The Auk

VOLUME 126, NUMBER 4, OCTOBER 2009
AN INTERNATIONAL JOURNAL OF ORNITHOLOGY

PUBLISHED BY THE AMERICAN ORNITHOLOGISTS' UNION

THE AUK

Vol. 126, No. 4, Pages 717–969

October 2009

The Auk 126(4):744–754, 2009

Printed in USA.

HIERARCHICAL SPATIAL GENETIC STRUCTURE OF COMMON EIDERS (*SOMATERIA MOLLISSIMA*) BREEDING ALONG A MIGRATORY CORRIDOR

Sarah A. Sonsthagen,[1,6] Sandy L. Talbot,[2] Richard B. Lanctot,[3] Kim T. Scribner,[4] and Kevin G. McCracken[1,5]

[1]*Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA;*
[2]*Alaska Science Center, U.S. Geological Survey, 4210 University Drive, Anchorage, Alaska 99508, USA;*
[3]*U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 E. Tudor Road, MS 201, Anchorage, Alaska 99503, USA;*
[4]*Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, Michigan 48824, USA; and*
[5]*University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, USA*

Abstract.—Documentation of spatial genetic discordance among breeding populations of Arctic-nesting avian species is important, because anthropogenic change is altering environmental linkages at micro- and macrogeographic scales. We estimated levels of population subdivision within Pacific Common Eiders (*Somateria mollissima v-nigrum*) breeding on 12 barrier islands in the western Beaufort Sea, Alaska, using molecular markers and capture–mark–recapture (CMR) data. Common Eider populations were genetically structured on a microgeographic scale. Regional comparisons between populations breeding on island groups separated by 90 km (Mikkelsen Bay and Simpson Lagoon) revealed structuring at 14 microsatellite loci ($F_{ST} = 0.004$, $P < 0.01$), a nuclear intron ($F_{ST} = 0.022$, $P = 0.02$), and mitochondrial DNA ($\Phi_{ST} = 0.082$, $P < 0.05$). The CMR data ($n = 34$) did not indicate female dispersal between island groups. Concordance between genetic and CMR data indicates that females breeding in the western Beaufort Sea are strongly philopatric to island groups rather than to a particular island. Despite the apparent high site fidelity of females, coalescence-based models of gene flow suggest that asymmetrical western dispersal occurs between island groups and is likely mediated by Mikkelsen Bay females stopping early on spring migration at Simpson Lagoon to breed. Alternatively, late-arriving females may be predisposed to nest in Simpson Lagoon because of the greater availability and wider distribution of nesting habitat. Our results indicate that genetic discontinuities, mediated by female philopatry, can exist at microgeographic scales along established migratory corridors. *Received 31 October 2008, accepted 3 May 2009.*

Key words: barrier islands, Beaufort Sea, Common Eider, dispersal, gene flow, microsatellites, mtDNA, philopatry, *Somateria mollissima,* spatial genetic structure.

Estructura Genética Jerárquica Espacial de Poblaciones Reproductivas de *Somateria mollissima* a lo largo de un Corredor Migratorio

Resumen.—La documentación de la discordancia genética espacial entre poblaciones reproductivas de especies de aves que crían en el Ártico es importante debido a que los cambios antropogénicos están alterando las conexiones ambientales a escalas micro y macrogeográficas. Utilizando marcadores moleculares y datos de captura, marcado y recaptura (CMR), estimamos los niveles de subdivisión poblacional en *Somateria mollissima v-nigrum* considerando las áreas de reproducción ubicadas en 12 islas de barrera en el oeste del Mar de Beaufort, Alaska. Las poblaciones estuvieron estructuradas a una escala microgeográfica. Las comparaciones regionales entre poblaciones que crían en grupos de islas separados por 90 km (Bahía de Mikkelsen y Laguna Simpson) mostraron estructura en 14 loci microsatélites ($F_{ST} = 0.004$, $P < 0.01$), un intrón nuclear ($F_{ST} = 0.022$, $P = 0.02$) y ADN mitocondrial ($\Phi_{ST} = 0.082$, $P < 0.05$). Los datos de CMR ($n = 34$) no indicaron que existiera dispersión de las hembras entre grupos de islas. La concordancia entre los datos genéticos y de CMR indica que las hembras que se reproducen en el oeste del Mar de Beaufort son fuertemente filopátricas a grupos de islas pero no a una isla en particular. A pesar de la aparentemente alta fidelidad a los sitios de las hembras, modelos de flujo génico basados en coalescencia sugieren que existe disperdsión asimétrica al oeste entre grupos de islas, lo que probablemente esté mediado por el hecho de que las hembras de la Bahía de Mikkelsen se detienen temprano durante la migración de otoño en la Laguna Simpson para reproducirse. Alternativamente, las hembras que arriban tarde podrían estar predispuestas a anidar en la Laguna Simpson debido a la mayor disponibilidad y distribución más amplia del hábitat de anidación. Nuestros resultados indican que, a escalas microgeográficas a lo largo de corredores de migración establecidos, pueden existir discontinuidades genéticas mediadas por la filopatría de las hembras.

[6]Present address: Alaska Science Center, U.S. Geological Survey, 4210 University Drive, Anchorage, Alaska 99508, USA.
E-mail: ssonsthagen@usgs.gov

The Auk, Vol. 126, Number 4, pages 744–754. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2009.08224

The degree to which avian populations are genetically structured at microgeographic scales is greatly influenced by dispersal. For many species, detecting dispersal is difficult, especially for mobile organisms that may travel long distances prior to and between breeding attempts. Birds are of particular interest, because most species that breed in Arctic or temperate regions migrate to other areas during the non-breeding season and, thus, show less geographic structure than other vertebrate groups (Avise 1996). Lack of population structure has been attributed to the environmental variability of Arctic and temperate regions (Scribner et al. 2001, Pearce et al. 2004), which increases dispersal and migratory behavior in birds and can homogenize gene frequencies (Winker et al. 2000). Conversely, many birds exhibit high natal- and breeding-site fidelity, which is expected to restrict gene flow among neighboring populations (Avise 1996), leading to population subdivision in the face of countervailing dispersal.

Differences in the degree of philopatry also may exist between males and females. Females of most waterfowl species typically exhibit greater natal and breeding philopatry than males (Rohwer and Anderson 1988). Males and females typically pair on the wintering grounds, and males accompany females back to the females' natal area to breed. Because ducks from different breeding areas frequently share a common wintering ground, males may disperse long distances. Additionally, males may not mate with the same female each year and, thus, individual males may breed in distant locations from year to year (Anderson et al. 1992). Therefore, male dispersal behavior is expected to cause genetic mixing among individuals from multiple breeding areas. Sex-biased dispersal is expected to result in distinct patterns of spatial variance when genetic markers with different modes of inheritance are used to characterize individuals from different breeding populations.

Common Eiders (*Somateria mollissima*) have a circumpolar distribution and inhabit coastal regions throughout the Holarctic (Goudie et al. 2000). Pacific Common Eiders (*S. m. v-nigrum*) breed on the barrier islands of western Canada and Alaska (Goudie et al. 2000) and have experienced a marked population decline (53%) since the mid-1970s (Suydam et al. 2000). Reasons for the decline are unknown, but recent surveys indicate that the population may have stabilized (R. Suydam pers. comm.). However, these birds are long lived and have a low reproductive rate, which may limit population growth (Goudie et al. 2000).

Satellite-telemetry studies indicate that adult female Common Eiders that nest on islands in the Beaufort Sea may intermix with other Common Eider populations during migration to wintering grounds in the Bering Sea between Alaska and the Chukotka Peninsula, Russia (Petersen and Flint 2002, L. Dickson pers. comm.). Females originating from Alaskan and Canadian breeding areas likely pair with males from other breeding populations during winter, thus mediating gene flow through male-biased dispersal, even if levels of female dispersal are low. Such gene flow would be expected to occur despite the observation that all transmitter-equipped females returned to their breeding areas in the western Beaufort Sea the following summer (Petersen and Flint 2002, L. Dickson pers. comm.). Thus, differences between male and female dispersal should be evident in contrasting levels of subdivision in maternally and biparentally inherited markers.

