2009

MIGRATORY PATTERNS AND POPULATION STRUCTURE AMONG BREEDING AND WINTERING RED-BREASTED MERGANSERS (MERGUS SERRATOR) AND COMMON MERGANSERS (M. MERGANSER) Характер миграций и популяционная структура у Mergus serrator и M. merganser вместах зимовок и гнез ований

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The Auk 126(4):784–798, 2009

Printed in USA.

MIGRATORY PATTERNS AND POPULATION STRUCTURE AMONG BREEDING AND WINTERING RED-BREASTED MERGANSERS (*MERGUS SERRATOR*) AND COMMON MERGANSERS (*M. MERGANSER*)

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Abstract.—Philopatry has long been assumed to structure populations of waterfowl and other species of birds genetically, especially via maternally transmitted mitochondrial DNA (mtDNA), yet other migratory behaviors and nesting ecology (use of ground vs. cavity sites) may also contribute to population genetic structure. We investigated the effects of migration and nesting ecology on the population genetic structure of two Holarctic waterfowl, the Red-breasted Merganser (*Mergus serrator*) and Common Merganser (*M. merganser*), using mtDNA control-region sequence data. Red-breasted Mergansers (a ground-nesting species) exhibited lower levels of population differentiation across their North American range, possibly as a result of post-Pleistocene range expansion and population growth. By contrast, Common Mergansers (a cavity-nesting species) breeding in western and eastern North America were strongly differentiated, as were continental groups in North America and Europe. Our hypothesis that population differentiation of breeding female Common Mergansers results from limited migration during non-breeding periods was not supported, in that equally heterogeneous mtDNA lineages were observed in males and females on several wintering areas. The interspecific differences in mtDNA patterns for these two closely related species may have resulted from factors related to nesting ecology (ground vs. cavity nesting) and responses to historical climate change. *Received 17 September 2008, accepted 20 April 2009.*

Key words: cavity nesting, Common Merganser, *Mergus merganser, M. serrator,* migratory connectivity, mitochondrial DNA, philopatry, Red-breasted Merganser, sea ducks, waterfowl.

Характер миграций и популяционная структура у *Mergus serrator* и *M. merganser* в местах зимовок и гнездований

Абстракт.—Давно считается, что особенности филопатрии определяют генетическую структуру популяций водоплавающих и других видов птиц с материнским наследованием митохондриальной ДНК (мтДНК), хотя другие характеристики миграционного поведения и гнездования (например, гнездование на земле или в дуплах) также могут вносить свой вклад в генетическую структуру популяции. Мы изучили влияние миграционной и гнездовой экологии на генетическую структуру популяций двух голарктических уток—*Mergus serrator* и *M. merganser*, используя данные секвенирования контрольного региона мтДНК. *M. serrator*, гнездящийся на земле, обнаружил низкий уровень популяционной дифференциации по всему его ареалу в Северной Америке, возможно, вследствие пост-плейстоценового расширения ареала и увеличения численности. Напротив, гнездовые популяции *M. merganser* (гнездящегося в дуплах), на западе и на востоке северной Америки, были сильно дифференцированы. Существенная дифференциация также отмечена между североамериканскими и европейскими образцами. Гипотеза, что дифференциация популяции гнездующихся самок *M. merganser* происходит вследствие их ограниченной миграции в негнездовой период, опровергается фактом, что в ряде мест зимующие популяции самцов и самок характеризуются равными показателями гетерогенности линий мтДНК. Наблюдаемые межвидовые различия в характере дифференциации мтДНК для этих двух близких видов рода *Mergus* могут быть следствием принципиальных отличий в экологии гнездования (на земле или в дуплах), приводящих к разной реакции на исторические изменения климата.

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The Auk, Vol. 126, Number 4, pages 784–798. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2009.08182

Analysis of factors that contribute to population genetic structure can provide valuable insights into the evolution, ecology, and conservation of migratory birds. Numerous studies have demonstrated how geographic distance and physical barriers influence dispersal and gene flow and shape genetic differentiation among populations (Avise 1994). This isolation-by-distance model is one of the cornerstones of population genetic theory and a predictor of genetic differentiation (Wright 1943). However, the movements of many bird species are often not hampered by geographic barriers and distance, and migratory behavior and ecology are increasingly being recognized as equally important variables to consider in hypotheses of population genetic structure (Smith et al. 2005, Lecomte et al. 2009). For example, in a meta-analysis of 53 seabird species, Friesen et al. (2007) found that geographic distance between nesting colonies appeared to have only a weak influence on the extent of population genetic structure, whereas migratory traits, such as segregation on non-breeding areas and limited movement away from nesting areas following breeding, were more strongly correlated with the degree of population structure. Such comparative approaches across taxonomically related species or those inhabiting similar habitats are useful for understanding the behavioral and ecological mechanisms, besides geographic distance and physical barriers, that may be responsible for population differentiation.

A trio of closely related sea ducks in North America, the Hooded Merganser (*Lophodytes cucullatus*), Red-breasted Merganser (*Mergus serrator*), and Common Merganser (*M. merganser*), also provide useful examples of how migratory patterns can be used to formulate and test hypotheses about population structure across breeding and non-breeding areas. Mergansers, and most other waterfowl species (Family Anatidae), exhibit female philopatry (natal site fidelity), which is often invoked as a predictor of population structure in this group (Greenwood 1980, Avise 2000). Female philopatry in waterfowl is, thus, the behavioral equivalent of isolation-by-distance, especially when genetic differentiation is measured with maternally inherited mitochondrial DNA (mtDNA). Because females continually return to natal areas to breed, clustering of related females should lead to population structure across a broad scale (Avise 2000). However, several waterfowl species examined across their ranges, including the Hooded Merganser (Pearce et al. 2008), demonstrate a wide range of mtDNA differentiation, which is inconsistent with predictions based solely on female philopatry (Cronin et al. 1996, Scribner et al. 2003, Peters and Omland 2007). Thus, conclusions drawn from assumed philopatry, and in the absence of other supporting evidence, should be made cautiously (reviewed in Pearce and Talbot 2006). Therefore, it seems useful to investigate other mechanisms, in addition to philopatry, that may also structure waterfowl populations, particularly those that are related to migratory patterns and nesting ecology. We tested hypotheses regarding genetic differentiation of North American and Eurasian Common and Red-breasted mergansers in relation to migratory patterns and nesting ecology that are either known or inferred from nongenetic data.

The Red-breasted Merganser is a Holarctic, ground-nesting species of tundra and boreal forest areas (Titman 1999). Limited banding or radiotelemetry data are available for generating hypotheses regarding population structure and migratory connectivity. The evolutionary timing and origin of ground-nesting behavior are unknown in this species, but this behavior is uncommon among other closely related sea ducks and appears to have arisen from an ancestral group of cavity-nesting species in the genus *Mergus* (Livezey 1995). Therefore, we hypothesize that ground-nesting behavior in Red-breasted Mergansers may have allowed for competitive avoidance of closely related cavity-nesting waterfowl species and an opportunity to expand into more northern latitude habitats where cavities of adequate size were rare. We hypothesize that such a northward population expansion should lead to an unstructured pattern of genetic differentiation across the North American range of this species. However, breeding populations across North America may segregate spatially during non-breeding periods, with Alaskan and western Canadian breeders wintering along the Pacific Coast and breeding birds from eastern Canada wintering along the Atlantic and Gulf coasts of North America. Here, we examine whether such migratory patterns are evident in the genetic structure of breeding and winter samples collected in western and eastern North America.

The Common Merganser is a Holarctic, cavity-nesting species of the boreal forest (Mallory and Metz 1999). Mark–recovery analyses of banding data suggest geographic and sex-specific variation in migratory tendency in North America (Pearce et al. 2005) and Europe (Little and Furness 1985, Hatton and Marquiss 2004). Satellite-telemetry data also suggest that males and females differ in their migratory patterns among breeding, molting, and wintering areas, with post-fledging males moving farther than females (Pearce and Petersen 2009). Recent genetic analyses revealed population structure among breeding groups in North America and Europe for mtDNA, but not for nuclear DNA (Hefti-Gautschi et al. 2009, Pearce et al. 2009), which suggests that males migrate seasonally or disperse among genetically differentiated breeding areas, or both. Here, we examine the population structure of Common Mergansers across North America and Eurasia and also test the hypothesis that population differentiation is related to limited migratory movements of females after breeding by comparing the mtDNA of males and females on multiple wintering grounds.

