FSTAT and ARLEQUIN, respectively. Interhaplotypic and interallelic sequence divergences were used to calculate pairwise Φ_{ST} (Excoffier et al. 1992), and nuclear intron alleles were paired by individual. MODELTEST 3.06 (Posada and Crandall 1998) was used to determine the minimum parameter nucleotide substitution model that best fit the mtDNA and intron sequence data under Akaike's information criterion (Akaike 1974). Pairwise genetic distances between unique haplotypes and alleles were calculated in PAUP* 4.0 (Swofford 1998) for mtDNA and in ARLEQUIN for nuclear introns. Additionally, pairwise comparisons were performed using ARLEQUIN to determine the magnitude of spatial variance in haplotypic and allelic frequencies between mainland and island colonies. The mainland group was composed of Hock Slough, Tutakoke, and Big Slough, and the island group was composed of Kigigak Island. An isolation-by-distance analysis was performed in IBD: Isolation by Distance v. 1.52 (Bohonak 2002) with microsatellite data and nuclear intron data using genotypic data inferred from the PHASE analysis, to determine if more geographically distant population pairs were also more genetically differentiated. IBD tests the statistical significance of the relationship between genetic and geographic distance using a Mantel test.

Finally, microsatellite data were analyzed in STRUCTURE 2.1 (Pritchard et al. 2000) to

detect the occurrence of population structure without a priori knowledge of putative populations. Data were analyzed using an admixture model assuming correlated frequencies to probabilistically assign individuals to putative populations with a burnin period of 10 000 iterations, 100 000 Markov chain Monte Carlo iterations, and number of possible populations (K) ranging from one to ten; this analysis was repeated five times to ensure consistency across runs.

Estimation of gene flow. Number of migrants per generation ($N_e m$) for nuclear microsatellites and nuclear introns or number of female migrants per generation ($N_f m$) for mtDNA were calculated in MIGRATE v. 2.0.6 (Beerli 1998, 2002, Beerli and Felsenstein 1999) among sampled sites. Nuclear intron alleles were treated as one common pool for each of the populations. Full models, θ ($4N_e\mu$ or $N_f\mu$, composite measure of effective population size and mutation rate), and all pairwise migration parameters were estimated individually from the data and were compared to a restricted island model for which θ was averaged and pairwise migration parameters were symmetrical between populations.

MIGRATE was run using maximum likelihood search parameters; ten short chains (1000 trees used out of 20 000 sampled), five long chains (10 000 trees used out 200 000 sampled), and five adaptively heated chains (start temperatures: 1, 1.5, 3, 6, and 12; swapping interval = 1). Full models were run three times to ensure the convergence of parameter estimates. Restricted models were run once. The alternative model was evaluated for goodness-of-fit given the data using a log-likelihood ratio test. The resulting statistic from the log-likelihood ratio test is equivalent to a χ^2 distribution with the degrees of freedom equal to the difference in the number of parameters estimated in the two models (Beerli and Felsenstein 2001).

RESULTS

GENETIC DIVERSITY

Biparentally inherited nuclear microsatellites. Multilocus genotypes from 14 microsatellite loci were collected for 125 individuals sampled in the YKD. Most of the microsatellite loci (79%) appeared to conform to the stepwise mutation model (SMM); three loci (*Smo*04, *Smo*07, and *Smo*12) had at least one allele that had a length change different from the repeat unit (one bp difference). Number of alleles per locus ranged from two to 38, with an average of 9.9 alleles per locus. The average number of alleles per population ranged from 5.6 to 7.6. The observed heterozygosity ranged from 17% to 96% for each population, with an overall observed heterozygosity of 58%. The inbreeding coefficient (F_{IS}) ranged from -0.328 to 0.662 across sampled sites, with an overall mean of 0.032. None of the inbreeding coefficients were significantly different from zero ($P > 0.05$). Significant fluctuations in population demography were detected by BOTTLENECK (Table 1). Heterozygote deficiency was observed under the SMM in Kigigak, Hock Slough, and Tutakoke colonies, and the overall YKD estimate suggested recent population growth in the past several generations (Table 1). However, Tutakoke and overall YKD estimates also had significant heterozygote excess under the infinite allele model (IAM), suggesting a recent population bottleneck (Table 1).

