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ORIGINAL PAPER

Genetic structure of rhinoceros auklets, *Cerorhinca monocerata*, breeding in British Columbia, Alaska, and Japan

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Abstract Data from eight microsatellite markers screened in 246 rhinoceros auklets (*Cerorhinca monocerata*) from across the North Pacific revealed multiple genetic groups. The east (North America) to west (Japan) split was clearly evident in all analyses. Within the eastern Pacific, a minimum of three genetic groups are present. Surprisingly, rhinoceros auklets from Triangle Island, British Columbia, were genetically isolated from other nearby populations, including the breeding colony on Pine Island (~100 km to the east). A fourth genetic cluster (Chowiet Is) was detected using principal coordinate's analysis; however, sample sizes were limited. Patterns of differentiation correspond to nonbreeding distributions with the eastern and western Pacific birds spending time off the west coast of North America and Japan, respectively, and may represent historical isolation in separate refugia during the Pleistocene glaciations. The patterns of genetic structure result from a combination of historical and contemporary factors influencing dispersal of rhinoceros auklets.

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Introduction

The rhinoceros auklet (*Cerorhinca monocerata*) breeds on islands in the North Pacific from California to Japan. Breeding colonies are not evenly distributed along the coastline nor are population numbers similar throughout the range with approximately 50 % of the birds breeding in British Columbia, Canada (Rodway 1991). Like other puffins (tribe Fraterculini), rhinoceros auklets lay a single-egg clutch in an enclosed burrow, but unlike closely related species each parent provisions its offspring at most once per night with food loads consisting of fish and large invertebrates (Gaston and Dechesne 1996b; Takahashi et al. 1999). Comprehensive vital rate estimates are available over a 15-year period (1994–2008) from Triangle Island, which supports one of the larger colonies in British Columbia.

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Auklets on Triangle Island have a relatively constant annual adult survival rate of ~86 % (Morrison et al. 2011); however, breeding success is extremely variable and strongly linked to oceanographic conditions (Hedd et al. 2006; Ito et al. 2009; Borstad et al. 2011). While global population estimates are sufficient to list rhinoceros auklets as "least concern" (BirdLife International 2013), mortality is known to occur from anthropogenic factors and some populations are declining. For example, rhinoceros auklets comprise a large proportion of seabird bycatch in salmon gillnet fisheries off Washington (Melvin et al. 2001; Thompson et al. 1998) and British Columbia (Smith and Morgan 2005). In species, such as the rhinoceros auklet, with a high natural fledgling survival, both adult and juvenile survival rates have a large impact on population trajectories (Sandvik et al. 2008), and any factors reducing the survival rate could have consequences on long-term population viability.

Concern for the population health and persistence for any seabird species experiencing high fisheries-related mortality is well founded. Bycatch of seabirds occurs on a global scale, and their life history characteristics of marine foraging, delayed sexual maturation, low annual fecundity, obligate biparental care, and high natural longevity (c.f. Friesen et al. 2007) make them especially vulnerable to declines. While seabirds are not targeted by fisheries operations, global population declines as a result of incidental bycatch are unfortunately all too common in seabirds (Brothers et al. 2010; Croxall et al. 2012). In several species, concern has been raised about extinction risks related to fisheries mortality. This has motivated studies estimating the magnitude and impact of bycatch mortality for individual species or fisheries (e.g., Lewison and Crowder 2003; Lewison et al. 2009; Lebreton and Véran 2012) and on mitigation strategies (e.g., Klaer and Polacheck 1998; Wilcox and Donlan 2007; Finkelstein et al. 2008).

