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INVITED REVIEW

Mechanisms of population differentiation in seabirds

V. L. FRIESEN, T. M. BURG* and K. D. McCOY†
Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3 N6

Abstract

Despite recent advances in population genetic theory and empirical research, the extent of genetic differentiation among natural populations of animals remains difficult to predict. We reviewed studies of geographic variation in mitochondrial DNA in seabirds to test the importance of various factors in generating population genetic and phylogeographic structure. The extent of population genetic and phylogeographic structure varies extensively among species. Species fragmented by land or ice invariably exhibit population genetic structure and most also have phylogeographic structure. However, many populations (26 of 37) display genetic structure in the absence of land, suggesting that other barriers to gene flow exist. In these populations, the extent of genetic structure is best explained by nonbreeding distribution: almost all species with two or more population-specific nonbreeding areas (or seasons) have phylogeographic structure, and all species that are resident at or near breeding colonies year-round have population genetic structure. Geographic distance between colonies and foraging range appeared to have a weak influence on the extent of population genetic structure, but little evidence was found for an effect of colony dispersion or population bottlenecks. In two species (Galapagos petrel, *Pterodroma phaeopygia*, and Xantus's murrelet, *Synthliboramphus hypoleucus*), population genetic structure, and even phylogeographic structure, exist in the absence of any recognizable physical or nonphysical barrier, suggesting that other selective or behavioural processes such as philopatry may limit gene flow. Retained ancestral variation may be masking barriers to dispersal in some species, especially at high latitudes. Allopatric speciation undoubtedly occurs in this group, but reproductive isolation also appears to have evolved through founder-induced speciation, and there is strong evidence that parapatric and sympatric speciation occur. While many questions remain unanswered, results of the present review should aid conservation efforts by enabling managers to predict the extent of population differentiation in species that have not yet been studied using molecular markers, and, thus, enable the identification of management units and evolutionary significant units for conservation.

Keywords: conservation genetics, meta-analysis, mtDNA, phylogeography, population genetic structure, seabird

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Correspondence: Vicki Friesen, Fax: (613) 533 6617; E-mail: friesenv@biology.queensu.ca.
*Present address: Department of Biological Sciences, 4401 University Drive, University of Lethbridge, Lethbridge, Alberta, Canada T1K 3M4.
†Present address: Génétique et Evolution des Maladies Infecteuses, CNRS IRD UMR 2724, IRD, 911 Avenue Agropolis, 34394 Montpellier, France

Introduction

Understanding mechanisms of population differentiation is important both for understanding evolution and for successful conservation. For example, population differentiation is the first step towards reproductive isolation under several models of speciation, and so may play a central role in diversification and adaptation (e.g. Mayr 1963; Coyne & Orr 2004). Although in theory population genetic structure

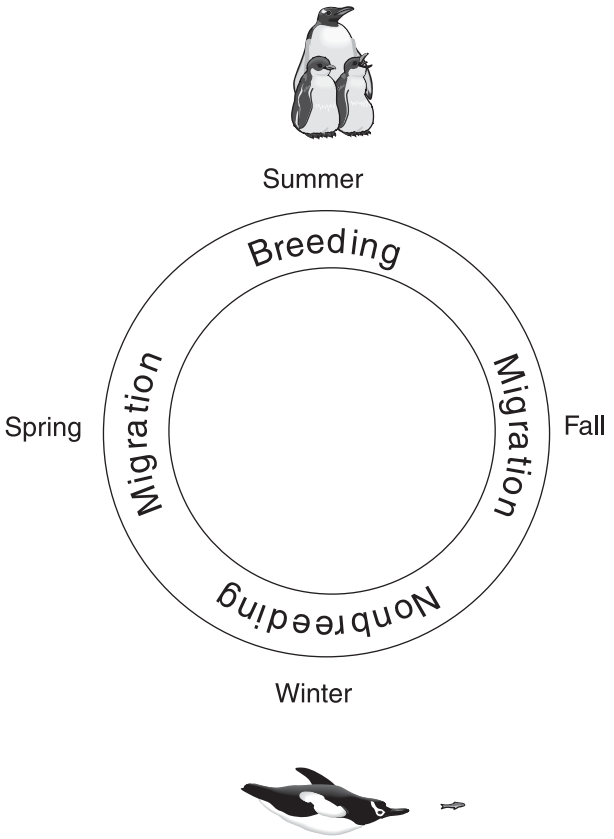

Fig. 1 Annual cycle of a typical seabird. Note that timing and duration of breeding, migration and molting vary among species, many species do not migrate, and some species take longer than a year to complete a breeding cycle (Hamer *et al*. 2002).

is a simple inverse function of gene flow (Wright 1931), in practice the factors that promote differentiation, especially the barriers that disrupt gene flow in different organisms, are multifaceted and many questions remain unanswered. For example, can geographic distance alone prevent gene flow in highly mobile organisms? Does segregation during the nonbreeding season prevent gene flow between populations of migratory animals?

Seabirds provide useful model systems for studying mechanisms of population differentiation. Seabirds are classically considered to include members of four avian orders: Sphenisciformes (penguins), Procellariiformes (albatrosses, petrels, shearwaters, storm-petrels and diving-petrels), Pelecaniformes (tropicbirds, gannets, boobies, cormorants, darters and frigatebirds) and Charadriiformes (skuas, gulls, terns and auks). With approximately 313 species totalling over 200 million breeding individuals, they represent significant components of both avian and marine diversity (reviewed in Schreiber & Burger 2002; Gaston 2004). Although seabirds are highly diverse, most species share several characteristics: pelagic (marine) distributions during the nonbreeding season (Fig. 1), marine foraging during reproduction, colonial breeding on cliffs or islands, delayed sexual maturation (first reproduction at 2 to 13 years, Jouventin & Dobson 2002), low annual fecundity (typically three or fewer chicks per year), biparental care, and long lives (up to 74 years, Sagar & Warham 1993). Colonial nesting makes this group relatively easy to study during the breeding season, so their reproductive ecology and behaviour are generally well characterized (Schreiber & Burger 2002; Gaston 2004). As methods for studying seabirds at sea improve, their foraging and wintering ecology are also becoming better understood (Shealer 2002; Croxall *et al*. 2005).