Biparentally inherited nuclear introns. PHASE reconstructed 31 unique alleles from 107 individuals for *lamin* A (Fig. 2A). Forty-seven (44%) individuals were homozygous at all variable sites, and 26 (24%) were polymorphic at one site. Probabilities of reconstructed haplotypes ranged from 0.82 to 1.00, except for five individuals that had probabilities ranging from 0.50 to 0.73. PHASE calculated the background recombination rate (ρ) as 0.50, with factors exceeding ρ ranging from 0.58 to 1.94 among 16 variable sites.

Twenty-one unique alleles for 85 individuals were reconstructed by PHASE for *gapdh* (Fig. 2B). Seven (8%) individuals were homozygous at all variable sites, and two (2%) individuals were polymorphic at only one site. Probabilities of reconstructed haplotypes ranged from 0.82 to 1.00, except for 14 individuals that had probabilities ranging from 0.50 to 0.76, which we attribute to potentially high levels of recombination occurring within this sequence (0.39–4.41 factors exceeded $\rho = 0.05$, among 15 variable sites) and autapomorphies (single novel polymorphisms occurring on one allele in one individual). There were seven variable sites that exceeded ρ by one or more factors: 2.12 factors between sites 16 and 22, 1.42 factors between sites 22 and 26, 1.12

TABLE 1. Analysis of historical fluctuations in population demography of Common Eiders breeding in the Yukon-Kuskokwim Delta (YKD), Alaska, assayed from 14 microsatellite loci tested using the infinite allele model (IAM), stepwise mutation model (SMM), and two-phase model of mutation (TPM) using BOTTLENECK (Cornuet and Luikart 1996), and with nuclear introns (*lamin* A and *gapdh*) and mtDNA sequence data tested using FLUCTUATE (Kuhner et al. 1995). Significant heterozygote deficiency (Hdef) indicates population growth, heterozygote excess (Hexc) indicates a population bottleneck, and nonsignificant values indicate populations are at equilibrium (Eq). Values significantly different from zero are marked with an asterisk ($P < 0.05$) or a double asterisk ($P < 0.003$).

	Big Slough	Hock Slough	Tutakoke	Kigigak	YKD
Microsatellite					
IAM	Eq	Eq	Hexc*	Eq	Hexc*
SMM	Eq	Hdef*	Hdef*	Hdef*	Hdef*
TPM	Eq	Hdef*	Eq	Eq	Eq
Lamin A					
θ^a	0.080 ± 0.051	0.167 ± 0.023**	0.193 ± 0.005**	0.016 ± 0.006*	0.122 ± 0.007**
g^a	632.1 ± 160.0**	975.1 ± 166.0**	392.2 ± 170.3**	407.8 ± 116.4*	550.8 ± 50.8**
Gapdh					
θ^a	0.028 ± 0.007**	0.015 ± 0.005*	0.027 ± 0.004**	0.019 ± 0.004**	0.047 ± 0.003**
g^a	1126.9 ± 160.0**	385.5 ± 166.0*	1066.5 ± 170.3**	322.2 ± 116.4*	400.0 ± 50.8**
MtDNA					
θ^a	0.005 ± 0.002*	0.005 ± 0.001**	0.004 ± 0.001**	0.005 ± 0.002*	0.023 ± 0.002**
g^a	140.5 ± 228.9	−38.0 ± 119.6	98.9 ± 173.3	−18.2 ± 117.3	534.1 ± 71.4**

[a] Parameter estimates θ ($N_f \mu$ for mtDNA, 4 $N_e \mu$ for nuclear DNA) and exponential growth rate (g) with the standard deviation (SD) for each population.

factors between sites 48 and 49, 1.02 factors between sites 136 and 145, 1.11 factors between sites 165 and 170, 1.36 factors between sites 186 and 192, and 4.41 factors between sites 232 and 252.

