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Spatial Genetic Structure of Long-tailed Ducks (*Clangula hyemalis*) among Alaskan, Canadian, and Russian Breeding Populations

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ABSTRACT. Arctic ecosystems are changing at an unprecedented rate. How Arctic species are able to respond to such environmental change is partially dependent on the connections between local and broadly distributed populations. For species like the Long-tailed Duck (*Clangula hyemalis*), we have limited telemetry and band-recovery information from which to infer population structure and migratory connectivity; however, genetic analyses can offer additional insights. To examine population structure in the Long-tailed Duck, we characterized variation at mtDNA control region and microsatellite loci among four breeding areas in Alaska, Canada, and Russia. We observed significant differences in the variance of mtDNA haplotype frequencies between the Yukon-Kuskokwim Delta (YKD) and the three Arctic locations (Arctic Coastal Plain in Alaska, eastern Siberia, and central Canadian Arctic). However, like most sea duck genetic assessments, our study found no evidence of population structure based on autosomal microsatellite loci. Long-tailed Ducks use multiple wintering areas where pair formation occurs with some populations using both the Pacific and Atlantic Oceans. This situation provides a greater opportunity for admixture across breeding locales, which would likely homogenize the nuclear genome even in the presence of female philopatry. The observed mtDNA differentiation was largely due to the presence of two divergent clades: (A) a clade showing signs of admixture among all breeding locales and (B) a clade primarily composed of YKD samples. We hypothesize that the pattern of mtDNA differentiation reflects some degree of philopatry to the YKD and isolation of two refugial populations with subsequent expansion and admixture. We recommend additional genetic assessments throughout the circumpolar range of Long-tailed Ducks to further quantify aspects of genetic diversity and migratory connectivity in this species.

Key words: *Clangula hyemalis*; Long-tailed Duck; philopatry; population genetic structure

RÉSUMÉ. Les écosystèmes de l’Arctique connaissent des changements sans précédent. La façon dont les espèces de l’Arctique réussissent à réagir aux changements environnementaux dépend, en partie, des liens entre les populations locales et les populations largement réparties. Dans le cas d’une espèce comme le harelde kakawi (*Clangula hyemalis*), nous disposons de peu de données de télémesure et de données prélevées au moyen des bagues pour déduire la structure de la population et la connectivité des déplacements migratoires. Les analyses génétiques peuvent toutefois offrir des connaissances supplémentaires. Afin d’examiner la structure de la population de hareldes kakawis, nous avons caractérisé la variation de la région de contrôle de l’ADNmt et des locus microsatellitaires de quatre aires de reproduction de l’Alaska, du Canada et de la Russie. Nous avons observé d’importantes différences en ce qui a trait à l’écart des fréquences de l’haplotype de l’ADNmt entre le delta Yukon-Kuskokwim (DYK) et les trois emplacements de l’Arctique (plaine côtière de l’Arctique en Alaska, Sibérie de l’Est et Arctique canadien central). Cependant, comme dans le cas de la plupart des évaluations génétiques des canards de mer, notre étude n’a trouvé aucune preuve de la structure de la population basée sur les locus microsatellitaires autosomiques. Le harelde kakawi se sert de diverses aires d’hivernage pour la formation de couples, et certaines populations favorisent tant l’océan Pacifique que l’océan Atlantique. Cette situation fournit de plus grandes possibilités de mélanges dans les lieux de reproduction, ce qui aurait vraisemblablement pour effet d’homogénéiser le génome nucléaire même en présence de la philopatrie chez les femelles. La différenciation observée de l’ADNmt était grandement attribuable à la présence de deux clades divergents : (A) un clade affichant des signes de mélange parmi tous les lieux de reproduction et (B) un clade principalement composé d’échantillons du DYK. Nous formulons l’hypothèse que le modèle de la différenciation de l’ADNmt reflète un certain degré de philopatrie dans le cas du DYK et l’isolement de deux populations réfugiales avec expansion et mélange subséquents. Nous recommandons la réalisation d’évaluations génétiques supplémentaires à l’échelle du domaine circumpolaire des hareldes kakawis afin d’être mieux en mesure de quantifier les aspects de la diversité génétique et de la connectivité des déplacements migratoires de cette espèce.

Mots clés : *Clangula hyemalis*; harelde kakawi; philopatrie; structure génétique de la population

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Резюме. Арктические экосистемы изменяются с беспрецедентной скоростью. Как арктические виды могут ответить на эти изменения окружающей среды частично зависит от взаимодействия локальных и широко распространенных популяций. Для таких видов, как утка морянка (*Clangula hyemalis*), с ограниченной информацией по телеметрии и данных по кольцеванию, генетический анализ может дать дополнительный взгляд на понимание популяционной структуры и миграционных связей. Для изучения популяционной структуры утки морянки мы показали генетическую изменчивость контрольного региона митохондриальной ДНК и микросателлитных локусов между четырьмя локальностями Аляски, Канады и России. Мы нашли значительное различие в дисперсии частот митохондриальных гаплотипов между локальностью в Дельте рек Юкон и Кускоквим (YKD) и тремя другими арктическими локальностями (арктическое побережье, восточная Сибирь и центральная канадская арктика). Однако, как и для большинства видов морских уток, мы не нашли подтверждения генетической структуры по аутосомным микросателлитным локусам. Морянки используют многочисленные места для зимовок, где происходит спаривание между особями популяций с Тихого и Атлантического океанов. Это дает большую возможность для смешения между местами размножения, которое, вероятно, стирает различия между ядерными геномами даже при наличии филопатрии у самок. Дифференциация по митохондриальной ДНК была обнаружена, в основном, за счет наличия двух дивергентных клад: клады (А), которая показывала признаки смешения между всеми локальностями для размножения, и клады (В), которая в основном состояла из особей YKD. Мы предполагаем, что такой характер дифференциации по митохондриальной ДНК отражает некоторую степень филопатрии к YKD и изоляции двух рефугиальных популяций с последующим распространеним и смешением. Мы рекомендуем дополнительные генетические исследования популяций утки морянки по всему приполярному ареалу для дальнейшего количественного анализа генетического разнообразия и миграционных связей этого вида.

Ключевые слова: *Clangula hyemalis*; Морянка; филопатрии; генетической структуры популяции

Перевёл Анна Горопашная Anya Goropashnaya.