Genetic methods can contribute to seabird conservation efforts in multiple ways (Edwards et al. 2001), including (1) the delineation of within-species groups that are sufficiently genetically divergent to warrant separate conservation priority (e.g., Burg and Croxall 2001; Smith et al. 2007; Welch et al. 2012); (2) the identification of geographic areas supporting high levels of biodiversity (i.e., "hotspots"; see Friesen et al. 2007); and (3) assisting fisheries bycatch or oiling event impact assessments, through molecular analyses to acquire species-specific data (Abbott et al. 2006) or population-specific data (e.g., Burg 2008). All of these require an understanding of how populations are genetically structured. A sufficient number of studies are now available, most having been conducted in the past decade, to confirm that levels of population differentiation among seabird populations are highly variable. As reviewed by Friesen et al. (2007) and exemplified in a comparative study in two species of albatross (Burg and Croxall 2001; Abbott and Double 2003), even between closely related species patterns of population differentiation can vary. At one extreme, there can be genetically homogenous populations indicative of total panmixia on a global scale (e.g., gray-headed albatrosses, *Thalassarche chrysostoma* and white-capped albatrosses, *Thalassarche steadi*), and at the other extreme, there can be strong genetic structuring among populations in both a population genetics and phylogeography context (e.g., black-browed albatrosses, *Thalassarche melanophris* and shy albatrosses, *Thalassarche cauta*) (Burg and Croxall 2001; Abbott and Double 2003).

Burg and Croxall (2001) proposed at-sea distributions may correspond to the levels of gene flow. A comprehensive review and analysis on seabird genetics (Friesen et al. 2007) and subsequent studies support this hypothesis (Rayner et al. 2011; Taylor et al. 2011). Rayner et al. (2011) eloquently demonstrated the presence of population-specific nonbreeding areas corresponding to genetically distinct colonies in Cook's petrel (*Pterodroma cookii*). Species that remained near their breeding colonies all year or had population-specific nonbreeding areas were genetically structured in almost all instances. Other factors considered, such as distance between colonies, foraging range, land barriers, colony dispersion, and population bottlenecks, had little effect (Friesen et al. 2007). Unfortunately, information about the nonbreeding distribution of rhinoceros auklets is limited, with a small number of banding returns suggesting that populations from southern British Columbia (Triangle and Pine Islands) winter mainly off central California (Triangle Island Research Station, unpubl. data; Gaston et al. 2009). As a result, associated inferences about genetic structuring in the absence of genetic data are uncertain, at best. The aim of this study was to determine the population genetic structure among rhinoceros auklets breeding in British Columbia, Alaska, and Japan to determine whether population level genetic differences need to be considered in fisheries bycatch mitigation efforts and impact assessments, as well as in conservation management.

Methods

Blood samples were taken from 246 rhinoceros auklets of unknown sex breeding at eight sites in the North Pacific (Fig. 1). Most of the sampling occurred in the summer of 2009, the exception being Triangle Is which was sampled in the summer of 2008. A small volume of blood was taken from the brachial vein. Whenever possible, chicks were sampled to ensure provenance of sampled birds, and all birds in British Columbia were banded to avoid resampling. Blood was stored in 70 % ethanol and DNA was later extracted using DNeasy Tissue Kit (QIAGEN).

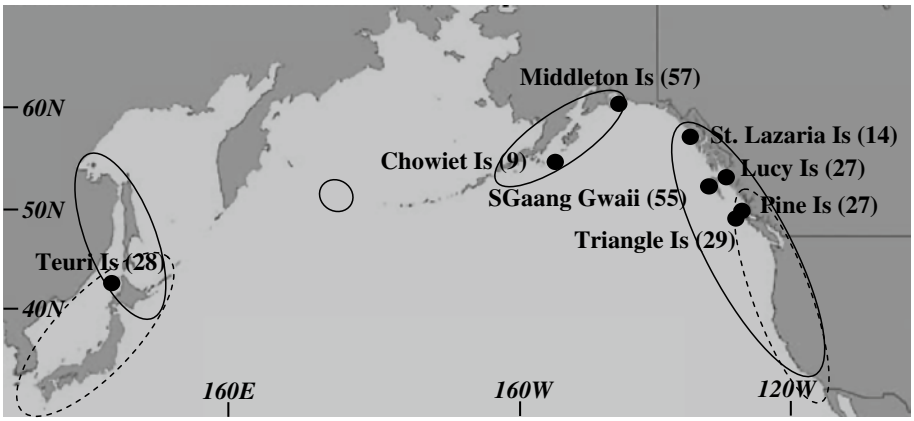

Fig. 1 Approximate locations (*black dots*) and number of birds analyzed (in *parentheses*) from each of eight rhinoceros auklet breeding colonies included in this study. Approximate breeding (*solid line*) and wintering (*dotted lines*) distributions are shown (BirdLife International 2013)