Haplotype (h) and nucleotide (π) diversity ranged from 0.849 to 0.912 and 0.008 to 0.009, respectively, for *lamin* A, and from 0.875 to 0.923 and 0.006 to 0.008, respectively, for *gapdh* (Table 2). Observed and expected heterozygosity for *lamin* A were 60% and 90%, respectively, which deviated significantly from Hardy-Weinberg equilibrium ($P < 0.05$). Observed and expected heterozygosity for *gapdh* were 94% and 90%, respectively, which also deviated from Hardy-Weinberg equilibrium ($P < 0.05$). Significantly negative values for Fu's *Fs* were observed for Hock Slough and Tutakoke (Table 2). Significant population growth rates (g) were detected by FLUCTUATE in all populations for both *lamin* A and *gapdh* (Table 1).

Maternally inherited mtDNA. Nine unique haplotypes were identified from 75 individuals with 13 variable sites (Fig. 2C). Haplotype (h) and nucleotide (π) diversity were high for most populations, with values ranging from 0.464 to 0.697 and 0.004 to 0.006, respectively (Table 2). The number of haplotypes per population ranged from three to six. Neutrality tests found no evidence for selection (Table 2). We did not detect any significant fluctuations in population demography for each population analyzed separately; however, a significant population growth rate (g) was detected when all colonies were combined (Table 1).

POPULATION SUBDIVISION

Biparentally inherited nuclear microsatellites. We did not detect any significant variations in allelic frequencies for the 14 microsatellite loci (Table 3), suggesting panmixia among sampled localities. In addition, there were no significant pairwise population comparisons for F_{ST} or R_{ST} (Table 3). The Bayesian clustering method, implemented by program STRUCTURE, indicated the most likely model generated from the microsatellite data was maximized when the total number of populations was one, which supports the interpretation of panmixia. In addition, the regional comparison between the mainland colonies and Kigigak Island was not significant (Table 3). Finally, we found no evidence of isolation by distance, as we did not detect a correlation between genetic and geographic distances ($r = 0.33$, $P = 0.30$).

Biparentally inherited nuclear introns. The nucleotide substitution model that best fit the