Methods

Sampling strategy.—To examine population-genetic and migratory patterns with mtDNA, we collected breeding and winter samples at sites throughout North America, Greenland, western Europe, and Russia (Figs. 1 and 2 and Appendix 1). Breeding samples were collected between March and August and came from adult females and pre-fledged young. Among breeding samples, the only adult males in the analysis were 8 Common Mergansers sampled on the Columbia River, Washington, from a total of 18. To examine samples from southeastern Alaska, we included nine putatively breeding Common Mergansers (two juvenile males, five juvenile females, and two adult females) collected in September and October from Prince of Wales Island, Alaska. Two subadult-plumaged birds (one male and one female), sampled incidentally, were also included to illustrate post-fledging movements (see below). Winter samples (collected between October and January) were obtained from tissues of male and female birds collected by hunters in North America and Eurasia (Figs. 1 and 2 and Appendix 1). To examine relationships between North American and European samples of Common Mergansers, we also included several

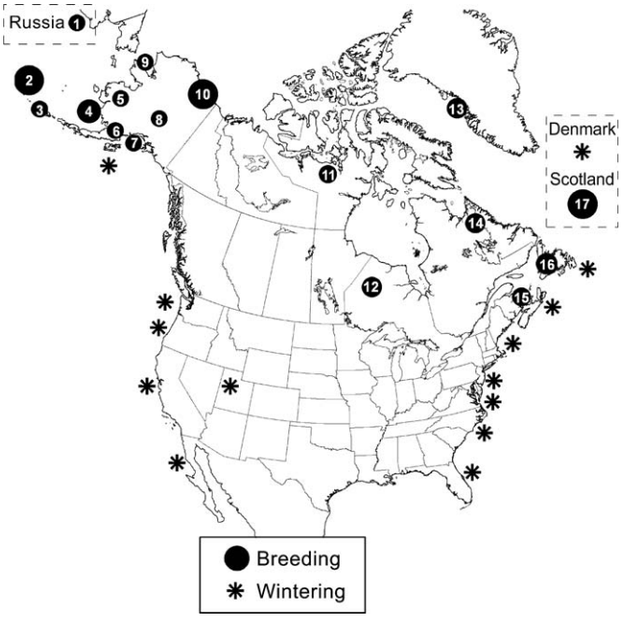

FIG. 1. Sampling localities for Red-breasted Merganser. Breeding samples are shown as circles and are proportional to sample size. Numbers within circles correspond to location names given in Appendices 1 and 2. Approximate locations of winter samples are shown with an asterisk.

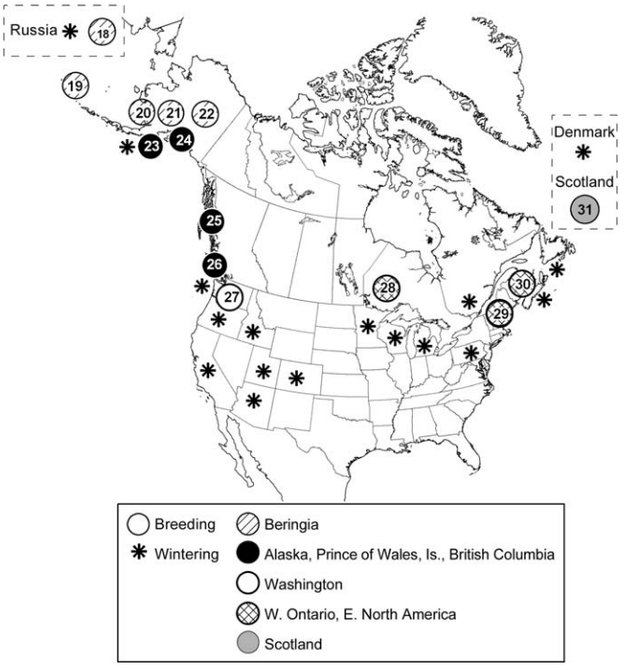

Fig. 2. Sampling localities for Common Merganser. Breeding samples are shown as circles and are shaded according to mtDNA haplogroup. Circle size is not proportional to sample size. Numbers within circles correspond to location names given in Appendices 1 and 2. Approximate locations of winter samples are shown with an asterisk.

mtDNA control-region haplotypes of the Goosander (*M. m. merganser*; Hefti-Gautschi et al. 2009). These included haplotype 01 from Switzerland and Italy; haplotypes 21, 22, and 23 from Norway; haplotypes 30 and 31 from Poland; and haplotypes 33, 35, and 36 from Iceland.

DNA extraction, sex determination, and mtDNA sequencing.—We extracted DNA from all samples using an overnight digestion at 55°C in a lysis buffer (50 mM Tris-HCl pH 8.0, 50 mM EDTA pH 8.0, 1% sodium dodecyl sulfate, 100 mM NaCl, and 1% 2-mercaptoethanol). Proteinase K (20 mg mL^{-1}) was added along with 100 mg mL^{-1} dithiothrietol (DTT) to feather samples, followed by salt extraction (Medrano et al. 1990). We verified the sex of samples using the P8 and P2 polymerase chain reaction (PCR) primers developed by Griffiths et al. (1998). The PCR cycling was performed on a Stratagene 96 Robocycler (La Jolla, California) using a profile of 94°C for 90 s (1 cycle), 40°C for 45 s, 72°C for 45 s, and 94°C for 30 s (40 cycles), 48°C for 60 s (1 cycle), and 72°C for 5 min (1 cycle). The PCR products were visualized on 6% polyacrylamide gels using a LI-COR 4200 DNA sequencer (LI-COR Biosciences, Lincoln, Nebraska).

We amplified and sequenced 439- and 425-base-pair (bp) fragments of the mtDNA control region (domain I) from Red-breasted (n = 139) and Common mergansers (n = 323), respectively. Taxon-specific primers and avoidance of blood samples, which contain a greater ratio of nuclear DNA to mtDNA, can reduce the likelihood of amplifying nuclear pseudogenes (Sorenson and Quinn 1998). Therefore, we used the MMCRL H and MMCRL R PCR primers developed for the Goosander (Hefti-Gautschi et al. 2009) and excluded blood samples from the study. The PCR products were amplified and then visualized on 5.5% polyacrylamide gels using methods described by Pearce et al. (2008). MtDNA sequences were aligned using ALIGNIR, version 2.0 (LI-COR), and collapsed into unique haplotypes using FABOX (Villesen 2007). Because insertion and deletion events can be an informative source of nucleotide variation (Pearce 2006), we included these sites in analyses after coding them as transitions. All haplotypes derived in the present study have been deposited in GenBank under accession numbers FJ191173–FJ191309 for Red-breasted Merganser and FJ190670–FJ190979 for Common Merganser.

Statistical analyses.—To quantify levels of genetic differentiation within each species, we used mtDNA haplotype spanning networks, generated by the median-joining method in NETWORK, version 4.2 (Bandelt et al. 1999). We used ARLEQUIN, version 3.11 (Excoffier et al. 2005), to calculate Φ_{ST} after incorporating the Tamura and Nei (1993) model of nucleotide substitution, as identified by MODELTEST (Posada and Crandall 1998), as the best fit to our data. To assess general patterns of migratory connectivity between breeding and wintering areas, we used haplotype networks and ARLEQUIN to examine differences among wintering-area samples collected across North America. For both species, Φ_{ST} was calculated after arranging winter samples into three groups: Alaska (Kodiak Island), western North America (may include Washington, Oregon, California, Arizona, Colorado, Utah, Idaho, and Baja Peninsula), and eastern North America (may include

Nova Scotia, Newfoundland, Maine, Massachusetts, New Jersey, Rhode Island, Virginia, Connecticut, and Florida). Inclusion of different localities in each of the three regional groups depended on the sampling distribution for each species (see Fig. 1 and Appendix 1). More specific groupings of locations were not possible with these data, because that would require *a-priori* knowledge regarding within-winter movements and little is known about the movements of mergansers during winter.

We determined the likely mtDNA group membership of Common Merganser winter samples, collected across five North American and two Eurasian sites, by comparing them with broad mtDNA haplogroup associations revealed by breeding-season samples. North American wintering sites included Alaska (Kodiak Island), western North America (Washington, Oregon, and California), the Intermountain West (Utah, Idaho, Colorado, and Arizona), the Great Lakes area (Minnesota, Wisconsin, and Michigan), and eastern North America (Pennsylvania, Québec, Newfoundland, and Nova Scotia). Eurasian wintering sites included Denmark and Vladivostok, Russia. MtDNA group membership was determined by first identifying identical haplotypes using FABOX (Villesen 2007). For haplotypes not observed among breeding samples, we determined mtDNA group membership using bootstrapped neighbor-joining trees (10,000 replicates) in MEGA, version 4.0 (Tamura et al. 2007), and by constructing haplotype networks of nonmatching sequences in relation to breeding-sample haplotypes.

We hypothesized that the Red-breasted Merganser data would show little differentiation across sampling areas. Thus, the results of standard tests of differentiation may offer little inferential power to differentiate between two possible scenarios: gene flow or insufficient time since divergence for genetic differences to accrue. Therefore, we used the program IM ("Isolation with Migration"; Nielsen and Wakeley 2001) to determine whether patterns of limited differentiation between populations were the result of incomplete lineage sorting, gene flow, or both. We used the IM analysis for three sets of comparisons: (1) between North American ($n = 89$) and European ($n = 30$) sequences from breeding and winter samples, (2) between groups of breeding samples from Alaska ($n = 37$) and Canada ($n = 9$), and (3) between groups of winter samples from the western ($n = 19$) and eastern ($n = 32$) coasts of North America. The first analysis was used to determine whether shared haplotypes between continents resulted from incomplete lineage sorting, whereas the second and third comparisons using North American samples were used to test hypotheses about migratory patterns and population differentiation. We hypothesized that if Alaskan and Canadian breeding populations of Red-breasted Mergansers are segregated on opposite coasts of North America during winter, estimates of the migration parameter (m) will be similar. If wintering areas are heterogeneous, composed of individuals from multiple and differentiated breeding areas, estimates of m should be greater than observed with the breeding data. For initial runs, we used wide priors that were assumed to be uninformative for each parameter. We then restricted the range of parameter values around the observed peaks for final runs. Migration rates (m_1, m_2) were set to be equal, and default settings were used for the heating mode. Following multiple runs to examine similarity of parameter estimates, a single long run (8×10^6 steps, minimum effective sample size for all parameters >1,000) was used to estimate final values for each of the three comparisons outlined above.