To characterize the genetic profile of each sampled population, individuals were genotyped at eight microsatellite loci (Table 1, Hasegawa et al. 2005). All loci were amplified using a 10 μL single-reaction nested polymerase chain reaction (PCR). Forward primers had a M13 sequence added to the 5′ end to allow incorporation of a fluorescently labeled M13(−21) primer (see Schuelke 2000). Reverse primers for CMms3, CMms14, and CMms22 were "PIG-tailed" to improve scoring (Brownstein et al. 1996). All loci except CMms4 were amplified using up to 300 ng of genomic DNA, 200 μM dNTP, 2 pmol each of fluorescently labeled M13 primer and reverse primer, 0.5 pmol of M13-labeled forward primer, 2.5 mM $MgCl_2$, and 0.5 U HotStar Taq DNA polymerase (QIAGEN) in 1 × PCR amplification buffer. PCR cycles were 15 min at 95 °C; a "touchdown" of 25 s at 95 °C, 25 s at 69–54 °C (dropping 3 °C every two cycles), 25 s at 72 °C; 25 cycles of 25 s at 95 °C, 25 s at 54 °C, 25 s at 72 °C, and one final cycle of 3 min at 72 °C. Locus CMms4 was amplified using the same reagent concentrations as above except 50–100 ng (1:4 dilution) of genomic DNA and 3.5 mM $MgCl_2$ were used. Thermal profiles for this locus had the same initial denaturation and final extension steps as above and the following touchdown: 25 s at 95 °C, 25 s at 62–54 °C (dropping 2 °C every two cycles), 25 s at 72 °C; 30 cycles of 25 s at 95 °C, 25 s at 54 °C, 25 s at 72 °C. PCR products from all loci for each individual were diluted, combined, and electrophoresed through a single capillary using an ABI 3130*xl* Genetic Analyzer. Data were analyzed using GeneMapper v4.0 (Applied Biosystems).

Analyses

Nine to fifty-seven individuals per sampled population were screened at eight microsatellite loci. Conformance of loci to Hardy–Weinberg equilibrium and linkage disequilibrium was assessed using GENEPOP (Raymond and Rousset 1995), with the dememorization number set at 1,000 and the number of batches at 300 batches (2,000 iterations per batch) for each test. The data were also checked for null alleles, drop out of large alleles, and scoring error due to stuttering using micro-checker 2.2.3 (van Oosterhout et al. 2004). GenAlEx v6.501 (Peakall and Smouse 2006) was used to characterize population genetic structure using the following methods: (1) an analysis of molecular variance (AMOVA, Excoffier et al. 1992) to determine how sampled genetic variance was partitioned among and within populations; and (2) estimates of F'_{ST} (Slatkin 1995) and F'_{ST} (Hedrick 2005) for the whole data set and for pairs of populations using 999 permutations to test significance. F'_{ST} adjusts the pairwise F_{ST} values by dividing each F_{ST} with the maximum possible F_{ST} for the data. This overcomes the problem of F_{ST} values being highly dependent on within-population diversity for multi-allelic markers (Meirmans and Hedrick 2011). Benjamini–Yekutieli's FDR (false discovery rate) corrections were applied to correct for multiple tests (Benjamini and Yekutieli 2001). GENEPOP was used to test for correlation between genetic and geographic distances using linearized pairwise F_{ST} values and straight line geographic distances. Significance was assessed with 10,000 permutations. A principal coordinate's analysis (PCA) was created in GenAlEx v6.3 using population genetic distance and standardized covariance. Structure v2.3.3 was used to determine the number of genetic clusters (Pritchard et al. 2000). A burn-in of 50,000 was performed followed by 50,000 Markov chains Monte Carlo (McMC) runs using correlated alleles and admixture model with location information (locprior). Ten runs were performed for each K from $K = 1$–7 and results were averaged across runs. A hierarchical AMOVA was also performed in GenAlEx using two to four groups based on the results from pairwise F_{ST}, PCA, and structure analyses to determine the most probable groupings.