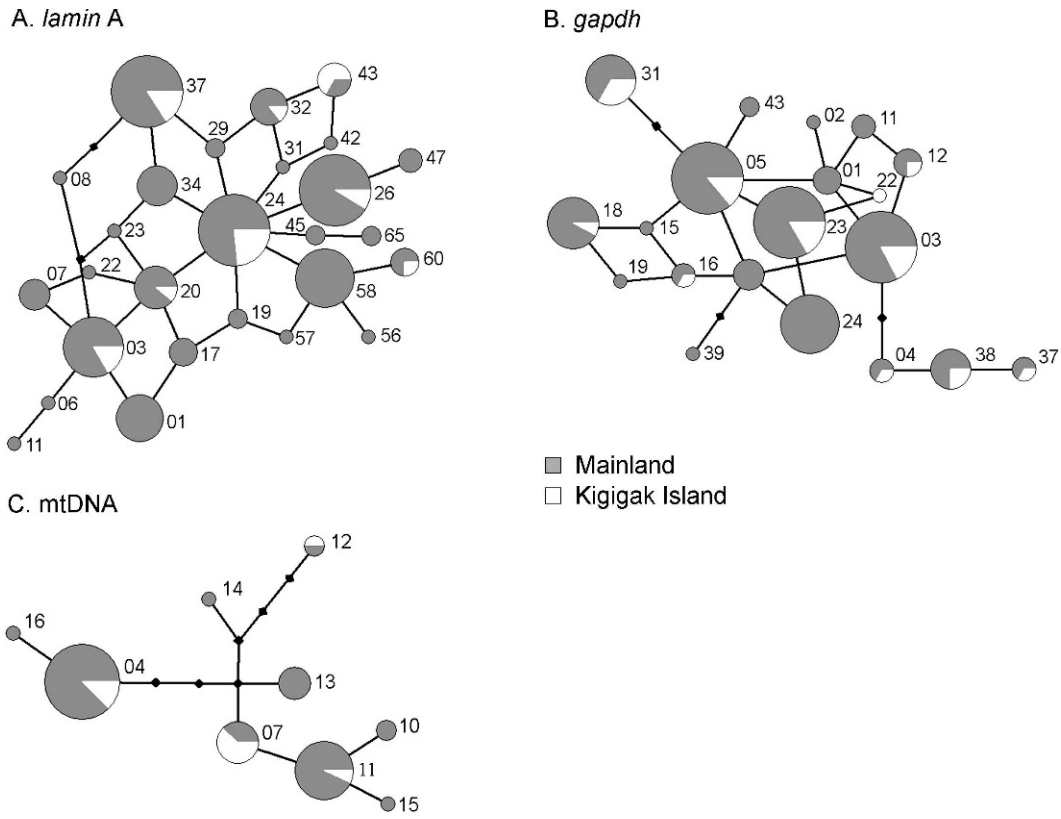

FIGURE 2. Networks illustrating relationships of (A) 31 *lamin* A alleles, (B) 21 *gapdh* alleles, and (C) nine mtDNA control region haplotypes assayed from Common Eiders breeding in the Yukon-Kuskokwim Delta. Size of the node corresponds to the frequency of each allele. Small black diamonds indicate intermediate ancestral alleles that were not sampled. Mainland colony (Big Slough, Hock Slough, and Tutatoke) alleles are illustrated in gray and Kigigak Island colony alleles are illustrated in white. Numbers correspond to haplotype or allele names.

lamin A and *gapdh* intron sequence data was the Tamura-Nei model (Tamura and Nei 1993) with an invariant site (TrN + I) parameter. We did not detect any significant intercolony differences in the allelic distribution for *lamin* A or *gapdh* (Table 3). However, a regional comparison showed low levels of structuring between mainland colonies and Kigigak Island for *lamin* A but not *gapdh* (Table 3). We also calculated F_{ST} values for each polymorphic site in ARLEQUIN. Significant F_{ST} values occurred at two of the 16 polymorphic positions in *lamin* A: site 90 ($F_{ST} = 0.046$, $P = 0.04$) and site 168 ($F_{ST} = 0.084$, $P = 0.04$). Intercolony comparisons were not significant. Two positions in *lamin* A yielded significant F_{ST} values between mainland colonies and Kigigak Island: site 168 ($F_{ST} = 0.231$, $P = 0.02$) and site 179 ($F_{ST} = 0.076$, $P = 0.04$). As observed for the microsatellite data, we did not detect any significant correlations between geographic and genetic distances for the nuclear introns when analyzed together ($r = 0.58$, $P = 0.18$), or separately (*gapdh*: $r = -0.44$, $P = 0.30$; *lamin* A: $r = -0.44$, $P = 0.22$).

Maternally inherited mtDNA. The nucleotide substitution model that best fit the mtDNA data was the Tamura-Nei model (Tamura and Nei 1993) with an invariant site parameter (TrN + I; substitute rate matrix: R[A–C] = 1.00, R[A–G] = 20.22, R[A–T] = 1.00, R[C–G] = 1.00, R[C–T] = 7.25, R[G–T] = 1.00, proportion of invariable sites = 0.83, A = 0.22, C = 0.31, G = 0.20, T = 0.28). Mean intercolony

TABLE 2. Estimates of genetic diversity of Common Eiders breeding in the Yukon-Kuskokwim Delta, Alaska, including nucleotide (π) and haplotype (h) diversity with standard deviation, number of unique alleles and haplotypes per population, and sample size (n), for *lamin* A, *gapdh*, and mtDNA control region.

	Big Slough	Hock Slough	Tutakoke	Kigigak
Lamin A				
h	0.912 ± 0.049	0.919 ± 0.022	0.895 ± 0.013	0.849 ± 0.041
π	0.009 ± 0.005	0.008 ± 0.005	0.009 ± 0.005	0.008 ± 0.005
Fu's *Fs*	−2.70	−9.76*	−10.18*	−1.19
Tajima's *D*	−0.20	−0.48	−0.42	−0.16
Unique alleles	8	23	22	8
n	7	33	37	13
Gapdh				
h	0.895 ± 0.033	0.923 ± 0.018	0.875 ± 0.017	0.899 ± 0.030
π	0.007 ± 0.004	0.007 ± 0.004	0.006 ± 0.003	0.008 ± 0.005
Fu's *Fs*	−1.08	−1.02	−3.79	−2.64
Tajima's *D*	−0.38	−0.32	−1.07	−0.18
Unique alleles	11	14	19	11
n	13	20	37	13
mtDNA				
h	0.464 ± 0.200	0.626 ± 0.067	0.638 ± 0.082	0.679 ± 0.090
π	0.004 ± 0.003	0.006 ± 0.004	0.005 ± 0.003	0.005 ± 0.003
Fu's *Fs*	1.61	3.22	0.76	1.95
Tajima's *D*	−0.56	0.32	1.06	−0.01
Unique haplotypes	3	5	6	4
n	8	19	36	12