Seabirds also present several challenges to the generally accepted mechanism of population differentiation. Most seabirds are strong fliers, with members of some species travelling hundreds or even thousands of kilometres on a single foraging trip (e.g. Hyrenbach *et al*. 2002; Croxall *et al*. 2005). Thus, they must encounter few physical (geographic) barriers to dispersal, and individuals can easily visit and breed at non-natal colonies (e.g. Harris 1983; Frederiksen & Petersen 2000; Inchausti & Weimerskirch 2002). Nonetheless, indirect evidence suggests that population differentiation can be strong. For example, geographic variation in morphology is extensive (reviewed in del Hoyo *et al*. 1992, 1996), ~15% of species and ~20% of subspecies breed only on single islands or archipelagos (del Hoyo *et al*. 1992, 1996), and evidence is accumulating that even sympatric populations can diverge genetically (e.g. Smith & Friesen 2007; Smith *et al*. 2007). Thus, nonphysical barriers to dispersal must play an important role in seabird diversification. Other authors have made similar observations. For example, Burg & Croxall (2001) found that black-browed albatrosses (see Appendix for scientific names) with different foraging grounds differ genetically despite a lack of physical barriers to dispersal between foraging areas; Liebers *et al*. (2001) noted that in yellow-legged gulls genetic differentiation is probably due to intrinsic reproductive barriers such as habitat preferences and mate choice; and Liebers & Helbig (2002) found that genetic divergence in lesser black-backed gulls is greatest between populations with no contemporary physical barriers to gene flow. Furthermore, recent population genetic studies of seabirds have revealed evidence for a role for multiple evolutionary processes, such as historical fragmentation, range expansion, isolation by distance, long range colonization, and ongoing gene flow, suggesting that mechanisms of population differentiation in seabirds may be complex. Here we review population-level studies of mitochondrial DNA (mtDNA) variation in seabirds to identify major factors promoting (and reducing) population differentiation in this group. Specifically, we ask (i) what, if any, physical barriers prevent gene flow among colonies? (ii) does population genetic structure exist in the absence of physical barriers to dispersal? and (3) if so, what nonphysical factors may be restricting gene

flow? We focus on studies of mtDNA because its greater sensitivity to population bottlenecks and restrictions in gene flow and its relative ease of analysis make it more useful than nuclear markers for investigating mechanisms of population differentiation (Avise 2004). A short-coming of mtDNA is that it reflects female-mediated gene flow and female effective population size only, and recent studies suggest it may be subject to periodic episodes of positive selection (Bazin *et al*. 2006). Population-level variation in nuclear DNA has been studied using a variety of markers in seabirds, and results to date indicate that the extent of population genetic structure is highly variable and not necessarily correlated with mtDNA variation (e.g. Burg & Croxall 2001; Riffaut *et al*. 2005; Friesen *et al*. 2006). Thus, the present analyses should ultimately be repeated with studies of nuclear DNA.

Methods

Selection of studies

Population studies of mtDNA variation in seabirds were collated from the literature. Several studies, particularly those involving the mitochondrial control region, reported ambiguous sequences, which were variously attributed to heteroplasmy, nuclear homologues, or tandem repeats (Berg *et al*. 1995; Friesen & Anderson 1997; Kidd & Friesen 1998b; Burg & Croxall 2001, 2004; Moum & Arnason 2001; Moum & Bakke 2001; Patirana *et al*. 2002; Abbott & Double 2003; Burg *et al*. 2003; Steeves *et al*. 2003; Abbott *et al*. 2005). In all but one (Friesen *et al*. 1996a), ambiguous sites were excluded from the original analyses and so do not affect the present results. However, different studies used genes with different mutation rates: 13 focused on the hypervariable Domain I of the mitochondrial control region, whereas 21 involved more slowly evolving genes (two involved Domains II and III, 11 involved cytochrome *b*, one involved ATPase 6 and 8, four involved RFLPs, and three involved a combination of these genes), and nine included a combination of Domain I and a more slowly evolving gene. These differences complicate comparisons among studies (e.g. Hedrick 1999). However, nine species have been studied using both Domain I and a less variable mitochondrial region with equivalent geographic sampling, and in most of these species different genes provided similar conclusions regarding both the extent of population genetic structure and the existence of phylogeographic structure. We therefore did not discriminate among studies based on different genes except in comparisons of Φ_{ST} or F_{ST} (see below). Note, however, that different genes lead to different conclusions regarding taxonomy and population history in two genera of albatrosses (*Diomedea* and *Thalassarche*; Robertson & Nunn 1998; Burg & Croxall 2001, 2004; Abbott & Double 2003).

Populations for which major parts of the breeding range were not sampled ('N' under 'Comprehensive sampling' in the Appendix), and species that breed predominantly inland (mew, herring, Caspian and Armenian gulls) were excluded from the comparative analyses. If more than one study has been done on a species, only the study with the more comprehensive sampling was included. In addition, note that the taxonomy of several groups of seabirds, especially the albatrosses and gulls, is in flux, and that taxonomy may affect the conclusions of a comparative analysis. In the present study, we used the most recent taxonomic recommendations that have been published and/or the recommendations of the studies given in the Appendix.

Comparative analyses

To investigate mechanisms of population differentiation, we examined the extent of both population genetic and phylogeographic structure. We use the term 'population' to include all individuals within a defined geographic area. We considered a population to be 'genetically structured' if haplotype frequencies differed significantly between two or more areas and/or if estimates of Φ_{ST} or F_{ST} were significantly different from 0 at $\alpha = 0.05$. We defined 'phylogeographic structure' as the existence of population-specific genealogical lineages, i.e. monophyly of one or more populations on the gene tree. Population genetic structure may or may not include phylogeographic structure; it can be assayed using standard statistical methods (e.g. Φ_{ST}; Excoffier *et al*. 1992), but statistically significant differences in allele frequencies may not reflect demographic or genetic independence (Hedrick 1999). In contrast, phylogeographic structure is generally indicative of prolonged (matrilineal) genetic isolation of populations (e.g. Neigel & Avise 1986).