INTRODUCTION

The climate is changing at an unprecedented rate, especially in the Arctic (Trenberth et al., 2007; Prowse et al., 2009), and these changes are predicted to continue in upcoming decades (IPCC, 2007). Environmental changes can have ecological consequences for species (Klenner and Aresenault, 2009) that can alter the connectivity between populations. Although the impact of environmental changes on population dynamics varies from species to species (see Gauthier and Berteaux, 2011; North American Bird Conservation Initiative Canada, 2012; Macdonald et al., 2012), changes in connectivity, via changes in migratory patterns or distributions, can ultimately affect how species are genetically structured across their range, or alter the genetic composition of locally adapted populations, or both. Understanding the level of sex-biased dispersal and connectivity among populations is an important aspect of conservation genetics (Haig et al., 2011) and can provide a better understanding of a species' flexibility in response to changes in the environment.

The degree of connectivity between local populations, and ultimately the evolutionary trajectories of each population, is dependent upon the level of interpopulational dispersal coupled with the potential for gene flow (effective dispersal; Waples and Gaggiotti, 2006). High effective dispersal can homogenize gene frequencies. However for migratory species, the return of individuals to their natal area (philopatry) and attendant fidelity to breeding areas is expected to restrict gene flow (Avise, 2000), which can lead to population differentiation despite countervailing dispersal. In addition, gender differences in degree of philopatry or dispersal can affect population genetic structure and the distribution of genetic diversity of a species (Fedy et al., 2008; Corrales and Höglund, 2012). Since levels of population structuring in migratory species depend at least in part on levels of philopatry in one or both sexes, investigations into levels of philopatry can inform hypotheses regarding migratory connectivity and population segregation (Scribner et al., 2001; Sonsthagen et al., 2011), especially for species with little-known migratory patterns, such as the Long-tailed Duck, *Clangula hyemalis* (Robertson and Savard, 2002; Petersen and Savard, 2015).

The Long-tailed Duck has a circumpolar distribution. It breeds in the tundra and taiga zones and winters primarily along the subarctic and temperate coastlines, as well as in the Great Lakes region of North America (Robertson and Savard, 2002; Mallory et al., 2006). Since the 1970s, Long-tailed Duck populations have declined by up to 50% in some breeding areas, in particular the Baltic Sea (Hodges et al., 1996; Dickson and Gilchrist, 2002; Bower, 2009; Skov et al., 2011). Although the reason for these declines remains unknown, they caused the species to be classified as "vulnerable" (BirdLife International, 2014). Over the last decade, population sizes in Alaska have remained stable on the Arctic Coastal Plain, but have declined significantly on the Yukon-Kuskokwim Delta (YKD) (Larned et al., 2012; Platte and Stehn, 2012; Flint, 2013). Despite these declines, the Long-tailed Duck remains the most abundant sea duck in North America.

The Long-tailed Duck is a short- to medium-distance migrant. Satellite telemetry data collected from birds breeding on the YKD (Petersen et al., 2003) and stable isotope analysis at Karrak Lake, Nunavut (Lawson, 2006), have

shown that female Long-tailed Ducks from the same breeding population use multiple wintering areas, which suggests weak migratory connectivity between single breeding and wintering areas. However, these studies assayed single populations only; other breeding areas have not been similarly examined, and thus levels of connectivity between wintering and breeding locations and among breeding areas are generally not well known (Robertson and Savard, 2002). Petersen et al. (2003) hypothesized that because pair formation occurs on wintering grounds, breeding areas should be connected via gene flow, homogenizing allele frequencies. However, females show some degree of breeding and wintering site fidelity (Alison, 1975; Robertson and Savard, 2002; Svazas et al., 2005; Sea Duck Joint Venture, 2012), which has been used as an indication of population structuring (but see Pearce et al., 2008). For species lacking detailed data on migratory patterns and levels of population structuring, genetic data can provide much needed insight into population connectivity and levels of philopatry both microgeographically and macrogeographically. Where breeding populations can be identified genetically, the same markers can be used to determine the origin of individuals in non-breeding aggregations (Pearce et al., 2000; Sonsthagen et al., 2014).

Here we test the degree of population differentiation among widespread sampling locations within the circumpolar distribution of the Long-tailed Duck. To evaluate whether breeding areas represent distinct lineages or form a panmictic population, we compared haplotypic frequencies from the maternally inherited mtDNA control region and allelic frequencies from 12 biparentally inherited autosomal microsatellite loci and two sex-linked microsatellite loci. The use of multiple markers with differing modes of inheritance facilitates greater understanding of the phylogeographic history of a species, since using only loci from one genome (mtDNA or nuclear) may not be consistent with the species' evolutionary history (Edwards and Bensch, 2009; Sonsthagen et al., 2009). For several taxa, multigene approaches have emphasized the role of sex-biased dispersal, which may not be evident when using a single marker type (e.g., Scribner et al., 2001; Illera et al., 2011; Peters et al., 2012; Dai et al., 2013). On the basis of Petersen et al. (2003) and Lawson (2006), who demonstrate that Long-tailed Ducks use multiple wintering areas where pair-formation occurs, we hypothesize that male-mediated gene flow will homogenize the populations. As a result, we predict that we will observe little or no population differentiation through analysis of the biparentally inherited microsatellite loci. However, assuming that high fidelity to breeding sites in females (Robertson and Savard, 2002) indicates philopatry, we predict that population subdivision, if it exists, would be observed in the maternally inherited mtDNA.

METHODS

Sample Collection

Long-tailed Ducks (n = 111) were sampled during summer from the two primary breeding locales within Alaska (the Arctic Coastal Plain and the YKD) and a representative locale in the central Canadian Arctic (Queen Maud Gulf Bird Sanctuary, Nunavut, Canada) (Fig. 1). On the Arctic Coastal Plain, blood (n = 26), feathers (n = 1), and one eggshell membrane (n = 1) were collected from nesting individuals or nests from Camp Island, Mary Sachs Island, and the Colville River Delta during other field research activities between 1998 and 2002 (K. Bollinger, pers. comm. 1998; Sonsthagen et al., 2009). On the YKD, blood (n = 61) and feathers (n = 3) were collected from nesting individuals or nests from the Kilbuk Mountains, Aropuk Lake, Kigigak Island, and Hock Slough, during mark-recapture studies (see Schamber et al., 2009). In addition, we sampled muscle from wings of spring migrants harvested on the Indigirka River Delta, Russia, from 3 to 13 June 1994. Bird surveys in that area found Long-tailed Duck nests beginning on June 22 in 1993 and June 25 in 1995 (J.M. Pearce, pers. comm. 2015). Given the date of collection and the fact that Long-tailed Ducks are known to nest in the greater Indigirka River Delta (Pearce et al., 1998), we assume that these spring samples represent a local population.