* Significant *P*-values for Fu's *Fs* ($P < 0.02$) and Tajima's *D* ($P < 0.05$).

variance in haplotypic frequency was significant (Table 3). In addition, there were significant intercolony comparisons between Hock Slough and all other colonies, and between Kigigak Island and Tutakoke (Table 3). However, when we applied the TrN + I model to the dataset, intercolony comparisons were no longer significant (Table 3). A regional comparison between mainland colonies and Kigigak Island uncovered moderate levels of genetic subdivision (Table 3). However, when we applied the TrN + I model to the dataset, this regional comparison also was no longer significant (Table 3).

GENE FLOW

Although the Bayesian clustering program STRUCTURE did not uncover population subdivision among YKD colonies, we tested a two-population geographic model between mainland (Big Slough, Hock Slough, and Tutakoke) colonies and Kigigak Island based on our inference of genetic partitioning at

TABLE 3. Pairwise F_{ST} and R_{ST} calculated from 14 microsatellite loci and Φ_{ST} from mtDNA control region, *lamin* A, and *gapdh* sequence data for each pair of Common Eider colonies studied in the Yukon-Kuskokwim Delta, Alaska, along with a regional comparison between mainland colonies (Big Slough, Hock Slough, and Tutatoke) and Kigigak Island. Significant intercolony comparisons are marked with an asterisk.

	Microsatellites		Nuclear introns		mtDNA	
Population pairs	F_{ST}	R_{ST}	*Lamin* A Φ_{ST}	*Gapdh* Φ_{ST}	F_{ST}	Φ_{ST}
Big Slough vs. Kigigak	0.009	−0.001	0.030	−0.021	0.076	0.083
Big Slough vs. Hock Slough	0.002	−0.019	0.014	−0.013	0.187*	0.136
Big Slough vs. Tutakoke	0.004	−0.016	0.004	−0.004	−0.007	0.001
Kigigak vs. Hock Slough	−0.001	0.000	0.019	−0.011	0.156*	−0.020
Kigigak vs. Tutakoke	0.002	−0.004	0.014	0.004	0.080*	0.027
Hock Slough vs. Tutakoke	−0.003	−0.010	−0.004	−0.002	0.074*	0.040
Mainland vs. Kigigak	0.002	0.003	0.026*	0.006	0.086*	0.008
Overall	0.001	−0.009	0.003	0.005	0.086*	0.034

nuclear intron *lamin* A and mtDNA. $N_e m$ and θ values calculated in MIGRATE from microsatellite genotypes, mtDNA, and nuclear intron sequence data ranged from 13.1 to 26.0 migrants per generation from mainland colonies to Kigigak Island, with θ ranging from 0.002 to 1.026, and 1.5 to 18.8 migrants per generation from Kigigak Island to mainland colonies with θ ranging from 0.006 to 0.548 (Table 4). The full model (all parameters allowed to vary independently) had significantly higher likelihood than the restricted island model (symmetric interpopulation migration rates and θ) across all marker types (Table 4), indicating asymmetrical gene flow between mainland colonies and Kigigak Island.

DISCUSSION

POPULATION STRUCTURE AND FLUCTUATIONS

Low levels or a lack of spatial population genetic subdivision at biparentally inherited nuclear markers might be attributable to aspects of Common Eider breeding and wintering biology. Common Eiders breeding in the YKD winter in nearshore waters of western Alaska within 400 km of nesting sites (Petersen and Flint 2002). In winter aggregations, females may form pair bonds randomly (Spurr and Milne 1976) with males from different breeding colonies. Male dispersal among breeding areas is thus expected to homogenize genetic diversity in the nuclear genome (Scribner et al. 2001). However, we observed low, albeit significant, intercolony variance between mainland populations and Kigigak Island for nuclear intron *lamin* A. Significant population subdivision between the mainland and Kigigak Island may be the result of assortative mating occurring on the wintering grounds, such that females preferentially form pair bonds with males from the same colony, though stochastic outcomes of lineage sorting may produce a similar pattern.