Data describing population genetic structure are available for European Common Eiders (*S. m. mollissima*) that breed in the Baltic Sea (colonies 133–1,010 km apart; Tiedemann et al. 1999) and Pacific Common Eiders that breed on the Yukon-Kuskokwim Delta, Alaska (colonies 9–63 km apart; Sonsthagen et al. 2007). High levels of structure in maternally inherited mitochondrial DNA (mtDNA) were observed among colonies in the Baltic Sea and Yukon-Kuskokwim Delta (Φ_{ST} = 0.262–0.343, F_{ST} = 0.074–0.187, $P < 0.05$). Significant, but lower, levels of structure were detected among Baltic Sea colonies at microsatellite loci (F_{ST} = 0.009–0.029, $P < 0.05$). Both Tiedemann et al. (1999) and Sonsthagen et al. (2007) attributed high levels of mtDNA spatial structure to high rates of female natal philopatry. Tiedemann et al. (1999) attributed proportionally lower structure at microsatellite loci to nonrandom mating by males on the wintering grounds (i.e., males mate with females from the same locality more often than expected).

Information on the degree of spatial population structure in Pacific Common Eiders in the western Beaufort Sea is of particular interest to management and industry agencies because of the proximity of nesting areas to petrochemical projects (Minerals Management Service 2003). Philopatry to barrier-island nesting sites that are close to industrial infrastructure (Reed 1975, Swennen 1990) makes this population particularly susceptible to human disturbance and climate change. In addition, increases in avian and mammalian predators near human developments, including petrochemical installations, may adversely affect nest success and duckling survival (Eberhardt et al. 1982, Johnson 2000, R. H. Day unpubl. data). Population risks may be exacerbated if genetically distinct populations occur in proximity to existing or proposed developments. Evaluation of population structure of Common Eiders breeding in the western Beaufort Sea thus provides a means to assess potential effects of oil and gas exploration, and of changes in Arctic ecosystems resulting from climate change, on populations of this species.

We estimated levels of spatial population structure in Pacific Common Eiders breeding on barrier islands within two island groups of the western Beaufort Sea using microsatellite genotypes and sequence information from the mtDNA control region and two nuclear introns, coupled with capture–mark–recapture (CMR) data. We hypothesized that the nuclear markers (microsatellites and intron sequences) would show little population genetic structure, because these markers are biparentally inherited and Common Eiders breeding on these islands share a common wintering ground with Common Eiders from several other breeding areas. Over time, male dispersal among breeding populations could contribute to high levels of gene flow throughout the nuclear genome. However, we predicted that population structure would be observed in maternally inherited mtDNA because of the high degree of female natal and breeding philopatry in Common Eiders.

Methods

Sample collection.—Blood or feather samples from breeding female Common Eiders and eggs from nests were collected during mark–recapture and monitoring efforts on the barrier islands in the Beaufort Sea, Alaska, between June and July of 2000–2003. Samples were collected from two island groups consisting of 12 islands (Fig. 1). The western group, hereafter called "Simpson

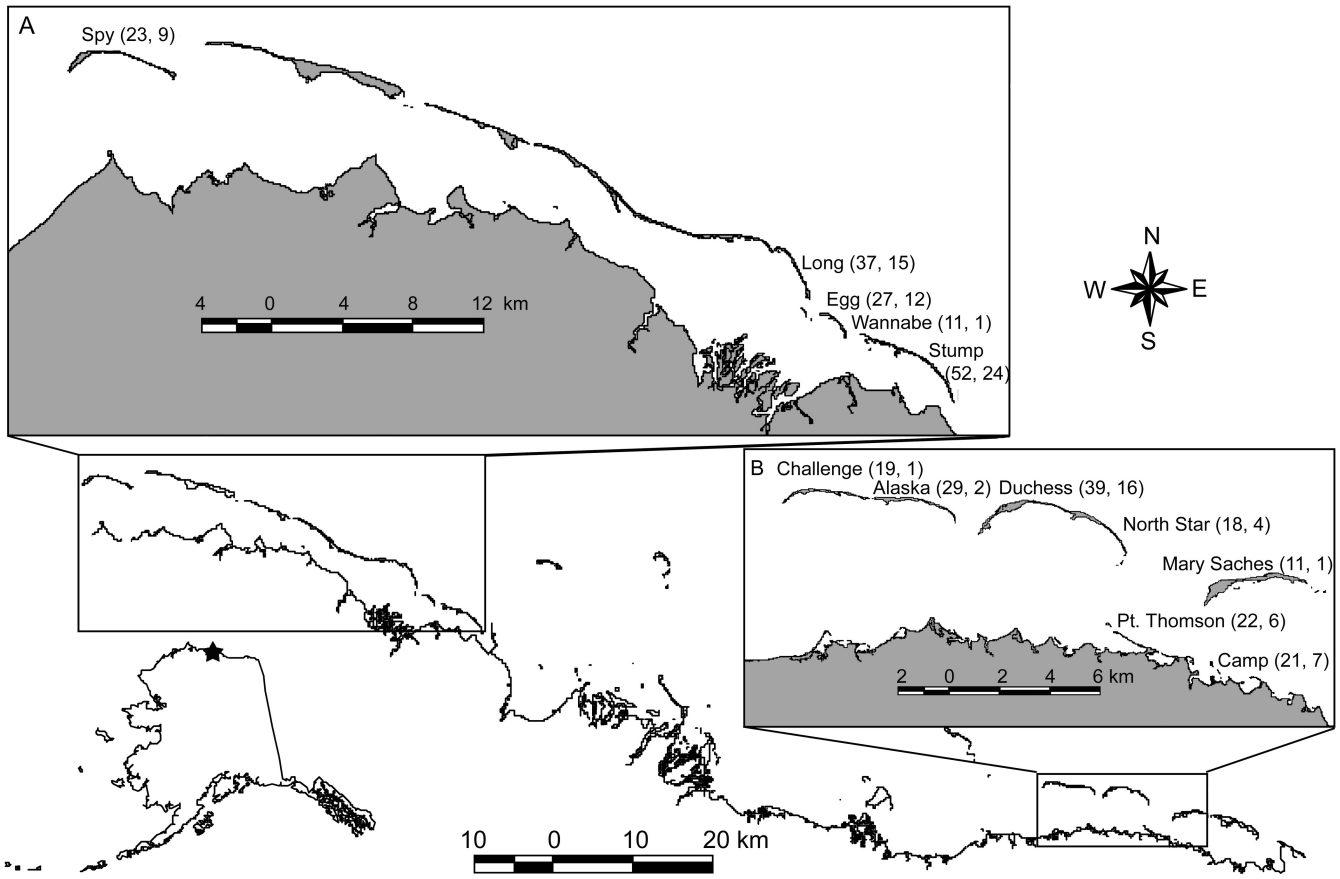

Fig. 1. Location of barrier islands in (A) Simpson Lagoon (western group) and (B) Mikkelsen Bay (eastern group) within the western Beaufort Sea. The number of Pacific Common Eiders sampled on each island is in parentheses; the first value is the number of samples (blood and feather) genotyped at 14 microsatellite loci, and the second value is the number of samples (blood) sequenced for mtDNA and two nuclear introns. "Wannabe" and "Camp" islands are designations used by the authors and are not official names of islands.

Lagoon," consists of five islands: Stump, "Wannabe," Egg, Long, and Spy islands (Fig. 1A). The eastern group, hereafter called "Mikkelsen Bay," consists of seven islands: "Camp," Point Thomson, Mary Saches, North Star, Duchess, Alaska, and Challenge islands (Fig. 1B). Distances between islands within each of the two groups ranged from 1.2 to 49.2 km, and distances between islands located in Simpson Lagoon and Mikkelsen Bay ranged from 78.1 to 143.1 km. Samples later identified as having identical genotypes and mother–offspring groups were not included in analyses (see below).