The sex of most samples was determined in the field by plumage and later confirmed by using the CHD molecular sexing protocol (Griffiths et al., 1998); however, six samples (three each from YKD and Queen Maud Gulf) failed to yield a product. Samples within Alaska were female-biased because they were collected as part of separate population dynamics studies that assessed, among other parameters, nest success and adult female survival (Schamber et al., 2009). As females are typically the more philopatric sex in waterfowl, analyzing a female-biased dataset allows for making inferences on female philopatry, whereas a male-biased sampling scheme may obscure any genetic signature of philopatry where males are the dispersing sex. Blood samples were taken from the jugular or tarsus veins and preserved in blood preservation buffer (Longmire et al., 1988). Feathers and eggshell membranes were stored dry at room temperature. All samples are archived at the Molecular Ecology Laboratory of the U.S. Geological Survey in Anchorage, Alaska.

Laboratory Techniques

Genomic DNA was extracted from blood, muscle, feather, or eggshell membranes using a "salting out" procedure described by Medrano et al. (1990) with modifications described in Sonsthagen et al. (2004) and from feathers and eggshell membranes using modifications outlined in Talbot et al. (2011). Genomic DNA concentrations were quantified using fluorometry and diluted to 50 ng mL^{-1} working solutions.

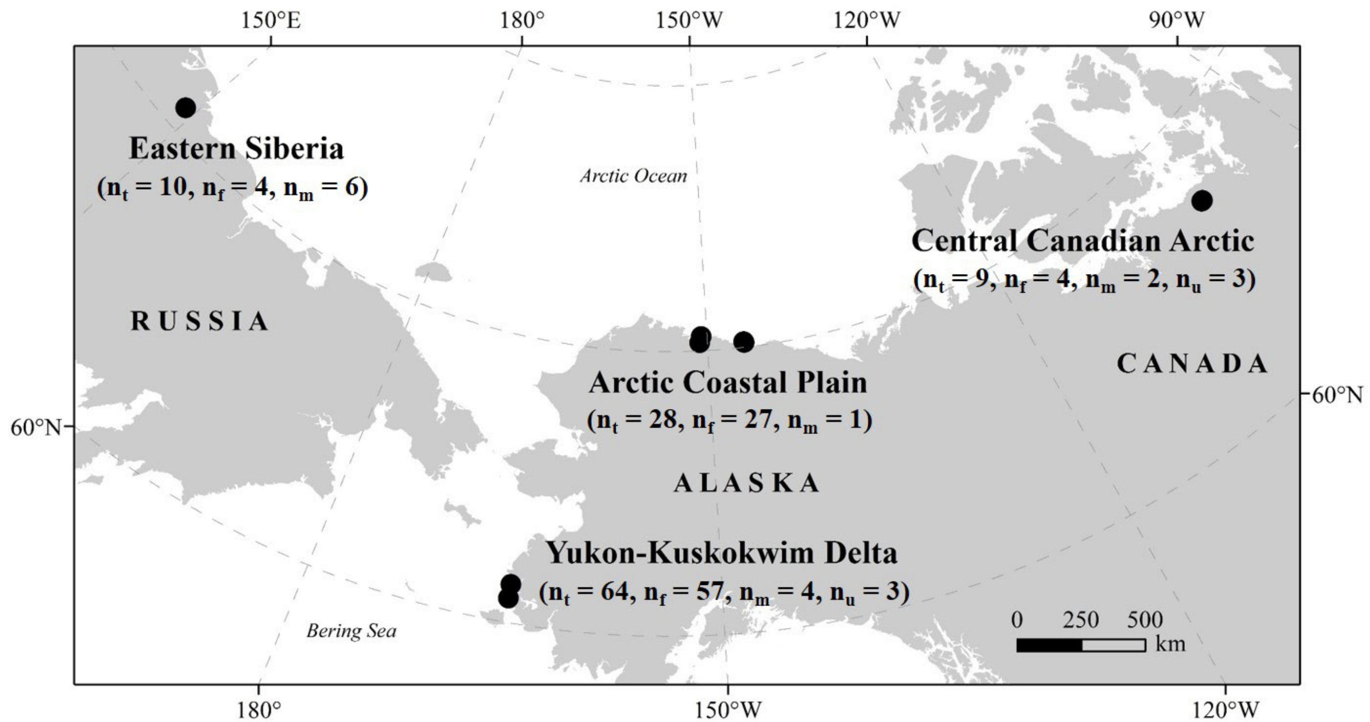

FIG 1. Sampling localities for Long-tailed Duck (*Clangula hyemalis*) used in this study, showing total sample size (n_t) and number of females (n_f), males (n_m), and unknown sex (n_u) sampled at each location.

Initially, 12 individuals were screened at 67 microsatellite loci known to be variable in other waterfowl species, namely Canada Goose (*Branta canadensis*; Buchholtz et al., 1998; Cathey et al., 1998; A. Baker, pers. comm. 2001); White-fronted Goose (*Anser albifrons*; Fields and Scribner, 1997); Mallard (*Anas platyrhynchos*; Maak et al., 2003); Harlequin Duck (*Histrionicus histrionicus*; Buchholz et al., 1998); Spectacled Eider (*Somateria fischeri*; S. Libants, K. Oswald, E. Olle, and K. Scribner, pers. comm. 1999); and Common Eider (*S. mollissima*; Paulus and Tiedemann, 2003; Sonsthagen, 2006). Nineteen autosomal loci were found to be polymorphic, and 12 of these (6AB, Aph02, Aph08, Aph19, Aph23, Bca10, Bca11, Hhiμ5, Sfiμ11, Smo07, Smo09, and CRG; online Appendix 1: Table S1) were in Hardy-Weinberg equilibrium and were selected for further analysis, as were two *Z*-linked microsatellite loci (Bca4 and Smo1; Sonsthagen, 2006). Polymerase chain reaction (PCR) amplification and electrophoresis followed protocols described in Sonsthagen et al. (2004). For quality control purposes, 10% of the samples were amplified and genotyped in duplicate for the 14 microsatellite loci. Analyses using the *Z*-specific (sex-linked) loci were conducted on females, and both males and females were used for analyses involving the 12 autosomal microsatellites. In birds, females are the heterogametic sex (ZZ/ZW system). In systems with male-biased dispersal, *Z*-linked alleles from females are transmitted to male offspring that disperse to other areas while female offspring receive their *Z*-linked allele from the adult male. Therefore, only analyzing females that show site fidelity allows for investigation into male site fidelity from the previous generation, as members of successive generations (or cohorts) would be unrelated in *Z*-linked genes (Lanctot et al., 1999; Haig, 2000). Microsatellite genotype data are accessioned at the USGS Alaska Science Center data repository (Wilson and Talbot, 2016).