Because the IM model is not well suited to data sets with multiple populations that are reciprocally monophyletic (or nearly so), we used an indirect method to examine the possibility of incomplete lineage sorting to explain shared haplotypes among Common Merganser breeding areas. Theoretically, when populations are isolated with no gene flow, lineage sorting should be complete when divergence time is equal to four times the effective population size. Therefore, we calculated the ratio (R) of divergence time to effective population size following the methodology presented in Friesen et al. (2007). Divergence time was estimated from the mean percentage sequence divergence (δ) between populations (haplogroups in this case), and the effective population size was indexed by nucleotide diversity (π).

Lastly, we used the site-frequency spectrum of segregating sites to test hypotheses about range and population expansion in Red-breasted Mergansers. First, we used ARLEQUIN to calculate Fu's F_s (Fu 1997) and Tajima's D (Tajima 1989), because population growth will influence the shape of gene trees and result in significant excess of low-frequency variants, as indicated by negative F_s and D, and this can be interpreted as evidence of population expansions (Fu 1997). Second, we examined the mismatch distribution for the observed number of differences between all pairs of haplotypes in the sample (Rogers and Harpending 1992). This analysis assumes that signatures in the distribution of pairwise nucleotide differences result from episodes of population growth and decline, though we acknowledge that different processes, such as population structure, may produce similar mismatch patterns. Calculations were performed on the entire North American Red-breasted Merganser data set.

Results

Red-breasted Merganser

Breeding samples.—Among 64 North American and Eurasian breeding samples, we observed 25 haplotypes defined by 29 variable sites that were characterized by one transversion and 28 transitions (Table 1). The most common haplotype (no. 1) was observed in 22% of all samples, including two samples from central Russia, one from Greenland, two from Scotland, and samples from multiple locations in Alaska and Canada (Table 1 and Appendix 2). Several lines of genetic evidence suggest a recent population expansion by the Red-breasted Merganser in North America. The mtDNA haplotype network revealed a star-like toplogy with only a single common haplotype (no. 1), from which radiated numerous low-frequency haplotypes (Fig. 3A). The mismatch distribution was unimodal for the North American data (Fig. 4) and did not differ from simulated distributions under models of sudden expansion ($P = 0.556$) or spatial expansion ($P = 0.795$). Fu's F_s (–8.20, $P < 0.001$) and Tajima's D (–1.85, $P = 0.012$) also were significantly negative.

Because few shared haplotypes were found among breeding areas (Table 1), an overall significant level of differentiation was observed for mtDNA ($\Phi_{ST} = 0.262$, $P < 0.001$). Pairwise comparisons among three breeding areas (Alaska, Canada, and Scotland) revealed that the greatest level of differentiation was observed between Alaska and Scotland ($\Phi_{ST} = 0.280$) and the lowest between

TABLE 1. MtDNA control-region haplotypes of Red-breasted Mergansers from North American and Eurasian breeding samples. Numbers above haplotype 1 identify the variable positions, and dots represent nucleotides identical to those in haplotype 1.

Haplotype	4	1	2	4	4	6	6	6	6	7	8	8	9	9	1 0	1 1	1 2	1 4	1 4	1 4	1 6	1 6	1 7	1 9	1 9	1 9	2 0	2 0	4 0	Sampling area and frequency: Alaska	Canada	Eurasia[a]
	4	1	5	8	9	4	5	7	9	3	5	7	2	3	0	1	0	0	1	5	1	8	2	6	7	8	4	8	8			
1	C	C	T	A	C	T	C	C	C	G	A	C	G	C	C	T	C	A	A	C	A	G	A	A	T	T	A	T	C	14	2	5
2	.	.	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	3		
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	1	1	
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	G	.	.	.	.	.	.	1		
5	.	.	C	G	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1		
6	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	2		
7	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2		
8	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3		
9	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	4		
10	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4		
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.	.	.	.	.	.	.	.	.	.	C	.	1		
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	G	.	.	1		
13	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	
14	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.		1	
15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	G	.	C	.	.	.		1	
16	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.		3	
17	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	C	.	.	.	.			1
18	.	.	.	G	T	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			2
19	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.			2
20	T	.	.	G	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			2
21	.	.	.	G	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			1
22	.	.	.	G	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			1
23	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.			2
24	.	.	.	G	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			1
25	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	.	.			1
Total																														37	9	18

[a]Includes breeding samples from Greenland, Russia, and Scotland.

Alaska and Canada (Φ_{ST} = 0.153). The presence of haplotype 1 in both North America and Europe suggested either long-distance gene flow or incomplete lineage sorting following a recent population expansion. Given the geographic distance between continents, the latter scenario seems more likely and was confirmed through an analysis of North American and European breeding samples using IM. The most probable estimate of the posterior distribution for the migration rate (*m*) between North American and western European samples was low (0.02), with confidence intervals that overlapped zero (95% highest posterior density [HPD]: 0.00–0.10). Thus, a hypothesis of no gene flow between continents cannot be rejected with these data. Within North America, a comparison between breeding samples from Alaska and Canada yielded a higher migration rate (0.71) and a broader confidence interval that did not overlap zero (95% HPD: 0.21–4.7).

Winter samples.—Among 75 North American and Eurasian winter samples, 38 haplotypes were observed. In North America, only six of these haplotypes were identical to those observed in breeding-area samples (nos. 1, 2, 7, 8, 9, and 13; Fig. 5A), and they occurred in 29% of winter samples. In the 15 winter samples from Denmark, only one haplotype (no. 23) matched breeding samples from Scotland, but it occurred in 40% of samples. Only haplotype 1 was shared between North American and Eurasian winter samples. Similar to breeding samples, haplotype 1 was the most common (13% of all winter samples), observed in Alaska (n = 3), western North America (n = 3), eastern North America (n = 3), and Denmark (n = 1). A large proportion of North American (65%) and Danish (53%) winter samples were novel haplotypes and not assignable to likely breeding areas. In a comparison of haplotype frequencies among three North American wintering areas (Alaska and western and eastern North America), we observed an overall significant level of population differentiation (Φ_{ST} = 0.101, P < 0.001), and all pairwise comparisons were also significant (P < 0.001). This result was supported by the IM analysis of winter samples from western and eastern North America, in that the migration rate (*m*) was low (0.13; 95% HPD: 0.04–0.84). The estimate for *m* also was lower than for the breeding data (above), which suggests that the two coastal wintering areas are not more heterogeneous than the breeding areas. Thus, the four haplotypes from Alaska breeding samples (nos. 2, 7, 8, and 9) that were observed in winter samples from Maine and