Nonrandom mating on the wintering grounds has been observed in Common Eiders (*S. m. mollissima*) breeding in the Baltic Sea (Tiedemann et al. 1999). Assortative mating on the wintering grounds could result from (1) individuals from the same colony arriving earlier on the wintering ground, coupled with a selective advantage for early pair formation (Spurr and Milne 1976), or (2) colonies

TABLE 4. Comparison of alternative models of Common Eider gene flow between mainland colonies (Big Slough, Hock Slough, and Tutakoke) and Kigigak Island in the Yukon-Kuskokwim Delta, Alaska. Full model migration matrix (allowing all parameters to vary independently) and restricted model (symmetrical gene flow) migration rates calculated from 14 microsatellite loci, *lamin* A and *gapdh*, and mtDNA control region.

				Mainland to Kigigak Island		Kigigak Island to mainland	
Marker	Hypothesis	Ln(L)[a]	*P*-value	$N_f m$ or $N_e m$[b]	θ[b]	$N_f m$ or $N_e m$[b]	θ[b]
Microsatellites	Full	−1454.4	<0.001	22.7 (20.2–25.2)	1.026 (0.962–1.093)	18.8 (16.8–21.2)	0.548 (0.516–0.584)
	Restricted	−1606.0		17.4	0.787	17.4	0.787
Nuclear introns	Full	−141.7	<0.001	13.1 (5.3–22.6)	0.002 (0.002–0.002)	5.5 (3.3–8.4)	0.006 (0.004–0.007)
	Restricted	−154.7		9.6	0.004	9.6	0.004
MtDNA	Full	15.5	<0.001	26.0 (6.2–191.7)	0.013 (0.010–0.017)	1.5 (0.5–4.1)	0.011 (0.004–0.055)
	Restricted	−16.0		14.8	0.012	14.8	0.012

[a] Likelihood of the data under each hierarchical model, evaluated for significance using a log likelihood ratio test (Beerli and Felsenstein 2001).
[b] Parameter estimates for number of migrants per generation ($N_f m$ for mtDNA, $N_e m$ for nuclear DNA) for population migration rates with 95% confidence intervals in parentheses.

wintering in different localities within the coastal waters of western Alaska and consequently pairing with individuals from the same colony. Satellite telemetry data from individuals breeding in Big Slough indicate that individuals from this colony winter in different locations (Petersen and Flint 2002). Although one YKD female ($n = 39$) wintered in an area not used by other marked birds (Petersen and Flint 2002), wintering areas were likely a mixture of YKD colonies, creating the potential for females to pair with males from different colonies in the YKD. Winter site fidelity has been observed in Common Eiders (Spurr and Milne 1976), and polynyas (openings in the ice) have been reported to occur regularly in coastal Alaskan waters (Petersen and Flint 2002). High winter site fidelity would have to occur over many generations to be detected genetically. Therefore, mainland colonies and the Kigigak Island colony would have to winter in different areas over evolutionary time, as one bout of random mating per generation between mainland and Kigigak Island populations might contribute to homogenization of allelic frequencies among colonies. Finally, unequal population sizes among mainland colonies and the Kigigak Island colony might bias estimators of population subdivision (Scribner et al. 2001). Individuals from colonies with larger population sizes would appear to mate assortatively simply because of the higher probability of mating with an individual from the same population, thus leading to an upward bias in estimates of F_{ST}.

Moderate levels of population structure were observed for the maternally inherited mtDNA control region. Genetic partitioning occurred at this locus among all sampled sites, except between Big Slough and Kigigak Island and Big Slough and Tutakoke, suggesting female natal and breeding philopatry over relatively short geographic distances. Banding data also indicate high breeding site fidelity, as only one breeding female has been observed to disperse between studied colonies (Tutakoke to Hock Slough; P. Flint, U.S. Geological Survey, pers. comm.). However, significant spatial genetic structuring was not evident when the nucleotide substitution model (TrN + I model) was applied to the dataset, suggesting that colonies have not been subdivided long enough for mutation to be driving differentiation among populations (Scribner et al. 2001). Evidence for recent range expansion is supported by significant positive growth rates observed at nuclear markers. Although we did not observe significant positive population growth rates for mtDNA, when sequence data were combined across all sampled sites, YKD as a whole had a positive growth signature, suggesting recent colonization (Waltari et al. 2004) of the YKD by Common Eiders.