Results

The eight microsatellite loci assayed had an overall mean heterozygosity across all samples and loci of 0.59 and

allelic diversity across all populations ranged from 3 to 22 alleles per locus (Supplemental Table, Table 1). Before FDR corrections, 13 of 64 locus-population comparisons showed significant departures from Hardy–Weinberg equilibrium, eight of which remained significant after the correction (Table 1). Deviations from Hardy–Weinberg proportions were not consistent for any locus or population and were not consistent with the single deviation (at locus CMms23) reported in this set of marker loci as tested on rhinoceros auklets breeding in Japan (Hasegawa et al. 2005). Micro-checker found no evidence of null alleles, large allele drop out, or scoring error for any of the loci or populations.

Overall F_{ST} was 0.107 and pairwise population F_{ST} values ranged from −0.007 (interpreted as 0) to 0.219. A total of 13 of the 28 F_{ST} values were significant after FDR correction, and these always included comparisons involving either Teuri or Triangle Is (Table 2). F'_{ST} values showed a wide range of values from −0.007 to 0.335 (Table 2). Hierarchical analyses of molecular variance (AMOVA) were significant for each level (among regions, among populations within regions, and within population) when breeding sites were divided into eastern and western Pacific (two groups: $\Phi_{RT} = 0.152$, $\Phi_{PR} = 0.028$, and $\Phi_{PT} = 0.176$; all $P = 0.01$). With three groups (Teuri Is, Triangle Is, and remaining populations), among-group and within-population differences were significant ($\Phi_{RT} = 0.135$ and $\Phi_{PT} = 0.137$; $P = 0.01$). Based on the PCA results (see below), we also ran a hierarchical AMOVA with Chowiet Is as a fourth group. Both within population and among region Φ values were significant ($\Phi_{RT} = 0.124$, $\Phi_{PR} = 0.000$, $P = 0.01$; and $\Phi_{PT} = 0.124$). The highest among group variance resulted when populations were divided into an eastern and western group; 12 % variance versus 8 % with three groups.

Table 1 Number of alleles sampled per locus (*Na*) and observed (H_o) and expected (H_e) heterozygosities for eight microsatellite loci in eight populations of rhinoceros auklets in the North Pacific

	CMms2	CMms3	CMms4	CMms9	CMms14	CMms22	CMms23	CMmc26
Triangle								
Na	3	14	5	2	3	4	4	5
H_o	0.520	0.808	0.5524	0.241	0.519	0.552	0.667	0.708
H_e	0.589	0.859	0.6154	0.307	0.479	0.542	0.642	0.588
SGaang								
Na	3	15	5	4	3	3	6	7
H_o	0.218[a]	0.727[a]	0.709	0.352	0.655	0.537	0.574[a]	0.778
H_e	0.348	0.878	0.663	0.325	0.568	0.568	0.639	0.722
Lucy								
Na	4	14	4	2	3	3	5	7
H_o	0.296	0.741	0.704	0.296	0.556	0.667	0.556	0.889
H_e	0.372	0.849	0.661	0.252	0.518	0.578	0.508	0.756
Pine								
Na	4	13	4	3	3	3	7	6
H_o	0.370	0.704[a]	0.600	0.333	0.370	0.596	0.815	0.704
H_e	0.438	0.879	0.706	0.359	0.514	0.522	0.658	0.762
St. Lazaria								
Na	3	11	4	4	2	6	6	6
H_o	0.214[a]	0.786	0.583	0.357[a]	0.462	0.644	0.786	0.714
H_e	0.513	0.819	0.656	0.441	0.497	0.649	0.714	0.686
Chowiet								
Na	3	8	4	2	3	3	5	5
H_o	0.222	0.625	0.778	0.222	0.556	0.222	0.778	0.375
H_e	0.364	0.805	0.623	0.198	0.586	0.427	0.704	0.422
Middleton								
Na	3	20	5	3	4	4	10	7
H_o	0.214[a]	0.792	0.620	0.351	0.439	0.526	0.614	0.740
H_e	0.437	0.880	0.654	0.311	0.554	0.555	0.666	0.759
Teuri								
Na	4	11	6	4	3	2	9	7
H_o	0.500	0.786	0.800	0.464	0.429	0.571	0.583[a]	0.816
H_e	0.669	0.803	0.702	0.493	0.404	0.491	0.726	0.742