We amplified a portion of domains I and II of the mtDNA control region using the primer pair L16620F (Liukkon-Anttila et al., 2002) and H581 (Quinn and Wilson, 1993; Ruokonen et al., 2000; online Appendix 1: Table S2). This process yielded 354 bp of sequence product for all individuals. PCR amplifications, cycle-sequencing protocols, and post-sequencing processing followed Sonsthagen et al. (2004). To increase sample size in the eastern Siberia and Canadian Arctic samples, we used both males and females, whereas only females were used from the Arctic Coastal Plain and YKD samples. Analyses showed similar results when only females were included for central Canadian Arctic and eastern Siberian populations, and any differences are noted in the results. Sequences were deposited in GenBank (accession numbers KT387850–KT387947).

An initial screen using the primer pair, L16620F–H581, revealed two distinct clades (Fig. 2). This high variability in mtDNA control region between populations in close proximity has also been reported for another sea duck, the Common Eider (*Somateria mollissima*; Tiedemann et al., 2004), as well as the Andean Goose (*Chloephaga melanoptera*; Bulgarella et al., 2014). However, because the occurrence of nuclear pseudogenes is common in avian species (Lopez et al., 1994; Sorenson and Quinn, 1998), we used the procedures outlined in Lanctot et al. (1999) to support our theory that the amplified sequences from the two clades were of mtDNA origin. Specifically, we designed clade-specific

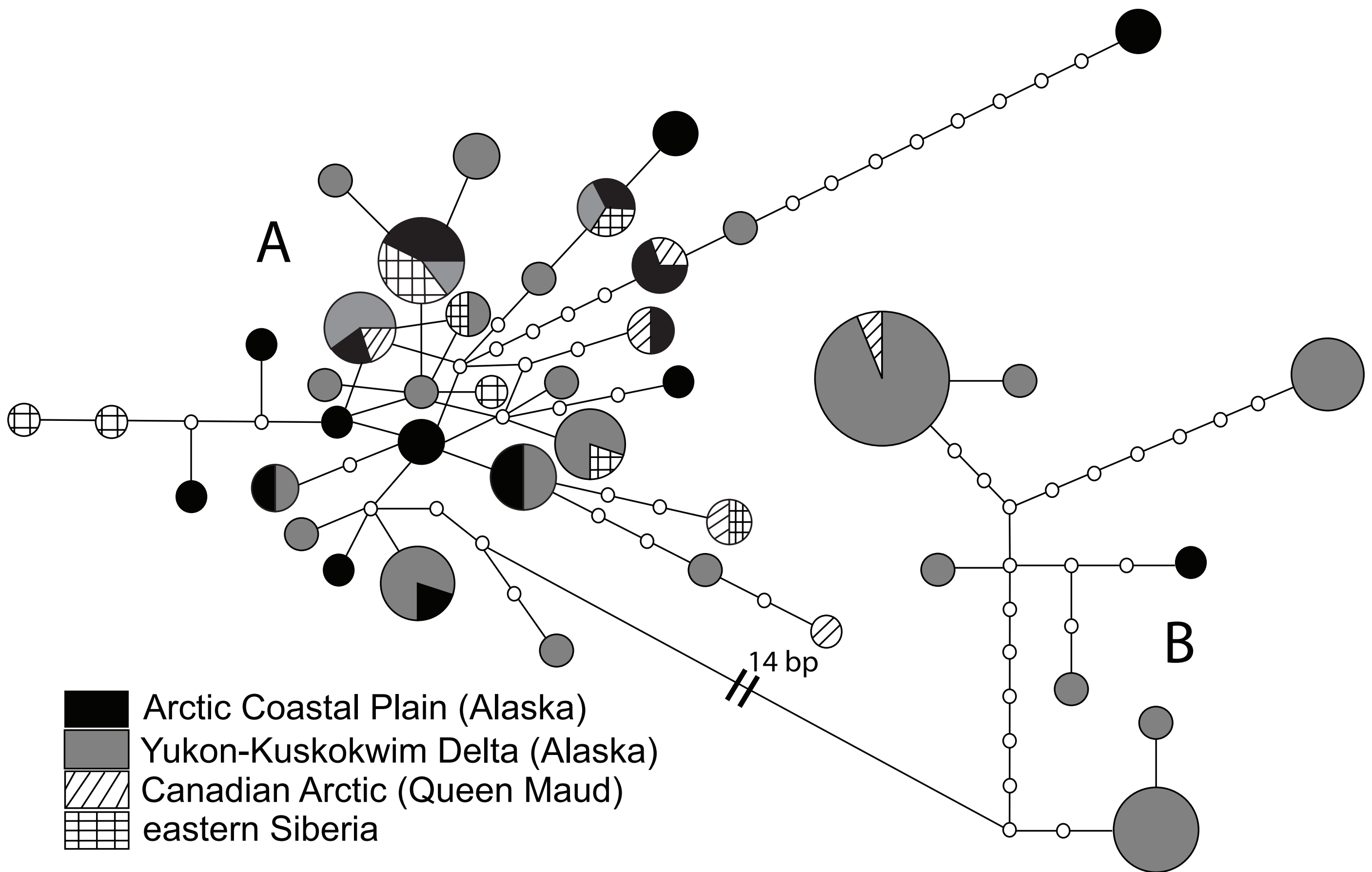

FIG 2. Unrooted haplotypic network for Long-tailed Duck mtDNA control region, showing two distinct clades (A and B). Sizes of circles are proportional to the frequency of each haplotype observed. Small white circles indicate haplotypes not observed in this study.

primers (three forward and two reverse for each group) to amplify each clade preferentially (online Appendix 1: Table S2). If both clades were mitochondrial in origin, we would either get the same sequence across primer pairs (general and clade-specific) or fail to amplify using clade-specific primers designed for the other group. Eight individuals from each group were selected and amplified using combinations of the clade-specific and general primers. All resulting sequences produced the same sequence as the original primer pair, L16620F–H581. In addition, we could not successfully amplify individuals using the opposing clade-specific primers, which further supported our conclusion that haplotypes from both clades and the original sequences are mitochondrial in origin.