Females ($n = 98$) were captured on nests using a dip net during initial nest searches and using a bow net when nests were revisited during late incubation (Sayler 1962). Blood was collected from brachial or jugular veins and placed in blood lysis buffer (Longmire et al. 1988). Feather samples ($n = 220$) were collected from nest bowls of unsampled females and stored in silica gel desiccant at room temperature. Tissues from eggs ($n = 9$ from five clutches) were collected opportunistically from abandoned or depredated nests to verify that sequences were mitochondrial (see below). Embryos were placed in tissue preservation buffer (4.0 M urea, 0.2 M NaCl, 10 mM EDTA, 0.5% N-lauroyl-sarcosine, and 100 mM tris-HCl [pH 8.0]; S. Talbot unpubl. data). Genomic DNAs were extracted using either a "salting out" protocol described by Medrano et al. (1990), with modifications described in Sonsthagen et al. (2004), or a Qiagen DNeasy Tissue Kit (Qiagen, Valencia, California). Genomic DNA extractions were quantified using fluorometry and diluted to 50 ng μL^{-1} working solutions.

Microsatellite genotyping.—Primers used for microsatellite genotyping of Common Eiders ($n = 327$) were obtained via cross-species screening of microsatellite primers developed for other waterfowl. We screened 12 individuals at 50 microsatellite loci reported to be variable in other waterfowl species and selected 14 microsatellite loci found to be polymorphic: Aph02, Aph08, Aph20, Aph23 (Maak et al. 2003); Bcaμ1, Bcaμ11, and Hhiμ3 (Buchholz et al. 1998); Cm09 (Maak et al. 2000); Sfiμ10 (Libants et al. unpubl. data); and Smo4, Smo7, Smo08, Smo10, and Smo12 (Paulus and Tiedemann 2003). Microsatellites were amplified using the polymerase chain reaction (PCR), and products were electrophoresed following protocols described in Sonsthagen et al. (2004) for tailed primers (Aph02, Aph08, Aph20, Aph23, Cm09,

Smo4, Smo7, Smo08, Smo10, and Smo12) and Pearce et al. (2005) for direct-labeled primers (Bcaμ1, Bcaμ11, Hhiμ3, and Sfiμ10). For quality-control purposes, 10% of the samples were randomly selected, re-amplified, and genotyped in duplicate.

Mitochondrial DNA and nuclear intron sequencing.—We amplified and sequenced a 545-base-pair (bp) portion of the control-region domain I and II (Baker and Marshall 1996) using primer pairs (L263 and H848) and protocols described in Sonsthagen et al. (2007). Sequences from opposite strands were assembled using SEQUENCHER, version 4.1.2 (Gene Codes, Ann Arbor, Michigan). Because of the existence of nuclear pseudogenes in avian species (Sorenson and Fleischer 1996), we verified that the amplified sequences were mtDNA control region by comparing sequences from heart and blood samples from five putative mother–offspring groups (e.g., Pearce et al. 2004). Individuals that contained double peaks within mtDNA electropherograms were resequenced. If co-amplified peaks were still detected, presumably because of nuclear pseudogenes present in this species (Tiedemann and von Kistowski 1998) or heteroplasmy, those individuals were removed (~10%). Sequences were deposited in GenBank (accession numbers EU019563–EU019596 and GQ405746–GQ405752).

Six nuclear introns were screened for variability in Common Eiders (Sonsthagen et al. 2007), and two polymorphic introns were selected for sequencing, lamin A (LMNA; 280 bp) and glyceraldehyde-3-phosphate dehydrogenase (GAPDH; 386–387 bp) (McCracken and Sorenson 2005). Introns were amplified using PCR and sequencing protocols described by Sonsthagen et al. (2007). 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 degeneracy codes and treated as polymorphisms. Gaps were coded as a fifth character state. Sequences were deposited in GenBank (accession numbers GQ405658–GQ405745 and GQ405753–GQ405854).

Estimation of genetic diversity.—To determine whether the same individual was sampled across multiple years (between feather and blood or feather and feather samples), probabilities of identity for a randomly mating population (PID) and among siblings (PID_{sib}) were calculated in GIMLET, version 1.3.3 (Valière 2002), using genotypes from the 14 microsatellite loci.

Data from islands with low sample sizes were pooled on the basis of geographic proximity (i.e., females captured within 3 km of each other on neighboring islands). Samples from Challenge Island were pooled with those from Alaska Island, samples from Mary Saches Island were pooled with those from North Star Island, and samples from "Wannabe Island" were pooled with those from Egg Island (Fig. 1).

Allelic phases for LMNA and GAPDH were inferred from diploid sequence data using PHASE, version 2.0 (Stephens et al. 2001), which uses a Bayesian approach to reconstruct haplotypes from population genotypic data and allows for recombination and the decay of linkage disequilibrium (LD) with distance. The PHASE analysis (parameters: 1,000 iterations with 1,000 burn-in iterations) was repeated three times to ensure consistency across runs. A four-gamete test was performed in DNASP, version 4.9 (Rozas et al. 2003), to estimate the minimum number of recombination events and identify inferred break points within nuclear intron sequences.

Using only adult breeding females, we calculated allelic richness, inbreeding coefficient (F_{IS}), expected and observed heterozygosities, Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium (LD) for each nuclear intron and microsatellite locus in FSTAT, version 2.9.3 (Goudet 1995; see Acknowledgments). Mitochondrial DNA control region and LMNA and GAPDH sequences 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, version 2.0 (Schneider et al. 2000). Critical significance values of 5% require a P value <0.02 for Fu's *Fs* (Fu 1997). Unrooted phylogenetic trees for each gene were constructed in NETWORK, version 4.1.0.8 (see Acknowledgments), using the reduced median network (Bandelt et al. 1995), to illustrate possible reticulations in the gene trees resulting from homoplasy or recombination.

Estimation of population subdivision.—The degrees of population subdivision among islands and between island groups were assessed by calculating overall and pairwise F_{ST}, R_{ST}, and Φ_{ST} for microsatellite and sequence data in ARLEQUIN, adjusting for multiple comparisons using Bonferroni corrections ($\alpha = 0.05$). Pairwise Φ_{ST} was calculated using a Tamura-Nei nucleotide substitution model with an invariant site parameter (Tamura and Nei 1993), as determined using MODELTEST, version 3.06 (Posada and Crandall 1998), and Akaike's information criterion (Akaike 1974). Because the upper possible F_{ST} value for a set of microsatellite loci is usually <1.0 (Hedrick 2005), we used RECODEDATA, version 1.0 (Meirmans 2006), to calculate the uppermost limit of F_{ST} for a given data set. Hierarchical analysis of molecular variance (AMOVA) was performed using ARLEQUIN to determine the magnitude of spatial variance in haplotypic and allelic frequencies among populations within and among island groups. In addition, a nested AMOVA was performed to assess the partitioning of genetic variation within individuals and among individuals within populations. An isolation-by-distance analysis was performed in IBD, version 1.52 (Bohonak 2002), with microsatellite data and nuclear intron data, to determine whether more geographically distant population pairs are also more genetically differentiated. IBD tests the statistical significance of the relationship between genetic and geographic distance using a Mantel test and calculates slope and intercept from reduced major axis regressions following Sokal and Rohlf (1981), with confidence limits.

Estimation of gene flow among populations.—We used MIGRATE, version 2.0.3 (Beerli and Felsenstein 1999, 2001; see Acknowledgments), to calculate the number of migrants per generation (N_em) for microsatellite and nuclear intron data and number of female migrants per generation (N_fm) for mtDNA between the two island groups. Individuals breeding in Mikkelsen Bay and Simpson Lagoon, respectively, were pooled and treated as two separate populations. Full models, θ ($4N_e\mu$; composite measure of effective population size and mutation rate), and all pairwise migration parameters (M), were estimated individually from the data and compared with restricted island models for which parameters θ and M were symmetrical among populations.