Seven factors potentially influencing population genetic structure were identified from population genetic theory and from previous seabird studies: land barriers (including ice), geographic distance between colonies, colony dispersion, nonbreeding distribution, foraging range, population bottlenecks, and retained ancestral variation. Data to test the importance of these factors were collated from the literature (Table 1), and two types of analyses were conducted: paired comparisons and meta-analyses.

Paired comparisons. Closely related species and conspecific populations that are separated by a physical barrier to dispersal are demographically independent but tend to be ecologically similar, and so form natural replicates. To identify potential barriers to gene flow, the extent of population genetic structure was compared (i) between closely related species, and (ii) between conspecific populations separated by contemporary or historical land (an apparently effective barrier to dispersal; see Results). This approach can be used to determine whether a factor

Table 1 Extent of genetic structure within seabird populations in the absence of contemporary or historical land or ice, and selected ecological characteristics of the populations. See the Appendix for study details. Conspecific populations separated by contemporary historical land barriers are entered separately

Species, Population	Global Φ_{ST} or F_{ST}*	Breeding range†	Colony dispersion‡	Non-breeding distribution§	Foraging range¶	Total population size**	Climate zone††
Domain I studies							
Wandering albatross	(0.09)	W	O	D	OS	3	ST
Antipodean albatross	0.05	R	O	D	OS	3	ST
Black-browed albatross	(0.27)‡‡,§§	W	O	M¶¶	OS	5	ST
Shy albatross	(0.10)	R	O	D	OS	4	ST
White-capped albatross	(0.01)	R	O	D	OS	4	ST
Grey-headed albatross	0.00	W	O	D	OS	4	ST
Cory's shearwater	‡‡,§§	I	O	M¶¶	OS	5	TR
Band-rumped storm-petrel, Atlantic	(0.46)‡‡,§§	W	O	D¶¶	OS	5	TR
Band-rumped storm-petrel, Pacific	(0.47)‡‡,§§	W	O	D¶¶	OS	5	TR
Leach's storm-petrel, Atlantic	0.03	W	O	M	OS	6	NT
Leach's storm-petrel, Pacific	0.13‡‡,§§	W	O	M¶¶	OS	6	TR, NT
Masked booby, Atlantic	0.32‡‡	W	O	R	OS	4	TR
Masked booby, Indiopacific	0.39‡‡	W	O	R	OS	4	TR
Yellow-legged gull	0.12‡‡	I	C	D	IS	4	TR
Lesser black-backed gull, W. Palearctic	(0.15)‡‡	I	C	M	IS	5	NT, NP
Lesser black-backed gull, E. Palearctic	0.07‡‡	I	C	M	IS	?	NT, NP
Black-legged kittiwake, Atlantic	(0.14)‡‡	W	O	D	M	6	NT, NP
Black-legged kittiwake, Pacific	0.03	W	O	D	M	6	NT, NP
Red-legged kittiwake	0.17‡‡	I	O	D	OS	5	NT
Common murre, Atlantic	0.12‡‡	W	O	D	M	6	NT
Common murre, Pacific	0.01	W	O	D	M	6	NT
Thick-billed murre, Atlantic	0.04‡‡	W	O	M	M	7	NP
Thick-billed murre, Pacific	0.09‡‡	W	O	D	M	7	NP
Razorbill	0.04‡‡	W	O	D	M	5	NT, NP
Pigeon guillemot	0.34‡‡	W	C	D/R	IS	5	NT, NP
Marbled murrelet	0.08‡‡	I	C	D/R	IS	5	NT
Kittlitz's murrelet	0.91‡‡,§§	I	C	D/R	IS	4	NT, NP
Xantus's murrelet	0.69‡‡,§§	R	O	D	OS	3	TR
Non-Domain I studies							
Black-footed albatross	0.91‡‡	I	O	D	OS	4	TR
Galapagos petrel	0.10‡‡	R	O	D	OS	3	TR
Sooty shearwater	(0.16)‡‡	I	O	M	OS	6	ST
Short-tailed shearwater	0.19	I	O	M	OS	6	ST
Yelkouan shearwater	‡‡,§§	I	O	M¶¶	OS	3	TR
European storm-petrel	0.90‡‡,§§	I	O	M¶¶	OS	5	TR, NT
Black guillemot	0.80‡‡,§§	W	C	D/R	IS	5	NT, NP
Crested auklet	0.01	W	O	D	M	6	NT, NP
Least auklet	0.02	W	O	D	M	7	NT, NP

*Parentheses indicate mean of pairwise comparisons of populations. Blank cells = Φ_{ST} or F_{ST} not estimated.
†W, widespread (breeding populations occur throughout most or all of the species' climate zone); R, species is restricted to a single island or archipelago; I, breeding distribution is neither widespread nor restricted (from del Hoyo *et al*. 1992, 1996).
‡O, nesting primarily in large colonies on offshore islands; C, nesting primarily in small colonies on coastal cliffs or islands.
§M, true migration (directed seasonal movements); D, dispersal from breeding colonies; R, year-round residency at breeding colonies. From del Hoyo *et al*. 1992, 1996, and references in the Appendix.
¶IS, inshore (foraging within ~8 km of land; Gaston 2004); OS, offshore; M, mixed. Modified from Schreiber & Burger 2002.
**Total number of breeding pairs expressed as an order of magnitude. From del Hoyo *et al*. 1992, 1996. ? = population size unknown.
††ST, Southern Temperate; TR, Subtropical/Tropical; NT, Northern Temperate; NP, Northern Polar. From del Hoyo *et al*. 1992, 1996.
‡‡Statistically significant population genetic structure, or significant difference in haplotype frequencies between at least two populations.
§§Phylogeographic structure.
¶¶Two or more population-specific nonbreeding grounds or seasons.

has an effect if all other variables are equal. However, it does not address the relative influence of different factors. The method also assumes that geographic sampling and molecular methods are equivalent between the units being compared; thus, not all possible comparisons were used.

Meta-analysis. To determine the relative importance of various factors (e.g. differences in nonbreeding distributions), the extent of population genetic and phylogeographic structure was compared among populations using a meta-analysis. Two types of tests were conducted for each factor: (i) the numbers of populations with or without (a) population genetic or (b) phylogeographic structure were compared between categories (e.g. migratory vs. resident) using Fisher's exact tests, and (ii) differences in mean Φ_{ST} or F_{ST} between categories were tested using analysis of variance (ANOVA). Because the theoretical maximum values of Φ_{ST} or F_{ST} based on hypervariable markers such as Domain I are lower than for less variable genes (Hedrick 1999), studies that did not include Domain I were excluded from ANOVAs. Meta-analyses have the advantage that they involve statistical tests, but have the drawback here that the number of studies is too small to control for the effects of multiple differences between populations. Thus, variables with weak effects may be masked by those with stronger or interactive effects.