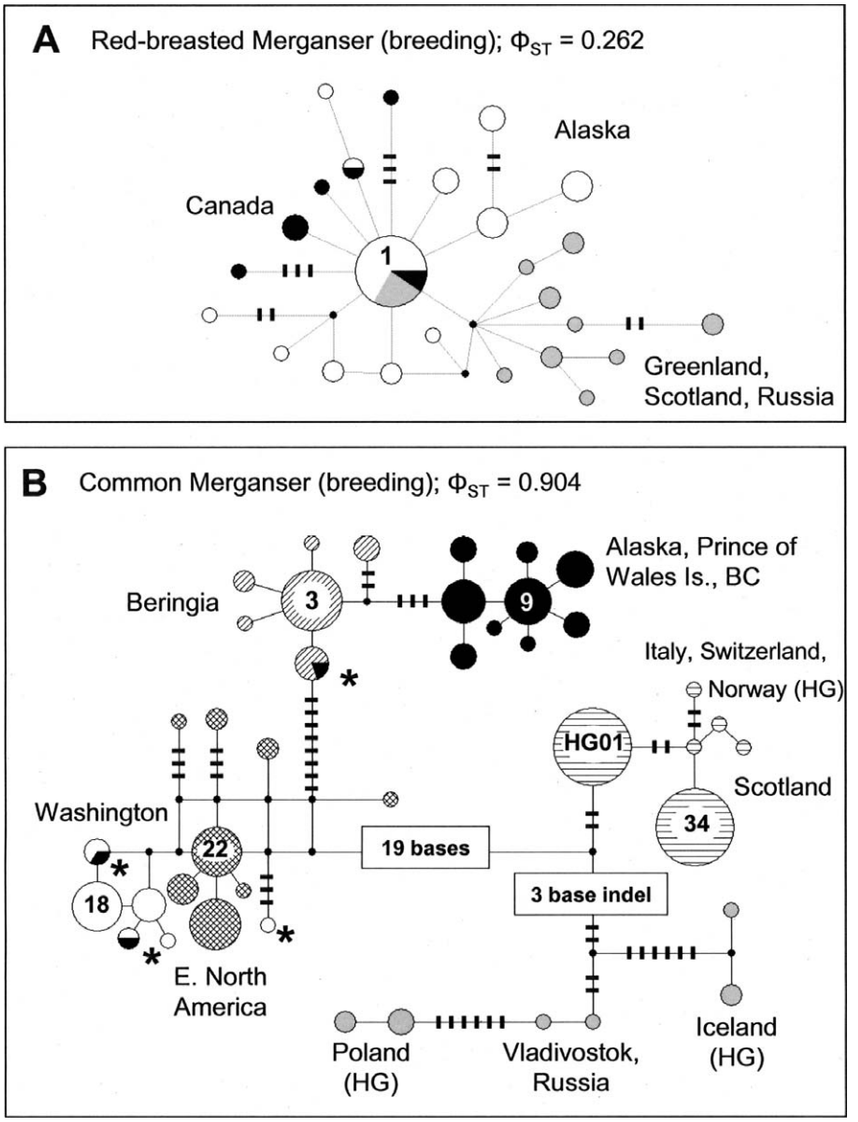

FIG. 3. MtDNA haplotype spanning networks for (A) Red-breasted Merganser and (B) Common Merganser breeding samples and overall levels of population differentiation (Φ_{ST}). In both panels, numbers within circles correspond to common haplotypes in Tables 1 and 2. A single site substitution links each circle except where bars or text denote additional substitutions. Circles are proportional to the number of each haplotype observed. Small black dots are inferred intermediate haplotypes. In panel B, haplotypes labeled "HG" are from Hefti-Gautschi et al. (2009, table 4). Winter samples from Vladivostok, Russia, that were more similar to European lineages also are included (see text). Circles are color-coded to match the major mtDNA haplogroups observed across North America as in Figure 2. Apparent dispersal or migratory events of four individuals are indicated by asterisks (see text).

Massachusetts likely resulted from incomplete lineage sorting and not from migratory connectivity between opposite coasts of North America.

Common Merganser

Breeding samples.—Among 130 North American and global breeding samples, we observed 32 haplotypes defined by 59 variable sites that were characterized by a 1-bp indel, 4 transversions, and 52 transitions (Table 2). Two transversions each occurred within North America and between North American and European samples. Twenty-nine haplotypes (nos. 1–29) were observed in North American breeding samples and three (34–37) in breeding samples from Scotland (Table 2 and Appendix 2). The three haplotypes from Scotland were identical to haplotypes 06 (from Sweden, Finland,

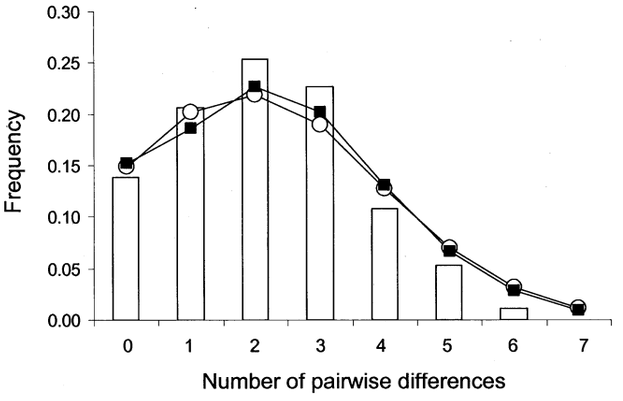

FIG. 4. Results of mismatch distribution analysis of mtDNA for Red-breasted Merganser. Bars represent the frequency of pairwise differences among all North American haplotypes. The line with open circles depicts the theoretical distribution as expected under a model of sudden expansion, whereas the line with closed squares depicts the distribution under a model of spatial expansion.

and Estonia), 24 (from Norway), and 09 (from Norway, Sweden, and Switzerland) observed by Hefti-Gautschi et al. (2009).

In contrast to Red-breasted Mergansers, Common Merganser breeding samples exhibited a pronounced pattern of population structure. The overall difference among sampling areas was high ($\Phi_{ST} = 0.904$, $P < 0.001$), and all pairwise tests were significant, including the smallest difference ($\Phi_{ST} = 0.05$) between western Ontario and eastern North America (Table 3). The level of differentiation did not change substantially when European samples were excluded from the analysis ($\Phi_{ST} = 0.857$, $P < 0.001$). Population structure was observed not only among distant sampling regions, but also at finer geographic scales. For example, we observed haplotype 3 in 10 of 11 samples from Fairbanks, haplotype 5 in 5 of 6 samples from Togiak River, and haplotype 8 among all Anchor River samples, which suggests that shared lineages are a result of long-term philopatry to individual river drainages. North American samples clustered into three major groups of haplotypes (Fig. 3B): Beringia (map locations 18–22; Fig. 2); Alaska, Prince of Wales Island, and British Columbia (AK–POW–BC; map locations 23–26); and Washington (map location 27), western Ontario (map location 28), and eastern North America (map locations 29–30). Samples from Scotland formed an additional group that differed from North America by an average of 19 site substitutions (Fig. 3B), corresponding to 5.3–7.1% uncorrected sequence divergence (Table 4).

The Beringia group included samples from not only Interior and western Alaska (locations 20–22; Fig. 2) that are classified as the North American subspecies (*M. m. americanus*), but also the western Aleutian Islands (location 19) and a single sample from near Magadan, Russia (location 18). Common Mergansers in the Aleutian Islands and Russia have historically been classified as Goosanders, the Eurasian subspecies, on the basis of adult male wing plumage (see Gibson and Byrd 2007). Male Goosanders have elongate white secondary wing coverts that cover a black wing bar that is more visible in males from Fairbanks, which do not have the elongate wing coverts. Furthermore, haplotype 3 was found in specimens from both Shemya Island and Fairbanks, Alaska (Table 2 and Fig. 2), even though males in these areas exhibit two distinct phenotypes. Samples that formed the AK–POW–BC group came from throughout south-central Alaska, Kodiak Island, the Kenai Peninsula, and Prince William Sound, and from Prince of Wales Island, Alaska, and Vancouver Island, British Columbia (Fig. 2).

The haplotype network for breeding samples displayed a close association between samples from Washington and eastern North America. In fact, some of the variation within eastern North America is as great as that between Beringia and AK–POW–BC. Multiple inferred haplotypes in the eastern North American portion of the network (Fig. 3B) suggest that additional mtDNA variation exists throughout the central portion of North America that was not sampled during the present study. The haplotype network (Fig. 3B) displayed some evidence for incomplete lineage sorting, gene flow, or both, in that four samples clustered outside their haplogroups. All four (one male and three females) were identified as either second-year or adult when collected. A second-year male in the Beringia group (haplotype 7) and two adult females from Washington (haplotypes 16 and 17) exhibited sequences more closely related to the AK–POW–BC group, whereas one second-year female sample in Washington (haplotype 20) showed a greater similarity to sequences from eastern North America. Calculations of the ratio (R) of mean percentage sequence divergence rate and nucleotide diversity were much greater than 4.0 (range: 63–580) for the three pairs of populations examined (Beringia vs. Alaska, Alaska vs. western North America, and Beringia vs. western North America), which suggests that these are recent dispersal or migratory events and not the result of incomplete lineage sorting.

Winter samples.—Among 193 North American and Eurasian winter samples, we observed 66 haplotypes (not shown). In North America, 19 of these haplotypes were identical to those observed among breeding-area samples and occurred in 67% of winter samples. In a comparison of haplotype frequencies among three North American wintering areas (Alaska and western and eastern North America), we observed an overall significant level of population differentiation ($\Phi_{ST} = 0.370$, $P < 0.001$), but this was much reduced from the breeding-area comparison ($\Phi_{ST} = 0.857$). In contrast to breeding samples, there were more shared haplotypes among wintering regions (Fig. 5B) and a greater occurrence of divergent lineages within areas.

In the 31 winter samples from Denmark, 15 haplotypes were observed, and 4 of these matched breeding samples from Scotland. In the seven winter samples from Vladivostok, four haplotypes were observed. Three samples were identical and matched haplotype 3 from the western Aleutian Islands and Fairbanks (Table 2), and another two samples differed by 1 bp from haplotype 4 observed in the western Aleutian Islands (V47 in Table 2). The remaining two winter samples from Russia (V50 and V51) were substantially different from haplotypes in Beringia (Table 2) and more closely related to European breeding samples (Fig. 3B). These two samples both contained a 3-bp insertion (AAC; Table 2) that also was observed among samples from Poland and Iceland (Hefti-Gautschi et al. 2009). Except for the Russian samples, there were no other occurrences of shared haplotypes between North American and Eurasian wintering locations.