[a] The three locus-population comparisons that showed deviations from Hardy–Weinberg equilibrium genotypic proportions after FDR correction

Table 2 Pairwise comparisons of F_{ST} (Wright 1978) below diagonal and F'_{ST} above diagonal

	Triangle	SGaang	Lucy	Pine	St. Lazaria	Chowiet	Middleton	Teuri
Triangle		**0.132**	**0.161**	**0.145**	**0.134**	**0.097**	**0.125**	**0.271**
SGaang	**0.089**		−0.008	0.004	0.014	0.021	0.001	**0.286**
Lucy	**0.112**	−0.007		−0.007	0.010	0.034	0.002	**0.335**
Pine	**0.091**	0.003	−0.005		0.000	0.010	0.004	**0.258**
St. Lazaria	**0.078**	0.010	0.008	0.000		0.071	−0.009	**0.323**
Chowiet	**0.062**	0.016	0.028	0.007	0.044		0.022	**0.326**
Middleton	**0.076**	0.001	0.001	0.003	−0.005	0.015		**0.265**
Teuri	**0.157**	**0.181**	**0.219**	**0.155**	**0.178**	**0.198**	**0.153**	

Values in bold are significant at $P < 0.05$ after FDR corrections

All P values (uncorrected) for significant values of F_{ST} are 0.010 except for the Chowiet–Triangle comparison ($P = 0.020$). The only other P value below 0.10 is the St. Lazaria–Chowiet comparison ($P = 0.07$)

The Mantel test for isolation by distance was not significant ($P = 0.065$) when all sampling sites were included. No significant isolation by distance pattern was observed ($P = 0.419$) when the Teuri population from the western Pacific was excluded from the analysis.

Fig. 2 Principal coordinates analysis of pairwise F_{ST} values for eight rhinoceros auklet populations in the North Pacific. Refer to Fig. 1 for location of sampling sites

Principal coordinate's analysis showed three main clusters (Fig. 2) with coordinates 1 (65.92 %) and 2 (24.92 %) explaining >90 % of the variation. Chowiet Is was separated from the other eastern Pacific populations by both the second and third coordinate (8.34 % of the variation; data not shown). Structure runs showed $K = 2$ consistently had the highest ln Pr (X|K) (−4,745, Bayes's factor Pr ($K = 2$) = 1) separating the eastern and western Pacific populations (Fig. 3). No further structure was detected by structure when the eastern Pacific populations were run separately.

Discussion

Molecular data from nuclear markers show the presence of at least two genetically distinct groups of rhinoceros auklets in the North Pacific. Further genetic separation

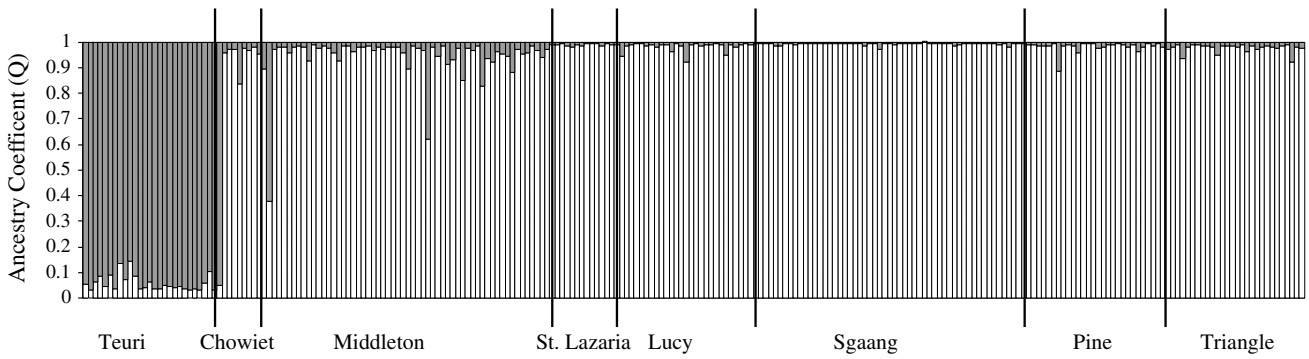

Fig. 3 Structure results at $K = 2$ showing ancestry coefficients (Q) for western Pacific (*dark gray*) and eastern Pacific (*white*) rhinoceros auklets. Ancestry is based on data from eight microsatellite loci. Each *bar* represents a single bird and the eight sampling sites are divided by the *long, black, vertical lines*