Genetic Diversity and Population Subdivision

We used FSTAT ver. 2.9.3 (Goudet, 1995) to calculate allelic richness by rarefaction, inbreeding coefficient (F_{IS}), and observed and expected heterozygosities and to test for Hardy-Weinberg equilibrium and linkage disequilibrium for each microsatellite locus and population. We used ARLEQUIN ver. 3.5.1.2 (Excoffier and Lischer, 2010) to estimate haplotype (h) and nucleotide (π) diversity at the mtDNA control region. An unrooted haplotype network for mtDNA control region was constructed in NETWORK 4.6.1.1 (Fluxus Technology Ltd., 2013) using the Reduced Median method (Bandelt et al., 1995) to illustrate possible reticulations in the gene tree because of homoplasy or recombination.

The degree of population genetic subdivision among Long-tailed Duck populations was assessed by calculating overall and pairwise F_{ST} and R_{ST} for microsatellite loci and Φ_{ST} for mtDNA sequence data using ARLEQUIN and adjusting for multiple comparisons using Bonferroni correction ($\alpha = 0.05$) for microsatellite data. Pairwise Φ_{ST} for mtDNA was calculated using the best-fit nucleotide substitution model as identified in Modeltest 3.06 (Posada and Crandall, 1998) under the Akaike information criterion (AIC; Akaike, 1974). Because the upper possible F_{ST} value for a set of microsatellite loci is usually below 1.0 (Hedrick, 2005), we used RECODEDATA, version 1.0 (Meirmans, 2006) to calculate the uppermost limit of F_{ST} for our data set. We used POWSIM 4.1 (Ryman and Palm, 2006) to assess the statistical power of detecting population genetic structure on the basis of the microsatellite data set and sample sizes assayed. We ran simulations in POWSIM (1000 dememorizations, 100 batches, 1000 iterations per batch, 1000 runs) with allele frequencies observed for the 12 microsatellite loci with the same sample sizes used in the present study. We performed five simulations

with varying effective population sizes (N_e = 50, 100, 250, 500, 750, 1000, 2000, and 2500) at 10 generations to test statistical power. To account for differences in effective population size between genomes, we compared the extent of mtDNA and nuclear differentiation among populations to the expected levels of divergence outlined in Zink and Barrowclough (2008).

We also used a Bayesian clustering program, STRUCTURE 2.2.3 (Pritchard et al., 2000) to determine the level of population structure in the autosomal microsatellite data set without providing a priori information on the geographic origin of the individuals. If no structure was observed, we used the LOCPRIOR option as well; with this model, we can potentially detect population structure in datasets with a weak signal of structure not detectable under standard models (Hubisz et al., 2009). We determined whether location was informative by the value of *r*, which parameterizes the amount of information contained by the location of the samples. Values of *r* greater than 1 indicate a lack of population structure, or structure independent of locality. STRUCTURE assigns individuals to populations by maximizing Hardy-Weinberg equilibrium and minimizing linkage disequilibrium. The analysis was run for K = 1 – 10 populations using an admixture model with 100 000 burn-in iterations and 1 000 000 Markov chain Monte Carlo (MCMC) iterations; the analysis was repeated 10 times for each K to ensure consistency across runs. We used the ΔK method of Evanno et al. (2005) and evaluated the estimate of the posterior probability of the data given K, Ln P(D), to determine the most likely number of groups at the uppermost level of population structure.

Historical Population Demography

Evidence for fluctuations in historical population demography was evaluated for 12 microsatellite loci using BOTTLENECK 1.2.02 (Cornuet and Luikart, 1996). BOTTLENECK compares the number of alleles and gene diversity at polymorphic loci under the infinite allele model (IAM; Maruyama and Fuerst, 1985), the stepwise mutation model (SMM; Ohta and Kimura, 1973), and the two-phase 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 whether the average of standardized differences between observed and expected heterozygosities is significantly different from zero (Cornuet and Luikart, 1996). Significant heterozygote deficiency relative to the number of alleles indicates recent population growth, whereas heterozygote excess relative to the number of alleles indicates a recent population bottleneck (Cornuet and Luikart, 1996). BOTTLENECK compares heterozygote deficiency and excess relative to number of alleles expected at mutation-drift equilibrium, and not deviations from Hardy-Weinberg equilibrium expectation (Cornuet and Luikart, 1996).

Demographic histories of Long-tailed Ducks were evaluated using two approaches: standard qualitative test statistics and coalescent-based estimations. To test for genetic signatures of recent effective population size changes, we calculated Fu's F_s (Fu, 1997) and Tajima's D (Tajima, 1989) on the basis of the site-frequency spectrum of segregating sites for mtDNA. Negative values of Tajima's D or Fu's F_s result when there is an excess of low-frequency polymorphisms, which can result from rapid population expansion or selective sweep acting on linked polymorphisms. Conversely, a positive value for either test statistic can indicate a population decline. We used a coalescent model in LAMARC 2.1.8 (Kuhner, 2006) to calculate the population growth rate parameter (g) for mtDNA from each population independently. We used a Bayesian analysis with 1 000 000 recorded genealogies sampled every 50 steps and a burn-in of 100 000 (10%) genealogies. Priors were flat, with the upper limit for growth set to 15 000.