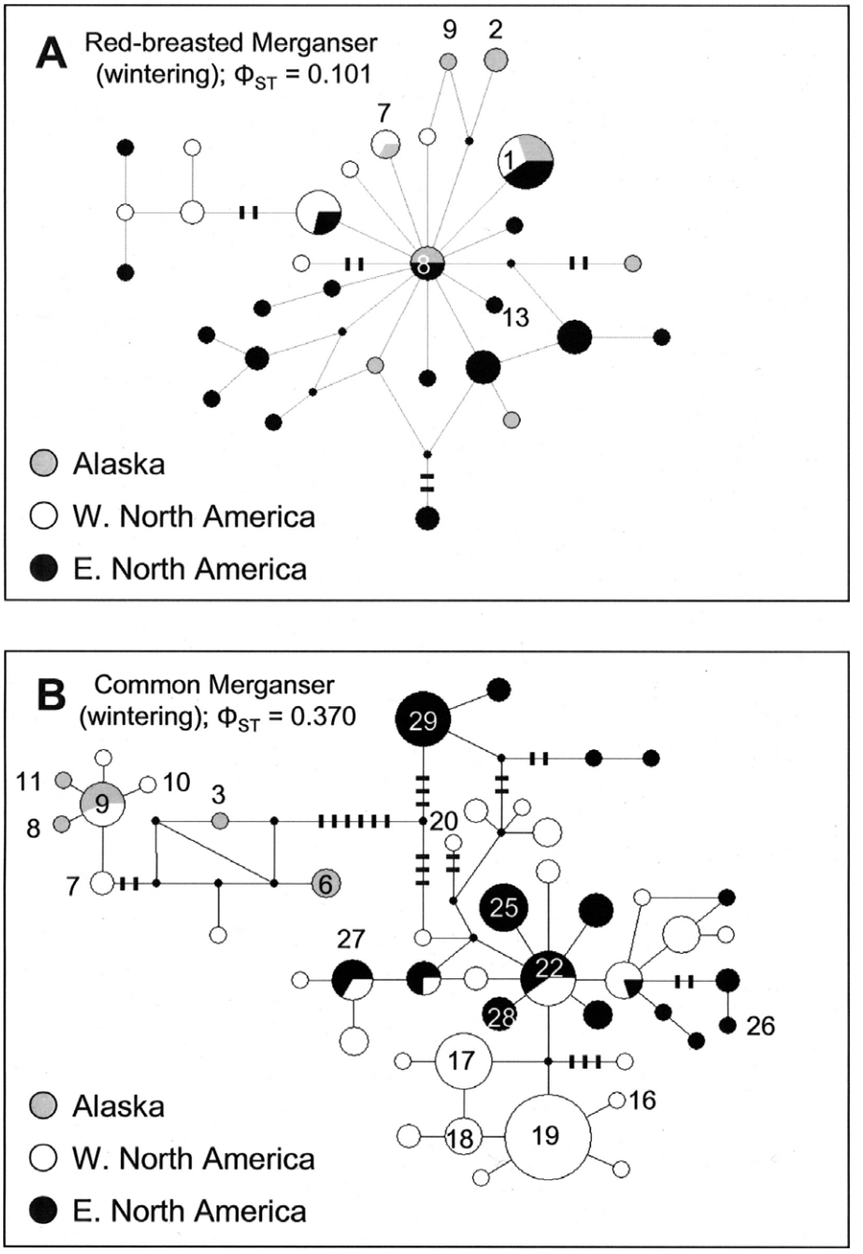

Fig. 5. MtDNA haplotype spanning networks for (A) Red-breasted Merganser and (B) Common Merganser winter samples and overall levels of population differentiation (Φ_{ST}). Circles are proportional to the number of each haplotype observed. Small black dots are inferred haplotypes. Numbers within circles correspond to haplotypes listed in Tables 1 and 2 that were observed within breeding samples.

On the basis of exact haplotype matches and mtDNA spanning network analysis, we observed that several wintering areas were composed of multiple mtDNA haplogroups, but we also observed geographic variation in the pattern of heterogeneity (Fig. 6). Individuals from >1 haplogroup were present in all winter areas except the Great Lakes, eastern North America, and Denmark, though multiple breeding areas may still be present within these areas (see below). In western North America and the Intermountain West, proportions of different mtDNA haplogroups were similar for male and female samples. In heterogeneous areas, approximately half of all samples originated from mtDNA haplogroups other than the resident group, and in western North America all four North American haplogroups were present. Most winter samples from Vladivostok were similar to those observed

TABLE 2. MtDNA control-region haplotypes of Common Mergansers, number (*n*), and location (Fig. 2) of each haplotype in North American and Eurasian breeding areas. Three haplotypes from wintering birds near Vladivostok, Russia (V47, 50, and 51), are also shown. Numbers above haplotype 1 identify the variable positions, and dots represent nucleotides identical to those in haplotype 1. Insertion and deletion events (indels) are shown as dashes.

Haplotype	1 1 1 1 2 2 2 3 3 4 4 4 5 6 7 7 7 7 8 8 8 8 9 9 2 2 3 3 3 3 4 4 4 4 5 5 5 5 7 7 8 9 9 0 0 0 0 1 1 1 1 1 1 2 2 2 2 2 5 7 7 0 4 5 6 8 3 5 8 3 5 0 2 6 7 3 4 6 8 9 2 5 6 7 3 7 2 3 0 1 3 8 1 2 3 9 0 1 4 9 2 9 1 1 3 3 4 6 9 3 5 6 7 8 9 1 3 5 6 7 6 0 3 3	*n*	Location
1	C A C C A C A C T C A A C C G C T T C C A A C C T C C A A C T T C C C C G C A C A C A T C T T C – C – – – G C C C A G C A C	2	18,19
2	. . . . . T . . . . . T	1	19
3	. . . . . T	15	19, 22
4	. . . . . T . . . . . T	1	19
5	. . . . . C . . . . . T	5	20
6	. . . . . T . C . . . . . T . . . . . T	3	21
7	. . . . . C . T . . . . . C . . . . . A . . . . . T	8	20, 25, 26
8	. . . . . C . T . . . . . C . . T . . . . . A	6	24
9	. . . . . C . T . . . . . C . . T . . . . . A . . . . . T	9	24, 25
10	. . . . . C . T . . . . . C . . T . . . . . C . . . . A . . . . . T	2	23
11	. . . . . C . T . . . . . C . . T . . . . . C . A . . . . . T	3	24
12	. . . T . . . . . C . T . . . . . C . . T . . . . . A . . . . . T	1	25
13	. . . . . C . T . . . . . T . . . . C . . . . . A . . . . . T	3	25
14	. . . . . A . . . . . C . T . . . . . C . . T . . . . . A . . . . . T	1	25
15	. . . . . C . T . . . . . C . . . . . C . . . . . A . . . . . T	3	26
16	. . . . G . . . . . C . . . . . C . . G . T . . T . T . . . . . G T C C . . C . A . . . . . T . T . . T . T	2	25, 27
17	. . . . G . . . . . C . . . . . C . . . . T . . . . T . . . . . G T C C . . C . A . . . . . T . T . . . . T	2	26, 27
18	. . . . G . . . . . C . . . . . C . . . . T . . T . T . . . . . G T C C . . C . A . . . . . T . T . . . . T	9	27
19	. . . . G . . . . . C . . . . . C . . . . T . . T . T . . . . . G T C C . . C . A . . . . . T . T . . T . T	5	27
20	. . . . G . . . . . T . . . C . . . . . T C . . . . T . . . . T . . . . . G . C C . . C . A . . . . . T	1	27
21	. . . . G . . . . T . . . . C . . . . . . C . . . . T . . T . T . . . . . G T C C . . C . A . . . . . T . T . . T . T	1	27
22	. . . . G . . . . . C . . . . . . C . . . . T . . . . T . . . . . G . C C . . C . A . . . . . T . . . . T . T	10	28, 29, 30
23	. . . . G . G . . . G . . T . . . C . . . . . T . . . . T . . . . . G . C C . . C . A . . . . . T . T . . T . T	1	28
24	. . . . G . . . . . C . T . . . . C . . . . T . . . . T . . . . . G . C C . . C . A . . . . . T . . . . T . T	1	28
25	. . . . G . . . . . C . . . . . . C . . . G T . . . . T . . . . . G . C C . . C . A . . . . . T . . . . T . T	11	29, 30
26	. . . . G . . . . . C . . . . . . T . . . . T . . . . . G . C C T . C . A T . . . . T . . . . . T	2	30
27	. . . . G . . . . . C . . . . . . T . . . . T . . . . T G . C C . . C . A . . . . . T . T	2	28, 29
28	. . . . G . . . . . C . . . . . C . . . . T C . . . T . . . . . G . C C . . C . A . . . . . T . . . . T . T	4	29
29	. . . . G . G . . . . . T . . . C . . . . . . T . . . . T . . . . . G . . C . . . . A . . . . . T . T	1	30
34	T . T . G T . . C . . G T . A A . . . . G G T . C T . C . T . C . T . . A . G . . . . C . C C . A . . . . . A . G T	1	31
36	T . T . G T . . C . . G T . A A . C . . G G T . C T . C . T . C . T . . A . G . . . . C . . C T A . . . . . G A . G T	13	31
37	T . T . G T . . C . . . T . A A . C . . G G T . C T . C . T . C . T . . A T G . . . . C . . C . A . . . . . A . G T	1	31
V47	. . . . . T . . . . T	2	18
V50	T G T . G T . . C T . . T . A . . C . . G . . . C T . C . T . C . T . T A . . . . . C . . C . A . A A C A . . . . A . G T	1	18
V51	T . T . G T . . C T . . T . A . . C . . G . . . C T . C . T . C . T . T A . . . . . C . . C . A . A A C A . . . . A . G T	1	18
Total		134	

Table 3. Pairwise Φ_{ST} among Common Merganser breeding samples across North America in comparison to European samples from Scotland and Denmark (*$P < 0.001$).