MIGRATE was run using maximum-likelihood search parameters: 10 short chains (1,000 used trees out of 20,000 sampled), five long chains (10,000 used trees out of 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. Competing models were evaluated for goodness-of-fit given the data using a log-likelihood ratio test and a chi-square 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

Microsatellites.—The number of alleles per locus at the 14 microsatellite loci ranged from 3 to 44, with an average of 11.3 alleles per locus. Allelic richness for each population ranged from 4.40 to 5.32. The observed heterozygosity for each population ranged from 11.9% to 91.8%, with an overall value of 57.7%. The inbreeding coefficients (F_{IS}) ranged from −0.071 to 0.060 across all islands, with an overall value of 0.027, and did not differ significantly from zero ($P > 0.05$).

Nuclear introns.—Twenty-five LMNA alleles were reconstructed from 108 individuals using PHASE (Fig. 2A). Sixty individuals (56%) were homozygous at all variable sites, and 22 individuals (20%) were heterozygous at one site. Pair probabilities of reconstructed haplotypes for individuals that were heterozygous for more than one site ranged from 0.82 to 0.99 ($n = 22$), except for two individuals with haplotype probabilities of 0.62 and 0.68. The background recombination rate (ρ) was 0.50, with factors exceeding ρ ranging from 0.58 to 1.94 among 14 variable sites. A minimum of five recombination events was identified in DNASP, with break points occurring between sites 55 and 98, 98 and 116, 116 and 160, 160 and 171, and 171 and 179.

Twenty-two GAPDH alleles were reconstructed from 88 individuals (Fig. 2B). Six individuals (7%) were homozygous at all variable sites, and one individual (1%) was heterozygous at one site. Pair probabilities of all other reconstructed haplotypes ranged from 0.82 to 1.00 ($n = 60$) and from 0.43 to 0.78 ($n = 21$), which may be attributable to potentially high levels of recombination occurring within this marker (0.39–4.41 factors exceeding ρ = 0.05, between 15 variable sites) and autapomorphies (single novel polymorphisms occurring on one allele in one individual). At least two recombination events were identified in DNASP, with break points occurring between sites 16 and 129 and sites 136 and 165.

Haplotype (h) and nucleotide (π) diversity ranges were 0.600–0.915 and 0.005–0.009, respectively, for LMNA, and 0.874–0.954 and 0.006–0.009, respectively, for GAPDH (Table 1). Observed and expected heterozygosity for LMNA were 41.6% and 87.9%, respectively, which significantly deviated from HWE ($P = 0.004$). Observed and expected heterozygosity for GAPDH was 92.4% and 89.9%, respectively, which also significantly deviated from HWE ($P < 0.001$). Significantly negative values for Fu's Fs ($P < 0.02$) were observed for North Star and Mary Saches, Duchess, and Long (Table 1) islands, indicating an excess of rare alleles, which may result from population expansion.

Mitochondrial DNA.—Eleven mtDNA control-region haplotypes were identified from 83 individuals (Fig. 2C) defined by 13 variable sites. Haplotype and nucleotide diversity were high for most populations, with values ranging from 0.000 to 0.891 and from 0.000 to 0.009, respectively (Table 1). Spy Island possessed a single haplotype. Other islands were represented by two to six haplotypes. Tajima's D and Fu's Fs were not significant (Table 1).

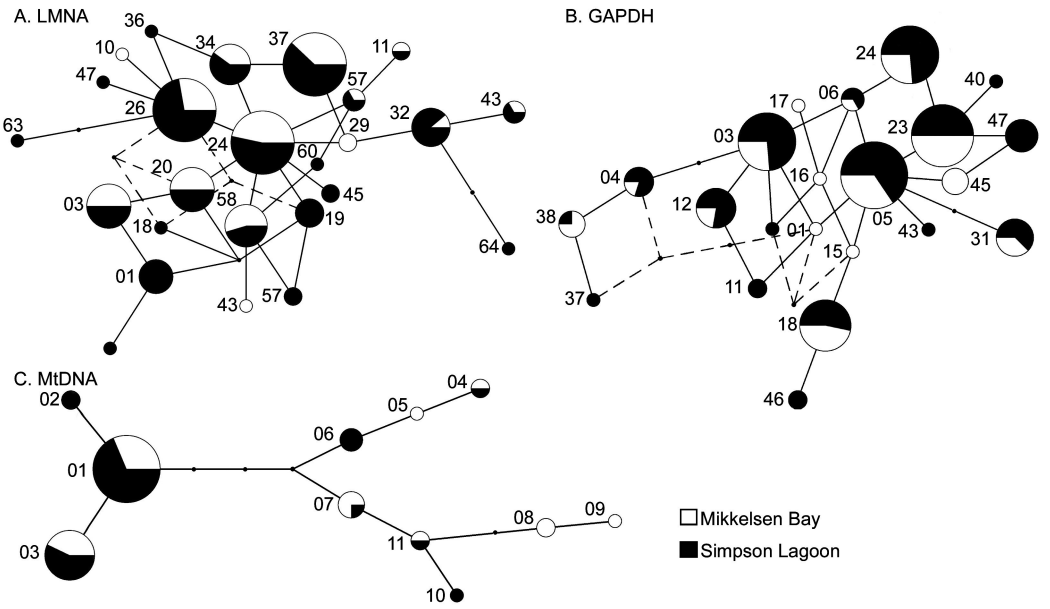

FIG. 2. Unrooted parsimony tree illustrating relationships of (A) 25 lamin A (LMNA) alleles, (B) 22 glyceraldehyde-3-phosphate dehydrogenase (GAPDH) alleles, and (C) 11 mtDNA control-region haplotypes. The 95% probability set of parsimony trees is illustrated with bold branches, with the size of the circle node corresponding to the frequency of each allele. Dashed lines indicate alternative branching patterns and possible reticulations. Small black circles indicate intermediate ancestral alleles that were not sampled.

Table 1. Estimates (± SD) of nucleotide (π) and haplotype (h) diversity for lamin A (LMNA), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), and mtDNA control region for Pacific Common Eiders sampled at islands in the western Beaufort Sea (Fig. 1). Fu's *Fs* and Tajima's *D* values in bold indicate significance (*Fs*, $P < 0.02$; *D*, $P < 0.05$).

	Spy	Long	"Wannabe" and Egg	Stump	Challenge and Alaska	Duchess	Mary Saches and North Star	Pt. Thomson	"Camp"
LMNA									
n	9	15	13	24	3	14	5	6	7
h	0.876 ± 0.045	0.915 ± 0.027	0.818 ± 0.052	0.849 ± 0.036	0.600 ± 0.215	0.884 ± 0.034	0.844 ± 0.103	0.864 ± 0.072	0.901 ± 0.047
π	0.008 ± 0.005	0.009 ± 0.006	0.007 ± 0.004	0.008 ± 0.005	0.005 ± 0.004	0.007 ± 0.005	0.005 ± 0.004	0.006 ± 0.004	0.009 ± 0.006
Fu's *Fs*	–1.896	**–4.943**	–3.033	–3.499	0.381	**–4.704**	**–2.690**	–2.004	–1.503
Tajima's *D*	0.070	–0.119	–0.126	–0.169	0.338	0.226	–0.682	–0.212	–0.147
GAPDH									
n	6	13	13	18	3	11	4	5	6
h	0.954 ± 0.047	0.886 ± 0.036	0.874 ± 0.032	0.900 ± 0.024	0.933 ± 0.122	0.909 ± 0.037	0.927 ± 0.084	0.911 ± 0.077	0.924 ± 0.058
π	0.007 ± 0.005	0.007 ± 0.004	0.006 ± 0.004	0.006 ± 0.004	0.008 ± 0.006	0.006 ± 0.004	0.007 ± 0.005	0.009 ± 0.006	0.006 ± 0.004
Fu's *Fs*	–2.162	–0.996	–0.773	–2.850	–1.466	**–3.602**	–0.930	–0.907	–1.584
Tajima's *D*	–0.964	–0.306	–0.836	–0.853	–0.631	–0.989	–0.856	–0.810	–0.323
MtDNA									
n	7	13	13	19	3	11	5	6	6
h	0.000 ± 0.000	0.654 ± 0.106	0.526 ± 0.152	0.579 ± 0.114	0.667 ± 0.314	0.891 ± 0.063	0.400 ± 0.237	0.800 ± 0.172	0.333 ± 0.215
π	0.000 ± 0.000	0.003 ± 0.002	0.003 ± 0.002	0.003 ± 0.002	0.001 ± 0.001	0.009 ± 0.005	0.001 ± 0.001	0.007 ± 0.004	0.002 ± 0.002
Fu's *Fs*	—	0.399	0.868	0.183	0.201	0.543	0.090	0.567	2.139
Tajima's *D*	0.000	–1.249	–0.167	–0.869	0.000	0.591	–0.817	–0.516	–1.295