RESULTS

Population Structure and Genetic Diversity

In the 111 Long-tailed Ducks examined, the number of alleles per autosomal microsatellite locus ranged from 3 to 17 (average 8.2 per locus). The average number of alleles per population ranged from 4.2 to 7.5, with allelic richness ranging from 4.0 to 4.2 (Table 1). Observed heterozygosity ranged from 55% to 59.6% for each population, with an overall value of 58.4%. The inbreeding coefficient (F_{IS}) ranged from −0.021 to 0.084 across sample sites, with an overall mean of 0.037. All populations were in Hardy-Weinberg equilibrium and no signature of linkage disequilibrium was detected between any pair of loci. In 92 females, we observed 10 and 11 alleles for *Z*-linked Bca4 and Smo1, respectively, and no signature of linkage disequilibrium was detected.

We identified 41 unique mtDNA haplotypes characterized by 59 variable sites among 98 individuals. Haplotype (h) diversity ranged from 0.93 to 1.00 and nucleotide (π) diversity from 0.015 to 0.047 (Table 1). The total number of mtDNA haplotypes per population ranged from 6 to 25, with allelic richness ranging from 6.00 to 9.18. Haplotypes were clustered into two clades that were separated at a minimum of 14 bp: Clade A was composed of all four populations intermixed and Clade B was predominately composed of YKD samples, with one individual each from the Canadian Arctic and the Arctic Coastal Plain (Fig. 2). Within the YKD population, 53% of individuals possessed a haplotype found within clade B. The YKD shared six haplotypes with the Arctic Coastal Plain, four with eastern Siberia, and two with the Canadian Arctic. In addition, the Arctic Coastal Plain shared three haplotypes with the central Canadian Arctic and two with eastern Siberia. Finally, eastern Siberia and the Canadian Arctic shared one haplotype.

TABLE 1. Estimates of genetic diversity of Long-tailed Ducks breeding in Alaska (Arctic Coastal Plain and Yukon-Kuskokwim Delta [YKD]), the central Canadian Arctic, and eastern Siberia. Average number of alleles, allelic richness,[1] observed and expected heterozygosities (H_o/H_e), inbreeding coefficient (F_{IS}), and sample size (n) were calculated from 12 autosomal microsatellite loci and two *Z*-linked microsatellite loci. Also shown are the number of haplotypes, haplotype (h) and nucleotide (π) diversity, Fu's F_s, and Tajima's D, which were calculated from 354 bp of mtDNA control region.

	Arctic Coastal Plain	YKD	Central Canadian Arctic	Eastern Siberia
Autosomal microsatellites:				
No. alleles	5.9	7.5	4.2	4.3
Allelic richness	4.1	4.2	4.0	4.0
H_o/H_e	55.5/60.3	59.6/62.4	57.5/56.4	55.0/58.4
F_{IS}	0.084	0.024	−0.021	0.061
n	28	64	9	10
Z-linked microsatellites:				
No. alleles	7	10.5	2.5	3
Allelic richness	4.0	4.2	2.5	3.0
h	0.906	0.934	0.857	0.857
n	27	57	4	4
mtDNA:				
No. haplotypes	17	25	6	8
Allelic richness	9.2	8.1	6.0	7.0
h	0.971	0.909	1.00	0.933
π	0.0266 (0.0141)	0.0472 (0.0236)	0.0437 (0.0264)	0.0147 (0.0088)
Fu's F_s	−4.19	−0.42	−0.54	−2.05
Tajima D	−0.90	1.15	−0.64	−0.87
n	24	58	6	10

[1] Allelic richness is based on the lowest sample size (9 for autosomal microsatellites, 4 for *Z*-linked microsatellite, and 6 for mtDNA).

Overall, population subdivision was not significant for autosomal microsatellite loci, and no pairwise comparisons were significant (Table 2). STRUCTURE also did not uncover any genetic partitioning within these populations: the likelihood given the data was maximized when $K = 1$, and locality information was not informative ($r > 5$). Simulations in POWSIM revealed significant power (> 80%) to detect genetic differentiation ($F_{ST} = 0.006 - 0.010$ for effective sizes ranging from 50 to 750). Simulations based on effective sizes greater than 1000 had low power (< 60%). In all cases, the alpha error remained below the expected $\alpha = 0.05$. Overall, the microsatellite data were consistent with the mtDNA results for the Arctic coast breeding populations, suggesting no population genetic structure. However, there was discord for comparisons involving the YKD, with mtDNA being more structured than microsatellites.

We did observe significant genetic structuring of the mtDNA control region and *Z*-linked microsatellite loci. The global Φ_{ST} for the mtDNA control region was moderately high, with significant population differences restricted to comparisons of the YKD to the Arctic Coastal Plain and eastern Siberia (Table 2). However, when we excluded males from the eastern Siberian and Canadian Arctic datasets, the YKD and central Canadian Arctic were significantly different ($\Phi_{ST} = 0.27$). The significance and magnitude of divergence among the other comparisons were similar whether or not males were included. Overall population differentiation in *Z*-linked loci was restricted to interpopulation comparisons involving the eastern Siberian spring migrant populations (Table 2). The F_{ST} value (0.105) also indicated a significant difference between the central Canadian Arctic and the YKD (Table 2).

Recent and Historical Demography

In the stepwise mutation model and the two-phase model of mutation, the YKD showed evidence of recent population growth (heterozygote deficiency; Table 3). There was no evidence of significant heterozygosity excess or deficit in any of the other populations, indicating population equilibrium, although we note that Wilcoxon signed-rank tests for recent population fluctuations in the central Canadian Arctic and eastern Siberian spring migrant populations likely lack power, given that each of those populations is represented by fewer than 20 individuals (Cornuet and Luikart, 1996). MtDNA patterns were consistent with long-term population stasis and a lack of clear demographic expansion for all populations sampled. Neither Tajima's D nor Fu's F_s were significant for the mtDNA control region (Table 1) and the 95% confidence interval around the metric for population growth (g) overlapped zero for each population (Table 3), which is consistent with a stable population size.

DISCUSSION

Understanding population connectivity and spatial organization of populations is an important factor when considering their potential responses to environmental change. Isolated areas or those with limited connectivity may be more susceptible to disturbances than areas that are interconnected. Although we failed to reject a null hypothesis of no spatial genetic structure across broadly distributed areas within the Arctic (Alaska, Canada, and Russia),

TABLE 2. Pairwise and overall values of F_{ST}, R_{ST}, and θ_{ST} calculated from 12 microsatellite loci and 354 bp of mtDNA control region for Long-tailed Ducks breeding in Alaska (Yukon-Kuskokwim Delta and Arctic Coastal Plain), the central Canadian Arctic, and eastern Siberia. Significant values are indicated in bold (α = 0.05).