Studies to date are heavily biased towards procellariiform and charadriiform species (Appendix), and because barriers to dispersal may differ among birds in different orders or families (e.g. albatrosses are stronger fliers than alcids), the possibility of phylogenetic constraints was addressed in two ways. First, paired comparisons inherently control for phylogeny. Second, the extent of population genetic structure was compared among species from different orders and families. We found that, in the absence of land barriers (see Results), the incidence of population genetic structure was slightly but not significantly lower in diomedeids (two of seven species had population genetic structure) than in procellariids (four of five species were structured) and hydrobatids (all of three species were structured; $P = 0.094$; Table 1). Otherwise, species in different orders or families did not differ either in the incidence of population genetic or phylogeographic structure, or in mean Φ_{ST} or F_{ST} (all $P > 0.10$). Data for species in different orders were therefore pooled. We acknowledge that this does not control for phylogenetic constraints, and that sample sizes for some families are small. The following analyses therefore should be repeated independently on each order when more studies become available.

These analyses are admittedly crude, but too few studies have been published for more sophisticated, multifactorial analyses. Our hope is that mechanisms of general importance should be apparent despite the limits of the tests, and that the present results will generate directions and hypotheses for more rigorous tests in future.

Results

At least 43 studies, including 53 species, have been completed to date (Appendix). Species include 1 sphenisciform, 21 procellariiforms, 5 pelecaniforms, and 26 charadriiforms. Results indicate that the extent of population genetic structure varies from virtual panmixia (e.g. grey-headed albatross) to reciprocal monophyly of populations (e.g. European storm petrel; Tables 1 and 2).

Table 2 Species whose breeding distribution is fragmented by (a) contemporary land, or (b) historical land, and the extent of genetic differentiation between the fragmented populations. See Appendix for study details

Species	Populations	Barrier(s)	Φ_{ST} or F_{ST}*
(a) Contemporary land			
Band-rumped storm petrel	Atlantic/Pacific	Americas, Africa	(0.77)†‡
Leach's storm petrel	Atlantic/Pacific	North America, Asia	0.15†
Masked booby	Atlantic/Indopacific	Americas, Africa	0.79†‡
Red-footed booby	Atlantic/Pacific	Americas, Africa	0.99†‡
Brown booby	Atlantic/Pacific	Americas, Africa	0.93†‡
Sooty tern	Atlantic/Pacific	Americas, Africa	0.38†‡
Common murre	Atlantic/Pacific	North America, Asia	0.47†‡
(b) Historical land			
Adelie penguin	Ross Sea/circum-Antarctic	Antarctic ice sheets	†
Glaucous gull	Nearctic/Palearctic	Pleistocene glaciers	†‡
Lesser black-backed gull	Eastern/Western Eurasia	Pleistocene glaciers	0.21†‡
Black-legged kittiwake	Atlantic/Pacific	Bering land bridge and Pleistocene glaciers	0.52†‡
Thick-billed murre	Atlantic/Pacific	Bering land bridge and Pleistocene glaciers	0.52†‡

*Parentheses indicate mean of pairwise comparisons of populations. Blank cells = Φ_{ST} or F_{ST} not estimated.
†Statistically significant population genetic structure, or significant difference in haplotype frequencies between at least two populations.
‡Phylogeographic structure.

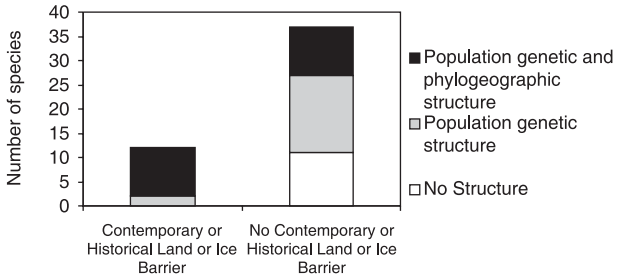

Fig. 2 Number of species exhibiting no significant population genetic structure (panmixia), statistically significant population genetic structure, or phylogeographic structure in the presence or absence of a contemporary land barrier between populations.

Land and ice

Despite their dispersal abilities, most seabirds will not fly across land or ice (hereafter, simply 'land') since many cannot find food on land and others cannot take flight easily from land. However, seabirds are often blown overland during storms, so the a priori importance of land as a barrier to gene flow is unclear. Of seven mtDNA studies of seabirds whose breeding distribution (or at least, sampling distribution) is fragmented by contemporary land, all found significant genetic differentiation between the fragmented populations and 6 also found phylogeographic structure (Table 2; Fig. 2). For 5 additional species, the breeding distribution would have been fragmented by land bridges and/or glaciers during the Pleistocene (i.e. birds would have had to fly over land to disperse between parts of the breeding range): all these species exhibit statistically significant population genetic structure, and all but one have phylogeographic structure (Table 2). These five species all had corroborating evidence, in the form of deep branches in the gene tree or results from nested clade analysis, for historical fragmentation (Table 3). Thus, land appears to present a significant physical barrier to gene flow in seabirds. Even the Isthmus of Panama, with a minimum width of only 35 km, appears to prevent gene flow between Atlantic and Pacific populations, possibly due to its elevation (Steeves *et al*. 2003, 2005).

However, land does not provide a complete explanation of population differentiation in seabirds. Genetic structure exists in the absence of either contemporary or known historical land barriers in 26 populations (involving 22 species), and phylogeographic structure exists in 10 of these populations (Table 1; Fig. 2). Thus, additional factors must be promoting population differentiation in seabirds. To help identify these factors, we assumed that populations separated by contemporary or historical land barriers (e.g. Atlantic vs. Pacific populations; Table 2) are demographically and genetically independent (since they are both physically separate and phylogenetically distinct), and treated them as separate entries in subsequent analyses. Thus, the following analyses are based on populations, rather than species, and include conspecific populations from different ocean basins. Whereas inclusion of multiple conspecific populations may involve pseudoreplication and so may bias the meta-analyses, the extent of population genetic structure often differed between these populations (e.g. Atlantic vs. Pacific populations of black-legged kittiwakes; Table 1), and random exclusion of one population from each species altered the result for only one test in the meta-analysis.