Population Structure

Microsatellites.—After removing mother–offspring groups and identical genotypes ($n = 18$) at 14 microsatellite loci, the overall F_{ST} (0.004, $P < 0.01$) was significant. The upper limit of F_{ST} calculated with RECODEDATA was 0.408. Therefore, the overall F_{ST} of 0.004 accounts for 1.0% of the maximum possible level of genetic structure. We did not observe a significant level of differentiation using R_{ST} (0.004, $P > 0.05$). Significant differences in allelic frequencies were observed within and among island groups on the basis of F_{ST} (0.007–0.016; Table 2). No significant comparisons were observed among adjacent islands. The regional comparison between Mikkelsen Bay and Simpson Lagoon was also significant ($F_{ST} = 0.004$; Table 3). The significant F_{ST} values we observed, albeit low, are noteworthy given the geographic proximity of the islands (1.2–143 km apart; Wright 1951). Hierarchical analyses of molecular variance uncovered low but significant variance within islands, among islands within a group, and within individuals (Table 3). We found no evidence of isolation-by-distance correlations between genetic and geographic distances ($r = 0.012$, $P = 0.46$).

Nuclear introns.—Significant differences in the spatial distribution of allelic frequencies were observed for LMNA among islands (overall $\Phi_{ST} = 0.023$, $P = 0.02$), between Mikkelsen Bay and Simpson Lagoon ($\Phi_{ST} = 0.022$; Table 3), and among islands within these waters ($\Phi_{ST} = 0.089–0.173$; Table 4). AMOVA analyses also detected significant variance among islands within island groups, within islands, among individuals within islands, and within individuals (Table 3). This pattern appears to be driven by a single C/T nucleotide polymorphism at one of 14 polymorphic positions in LMNA: site 116 ($F_{ST} = 0.153 \pm 0.084$ between Mikkelsen Bay and Simpson Lagoon). Pairwise F_{ST} comparisons among islands ranged from 0.053 to 0.352 (Table 4). However, site 116 was monomorphic for all islands in Mikkelsen Bay.

No population structure was observed for GAPDH (overall $\Phi_{ST} = -0.071$, $P = 0.94$; Table 3). As with the microsatellite data, we detected no significant correlations between genetic and geographic distances for LMNA and GAPDH combined ($r = 0.096$, $P = 0.28$) or analyzed separately (LMNA $r = -0.012$, $P = 0.050$; GAPDH $r = 0.142$, $P = 0.20$).

Mitochondrial DNA.—AMOVA analysis detected significant variance within islands and among islands within each island group (Table 3). Mean inter-island variance in haplotypic frequency was low but significant ($\Phi_{ST} = 0.070$, $P = 0.05$). Regional comparison between Mikkelsen Bay and Simpson Lagoon was also significant ($\Phi_{ST} = 0.082$, $P < 0.05$; Table 3). High levels of genetic discordance were observed between Duchess Island, located in Mikkelsen Bay, and all four islands located in Simpson Lagoon ($\Phi_{ST} = 0.135–0.271$; Table 2).

Estimates of Gene Flow

Asymmetrical dispersal was observed between Mikkelsen Bay and Simpson Lagoon across all three marker types, and the full model (all parameters allowed to vary independently) was found to have significantly higher likelihoods than the restricted island model (equal interpopulation migration rate and equal θ across populations; Table 5). The biases in the variances and the means indicate that, on average over generations, gene flow has been greater from Mikkelsen Bay to Simpson Lagoon (east to west) than vice

TABLE 2. Pairwise inter-island F_{ST} calculated from 14 microsatellite loci (above diagonal) and pairwise inter-island ϕ_{ST} calculated from mtDNA control region (below diagonal) for Pacific Common Eiders breeding in the western Beaufort Sea, Alaska. Significant comparisons ($\alpha = 0.05$) are in bold.

Islands	Spy	Long	Egg	"Wannabe"	Stump	Challenge	Alaska	Duchess	North Star	Mary Saches	Pt. Thomson	"Camp"
Spy	—	**0.009**	**0.010**	0.000	0.008	**0.012**	0.007	0.000	**0.016**	0.007	0.007	0.008
Long	0.029	—	0.006	0.001	0.005	**0.016**	**0.010**	0.001	**0.014**	0.002	0.001	0.007
Egg				0.002	−0.003	0.000	0.002	0.003	**0.008**	0.013	0.000	0.003
"Wannabe"	0.068	0.037	—	—	0.001	0.008	0.003	−0.007	0.011	0.006	−0.010	−0.004
Stump	0.008	−0.023	−0.010	NA	—	0.007	**0.007**	0.001	0.003	0.013	−0.002	0.000
Challenge						—	0.002	0.006	0.013	0.013	−0.001	0.007
Alaska	0.300	−0.199	−0.002	NA	−0.141	NA	—	0.002	0.001	0.006	−0.003	0.004
Duchess	**0.271**	**0.230**	**0.135**	NA	**0.183**	NA	0.116	—	0.007	0.002	−0.004	0.002
North Star									—	0.017	0.004	0.002
Mary Saches	0.073	−0.095	0.040	NA	−0.066	NA	−0.299	0.201	NA	—	−0.002	**0.020**
Pt. Thomson	0.127	0.026	−0.082	NA	−0.024	NA	−0.174	−0.024	NA	0.032	—	−0.005
"Camp"	0.028	0.000	−0.082	NA	−0.083	NA	−0.058	0.097	NA	−0.018	−0.085	—

TABLE 3. Hierarchical nested analyses of molecular variance (AMOVA) of allelic and haplotypic frequencies (LMNA = lamin A, GAPDH = glyceraldehyde-3-phosphate dehydrogenase, and μsats = microsatellite loci) for Pacific Common Eiders sampled from islands within Mikkelsen Bay and Simpson Lagoon. Significant comparisons ($P < 0.05$) are in bold.

Sources of variation	μsats	LMNA	GAPDH	MtDNA
Among groups (F_{CT})	0.001	−0.003	−0.000	0.028
Among islands within groups (F_{SC})	**0.004**	**0.025**	−0.019	**0.055**
Within populations (F_{ST})	**0.004**	**0.022**	−0.019	**0.082**
Among individuals within islands (F_{IS})	0.014	**0.682**	0.073	—
Within individuals (F_{IT})	**0.019**	**0.678**	0.051	—

versa (Table 5). N_em and θ ($4N_e\mu$) values calculated in MIGRATE from microsatellite genotypes, mtDNA, and nuclear intron sequence data ranged from 5.1 to 24.2 migrants per generation from Simpson Lagoon to Mikkelsen Bay, with θ ranging from 0.001 to 0.683, and from 24.4 to 34.2 migrants per generation from Mikkelsen Bay to Simpson Lagoon, with θ ranging from 0.006 to 0.635 (Table 5).