	Autosomal microsatellite		*Z*-linked microsatellite		mtDNA	
	F_{ST}	R_{ST}	F_{ST}	R_{ST}	F_{ST}	θ_{ST}
Arctic Coastal Plain:						
YKD	−0.005	−0.002	0.000	0.004	**0.050**	**0.258**
Canada	0.004	−0.023	0.085	0.007	−0.012	−0.058
Siberia	0.003	−0.020	**0.110**	**0.423**	0.005	0.050
YKD:						
Canada	0.007	−0.013	**0.105**	−0.034	0.001	0.111[1]
Siberia	0.007	−0.021	0.069	**0.247**	**0.067**	**0.310**
Canada:						
Siberia	−0.017	−0.024	**0.269**	**0.454**	0.019	0.079
Overall	0.000	−0.011	**0.031**	**0.064**	**0.040**	**0.238**

[1] p value = 0.07. When only females were included in this population, θ_{ST} = 0.24 and is significant ($p < 0.05$). All other comparisons, whether males were included or excluded from the Siberia and Canada populations, were similar.

we did observe significant mtDNA differentiation between Arctic populations and the subarctic YKD population, although we observed a large number of both clade A and B haplotypes on the YKD. Their presence likely reflects the intermixing of formerly isolated and refugial populations, while the predominance of clade A haplotypes among Arctic populations suggests historical co-ancestry with recent expansion into the YKD region.

Population Structure: Female Philopatry

Long-tailed Ducks use numerous wintering areas, where pair formation occurs (Petersen et al., 2003; Lawson, 2006; Sea Duck Joint Venture, 2012). Thus winter aggregations are most likely composed of individuals from multiple breeding locales, which probably serves to homogenize allelic frequencies in the nuclear genome via male dispersal and interbreeding. Although females in the central Arctic and eastern North American populations exhibit some degree of fidelity to breeding sites, as well as to wintering areas (Alison, 1975; Robertson and Savard, 2002; Sea Duck Joint Venture, 2012), our analyses suggest that these behaviors are not structuring breeding populations genetically (e.g., limited or no philopatry). Alison (1977), in the only study to investigate the degree of philopatric behavior, found that it occurred at a low rate at Churchill, Manitoba (4 of 26 marked subadults returned to their natal area the following year). As philopatry is expected to restrict gene flow among neighboring populations, resulting in population structure, our lack of significant fixation indices (F_{ST} and Φ_{ST}) at mtDNA and autosomal microsatellites and the observation of shared mtDNA haplotypes across the Arctic suggest that there is some effective dispersal for both males and females among these disparate areas within the Arctic.

The two divergent clades, with YKD samples spread throughout but with mostly YKD females in clade B, suggest that this area may be composed of individuals whose ancestors were isolated in two different refugial populations that subsequently came back into contact, as hypothesized for the Snow Goose (*Chen caerulescens*; Quinn, 1992). On the basis of the current distribution of the species, Ploeger (1968) proposed a number of last glacial refugia for Long-tailed Ducks, including the shelf area north of the Bering Strait and the northwestern Canadian Archipelago, both possible source refugia for the locales included here. In addition, the finding that clade B (see Fig. 2) is composed almost entirely of YKD females suggests that females in this area do exhibit some degree of philopatry despite potential mixing from other areas on various wintering grounds. This pattern further suggests that the interaction between populations is asymmetrical, with more females dispersing into the YKD than vice versa. If admixture were symmetrical and occurring at a high rate, we would expect to find a higher representation of haplotypes from clade B in the other breeding sites. As Long-tailed Ducks are short- to medium-distance migrants, it is possible that the Arctic populations may use more northern sites along the coast, or open areas within the sea ice (polynyas), more frequently than they use southern sites. This pattern would allow only partial overlap in wintering areas, as observed for the Arctic Coastal Plain and YKD populations of Common Eiders (Petersen and Flint, 2002). Non-breeding females banded on the Arctic Coastal Plain during molt use many of the same wintering sites as the YKD population (M.R. Petersen, unpubl. data). However, the breeding location of molting birds banded on the Arctic Coastal Plain is unknown. Long-tailed Ducks are known to molt at great distances from their breeding areas; for example, many birds in Alaska migrate to coastal Russia to molt (Baldassare, 2014). Thus, these banded birds may not accurately represent the population of the Arctic Coastal Plain. More information on the migration patterns of ducks in breeding locales on the Arctic Coastal Plain and in Canada is needed to determine the degree of wintering distribution overlap with subarctic populations and what role wintering or molting habitat selection may play in the distribution of genetic diversity.

TABLE 3. Analysis of historical fluctuations in population demography of Long-tailed Duck populations from 12 microsatellite loci tested using the infinite allele model (IAM), stepwise mutation model (SMM), and two-phase model of mutation (TPM). Also shown is the population growth parameter (*g*) for mtDNA control region. Significant estimates are in bold.

	Microsatellites			mtDNA	
	IAM	SMM	TPM	θ	*g*
Arctic Coastal Plain	Eq	Eq	Eq	0.06 (0.03–0.09)	29.6 (−37.0–96.2)
YKD	Eq	**Hdef**	**Hdef**	0.06 (0.03–0.09)	37.1 (−28.7–111.3)
Canadian Arctic	Eq	Eq	Eq	0.18 (0.04–4.20)	84.4 (−8.7–301.9)
Eastern Siberia	Eq	Eq	Eq	0.09 (0.01–0.10)	180.9 (−29.6–618.2)

Although our results of lack of genetic differentiation across the Arctic agree with those of Humphries and Winker (2010), our conclusions could also suffer from low statistical power because of the small sample sizes in the Canadian Arctic and Siberia. Power simulations based on the microsatellite data set show that these markers have relatively high power to detect low levels of nuclear differentiation (F_{ST} of 0.006 to 0.010) as long as the effective size for each population is below 1000. Effective populations sizes are typically lower than census sizes, with some ratios (N_e/N) in wild populations as low as 0.01 (Palstra and Fraser, 2012); however, since Long-tailed Ducks are one of the most abundant sea ducks, it is possible that in this case the effective population size for each area exceeds 1000. Therefore, additional samples from these two areas are needed to confirm the levels of differentiation observed and to provide information on overlap of wintering sites of subarctic and Arctic populations in the Pacific Ocean.