Low to high interpopulation variances in haplotypic frequencies have been observed in another population of Pacific Common Eiders. Common Eiders breeding in the central Beaufort Sea exhibited population structuring within mtDNA (pairwise $\Phi_{ST} = 0.135$–0.271) among islands approximately 85–135 km apart (Sonsthagen 2006). However, genetic discordance was not observed among islands within the same island group, indicating that Beaufort Sea females are philopatric to island groups rather than particular islands. The degree of philopatry differs among YKD females, as moderate levels of population subdivision were observed among colonies approximately 10–63 km apart. In contrast to the Beaufort Sea population, females breeding in the YKD appear to be philopatric to individual colonies, as also observed for *S. m. dresseri* by Wakely and Mendall (1976). Differences in the degree of philopatry among Beaufort Sea and YKD females may be attributed to a more stochastic arctic environment. Seasonal arctic storms in the Beaufort Sea alter the location of available nesting habitat annually, potentially causing females to disperse among adjacent islands (Sonsthagen 2006). Conversely, Common Eiders in the YKD nest in sedges in coastal wetland tundra habitat (Kincheloe and Stehn 1991, Flint et al. 1998) that remains relatively unchanged across seasons (Stehn et al. 1993). Spatial stability in the availability of nesting habitat through intergenerational time would enable females to nest in the same area across years. Coupled with high natal philopatry, temporal and spatial stability of nesting habitat would create genetic discordance among adjacent colonies at mtDNA despite gene flow through male-mediated dispersal.

Interisland comparisons in mtDNA haplotypic frequencies (Φ_{ST}) among Beaufort Sea Common Eiders were an order of magnitude greater than intercolony estimates observed in

the YKD (Sonsthagen 2006). Larger estimates of population subdivision may be explained, in part, by the historical population demography of the northern Alaskan population. The Beaufort Sea population did not exhibit a genetic signature of sudden population expansion, suggesting that northern Beringia may have served as a glacial refugium for Common Eiders during the Pleistocene (Sonsthagen 2006). Long-term persistence of Beaufort Sea Common Eiders in a Pleistocene refugium, coupled with female natal philopatry, would result in greater spatial population genetic structure observed for mtDNA when compared to the potentially recently colonized YKD.

The comparatively higher levels of population subdivision observed for mtDNA than nuclear DNA could also be attributed to lineage sorting. MtDNA has a lower effective population size relative to nuclear DNA. Therefore, when mutation rate and selection are held constant, genetic drift has a larger effect on mtDNA than nuclear DNA (Avise 2004), translating into higher estimates of population subdivision (F_{ST}). The effects of lineage sorting and sex-biased differences in philopatry on spatial genetic subdivision are not mutually exclusive and both may be playing a role in the degree of population structure observed. However, microsatellite loci have a high rate of mutation relative to mtDNA control region (Avise 2004), resulting in new mutations arising more frequently within populations. By chance alone, one would expect new mutations to increase in frequency among isolated populations and dampen the effects of incomplete lineage sorting within microsatellite loci. Given differences in the degree of philopatry between the sexes in Common Eiders and congruence in results between microsatellite and nuclear intron loci, differences in estimates of population subdivision may be more attributable to male dispersal and high natal and breeding philopatry in females than to incomplete lineage sorting for the YKD population.