Geographic distance

The distribution of habitat suitable for foraging and nesting is patchy, with large areas of ocean being unusable for most species (e.g. the Eastern Pacific Basin). If gene flow declines with distance between colonies and/or if seabirds do not cross large expanses of open ocean (e.g. Steeves *et al*. 2003), then genetic divergence should increase with geographic distance between colonies, i.e. seabirds should show isolation by distance. Some results indicate that geographic distance may promote population differentiation in seabirds: In paired comparisons, Φ_{ST} was slightly higher in the widely distributed wandering albatross than in the more geographically restricted Antipodean albatross (Table 4). And in the meta-analysis, the existence of population genetic structure was slightly (but not significantly) less likely in populations with restricted ('R' in Table 1) vs. nonrestricted ('I' and 'W' in Table 1) breeding ranges (Table 5; although only five species had restricted ranges).

However, a simple model of isolation by distance does not provide a complete explanation for population differentiation in the absence of land barriers in seabirds: Several species show genetic differentiation within single islands or archipelagos (Galapagos petrel, band-rumped storm-petrel, Leach's storm-petrel). In paired comparisons, population genetic structure was no greater in the black-legged kittiwake than in its less widespread congener (Table 4). Evidence of isolation by distance was not necessarily associated either with statistically significant values of Φ_{ST} or F_{ST} or with phylogeographic structure (Table 3; Fisher's exact tests, $P > 0.10$, although sample sizes were low). In the meta-analysis, the incidence of phylogeographic structure did not differ between populations with restricted ranges (Table 5). And mean Φ_{ST} or F_{ST} did not differ between populations with restricted vs. nonrestricted ranges (Table 5). Furthermore, six studies found explicit evidence for long-range colonization (Table 3), suggesting that distance is not a barrier to dispersal. Thus, geographic distance provides only a weak explanation of the extent of population genetic structure in seabirds.

Table 3 Results of tests for historical demographic changes in seabird populations, including estimates of Φ_{ST} or F_{ST}; evidence from mtDNA sequences for historical fragmentation (Hist. Frag'n), isolation by distance (IBD), a population bottleneck (Bottleneck) or expansion (Pop. Exp'n), range expansion (Range Exp'n), or long-range colonization (LRC); and tests used to infer the change. See Appendix for scientific names and study details. Only results of explicit tests are included. Populations separated by contemporary or historical land are entered separately

Species	Global Φ_{ST} or F_{ST}*	Hist. Frag'n	IBD	Bottleneck	Pop. Exp'n	Range Exp'n	LRC	Tests used†
Adelie penguin	‡	Y	Y	Y	Y	Y		1–4
Wandering albatross	(0.09)						Y	5
Shy albatross	(0.10)		Y	Y				5
White-capped albatross	(0.01)		Y					5
Northern fulmar	0.03		Y	N				6
Fairy prion	0.17			Y				1, 7
Short-tailed shearwater	0.19			Y	Y			1, 7
Band-rumped storm petrel (Atlantic)	(0.46)‡§	Y	Y		Y	Y	Y	2, 3, 5
Band-rumped storm petrel (Galapagos)	0.03‡				Y			2, 3, 5
Masked booby (Indopacific)	0.39‡§		Y		Y		Y	3, 5, 8
Black-tailed gull				Y	Y			2, 8
Glaucous gull	‡§	Y						2, 5, 8
Yellow-legged gull	0.12‡			N	N			8
Slaty-backed gull					N			2, 8
Lesser black-backed gull (E. Palearctic)	0.07‡	Y	Y		Y	Y		1, 2, 6
Lesser black-backed gull (W. Palearctic)	0.15‡	Y			Y			1, 2, 6
Black-legged kittiwake (Atlantic)	0.14‡	Y	N	N	N			1, 2, 6, 8
Black-legged kittiwake (Pacific)	0.03	Y	N	N	N			1, 2, 6, 8
Red-legged kittiwake	0.17‡	Y		N	N	N		5
Sooty tern (Indopacific)		N		Y	Y			1, 2, 8
Common murre (Atlantic)	0.12‡		Y	Y	Y	Y		2, 5, 6
Common murre (Pacific)	0.011	N	Y		Y	Y		2, 5, 6
Thick-billed murre (Atlantic)	0.02	Y	Y		Y	Y	Y	2, 5, 6
Thick-billed murre (Pacific)	0.13‡	Y	Y			Y	Y	2, 5, 6
Razorbill	0.04‡	Y			Y	Y		1, 2, 8
Black guillemot	0.80‡§	Y	N	N	N			1, 2, 6, 8
Pigeon guillemot	0.34‡	Y	Y		Y	Y	Y	2, 5, 6
Marbled murrelet	0.08‡	N	Y		Y	Y		2, 5, 6
Kittlitz's murrelet	0.91‡§	Y						1
Xantus's murrelet	(0.69)‡§	Y						1, 2, 8
Crested auklet	0.02			N	N			2, 3
Least auklet	0.01			N	N			2, 3

*Parentheses indicate mean of pairwise comparisons of populations. Blank cells = Φ_{ST} or F_{ST} not estimated.
†1 = sequence divergence; 2 = neutrality tests (e.g. Tajima's D; Tajima 1989); 3 = coalescent theory-based Bayesian inference; 4 = $\times^2$; 5 = nested clade analysis; 6 = Mantel's tests; 7 = diversity indices; 8 = mismatch distributions.
‡Statistically significant population genetic structure or significant difference in haplotype frequencies between at least two populations.
§Phylogeographic structure.