Female Site Fidelity

Using GIMLET, we calculated an overall PID of 3.2×10^{-12} for a population composed of randomly mating individuals and 5.3×10^{-5} for siblings using genotypes collected from 14 microsatellite loci. These denominator values are much larger than the population breeding on islands in the western Beaufort Sea (~660 nests found on the islands; Noel et al. 2005), which gave us confidence that identical genotypes for samples taken in different years were from the same individual.

Throughout the course of the four-year study, 34 females were detected breeding in multiple years (based on observations of banded individuals and genetic techniques). Most ($n = 21$ of 34; 62%) nested on the same islands, whereas 13 (38%) moved to a new island within the same island group. Inter-nest distances between breeding attempts ranged from 1.1 to 12.1 km on the basis of observations using band CMR data (J. Reed unpubl. data) and from 1.1 to 12.5 km on the basis of a comparison of genetic samples. We found no evidence of female dispersal between Mikkelsen Bay and Simpson Lagoon island groups. Females that dispersed to a different nest site between years generally moved to an adjacent island within the same island group to breed (9 of 13, or 69%). However, three females breeding in Mikkelsen Bay moved from islands in the ocean to islands near the coast (Alaska Island to Pt. Thomson Island, 12.1 km and 12.5 km; Duchess Island to "Camp Island," 10.2 km; Fig. 1). One female breeding in Simpson Lagoon dispersed three islands east of its original nest site (Long Island to Stump Island, 10.0 km).

DISCUSSION

Population genetic structure.—Population subdivision was observed in three types of genetic markers in the Pacific Common Eiders sampled in the western Beaufort Sea. Higher levels of spatial structure were observed at maternally inherited mtDNA than at biparentally inherited nuclear introns and microsatellite loci for inter-island comparisons, which is consistent with our prediction

Table 4. Pairwise inter-island ϕ_{ST} values calculated for lamin A (complete sequence below diagonal and site 116 above diagonal) for Pacific Common Eiders breeding on islands in the western Beaufort Sea, Alaska. Significant comparisons ($\alpha = 0.05$) are in bold.

	Simpson Lagoon				Mikkelsen Bay				
Islands	Spy	Long	"Wannabe" and Egg	Stump	Alaska and Challenge	Duchess	Mary Saches and North Star	Pt. Thomson	"Camp"
Spy	—	−0.086	**0.284**	**0.352**	**0.053**	**0.330**	**0.151**	**0.182**	0.208
Long	0.022	—	**0.169**	0.217	−0.006	**0.205**	0.078	0.102	0.121
"Wannabe" and Egg	**0.106**	0.025	—	−0.024	−0.091	−0.007	−0.050	−0.040	−0.032
Stump	**0.092**	0.022	−0.012	—	−0.092	−0.012	−0.051	−0.042	−0.035
Alaska and Challenge	**0.148**	0.024	−0.042	0.003	—	—	—	—	—
Duchess	0.053	0.007	−0.002	−0.007	0.024	—	—	—	—
Mary Saches and North Star	0.033	0.003	0.003	−0.025	0.119	−0.029	—	—	—
Pt. Thomson	**0.089**	0.024	0.059	0.037	**0.173**	0.009	0.034	—	—
"Camp"	0.052	0.026	0.027	0.074	0.088	0.001	−0.007	−0.034	—

and known patterns of male-biased dispersal (Swennen 1990). We observed higher differentiation among colonies separated by similar geographic distance than that reported in European Common Eiders in the Baltic Sea (Tiedemann et al. 1999) and Pacific Common Eiders in the Yukon-Kuskokwim Delta (Sonsthagen et al. 2007). Tiedemann et al. (1999) proposed that differences in migration phenology among geographic regions coupled with a selective advantage for early pair formation were the main mechanisms promoting genetic subdivision among populations in the Baltic Sea. These mechanisms may not provide a satisfactory explanation in our study area, because differences in migratory phenology do not appear to occur among island groups, and satellite telemetry data indicate that there is no difference in the start of autumn migration among Common Eiders breeding in northern and western Alaska (~1,250 km apart; Petersen and Flint 2002). Lack of differences in migration phenology may explain, in part, the lower levels of differentiation observed at nuclear markers, because Common Eiders from different island groups likely admix on the wintering grounds.

We observed higher levels of population structure at mtDNA. Population subdivision was observed between Duchess Island, located in Mikkelsen Bay, and all islands located in Simpson Lagoon. Although we did not detect significant pairwise comparisons among all islands in Mikkelsen Bay and Simpson Lagoon, we believe that the structuring observed is noteworthy given that Duchess Island is the only island that contains a colony of breeding Common Eiders in Mikkelsen Bay. Nests on the other islands in Mikkelsen Bay were scattered thinly, with relatively few nests per island. The presence of a colony on Duchess Island is likely driving the significant pairwise comparisons observed at this marker, given that when Duchess Island was removed from the analysis the overall Φ_{ST} was no longer significant (mtDNA $\Phi_{ST} = -0.018$, $P = 0.61$). Common Eiders are typically colonial nesters (Goudie et al. 2000), and the low-density nesters in Mikkelsen Bay could be "overflow" from Duchess Island, though demographic data are needed to support this hypothesis. Although there also are colonies on three islands in Simpson Lagoon (Egg, Long, and Stump islands), these colonies occur on islands that are adjacent to each other (within several hundred meters) and, thus, unlikely to become genetically isolated because birds may disperse among islands. Although we do not have natal-dispersal data for this population, we have breeding-dispersal distances from recaptured individuals. Given that no breeding females were observed dispersing between Mikkelsen Bay and Simpson Lagoon, we hypothesize that females breeding in the western Beaufort Sea are strongly philopatric to island groups rather than to a particular island. This differs from observations of *S. m. dresseri* breeding

Table 5. Comparison of alternative models of gene flow between Pacific Common Eiders in Mikkelsen Bay and Simpson Lagoon. Full-model migration matrix (allowing all parameters to vary independently) and restricted-model (symmetrical gene flow) migration rates calculated from 14 microsatellite loci, nuclear introns lamin A and glyceraldehyde-3-phosphate dehydrogenase, and mtDNA control region, were evaluated for significance using a log likelihood ratio test (df = 4). Ninety-five percent confidence intervals are in parentheses.

				Simpson Lagoon to Mikkelsen Bay		Mikkelsen Bay to Simpson Lagoon	
Marker	Hypothesis	Ln(L)	*P*	*Nfm* or *Nem*	θ	*Nfm* or *Nem*	θ
Microsatellites	Full	−8,782.1	<0.001	18.8 (17.8–20.3)	0.683 (0.650–0.717)	27.1 (25.4–29.6)	0.635 (0.612–0.659)
	Restricted	−8,888.0		78.3	2.247	78.3	2.247
MtDNA	Full	1.9	<0.001	5.1 (0.9–28.1)	0.001 (0.000–0.002)	24.4 (2.4–95.9)	0.006 (0.005–0.015)
	Restricted	−12.0		12.3	0.003	12.3	0.003
Nuclear introns	Full	−401.8	<0.001	24.2 (18.6–31.5)	0.003 (0.003–0.004)	34.2 (26.7–43.7)	0.010 (0.009–0.011)
	Restricted	−468.9		22.3	0.006	22.3	0.006

in Maine (Wakeley and Mendall 1976). Distances among islands in Maine are similar to those observed in our study (1.7–24.3 km apart); however, 71% of females returned to their previous breeding island, and only 2% dispersed to neighboring islands, compared with the 38% observed in our study (Wakeley and Mendall 1976). Over many generations, females dispersing among neighboring islands would have a homogenizing effect within island groups, while maintaining population subdivision between island groups.

Behavioral responses to a stochastic Arctic environment may play a role in the inferred degree of breeding philopatry we observed between populations in Maine and the Beaufort Sea. Common Eider nests in the western Beaufort Sea are associated with driftwood (Goudie et al. 2000, Johnson 2000), and changes in driftwood distribution and abundance will affect where Common Eiders nest. Storms dramatically modify the shape and topography of these barrier islands, thus changing where available habitat is located annually (Noel et al. 2005). Finally, Common Eiders breeding on the Beaufort Sea postpone nesting attempts until the island is surrounded by open water, reducing predation risk (Schamel 1977). Islands located in the same vicinity may not be surrounded by water at the same time (S. Sonsthagen pers. obs.). Therefore, in years when ice break-up is late, Common Eiders may initiate nesting on the first "suitable" island, regardless of where they nested in previous years or where they hatched, because of the presumed selective advantage of nesting early (Milne 1974).