Population bottleneck signals observed with microsatellite loci under the infinite allele model (IAM) are consistent with demographic data indicating population decline (Stehn et al. 1993). Differences in population fluctuations among models (IAM and stepwise mutation model [SMM]) may be because of the underlying assumptions of mutation models, such that IAM does not allow for homoplasy (i.e., each mutation results in a new allele) and SMM allows for mutations to existing allelic states (homoplasy). When mutation rate is held constant, IAM will have more distinct allelic states and a higher expected heterozygosity under mutation drift equilibrium, and therefore may be better able to detect population declines. Simulation data indicate that IAM may also better detect weak population bottlenecks than SMM (Cornuet and Luikart 1996), and empirical data suggest SMM may not be as able to detect recent population declines (Cornuet and Luikart 1996). Therefore, differences in directionality of population fluctuations between mutation models may reflect differences in population size over evolutionary time, with IAM detecting the recent population decline observed by Stehn et al. (1993) and SMM detecting long-term population growth.

GENE FLOW

Common Eiders breeding in the YKD appear to be exhibiting asymmetrical gene flow between mainland colonies and Kigigak Island across all marker types, with more individuals dispersing from mainland populations to Kigigak Island. Congruence of asymmetry in dispersal across all marker types indicates that this is a consistent behavior over evolutionary time. Colonization of the YKD during the last glacial retreat could explain, in part, the directionality of gene flow observed for mtDNA and nuclear introns. Significant positive growth rates and changes in effective population size across all marker types indicate that the YKD was colonized recently (Waltari et al. 2004). Ploeger (1968) hypothesized that during the last glacial period, the Common Eider breeding distribution was restricted to the southern edge of the Bering Land Bridge, southwest of the YKD. Assuming the YKD was colonized by eiders residing on the southern edge of the Bering Land Bridge, we would expect to observe more individuals dispersing south to north. However, females breeding in the YKD are exhibiting asymmetrical gene flow from north to south. Therefore, the observed pattern is more consistent with colonization of the YKD by Common Eiders from glacial refugia north of the current breeding site (Sonsthagen 2006).

Unsampled populations may have effects on the estimation of population size (θ) and immigration rates (*M*; Beerli 2004). Simulation data indicate that estimates of θ and *M* show an upward bias with increasing immigration from unsampled populations and that biases in the estimate of number of migrants per generation closely follow biases of θ (Beerli 2004). Despite upward biases in estimators of gene flow in the absence of samples from larger, more influential, populations, directionality of gene flow does not appear to be affected in this study. Furthermore, in source-sink populations, which may describe the population dynamics observed in the YKD, θ is estimated accurately (Beerli 2004). Therefore, the directionality of gene flow observed between the mainland and Kigigak Island colonies is likely not influenced by unsampled mainland populations. However, the magnitude of gene flow may have an upward bias if unsampled populations in the YKD have a larger influence on the exchange of alleles among populations than sampled mainland populations.

COMPARISON WITH OTHER WATERFOWL

Spatial genetic structuring, although low, observed at such a microgeographic scale for Common Eiders breeding in the YKD is noteworthy, especially when compared to other arctic-breeding waterfowl. Studies of King Eiders (*S. spectabilis*; Pearce et al. 2004) and Harlequin Ducks (*Histrionicus histrionicus*; Lanctot et al. 1999) did not detect significant levels of population genetic structure among sampled sites for microsatellite genotype or mtDNA sequence data. Steller's Eiders (*Polysticta stelleri*) breeding in Alaska and Russia exhibited low levels of population differentiation among sites at microsatellite loci (Pearce et al. 2005). Higher levels of population genetic subdivision were observed among breeding populations of Spectacled Eiders (*S. fisheri*) for mtDNA (Scribner et al. 2001) and Canada Geese (*Branta canadensis*) for mtDNA and nuclear microsatellite loci (Scribner et al. 2003). However, these studies were conducted at much larger spatial scales relative to our study.

Differences in the degree of population subdivision could be attributed to behavioral characteristics of individual species. Several aspects of the biology of many of these species are similar to those of Common Eiders, including: (1) exhibition of some degree of breeding site fidelity, (2) seasonal migratory behavior, (3) population mixture in large winter aggregations, (4) formation of pair bonds in winter months with males following females back to breeding sites, and (5) seasonal monogamy (Andersen et al. 1992). In contrast to Common Eiders, many waterfowl species are monotypic across their range and show little to no population structuring (Newton 2003). Species that exhibit fine-scale spatial structure likely have high natal, breeding, and winter site philopatry, as has been indicated for Common Eiders (Goudie et al. 2000).

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