Colony dispersion

Gene flow is less effective at countering genetic drift under a one-dimensional stepping-stone model of dispersal (where individuals disperse primarily to neighbouring colonies along a linear distribution) than in an *n*-island model (where dispersal is random; Kimura & Weiss 1964; Slatkin 1993). Thus, population genetic structure should be stronger, or at least more likely to exist, in species that follow a predominantly one-dimensional stepping-stone pattern of dispersal than in those approximating an *n*-island model. Due to the generally low rates of band (ring) returns for seabirds, dispersal patterns have not been described in many species (Weimerskirch 2002). However, Storer (1952) suggested that the greater geographic variation in morphology in guillemots (*Cepphus* spp.) compared to murres (*Uria* spp.) may be the result of differences in colony distributions: guillemots nest primarily in small colonies on coastal cliffs and nearshore islands, whereas murres nest in a few large colonies on offshore islands. We therefore categorized species as either nesting primarily in a few large colonies on offshore islands (potentially approximating

Table 4 Closely related species, estimates of Φ_{ST} or F_{ST}, and the main ecological and historical demographic differences (if any) between the species. Dashed lines separate species used for paired comparisons. See Appendix for scientific names and study details, and Tables 1 and 3 for ecological characteristics and historical demographic changes

Species	Global Φ_{ST} or F_{ST}*	Main ecological and historical differences
Wandering albatross	(0.09)	(1) widespread breeding distribution
Antipodean albatross	0.05	(1) restricted breeding distribution
Black-browed albatross	(0.27)†‡	(1) multiple population-specific nonbreeding areas; (2) 10^5 pairs
Grey-headed albatross	0.00	(1) nonbreeders disperse from colonies; (2) 10^4 pairs
Shy albatross	(0.10)	(1) population bottleneck
White-capped albatross	(0.01)	(1) no population bottleneck
Sooty shearwater	0.16†	
Short-tailed shearwater	0.19	
Band-rumped storm petrel (Atlantic)	(0.46)†‡	(1) population-specific nonbreeding seasons; (2) 10^5 pairs; (3) tropical/subtropical
Leach's storm petrel (Atlantic)	0.03	(1) long-distance migration; (2) 10^6 pairs; (3) temperate
Band-rumped storm petrel (Pacific)	(0.47)†‡	(1) 10^5 pairs; (2) tropical/subtropical
Leach's storm petrel (Pacific)	0.13†‡	(1) 10^6 pairs; (2) temperate to subtropical
Yellow-legged gull	0.12†	(1) nonbreeders disperse from colonies; (2) 10^4 pairs; (3) subtropical
Lesser black-backed gull (W. Palearctic)	(0.15)†	(1) long-distance migration to a single nonbreeding area; (2) 10^5 pairs; (3) temperate to polar
Black-legged kittiwake (Pacific)	0.03	(1) widespread; (2) mixed foraging distance; (3) 10^6 pairs
Red-legged kittiwake	0.17†	(1) not widespread; (2) offshore foraging; (3) 10^5 pairs
Common murre (Atlantic)	0.12†	(1) nonbreeders disperse from colonies; (2) 10^6 pairs
Thick-billed murre (Atlantic)	0.04†	(1) long-distance migration to a single nonbreeding area; (2) 10^7 pairs
Common murre (Pacific)	0.01	(1) 10^6 pairs; (2) no historical fragmentation
Thick-billed murre (Pacific)	0.09†	(1) 10^7 pairs; (2) historical fragmentation
Black guillemot	0.30†	(1) no isolation by distance; (2) no population expansion
Pigeon guillemot	0.34†	(1) isolation by distance; (2) population expansion
Marbled murrelet	0.08†	(1) 10^5 pairs; (2) no historical fragmentation
Kittlitz's murrelet	0.91†‡	(1) 10^4 pairs; (2) historical fragmentation
Crested auklet	0.02	(1) 10^6 pairs
Least auklet	0.01	(1) 10^7 pairs

*Parentheses indicate mean of pairwise comparisons of populations.
†Statistically significant population genetic structure.
‡Phylogeographic structure.

an *n*-island model; 'O' in Table 1) or in many small colonies on mainland cliffs or nearshore islands along coastlines (potentially approximating a one-dimensional stepping-stone model of dispersal; 'C' in Table 1). Colony dispersion appears to have some effect: All populations with small, coastal colonies had population genetic struc-ture, and two showed phylogeographic structure (Table 5). However, no significant differences were found between populations with island vs. coastal arrangements of colonies either in the incidence of phylogeographic structure, or in mean Φ_{ST} or F_{ST} (Table 5). Thus, colony dispersion appears to have only a weak influence on population genetic structure.

Nonbreeding distribution

If individuals either remain near their breeding colonies during the nonbreeding season or travel to a population-specific nonbreeding area, their probability of encountering, and therefore potentially breeding at, other colonies, may be lower. Thus, population genetic structure may be

Table 5 Results of tests of the importance of different factors in shaping population genetic and phylogeographic structure in seabirds. Significant results are highlighted in bold. Data from Table 1

			Meta-analysis				
			Genetic structure†		Phylogeographic structure†		
Independent variable	Categories	Paired comparisons*	No	Yes	No	Yes	F_{ST} or Φ_{ST}‡
Breeding range	Breeding range restricted	1/1	3	2	4	1	0.21 ± 0.32
	Breeding range not restricted		8	24	23	9	0.19 ± 0.21
			$P = 0.08$		$P = 0.80$		$F_{1,25} = 0.02$; $P = 0.88$
Colony dispersion	Island	i.d.	11	19	22	8	0.28 ± 0.32
	Coastal		0	7	5	2	0.17 ± 0.19
			$P = 0.05$		$P = 0.82$		$F_{1,25} = 1.03$; $P = 0.32$
Nonbreeding distribution	Long-distance migration, or dispersal	3/0	11	13	23	1	0.11 ± 0.15
	Resident, or population-specific nonbreeding grounds/seasons		0	13	4	9	0.37 ± 0.24
			$P = 0.002$		**$P = 0.00003$**		**$F_{1,25} = 12.2$; $P = 0.002$**
Foraging range	Inshore	i.d.	0	7	5	2	0.29 ± 0.32
	Mixed, or offshore		11	19	22	8	0.23 ± 0.25
			$P = 0.05$		$P = 0.82$		$F_{1,27} = 0.31$; $P = 0.58$
Population size	Less than 10^6 breeding pairs	7/3	5	19	15	9	0.26 ± 0.25
	10^6 or more breeding pairs		6	6	11	1	0.07 ± 0.05
			$P = 0.09$		$P = 0.08$		$F_{1,24} = 4.19$; $P = 0.052$
Climate zone	Temperate to polar	3/1	11	14	22	3	0.14 ± 0.20
	Mostly tropical to subtropical		0	12	5	7	0.37 ± 0.20
			$P = 0.004$		**$P = 0.003$**		**$F_{1,25} = 6.85$; $P = 0.015$**§