	Alaska, Prince of Wales Island, and British Columbia	Washington	Western Ontario	Eastern North America	Scotland and Denmark
Beringia	0.752*	0.918*	0.881*	0.858*	0.938*
Alaska, Prince of Wales Island, and British Columbia		0.918*	0.887*	0.871*	0.939*
Washington			0.679*	0.642*	0.941*
Western Ontario				0.052*	0.921*
Eastern North America					0.918*

[a] Haplogroups include the following areas: (1) Beringia; (2) Alaska, British Columbia, Canada, and Prince of Wales Island, Alaska; (3) Washington, western Ontario, Canada, and eastern North America; and (3) Scotland and Denmark.

in Iceland and Poland by Hefti-Gautschi et al. (2009), in that they contained the 3-bp indel (Table 2). This indel was not observed in any of the 31 winter samples from Denmark. After accounting for the shorter control-region fragment sequenced in the present study, 93% of winter samples from Denmark were identical to haplotypes from central and northern European areas identified by Hefti-Gautschi et al. (2009).

Discussion

Red-breasted Mergansers within North America yielded a pattern of population expansion that is common to many species that have expanded their ranges to more northerly latitudes following the last glacial maximum in North America (Avise 2000, Milá et al. 2006). However, differentiation exists on broad scales, and mtDNA lineages that are shared between North America and Europe are more likely the result of insufficient time since range expansion (i.e., incomplete lineage sorting) than of gene flow. The analysis of winter samples suggests that birds on opposite coasts of North America are distinct. The lower estimate and narrower confidence limits on the estimate of migration for wintering than for breeding data suggest that further sampling across the breeding range is needed to refine possible population boundaries. Information from other independent markers, such as stable-isotope, mark–recapture, or satellite-telemetry data, could also be used to assess where broad population boundaries and migratory pathways between breeding and wintering areas occur. By contrast, mtDNA from Common Mergansers revealed substantial population structure, which suggests limited female-mediated gene flow. Evidence of female philopatry was found not only in the differentiation among sampling regions but also at finer scales. Among samples from single localities in Alaska, such as Fairbanks and the Togiak and Anchor rivers, independent samples had identical haplotypes, which suggests shared lineages as a result of philopatry to individual river drainages. Despite the disappearance of Pleistocene barriers throughout North America that may have limited past dispersal, we observed no evidence of secondary contact among historically isolated groups of Common Mergansers.

Genetic evidence from wintering Common Mergansers suggests that males and females appear to move across phylogeographic boundaries along the Pacific Coast, which is similar to movements observed with satellite transmitters (Pearce and Petersen 2009). These movements by females may facilitate male dispersal and gene flow if females pair during winter and away from natal breeding grounds. For male Common Mergansers,

Table 4. Uncorrrected percent sequence divergence of mtDNA among sampling areas for Common Mergansers in North America and Europe. Between-area divergence values are shown below the diagonal, whereas within-group divergence levels are shown along the diagonal.

	Haplogroup[a]			
	1	2	3	4
1	0.23–1.15			
2	1.15–1.83	0.23–0.69		
3	2.52–3.90	2.29–4.36	0.46–2.29	
4	5.50–6.42	5.50–7.11	5.28–7.11	0.23–1.38

[a] Haplogroups include the following areas: (1) Beringia; (2) Alaska, British Columbia, Canada, and Prince of Wales Island, Alaska; (3) Washington, western Ontario, Canada, and eastern North America; and (3) Scotland and Denmark.

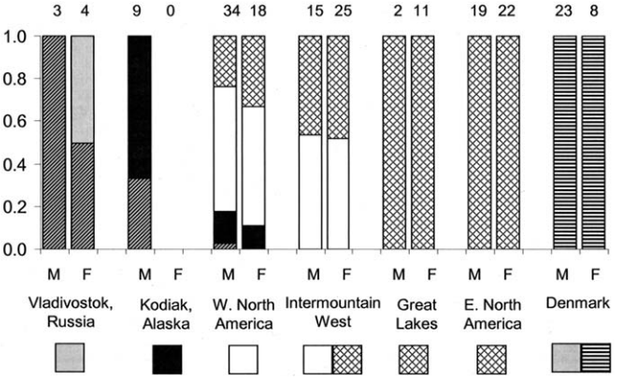

Fig. 6. Frequency of mtDNA haplogroups among winter samples of male (M) and female (F) Common Mergansers across five North American and two Eurasian sites. Samples from Vladivostok, Russia, were a mixture of wintering and putatively wintering birds, collected during October–April. Shading of bars corresponds to colors used in Figure 3B. Expected haplogroup composition of each wintering area, based on mtDNA of breeding samples, is shown in boxes below location names. Sample sizes appear above each bar.

population heterogeneity on wintering areas likely results from both seasonal migration and dispersal among divergent breeding grounds. Both of these behaviors were observed among molting Common Mergansers in Alaska (Pearce et al. 2009). Thus, the finding of a Beringian haplotype in western North America during winter could mean that this individual either dispersed to a new breeding area or migrated south for the winter.

Common Merganser samples from wintering areas such as western North America and Vladivostok comprised individuals with very different mtDNA lineages, because these areas are adjacent to major phylogeographic breaks. Although wintering areas such as the Great Lakes and eastern North America appear to be homogeneous, they likely contain individuals from multiple breeding areas that may be differentiated on a lesser scale than in western North America. Interestingly, none of the 31 winter samples from Denmark contained the unique 3-bp insertion (AAC), despite the occurrence of this mutation in breeding birds in Iceland and Poland (see Hefti-Gautschi et al. 2009). This insertion was also lacking among Danish breeding birds (Hefti-Gautschi et al. 2009). Band-recovery data from central Europe and Scandinavia show that Danish wintering birds originate from Norway, Sweden, Finland, and the northern coast of western Russia (Bønløkke et al. 2006). There may be geographic variation in migratory tendency and limited dispersal by males among some breeding populations in Europe, a pattern also observed in band-recovery data across North America (Pearce et al. 2005). Additional breeding and winter samples of Common Mergansers from Europe and Russia would improve our interpretation of migratory patterns and population structure.

We conclude that the four cases of apparent dispersal among haplogroups of Common Mergansers (Fig. 3B) are either dispersal by males or seasonal migratory movements by females. Dispersal by males is suggested by the lack of population differentiation for nuclear markers across Europe and North America (Hefti-Gautschi et al. 2009, Pearce et al. 2009), whereas migratory movement by females is supported by limited satellite telemetry (Pearce and Petersen 2009) and the genetic data from wintering areas presented here. Furthermore, indirect genetic evidence using the ratio of sequence divergence to nucleotide diversity ($R = \delta/\pi$) suggests that these dispersal or migratory events are not the result of incomplete lineage sorting. With $R > 4$, populations should be differentiated at nuclear loci in the absence of male gene flow, similar to waterfowl species in which males do not disperse (e.g., Scribner et al. 2003).

The relationship of Common Merganser haplotypes in the mtDNA network for Beringia and areas farther south (Fig. 3B) does not imply a northward post-Pleistocene, stepping-stone colonization pattern along the Pacific Coast. Instead, the AK–POW–BC haplogroup appears to be derived from the Beringian group. Additionally, all samples from Beringia are more closely related to North America than to Asia, which differs from New World–Old World patterns of several avian taxa with ranges that span the Bering Sea (Zink et al. 1995, 2006; Drovetski et al. 2004). However, such a split may occur farther west in the Russian Far East, as suggested by the admixture of New World–Old World lineages among wintering birds near Vladivostok (Table 2 and Fig. 6).

The contrasting patterns of genetic differentiation in Red-breasted and Common mergansers raise questions about the evolutionary and ecological constraints of nesting behavior for species that nest on the ground and in cavities. If Red-breasted Mergansers evolved from a cavity-nesting ancestor, the switch to ground nesting has allowed colonization of more northern breeding habitats than other merganser species that rely on cavities. Whether this switch has led to lower rates of annual survival, which are more characteristic of *r*-selected ground-nesting waterfowl than of sea ducks (Krementz et al. 1997), is unknown, because no data on survivorship are available (Titman 1999). In the cavity-nesting Common Merganser, female population structure appears to be maintained by philopatry. Although philopatry has often been viewed as a constraint, placing populations at risk if local habitat or forage is disturbed, our genetic data suggest that female movements during non-breeding periods could facilitate dispersal if natal nesting areas became unsatisfactory. But then why be philopatric? Among cavity-nesting species of waterfowl, Common Mergansers have the largest body size and, thus, may be limited to a smaller proportion of natural cavities than their smaller-bodied congeners. Thus, there may be a cost of dispersal in terms of locating large cavities in unfamiliar habitats. By contrast, smaller-bodied cavity-nesting waterfowl may exhibit more inconsistent patterns of site fidelity because smaller cavities may be more abundant and easier to locate, making dispersal more common (see Pearce et al. 2008). Cavity nesting by Common Mergansers also raises the question of what nesting habitat existed historically in the North Pacific when Beringian populations diverged from western and eastern North America and whether Common Mergansers nested on the ground in the past. Both pollen and macrofossil data suggest that the most common tree genera (*Populus*, *Picea*, and *Pinus*) associated with nest cavities survived within Beringia during the last glacial maximum, around 15,000–28,000 years ago (Brubaker et al. 2005). However, little is known about the size and structure of these forests and whether they could have supported cavities suitable for nesting. Two records of Common Merganser broods from the western and central Aleutian Islands need further substantiation, given that these treeless islands do not support tree cavities and that breeding Red-breasted Mergansers are common there (Gibson and Byrd 2007).