may be present in the eastern Pacific with birds on Triangle Is forming a third genetically distinct group (PCA and F_{ST}) and possibly a fourth group on Chowiet Is (PCA). Range-wide patterns are consistent with those found in other marine taxa showing an east–west split in the North Pacific (Cronin et al. 1996; Stanley et al. 1996; Congdon et al. 2000; Holder et al. 2000; Canino et al. 2010; Liu et al. 2011). Most of these species are dependent on land for at least one stage of their life history, while a few rely on shallow waters adjacent to coastlines. The eastern and western lineages of marine taxa are proposed to have originated during the Pleistocene and are maintained to different extents by restricted gene flow. For example, Pacific herring (*Clupea pallasii*) contained two evolutionary lineages that subsequently mixed in the eastern Pacific, yet have remained isolated from a third lineage in the western Pacific (Liu et al. 2011). During the last glacial maximum, the rhinoceros auklets were likely further south or had a reduced range due to the presence of ice throughout much of the North Pacific, with the exception of Beringia, restricting breeding habitat and altering prey distributions. A southwards range shift during the Pleistocene would have isolated the breeding populations into eastern and western Pacific refugia allowing divergence to occur. We cannot rule out the possibility that the east–west split predates the last glacial maximum (LGM) and was maintained during the LGM. To test the hypothesis of an early Pleistocene split, the divergence time needs to be estimated using sequence data.

The observed population genetic structure in rhinoceros auklets likely reflects historical factors and not just contemporary conditions. This scenario is considered likely for species whose current geographic distribution is the result of post-Pleistocene range expansion (Cronin et al. 1996; Stanley et al. 1996; Congdon et al. 2000; Holder et al. 2000; Friesen et al. 2007; Canino et al. 2010; Liu et al. 2011). The current distribution of rhinoceros auklets (BirdLife International 2013) is not continuous. During the nonbreeding season, birds are found along the coastlines of the eastern (California to British Columbia) and western (Japan) Pacific (Fig. 1; BirdLife International 2013), possibly as a result of historical isolation. While the breeding distribution is more fragmented with four clusters of breeding sites (western Sea of Okhotsk, western Aleutian Islands, Gulf of Alaska, and British Columbia/southeast Alaska), population genetic patterns observed here correspond to the auklet's nonbreeding distribution. This is consistent with findings that levels of population genetic structure for seabirds are best explained by their nonbreeding distribution (Burg and Croxall 2001; Friesen et al. 2007).

Contemporary processes and their effects on population differentiation are evident by looking at the time required for newly isolated populations to arrive at mutation-migration-drift equilibrium and to diverge sufficiently as to lose the genetic imprint of their past association. Indeed, populations of common murre (*Uria aalge*), an alcid whose broad geographic distribution includes the North Pacific, are considered not to be in genetic equilibrium (Morris-Pocock et al. 2008). We found deviations from Hardy–Weinberg proportions in rhinoceros auklets that were not found when the same markers were applied to birds of this species breeding in Japan (Hasegawa et al. 2005) and thus may be modest evidence that these populations are out of mutation-migration-drift equilibrium.

Isolation by distance is an appealing hypothesis for rhinoceros auklets as it is consistent with the stepping-stone model of colonization (Kimura and Weiss 1964), whereby proximate populations are genetically more similar than those located more distantly. It is generally considered the most likely scenario for seabirds and has particular intuitive appeal for coastal species like rhinoceros auklets whose breeding colonies are linearly distributed along the coastline. Range-wide we had weak support for isolation by distance ($P = 0.065$); however, once the western Pacific population was excluded, this pattern disappeared. The small number of sampled populations is likely precluding a valid statistical assessment of isolation by distance in rhinoceros auklets as it offers only a few pairwise population comparisons, and sampling sites were not evenly distributed along the coastline. If the populations are relatively young, genetic drift and gene flow may not have had enough time to allow for a pattern of isolation by distance to form (Hutchison and Templeton 1999). Additionally, patterns in the eastern Pacific show that population differences do not always correspond to geographic distances (i.e., Triangle Island).