The population structure observed in the present study also was likely influenced by differences in the rates of lineage sorting between the nuclear and mitochondrial genomes (Avise 2004). Mitochondrial DNA has a lower effective population size than nuclear DNA. Thus, genetic drift has a larger effect on mtDNA than on nuclear DNA (Avise 2004), which translates 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 play a role in the degree of population structure observed.

Gene flow.—We do not completely understand the factors that influence the degree of migratory and homing behavior in this species. Common Eiders appear to move the minimum distance to wintering areas (Petersen and Flint 2002), and the degree of movement is likely environmentally induced (Swennen 1990). This may explain, in part, the directionality of gene flow observed. Microsatellite, nuclear intron, and mtDNA loci all indicate significant asymmetrical gene flow, such that, on average, more individuals dispersed from Mikkelsen Bay to Simpson Lagoon (i.e., east to west). Because islands become ice-free about two weeks earlier in Simpson Lagoon than in Mikkelsen Bay (Schamel 1977), female Common Eiders from Mikkelsen Bay may benefit from short-stopping migration and initiating nests at Simpson Lagoon, enabling them to hatch broods sooner. Should these females successfully hatch young, they may be more likely to nest in Simpson Lagoon in succeeding years (Milne 1974). Thus, earlier nest initiation and previous nest success may be factors that influence females that hatched in Mikkelsen Bay to breed in Simpson Lagoon and to return there in successive years. The relatively earlier ice break-up in Simpson Lagoon may have driven the westward bias in dispersal.

Alternatively, Common Eiders may be dispersing west because of the more abundant and broader distribution of available nesting habitat in Simpson Lagoon (based on number of nests found in each island group between 1998 and 2002 [Noel et al. 2005] and driftwood distribution [R. Lanctot and S. Sonsthagen pers. obs.]). This differential distribution of nesting habitat may especially affect first-time breeding females from Mikkelsen Bay that tend to arrive later from the wintering grounds (Johnson et al. 1992), because females arriving earlier on the breeding grounds may have already secured suitable nest sites.

Comparison with other waterfowl.—The fine-scaled spatial genetic structuring we observed in Pacific Common Eiders breeding on island groups 90 km apart in the western Beaufort Sea is noteworthy, especially when compared with other Arctic-nesting waterfowl. King Eiders (*S. spectabilis*) sampled from Russia, Alaska, and Canada exhibited evidence of high levels of dispersal among western and eastern Arctic populations using mtDNA and six nuclear microsatellite loci (Pearce et al. 2004). Among Harlequin Duck (*Histrionicus histrionicus*) populations that breed in Alaska, no evidence of genetic discordance among sampled sites was found in analyses of four autosomal microsatellite loci, two Z-specific microsatellite loci, and mtDNA (Lanctot et al. 1999). Lack of structure was attributed to recent range expansion. Steller's Eiders (*Polysticta stelleri*) that breed in Alaska and Russia exhibit low population subdivision at nuclear markers (Pearce et al. 2005). However, estimates based on mtDNA were not significant. Scribner et al. (2001) documented high levels of differentiation in mtDNA among sampled sites in Spectacled Eiders (*S. fisheri*), but they did not detect any differences in allelic frequencies at autosomal or Z-linked microsatellite loci. Canada Geese (*Branta canadensis*) exhibit high levels of genetic differentiation among sampled sites at autosomal and Z-linked microsatellite loci and mtDNA (Scribner et al. 2003). Several recent studies of dabbling ducks (*Anas* spp.) also have shown a range of differentiation at continental scales (Kulikova et al. 2005, Peters et al. 2008, McCracken et al. 2009). Although these studies all documented significant differences in gene frequencies among sampled sites, they were conducted at much larger spatial scales than our study.

Conclusion.—Oil and gas development has occurred and is being planned for barrier islands where Common Eiders currently nest in the Beaufort Sea. We observed females dispersing ≤12.5 km between years to nest. Thus, females may exhibit some plasticity in choosing their nesting sites; however, it is unclear how much plasticity occurs at the population level. The presence of microgeographic genetic structure between the island groups for all marker types assayed in the present study indicates that this plasticity may be limited. Furthermore, it is unclear how much genetic variation might be lost should these barrier-island populations be extirpated. Additional genetic analyses are needed to quantify the genetic diversity and levels of population structure present across the Pacific Common Eider's entire breeding range.

Acknowledgments

Funding was provided by Mineral Management Service (1435-01-98-CA-309) through the Coastal Marine Institute, University of Alaska Fairbanks, U.S. Geological Survey, Alaska EPSCoR Graduate Fellowship (NSF EPS-0092040), University of Alaska Foundation Angus Gavin Migratory Bird Research Fund, and BP Exploration (Alaska), Inc. We thank all the U.S. Geological Survey researchers and biologists that worked on the Beaufort

Sea Common Eider project, especially P. Flint, J. C. Franson, D. LaCroix, and J. Reed, as well as J. Gust and G. K. Sage, who provided laboratory assistance. J. Gleason, C. Monnett, J. Pearce, M. Petersen, and J. Gust, U.S. Geological Survey, and three anonymous reviewers provided valuable comments on earlier drafts of the manuscript. MIGRATE software and documentation are available from P. Beerli at popgen.scs.fsu.edu/migrate.download.html. NETWORK is available at www.fluxus-engineering.com. FSTAT is available from J. Goudet at www2.unil.ch/popgen/softwares/fstat.htm.

Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Anderson, M. G., J. M. Rhymer, and F. C. Rohwer. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 *in* Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Avise, J. C. 1996. Three fundamental contributions of molecular genetics to avian ecology and evolution. Ibis 138:16–25.

Avise, J. C. 2004. Molecular Markers, Natural History, and Evolution, 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

Baker, A. J., and H. D. Marshall. 1996. Mitochondrial control region sequences as tools for understanding evolution. Pages 51–79 *in* Avian Molecular Evolution and Systematics (D. Mindell, Ed.). Academic Press, San Diego, California.

Bandelt, H.-J., P. Forster, B. C. Sykes, and M. B. Richards. 1995. Mitochondrial portraits of human populations using median networks. Genetics 141:743–753.

Beerli, P., and J. Felsenstein. 1999. Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. Genetics 152:763–773.

Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. Proceedings of the National Academy of Sciences USA 98:4563–4568.

Bohonak, A. J. 2002. IBD (isolation by distance): A program for analyses of isolation by distance. Journal of Heredity 93:153–154.

Buchholz, W. G., J. M. Pearce, B. J. Pierson, and K. T. Scribner. 1998. Dinucleotide repeat polymorphisms in waterfowl (family Anatidae): Characterization of a sex-linked (Z-specific) and 14 autosomal loci. Animal Genetics 29:323–325.

Eberhardt, L. E., W. C. Hanson, J. L. Bengtson, R. A. Garrott, and E. E. Hanson. 1982. Arctic fox home range characteristics in an oil-development area. Journal of Wildlife Management 46:183–190.

Fu, Y.-X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925.

Goudet, J. 1995. FSTAT (version 1.2): A computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

Goudie, M. L., G. J. Robertson, and A. Reed. 2000. Common Eider (*Somateria mollissima*). *In* The Birds of North America, no. 546 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Hedrick, P. W. 2005. A standardized genetic differentiation measure. Evolution 59:1633–1638.

Johnson, D. H., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446–485 *in* Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Johnson, S. R. 2000. Pacific Eider. Pages 259–275 *in* The Natural History of an Arctic Oil Field: Development and the Biota (J. C. Truett and S. R. Johnson, Eds.). Academic Press, San Diego, California.