*Number of comparisons in Tables 4 and 6 that support/do not support an effect of the variable on population genetic structure.
i.d., insufficient data.
†Number of populations in first (top number) and second (bottom number) category, without vs. with population genetic or phylogeographic structure (from Table 1), and significance from Fisher's exact test for a difference in frequency.
‡Mean ± standard deviation for estimates of Φ_{ST} or F_{ST} for species in first (top number) and second (bottom number) category, and estimate and significance of F from ANOVA.
§Significance lost if only one population from each species used.

stronger in species that remain at or near colonies year round or have multiple population-specific nonbreeding grounds compared to species that migrate to a single common nonbreeding area or simply disperse. For example, Burg & Croxall (2001) found genetic differences among albatross populations with different nonbreeding areas. Classifying populations according to nonbreeding distribution is difficult since migratory habits are variable within many species. We therefore classified species generally as having (i) true migration (regular seasonal movements with predictable timing and destination; del Hoyo *et al*. 1992; 'M' in Table 1); (ii) dispersal (movement away from the colony but no specific nonbreeding site; 'D' in Table 1), or (iii) year-round residency at colonies ('R' in Table 1). In addition, we noted whether species had multiple population-specific nonbreeding grounds (or seasons, in the case of sympatric hot- and cool-season breeding populations of band-rumped and Leach's storm-petrels; '¶¶' in Table 1).

There was strong support for an effect of nonbreeding distribution on population genetic structure. In paired comparisons, genetic structure was greater in species with multiple population-specific nonbreeding areas or seasons than in those with simple dispersal (Tables 4 and 6). In the meta-analysis, population genetic and phylogeographic structure were more likely to be found in species with multiple nonbreeding grounds or seasons or with year-round residency than in those with simple dispersal or a single nonbreeding area (Table 5). Most notably, all 13 populations that either are year-round residents at breeding colonies ('R' and 'D/R' in Table 1), or have multiple population-specific nonbreeding grounds or seasons ('M¶¶' and 'D¶¶' in Table 1) showed population genetic structure. Furthermore, nine of these populations had phylogeographic structure.

Table 6 Conspecific populations separated by contemporary or historical land, estimates of Φ_{ST} or F_{ST} within each population, and the main ecological and historical demographic differences (if any) between them. See Appendix for scientific names and study details, and Tables 1 and 3 for ecological characteristics and historical demographic changes. Studies that did not address genetic structure within both populations were not included

Species	Population	Global Φ_{ST} or F_{ST}*	Main ecological & historical differences
Band-rumped storm petrel	Atlantic	(0.46)†‡	
	Pacific	(0.47)†‡	
Leach's storm petrel	Atlantic	0.00	(1) long-distance migration to a single nonbreeding area; (2) temperate
	Pacific	0.63†‡	(1) population-specific nonbreeding seasons; (2) temperate/subtropical
Masked booby	Atlantic	0.32†	
	Indopacific	0.39†	
Lesser black-backed gull	W. Palearctic	(0.15)†	
	E. Palearctic	0.07†	
Black-legged kittiwake	Atlantic	(0.14)†	
	Pacific	0.03	
Common murre	Atlantic	0.12†	
	Pacific	0.01	
Thick-billed murre	Atlantic	0.04†	(1) long-distance migration to a single nonbreeding area
	Pacific	0.09†	(1) nonbreeders disperse from colonies

*Parentheses indicate mean of pairwise comparisons of populations.
†Statistically significant population genetic structure.
‡Phylogeographic structure.

Conversely, only 1 of 24 populations that either disperse during the nonbreeding season ('D' in Table 1) or migrate to a single common nonbreeding ground ('M' in Table 1) had phylogeographic structure. And estimates of Φ_{ST} and F_{ST} were significantly higher in populations with year-round residency or multiple population-specific nonbreeding grounds or seasons than in those that disperse or migrate to a single nonbreeding ground (Table 5). Thus, nonbreeding distribution appears to explain much of the variation in population genetic and phylogeographic structure in seabirds.

Foraging range

As for nonbreeding ranges, gene flow may be reduced if individuals either remain near colonies while foraging or use multiple, population-specific foraging areas rather than travelling to a single common foraging ground. For example, Burg & Croxall (2001, 2004) found that genetic differences among albatross taxa correspond to differences in foraging distributions. We tested whether genetic differentiation is greater in inshore foragers (those that generally forage within ~8 km of land, Gaston 2004; 'IS' in Table 1) than in populations that either forage offshore or have variable foraging distances ('OF' or 'M' in Table 1). This hypothesis received previous support (Friesen 1997), and in the present review, all of seven inshore-foraging species had population genetic structure, and two had phylogeographic structure (Tables 1 and 5). Otherwise, foraging range explained little of the variation in population genetic structure (Table 5).

Population bottlenecks

Population bottlenecks and founder events may promote genetic differentiation through drift, and may even lead to speciation (e.g. Slatkin 1996; Templeton 1996; Liebers *et al*. 2001; Abbott & Double 2003). A role for population bottlenecks in promoting genetic differentiation in seabirds received some support from paired comparisons: Φ_{ST} was higher in the shy albatross, which shows evidence of a recent population bottleneck, than in the white-capped albatross (Table 4). However, too few studies have been done to test the general importance of bottlenecks in promoting population differentiation in seabirds.