Acknowledgments

We thank D. Derksen, P. Flint, S. Talbot, C. Dau, J. Peters, J. Gust, K. Sage, and M. Marquiss. Numerous individuals and agencies donated DNA samples, including P. Padding and K. Bollinger (U.S. Fish and Wildlife Service); K. Timm, R. McNeil, and B. Braune (National Wildlife Research Center, Canadian Wildlife Service); M. Marquiss (Centre for Ecology and Hydrology, Scotland); D. Boertmann (National Environmental Research Institute, Denmark); S. Birks and R. Faucett (Burke Museum of Natural History and Culture); L. Savoy (BioDiversity Research Institute); J. Smith and J. Parrish (University of Washington); T. Sutter (New York Department of Environmental Conservation); K. Winker, S. Sonsthagen, and R. Wilson (University of Alaska, Fairbanks); P. Abraham and T. Allen (Togiak National Wildlife Refuge); S. Kendall (Arctic National Wildlife Refuge); D. Zwiefelhofer (Kodiak National Wildlife Refuge); J. Morton and T. Eskelin (Kenai National Wildlife Refuge); and D. Sonneborn, M. Schwitters, and staff of the U.S. Coast Guard (Attu Loran Station). This research was supported primarily by the North American Sea Duck Joint Venture. Additional funding and support was provided by the U.S. Geological

Survey Alaska Science Center and by the Department of Biology and Wildlife at the University of Alaska, Fairbanks. K. Winker, M. Olson, M. Lindberg, P. Flint, D. Derksen, J. Klicka, and two anonymous reviewers provided comments on earlier drafts of the manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Avise, J. C. 1994. Molecular Markers, Natural History and Evolution. Chapman & Hall, New York.

Avise, J. C. 2000. Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, Massachusetts.

Bandelt, H.-J., P. Forster, and A. Röhl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37–48.

Bønløkke, J., J. J. Madsen, K. Thorup, K. T. Pedersen, M. Bjerrum, and C. Rahbek. 2006. Dansk Trækfugleatlas [The Danish Bird Migration Atlas]. Rhodos, Humlebæk, Denmark.

Brubaker, L. B., P. M. Anderson, M. E. Edwards, and A. V. Lozhkin. 2005. Beringia as a glacial refugium for boreal trees and shrubs: New perspectives from mapped pollen data. Journal of Biogeography 32:833–848.

Cronin, M. A., J. B. Grand, D. Esler, D. V. Derksen, and K. T. Scribner. 1996. Breeding populations of Northern Pintails have similar mitochondrial DNA. Canadian Journal of Zoology 74:992–999.

Drovetski, S. V., R. M. Zink, S. Rohwer, I. V. Fadeev, E. V. Nesterov, I. Karagodin, E. A. Koblik, and Y. A. Red'kin. 2004. Complex biogeographic history of a Holarctic passerine. Proceedings of the Royal Society of London, Series B 271:545–551.

Excoffier, L., G. Laval, and S. Schneider. 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Friesen, V. L., T. M. Burg, and K. D. McCoy. 2007. Mechanisms of population differentiation in seabirds. Molecular Ecology 16:1765–1785.

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

Gibson, D. D., and G. V. Byrd. 2007. Birds of the Aleutian Islands, Alaska. Series in Ornithology, no. 1. Nuttall Ornithological Club and American Ornithologists' Union, Washington, D.C.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Hatton, P. L., and M. Marquiss. 2004. The origins of moulting Goosanders on the Eden Estuary. Ringing & Migration 22:70–74.

Hefti-Gautschi, B., M. Pfunder, L. Jenni, V. Keller, and H. Ellegren. 2009. Identification of conservation units in the European *Mergus merganser* based on nuclear and mitochondrial DNA markers. Conservation Genetics 10:87–99.

Krementz, D. G., R. J. Barker, and J. D. Nichols. 1997. Sources of variation in waterfowl survival rates. Auk 114:93–102.

Lecomte, N., G. Gauthier, J.-F. Giroux, E. Milot, and L. Bernatchez. 2009. Tug of war between continental gene flow and rearing site philopatry in a migratory bird: The sex-biased dispersal paradigm reconsidered. Molecular Ecology 18:593–602.

Little, B., and R. W. Furness. 1985. Long distance moult migration by British Goosanders, *Mergus merganser*. Ringing & Migration 6:77–82.

Livezey, B. C. 1995. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor 97:233–255.

Mallory, M., and K. Metz. 1999. Common Merganser (*Mergus merganser*). *In* The Birds of North America, no. 442 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

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

Milá, B., T. B. Smith, and R. K. Wayne. 2006. Postglacial population expansion drives the evolution of long-distance migration in a songbird. Evolution 60:2403–2409.

Nielsen, R., and J. Wakeley. 2001. Distinguishing migration from isolation: A Markov chain Monte Carlo approach. Genetics 158:885–896.

Pearce, J. M. 2006. Minding the gap: Frequency of indels in mtDNA control region sequence data and influence on population genetic analyses. Molecular Ecology 15:333–341.

Pearce, J. M., P. Blums, and M. S. Lindberg. 2008. Site fidelity is an inconsistent determinant of population structure in the Hooded Merganser (*Lophodytes cucullatus*): Evidence from genetic, mark–recapture, and comparative data. Auk 125:711–722.

Pearce, J. M., and M. R. Petersen. 2009. Post-fledging movements of juvenile Common Mergansers (*Mergus merganser*) in Alaska as inferred by satellite telemetry. Waterbirds 32:133–137.

Pearce, J. M., J. A. Reed, and P. L. Flint. 2005. Geographic variation in survival and migratory tendency among North American Common Mergansers. Journal of Field Ornithology 76:109–118.

Pearce, J. M., and S. L. Talbot. 2006. Demography, genetics, and the value of mixed messages. Condor 108:474–479.

Pearce, J. M., D. Zwiefelhofer, and N. Maryanski. 2009. Mechanisms of population heterogeneity among molting Common Mergansers on Kodiak Island, Alaska: Implications for genetic assessments of migratory connectivity. Condor 111:283–293.

Peters, J. L., and K. E. Omland. 2007. Population structure and mitochondrial polyphyly in North American Gadwalls (*Anas strepera*). Auk 124:444–462.

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

Rogers, A. R., and H. C. Harpending. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Molecular Biology and Evolution 9:552–569.

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.

Smith, T. B., S. M. Clegg, M. Kimura, K. C. Ruegg, B. Milá, and I. J. Lovette. 2005. Molecular genetic approaches to linking breeding and overwintering areas in five Neotropical migrant passerines. Pages 222–234 *in* Birds of Two Worlds:

The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Sorenson, M. D., and T. W. Quinn. 1998. Numts: A challenge for avian systematics and population biology. Auk 115:214–221.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software, version 4.0. Molecular Biology and Evolution 24:1596–1599.

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.

Titman, R. D. 1999. Red-breasted Merganser (*Mergus serrator*). *In* The Birds of North America, no. 443 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Villesen, P. 2007. FaBox: An online toolbox for FASTA sequences. Molecular Ecology Resources 7:965–968.

Wright, S. 1943. Isolation by distance. Genetics 28:114–138.

Zink, R. M., A. Pavlova, S. Rohwer, and S. V. Drovetski. 2006. Barn Swallows before barns: Population histories and intercontinental colonization. Proceedings of the Royal Society of London, Series B 273:1245–1251.

Zink, R. M., S. Rohwer, A. V. Andreev, and D. L. Dittmann. 1995. Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. Condor 97:639–649.

Associate Editor: J. Klicka

Appendix 1. Geographic areas, sampling sites (number in brackets corresponds to general map locations in Figs. 1 and 2), season of collection, sample source, size (*n*), and coordinates for Red-breasted and Common mergansers included in the present study. Specific sampling-site names and coordinates were unavailable for many wintering areas in U.S. states and Canadian provinces and are left blank.