Kulikova, I. V., S. V. Drovetski, D. D. Gibson, R. J. Harrigan, S. Rohwer, M. D. Sorenson, K. Winker, Y. N. Zhuravlev, and K. G. McCracken. 2005. Phylogeography of the Mallard (*Anas platyrhynchos*): Hybridization, dispersal, and lineage sorting contribute to complex geographic structure. Auk 122:949–965.

Lanctot, R., B. Goatcher, K. Scribner, S. Talbot, B. Pierson, D. Esler, and D. Zwiefelhofer. 1999. Harlequin Duck recovery from the Exxon Valdez oil spill: A population genetics perspective. Auk 116:781–791.

Longmire, J. L., A. K. Lewis, N. C. Brown, J. M. Buckingham, L. M. Clark, M. D. Jones, L. J. Meincke, J. Meyne, R. L. Ratliff, F. A. Ray, and others. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics 2:14–24.

Maak, S., K. Neumann, G. von Lengerken, and R. Gattermann. 2000. First seven microsatellites developed for the Peking Duck (*Anas platyrhynchos*). Animal Genetics 31:233.

Maak, S., K. Wimmers, S. Weigend, and K. Neumann. 2003. Isolation and characterization of 18 microsatellites in the Peking Duck (*Anas platyrhynchos*) and their application in other waterfowl species. Molecular Ecology Notes 3:224–227.

McCracken, K. G., M. Bulgarella, K. P. Johnson, M. K. Kuhner, J. Trucco, T. H. Valqui, R. E. Wilson, and J. L. Peters. 2009. Gene flow in the face of countervailing selection: Adaptation to high-altitude hypoxia in the βA hemoglobin subunit of Yellow-billed Pintails in the Andes. Molecular Biology and Evolution 26:815–827.

McCracken, K. G., and M. D. Sorenson. 2005. Is homoplasy or lineage sorting the source of incongruent mtDNA and nuclear gene trees in the stiff-tailed ducks (*Nomonyx–Oxyura*)? Systematic Biology 54:35–55.

Medrano, J. F., E. Aasen, and L. Sharrow. 1990. DNA extraction from nucleated red blood cells. Biotechniques 8:43.

Meirmans, P. G. 2006. Using the AMOVA framework to estimate a standardized genetic differentiation measure. Evolution 60:2399–2402.

Milne, H. 1974. Breeding numbers and reproductive rate of eiders at the Sands of Forvie National Nature Reserve, Scotland. Ibis 116:135–154.

Minerals Management Service. 2003. Alaska Annual Studies Plan Final FY 2004. U.S. Department of the Interior, Minerals Management Service, Alaska Outer Continental Shelf Region, Anchorage, Alaska.

Noel, L. E., S. R. Johnson, G. M. O'Doherty, and M. K. Butcher. 2005. Common Eider (*Somateria mollissima*) nest

cover and depredation on central Alaskan Beaufort Sea barrier islands. Arctic 58:129–136.

Paulus, K. B., and R. Tiedemann. 2003. Ten polymorphic autosomal microsatellite loci for the eider duck *Somateria mollissima* and their cross-species applicability among waterfowl species (Anatidae). Molecular Ecology Notes 3:250–252.

Pearce, J. M., S. L. Talbot, M. R. Petersen, and J. R. Rearick. 2005. Limited genetic differentiation among breeding, molting, and wintering groups of threatened Steller's Eider: The role of historic and contemporary factors. Conservation Genetics 6:743–757.

Pearce, J. M., S. L. Talbot, B. J. Pierson, M. R. Petersen, K. T. Scribner, D. L. Dickson, and A. Mosbech. 2004. Lack of spatial genetic structure among nesting and wintering King Eiders. Condor 106:229–240.

Peters, J. L., Y. N. Zhuravlev, I. Fefelov, E. M. Humphries, and K. E. Omland. 2008. Multilocus phylogeography of a Holarctic duck: Colonization of North America from Eurasia by Gadwall (*Anas strepera*). Evolution 62:1469–1483.

Petersen, M. R., and P. L. Flint. 2002. Population structure of Pacific Common Eiders breeding in Alaska. Condor 104:780–787.

Posada, D., and K. A. Crandall. 1998. MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817–818.

Reed, A. 1975. Migration, homing, and mortality of breeding female eiders *Somateria mollissima dresseri* of the St. Lawrence estuary, Quebec. Ornis Scandinavica 6:41–47.

Rohwer, F. C., and M. G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Pages 187–221 *in* Current Ornithology, vol. 5 (D. M. Power, Ed.). Plenum Press, New York.

Rozas, J., J. C. Sánchez-DelBarrio, X. Messeguer, and R. Rozas. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19:2496–2497.

Sayler, J. W. 1962. A bow-net trap for ducks. Journal of Wildlife Management 26:219–221.

Schamel, D. 1977. Breeding of the Common Eider (*Somateria mollissima*) on the Beaufort Sea Coast of Alaska. Condor 79:478–485.

Schneider, S., D. Roessli, and L. Excoffier. 2000. ARLEQUIN, version 2.0: A software for population genetic data analysis. Genetics and Biometry Laboratory, University of Geneva, Geneva, Switzerland.

Scribner, K. T., M. R. Petersen, R. L. Fields, S. L. Talbot, J. M. Pearce, and R. K. Chesser. 2001. Sex-biased gene flow in Spectacled Eiders (Anatidae): Inferences from molecular markers with contrasting modes of inheritance. Evolution 55:2105–2115.

Scribner, K. T., S. L. Talbot, J. M. Pearce, B. J. Pierson, K. S. Bollinger, and D. V. Derksen. 2003. Phylogeography of Canada Geese (*Branta canadensis*) in western North America. Auk 120:889–907.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman, New York.

Sonsthagen, S. A., S. L. Talbot, and K. G. McCracken. 2007. Genetic characterization of Common Eiders breeding in the Yukon-Kuskokwim Delta, Alaska. Condor 109:878–893.

Sonsthagen, S. A., S. L. Talbot, and C. M. White. 2004. Gene flow and genetic characterization of Northern Goshawks breeding in Utah. Condor 106:826–836.

Sorenson, M. D., and R. C. Fleischer. 1996. Multiple independent transpositions of mitochondrial DNA control region sequences to the nucleus. Proceedings of the National Academy of Sciences USA 93:15239–15243.

Stephens, M., N. Smith, and P. Donnelly. 2001. A new statistical method for haplotype reconstruction from population data. American Journal of Human Genetics 68:978–989.

Suydam, R. S., D. L. Dickson, J. B. Fadely, and L. T. Quakenbush. 2000. Population declines of King and Common eiders of the Beaufort Sea. Condor 102:219–222.

Swennen, C. 1990. Dispersal and migratory movements of eiders *Somateria mollissima* breeding in The Netherlands. Ornis Scandinavica 21:17–27.

Tajima, F. 1989. The effect of change in population size on DNA polymorphism. Genetics 123:597–601.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

Tiedemann, R., and K. G. von Kistowski. 1998. Novel primers for the mitochondrial control region and its homologous nuclear pseudogene in the eider duck *Somateria mollissima*. Animal Genetics 29:468.

Tiedemann, R., K. G. von Kistowski, and H. Noer. 1999. On sex-specific dispersal and mating tactics in the Common Eider *Somateria mollissima* as inferred from the genetic structure of breeding colonies. Behaviour 136:1145–1155.

Valière, N. 2002. GIMLET: A computer program for analysing genetic individual identification data. Molecular Ecology Notes 2:377–379.

Wakeley, J. S., and H. L. Mendall. 1976. Migrational homing and survival of adult female eiders in Maine. Journal of Wildlife Management 40:15–21.

Winker, K., G. R. Graves, and M. J. Braun. 2000. Genetic differentiation among populations of a migratory songbird: *Limnothlypis swainsonii*. Journal of Avian Biology 31:319–328.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics 15:323–354.

Associate Editor: D. B. McDonald