Population Structure: Male Fidelity

Sex-linked and autosomal loci are often at different stages of divergence. Traits involved in mating patterns such as plumage and recognition have been suggested to be sex-linked, implying that sex chromosomes are important for the formation of reproductive isolation (Sætre et al., 2003; Ellegren et al., 2012). If male-mediated gene flow were the only factor contributing to the mitochondrial-nuclear discord, we would expect to find *Z*-linked loci to be the least structured because males carry two copies, but females only a single copy. However, the central Canadian Arctic population and eastern Siberian populations show significant differences at two *Z*-linked microsatellites, which suggests restricted male gene flow in the previous generation. Significant differentiation at *Z*-linked loci has also been found between Old World and New World populations of other Arctic waterfowl species (Peters et al., 2014). Although seasonal pair bonds are typical of Holarctic ducks and movements between breeding areas likely do occur, there is evidence that pair bonds re-form on the wintering grounds, especially in sea ducks (Bengston, 1972; Alison, 1975; Spurr and Milne, 1976; Savard, 1985; Gauthier, 1987). In addition, wintering site fidelity has been reported for many of the sea ducks (Anderson et al., 1992); for example, Barrow's Goldeneye (*Bucephala islandica*) males show similar levels of breeding site and winter site fidelity, which may facilitate reunion of pairs (Savard, 1985). The formation of long-term pair bonds could affect the genetic structure among populations on a short time scale, as it would temporally restrict dispersal among breeding areas. However, the degree of male philopatry in Long-tailed Ducks is currently unknown, and it is likely that long-term pair bonds do not occur often enough to influence the spatial pattern of allelic frequencies.

Alternatively, we may have preferentially sampled individuals representing one major wintering area. The central Canadian Arctic may represent a region of contact between Arctic and subarctic populations, as known suture zones (e.g., the Mackenzie River) are located there (Holder et al., 2000; Fedorov and Stenseth, 2002; Sonsthagen et al., 2011). The breeding population at Karrak Lake within the Queen Maud Gulf Bird Sanctuary includes Long-tailed Ducks that winter on both North American coasts, as well as the Great Lakes region (Larson, 2006). Therefore, it is possible that our small samples from Canada and eastern Siberia may have overrepresented individuals that winter in one geographic region and that our results reflect genetic structure on a much larger scale (e.g., east coast vs. west coast). More genome-wide approaches and extensive sampling are needed to determine the role of the *Z* chromosome in population divergence and to distinguish between Haldane's Rule and male-mediated gene flow (see Peters et al., 2014).

Population Demography

Globally, Long-tailed Duck populations have declined since the 1970s, but nevertheless the species remains one of the most abundant ducks in the North American Arctic. Recent surveys suggest that the size of the Arctic Coastal Plain population has stabilized over the past 20 years with a growth rate of 0.995, while the YKD population has shown significant declines over the past 10 years (Larned et al., 2012; Platte and Stehn, 2012). MtDNA and nuclear microsatellites showed a signature of long-term population equilibrium for the northern coastal populations. However, a signature of long-term population growth (SMM

and TPM microsatellite mutation models) with short-term population stasis (IAM) was detected for the YKD population, although this picture is inconsistent with population demography data that indicate a significant decline since 2001 (Platte and Stehn, 2012). Even with a recent collection of samples, the population decline is most likely not severe enough (under 25 effective breeders) on the YKD for the IAM model to detect the genetic signature of decline (see Cornuet and Luikart, 1996).

Comparison to Other Sea Duck Species

The lack of population differentiation in nuclear markers with structure in mtDNA observed in Long-tailed Ducks is consistent with the pattern found in other sea ducks. Spectacled and Common Eiders showed similar levels of genetic relationships between Alaska breeding populations on the Arctic Coastal Plain and YKD in both mtDNA and microsatellite loci (Scribner et al., 2001; Sonsthagen et al., 2011). These two species have differing wintering distributions, but both exhibit a high degree of female philopatry (98% in Common Eiders; Swennen, 1990). As mentioned above, only a small percentage of Common Eiders from each population (6% of marked birds) share wintering areas, while virtually the entire global population of Spectacled Eiders winters in the same region in the Bering Sea (Petersen et al., 1999; Petersen and Flint, 2002; Petersen and Douglas, 2004). Like the Long-tailed Duck, the King Eider (*Somateria spectabilis*) within the Central Canadian Arctic uses wintering areas on both sides of North America (Mehl et al., 2004). Females in this area showed low levels of fidelity (Kellett and Alisaukas, 1997), but fidelity may be higher on the Arctic Coastal Plain (Phillips and Powell, 2006). However, philopatry has not been assessed in this species, and lack of genetic differentiation across the northern Arctic coast of Alaska and Canada (Pearce et al., 2004) suggests that it is low.

The degree of philopatry can be variable within species and between sister taxa, and it is strongly influenced by ecological factors (Weatherhead and Forbes, 1994) and historical biogeography (Avise, 2000). This variability may be influencing the varying spatial patterns of genetic structure seen in sea ducks (Scribner et al., 2001; Pearce et al., 2004, 2014; Sonsthagen et al., 2011; this study). As Arctic environments change, species and even populations of the same species may respond differently via recruitment from other areas or in the colonization of new areas. Comparison of sea duck population connectivity highlights this differential response and illustrates that it is important to not make generalizations across species. It is unclear whether the discord between mtDNA and nuclear differentiation among Long-tailed Ducks in this study is due to isolation of populations in different refugia with asymmetrical secondary contact, ecological factors promoting differing levels of female philopatry, differing wintering site selection within populations, or a combination of these factors. Additional range-wide sampling and application of genome-wide approaches have the potential to distinguish these and other processes driving the biogeographic pattern of genetic variation found in Long-tailed Ducks.

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APPENDIX 1

The following tables are available in a supplementary file to the online version of the article at:
http://arctic.journalhosting.ucalgary.ca/arctic/index.php/arctic/rt/suppFiles/4548/0

TABLE S1. Primer sequences for autosomal and sex-linked (*Z*-specific) microsatellites used for Long-tailed Ducks.

TABLE S2. General and clade specific primers (see Fig. 2) used to amplify the mtDNA control region for Long-tailed Ducks.

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