Geographic area (location code)	Sampling site	Sample source[a]	*n*	Latitude	Longitude
		Red-breasted Merganser			
Breeding samples					
Russia (RUS)	Yamalo-Nenetski (1)	UWBM 59478, 59567 KGM 831, KGM 839, UAMX 4610, 4611, 4626, 4627, 4631, 4632, 4637,	2	68.01	68.36
Alaska (AKal)	Attu Island, Aleutian Islands (2)	4638, 4643	11	52.50	–173.10
Alaska (AKal)	Amchitka Island, Aleutian Islands (3)	Nest	1	51.30	–179.00
Alaska (AKgn)	Good News River (4)	Tissue	5	59.07	–161.35
Alaska (AKjo)	Johnson River (5)	Tissue	3	60.47	–161.45
Alaska (AKbr)	Brooks River (6)	Feather, tissue	2	58.33	–155.47
Alaska (AKsk)	Skilak Lake (7)	Tissue	2	60.28	–150.28
Alaska (AKfbk)	Fairbanks (8)	Tissue	3	64.49	–147.44
Alaska (AKce)	Cape Espenberg (9)	Nest	1	66.34	–163.44
Alaska (AKiv)	Ivishak River (10)	Tissue	9	68.42	–146.53
Nunavut (CANkl)	Karrak Lake (11)	Nest	1	67.14	–100.14
Ontario (ON)	Big Trout Lake (12)	Tissue	1	53.45	–90.00
Greenland (GRN)	Greenland (13)	Nest	1	68.10	–52.50
Quebec (PQ)	George River (14)	Tissue	2	58.30	–65.50
New Brunswick (NB)	Kouchibouguac National Park (15)	Nest	4	46.50	–64.58
Newfoundland (NF)	Newfoundland (16)	Tissue	1	49.00	–57.50
Scotland (UK)	Montrose (17)	Tissue	15	56.42	2.28
Wintering samples					
Alaska (AKw)	Kodiak Island	Tissue	12	57.45	–152.23
Washington (WAw)		Wing	1	47.30	–120.00
Oregon (ORw)		Wing	1	44.00	–120.35
California (CAw)		Wing	1	36.50	–120.00
Baja (MEXw)	Bahia de San Quintin	Wing	4	30.24	–115.58
Utah (UTw)		Wing	9		
Newfoundland (NFw)		Wing	3		
Nova Scotia (NSw)		Wing	3		
Maine (MEw)		Wing	3		
Massachusetts (MAw)		Wing	3		
New Jersey (NJw)		Wing	6		
Rhode Island (RIw)		Wing	3		
Connecticut (CNw)		Wing	1		
Virginia (VAw)		Wing	6		
North Carolina (NCw)		Wing	1		
Florida (FLw)		Wing	3		
Denmark (DEw)	Limfjorden	Wing	15	57.00	9.00

(*Continued*)

APPENDIX 1. Continued.

Geographic area (location code)	Sampling site	Sample source [a]	*n*	Latitude	Longitude
		Common Merganser			
Breeding samples					
Russia (RUS)	Magadan (18)	UWBM 43819	1	59.32	150.52
Alaska (AKal)	Shemya Island, Aleutian Islands (19) b	Tissue (2), UAM 24117, 24299, 24306	5	52.42	–174.06
Alaska (AKto)	Togiak River (20)	Tissue	6	59.02	–160.24
Alaska (AKno)	Novi River (21)	Tissue	2	62.56	–155.32
Alaska (AKnw)	Nowitna River (21)	Tissue	1	62.56	–155.32
Alaska (AKfbk)	Fairbanks (22)	Tissue (8), nest (3)	11	64.49	–147.44
Alaska (AKdj)	Delta Junction (22)	Tissue	1	64.04	–145.42
Alaska (AKdh)	Dalton Highway (22)	UAM 21870	1	68.00	–149.59
Alaska (AKko)	Kodiak Island (23)	Nest	2	57.45	–152.23
Alaska (AKar)	Anchor River (24)	Nest	6	59.46	–151.49
Alaska (AKkr)	Kenai River (24)	Tissue	3	60.28	–150.28
Alaska (AKho)	Hope (24)	Tissue	2	60.53	–149.37
Alaska (AKcrd)	Cordova (24)	Tissue	6	60.32	–145.45
Alaska (AKpow)	Prince of Wales Island (25)	Wing	9	57.32	–134.30
British Columbia (BC)	Port Alberni (26)	Tissue	4	49.14	–124.48
British Columbia (BC)	Gold River (26)	Tissue	5	49.41	–126.07
Washington (WA)	Columbia River (27)	Tissue	18	47.30	–120.10
Ontario (ON)	Western Ontario (28)	Tissue	8	50.40	–94.25
Vermont (VT)	Vermont (29)	Tissue	11	44.00	–72.50
Maine (ME)	Aziscohos Lake (29)	Nest	1	45.00	–71.00
New Brunswick (NB)	Restigouche River (30)	Tissue	12	48.04	–66.20
Scotland (UK)	Aberdeen (31)	Tissue	15	57.08	2.05
Wintering samples					
Russia (RUSw)	Vladivostok	Wing	7	43.13	131.41
Denmark (DEw)	Limfjorden	Wing	31	57.00	9.00
Alaska (AKw)	Kodiak Island	Tissue	9	57.45	–152.23
Washington (WAw)		Wing	10		
Oregon (ORw)		Wing	33		
California (CAw)		Wing	9		
Arizona (AZw)		Wing	6		
Utah (UTw)		Wing	17		
Idaho (IDw)		Wing	7		
Colorado (COw)		Wing	10		
Minnesota (MNw)		Wing	2		
Michigan (MIw)		Wing	6		
Wisconsin (WIw)		Wing	5		
Pennsylvania (PAw)		Wing	22		
Quebec (PQw)		Wing	6		
Newfoundland (NFw)		Wing	10		
Nova Scotia (NSw)		Wing	3		

[a] Numbers in parentheses refer to samples of the following tissue types: "wing" = tissue collected from U.S., Canadian, and Danish parts collection surveys; "feather" = sampled from salvaged or captured bird; "nest" = nesting material (i.e., egg-shell membranes and feathers). Vouchered museum specimens are indicated as follows: UWBM = University of Washington Burke Museum; KGM, UAM, and UAMX = University of Alaska Museum. All other samples are currently held at the U.S. Geological Survey Alaska Science Center.

[b] Considered breeding samples in the present study, but Common Mergansers in the Aleutian Islands are likely migrants, given that breeding records are unsubstantiated (Gibson and Byrd 2007).

APPENDIX 2. Geographic areas, sampling sites (number in brackets corresponds to general map locations in Figs. 1 and 2), number of each haplotype observed, and total sample size per area for Red-breasted and Common mergansers included in the present study.

Geographic area (location code)	Sampling site	Haplotypes observed (count)	*n*
		Red-breasted Merganser	
Russia (RUS)	Yamalo-Nenetski (1)	1 (2)	2
Alaska (AKal)	Attu Island, Aleutian Islands (2)	1 (5), 8 (1) 10 (3), 11 (1), 12 (1)	11
Alaska (AKal)	Amchitka Island, Aleutian Islands (3)	10 (1)	1
Alaska (AKgn)	Good News River (4)	5 (1), 6 (2), 7 (2)	5
Alaska (AKjo)	Johnson River (5)	4 (1), 8 (2)	3
Alaska (AKbr)	Brooks River (6)	1 (1)	1
Alaska (AKsk)	Skilak Lake (7)	2 (1), 9 (1)	2
Alaska (AKfbk)	Fairbanks (8)	1 (1), 9 (2)	3
Alaska (AKce)	Cape Espenberg (9)	2 (1)	1
Alaska (AKiv)	Ivishak River (10)	1 (7), 2 (1), 3 (1)	9
Nunavut (CANkl)	Karrak Lake (11)	3 (1)	1
Ontario (ON)	Big Trout Lake (12)	13 (1)	1
Greenland (GRN)	Greenland (13)	1 (1)	1
Quebec (PQ)	George River (14)	1 (2)	2
New Brunswick (NB)	Kouchibouguac National Park (15)	15 (1), 16 (3)	4
Newfoundland (NF)	Newfoundland (16)	14 (1)	1
Scotland (UK)	Montrose (17)	1 (2), 17 (1), 18 (2), 19 (2), 20 (2), 21 (1), 22 (1), 23 (2), 24 (1), 25 (1)	15
		Common Merganser	
Russia (RUS)	Magadan (18)	1 (1)	1
Alaska (AKal)	Shemya Island, Aleutian Islands (19)	1 (1), 2 (1), 3 (2), 4 (1)	5
Alaska (AKto)	Togiak River (20)	5 (5), 7 (1)	6
Alaska (AKno)	Novi River (21)	6 (2)	2
Alaska (AKnw)	Nowitna River (21)	6 (1)	1
Alaska (AKfbk)	Fairbanks (22)	3 (11)	11
Alaska (AKdj)	Delta Junction (22)	3 (1)	1
Alaska (AKdh)	Dalton Highway (22)	3 (1)	1
Alaska (AKko)	Kodiak Island (23)	10 (2)	2
Alaska (AKar)	Anchor River (24)	8 (6)	6
Alaska (AKkr)	Kenai River (24)	9 (3)	3
Alaska (AKho)	Hope (24)	9 (2)	2
Alaska (AKcrd)	Cordova (24)	9 (0.5), 11 (0.5)	6
Alaska (AKpow)	Prince of Wales Island (25)	7 (2), 9 (1), 12 (1), 13 (3), 14 (1), 16 (1)	9
British Columbia (BC)	Port Alberni (26)	7 (3), 17 (1)	4
British Columbia (BC)	Gold River (26)	7 (2), 15 (3)	5
Washington (WA)	Columbia River (27)	16 (1), 17 (1), 18 (9), 19 (5), 20 (1), 21 (1)	18
Ontario (ON)	Western Ontario (28)	22 (5), 23 (1), 24 (1), 27 (1)	8
Vermont (VT)	Vermont (29)	22 (3), 25 (4), 27 (1), 28 (3)	11
Maine (ME)	Aziscohos Lake (29)	28 (1)	1
New Brunswick (NB)	Restigouche River (30)	22 (2), 25 (7), 26 (2), 29 (1)	12
Scotland (UK)	Aberdeen (31)	34 (1), 36 (13), 37 (1)	15