For many seabirds, the breeding distribution represents a number of discrete areas owing to their breeding on islands. However, the nonbreeding distribution and at-sea distribution create opportunities for mixing in the same way as migration of terrestrial species to a common wintering ground (Lovette et al. 2004). Three of the four disjunct breeding areas of rhinoceros auklets were sampled in our study, and while Chowiet Is appears to be genetically isolated from the others in the eastern Pacific, Middleton Is located to the northeast of Chowiet Is and in the same "breeding area" in the Gulf of Alaska is not genetically distinct from the populations in British Columbia. Further work sampling the remaining disjunct breeding area in the Sea of Okhotsk and additional samples from the Gulf of Alaska may well reveal additional genetically distinct populations.

Triangle Island

The Triangle Is population revealed surprising results. It showed significant differences in allele frequencies from

all other populations, including nearby Pine Is (~100 km away). Reductions in gene flow over short geographic distances have been reported for other seabirds (Abbott and Double 2003; Levin and Parker 2012; Welch et al. 2012). Microsatellite analyses of Nazca boobies (*Sula granti*), a seabird restricted to the eastern tropical Pacific, showed that genetic isolation in this species does not correspond to geographic distances (Levin and Parker 2012). Individuals breeding on Espanola show significant allele frequency differences from birds breeding on San Cristobal (~35 km away), but are not significantly different from individuals on Genovesa (~150 km away). Seabirds are generally known for their strong natal philopatry (Friesen et al. 2007), which could promote genetic differentiation among different breeding sites if gene flow were sufficiently limited. For rhinoceros auklets, data from banding hundreds of adult individuals in British Columbia (Hifner unpublished) showed no evidence of dispersal to other sites. However, limited data are available for nestlings and as such dispersal could be occurring prior to recruitment. More information is needed on both post-breeding dispersal and juvenile movement as both would be expected to promote gene flow. As mentioned earlier, at-sea distribution in seabirds is an important factor, and in a number of instances, populations with different nonbreeding distributions are genetically isolated from each other (Burg and Croxall 2001; Friesen et al. 2007; Rayner et al. 2011; Taylor et al. 2011).

Conservation

The conservation implications of the results presented here are somewhat equivocal. Management units as defined by Moritz 1994) are "populations with significant divergence of allele frequencies." While Pine Is and Lucy Is clearly do not represent management units, Triangle Is is sufficiently divergent from both of them, and the other eastern Pacific breeding sites have to be considered a separate management unit. Furthermore, as PCA shows Chowiet Is in Alaska is separated from the other islands, it may merit separate conservation priority. While structure only detected two clusters, Pritchard et al. (2000) note the program may underestimate the number of clusters when structure is weak. Caution is warranted as the four units represent the minimum number of distinct genetic groups based on our sampling and additional samples from western Alaska in particular, and inclusion of other markers may reveal further population genetic differences in the North Pacific. A more in-depth study with more comprehensive sampling of rhinoceros auklet populations including birds from wintering areas and information on at-sea distributions will aid in the interpretation of our results adding an important temporal component. As the nonbreeding distribution of different breeding colonies is not known, genotyping samples collected during the winter will help gather this critical information. In addition, as genetic homogeneity of populations at a relatively small spatial scale of this study was rejected, it is reasonable to hypothesize that higher levels of population structure exist across their full geographic range, which spans from California to Japan (Gaston and Dechesne 1996a). More comprehensive sampling in both the eastern and western Pacific is needed to determine whether genetic patterns are the same in the east and west and will better elucidate the extent of population differentiation in rhinoceros auklets at micro-geographic scales. This would be worth investigating to determine whether there are distinct units for conservation purposes on a range-wide scale and, if so, to facilitate the development of genetic tools for determining provenance of fisheries bycatch birds to aid impact assessments and monitoring efforts.

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