Retained ancestral variation

Populations need time to diverge genetically after separating. Thus, recently separated populations could mask mechanisms driving population divergence in a comparative analysis due to retained ancestral variation. Several mtDNA studies of seabirds attributed a lack of population genetic structure to recent population establishment or recent separation of populations (e.g. Birt-Friesen *et al*. 1992; Austin *et al*. 1994; Liebers & Helbig 2002; Burg *et al*. 2003), although few actually tested for retained ancestral variation (e.g. Kidd

Table 7 Net percentage sequence divergence among populations (δ) and mean percent nucleotide diversity within populations (π) for species of seabirds for which both estimates are available, the presence of population pairs with ratios (R) of δ to π < 4, and estimates of Φ_{ST} or F_{ST}

Species	Populations analysed	δ (range)	π (range)	Population pairs with $R < 4$?	Global Φ_{ST} or F_{ST}*
Black-footed albatross	Hawaii vs. Japan	0.59	0.05 (0.00–0.12)	no	0.91†
Northern fulmar	N. Atlantic colonies	0.05 (0.00–1.80)	1.07 (0.79–1.39)	all	0.02
Galapagos petrel	Galapagos Is.	0.00 (0.00–0.01)	0.02 (0.00–0.05)	all	0.10†
Fairy prion	Tasmanian colonies	~0.01	0.26 (0.00–0.51)	all	0.17
Sooty shearwater	S. Pacific colonies	0.55 (–0.04–2.01)	≤ 0.4	most	(0.16)†
Short-tailed shearwater	S. Australian colonies	~0.01 (0.00–0.02)	0.25 (0.20–0.30)	all	0.19
European storm-petrel	Atlantic vs. Mediterranean	0.76 (0.72–0.79)	0.05 (0.00–0.11)	no	(0.94)†‡
Band-rumped storm-petrel	all colonies sampled	3.26 (0.00–6.54)	1.3 (0.6–1.0)	some	0.74†‡
Leach's storm-petrel	all colonies sampled	0.42 (0.01–1.28)	0.91 (0.30–5.15)	most	(0.23)†‡
Masked booby	Atlantic vs. Indopacific	7.08 (6.80–7.37)	1.13 (0.91–1.38)	no	0.79†‡
	Atlantic colonies	0.80	1.09 (0.91–1.26)	all	0.32†
	Indopacific colonies	0.74 (0.08–1.29)	1.21 (0.61–1.96)	most	0.39†
Lesser black-backed gull	eastern vs. western Eurasian subspecies	–0.05	0.28 (0.18–0.42)	all	(0.32)†
Black-legged kittiwake	N. Atlantic colonies	0.11 (0.00–0.42)	0.48 (0.30–0.90)	all	0.14†
Red-legged kittiwake	all colonies sampled	0.30 (0.16–0.48)	1.5 (1.1–1.6)	all	0.17†
Sooty tern	Atlantic vs. Pacific	1.5	2.1 (1.8–2.6)	all	0.38†‡
Common murre	N. Atlantic colonies	−0.08 (−0.03–0.00)	0.53 (0.42–0.66)	all	0.00
Common murre	N. Pacific colonies	0.00 (–0.08–0.20)	0.26 (0.08–1.30)	all	0.01
Thick-billed murre	all colonies sampled	0.55 (–0.10–1.59)	0.76 (036–1.56)	most	0.44†‡
Razorbill	all colonies sampled	0.04 (0.00–0.10)	1.30 (0.93–1.98)	all	0.04†
Black guillemot	all colonies sampled	0.57 (0.00–1.02)	0.30 (0.00–0.58)	most	0.80†‡
Pigeon guillemot	all colonies sampled	0.51 (0.04–1.52)	0.87 (0.47–1.70)	most	0.34†
Xantus's murrelet	all colonies sampled	1.18 (–0.01–1.8)	0.58 (0.20–0.94)	some	0.47†‡
Ancient murrelet	E vs. W. N. Pacific	0.00	0.42 (0.40–0.44)	all	0.00
Marbled murrelet	all colonies sampled	0.40 (−0.05–1.11)	0.70 (0.28–1.04)	all	0.08†
Kittlitz's murrelet	all colonies sampled	0.60 (–0.07–0.93)	0.24 (0.17–0.30)	some	0.87†‡

*Parentheses indicate mean of pairwise comparisons of populations rather than global estimate.†Statistically significant population genetic structure, or significant difference in haplotype frequencies between at least two populations.
‡Phylogeographic structure.

& Friesen 1998a). Theoretically, the time required for populations to lose the genetic signature of historical association (i.e. ancestral variation) is directly related to the genetically effective population size (Neigel & Avise 1986). In practice, determining whether populations retain ancestral variation or are still exchanging genes (i.e. have no contemporary barriers to gene flow) is difficult because contemporary migration rates and effective population sizes are difficult to estimate (but see, for example, Kuhner *et al*. 1998; Nielsen & Wakeley 2001). We therefore used four indirect methods to examine the influence of retained ancestral variation on seabird population genetic structure: the ratio of divergence time to effective population size, current population size, recent range expansion, and climate zone.

Ratio of divergence time to effective population size. Theoretically, if populations are genetically isolated (i.e. no gene flow occurs), lineage sorting should be complete (i.e. no ancestral variation should remain) when $t \cong 4N_f g$, where t is divergence time, N_f is female effective population size and g is generation time (Neigel & Avise 1986). Substituting δ/d for t (where δ is mean percentage sequence divergence between populations, and d is divergence rate; Wilson *et al*. 1985) and $\pi/d\,g$ for N_f (where π is nucleotide diversity; Nei & Li 1979), lineage sorting should be complete when $\delta \cong 4\pi$. We calculated the ratio (R) of δ to π for seabird populations for which both estimates were available (Table 7). R was greater than 4 for some or all population pairs for 12 of 26 analyses ('no', 'some populations' or 'most populations' under 'Population pairs with $R < 4$?' in Table 7). Accordingly, all of these analyses found genetic structure, and most (eight) also found phylogeographic structure. However, R was less than 4 for all population pairs for 14 analyses ('all' under 'Population pairs with $R < 4$?' in Table 7). Only one such analysis (the sooty tern) showed phylogeographic structure; the

remaining analyses found little or no population genetic structure. In these cases, populations either may have ongoing gene flow, or they may be genetically isolated but retain ancestral variation.

Population size. If populations retain historical variation, and if lineage sorting depends on effective population size (above), then genetic and phylogeographic structure should be stronger in populations with smaller effective sizes. Few researchers have estimated genetically effective population sizes for seabirds (but see Friesen *et al*. 1996a; Moum & Arnason 2001; Walsh *et al*. 2005). However, census size tends to correlate with effective population size (Frankham 1996; but see Bazin *et al*. 2006), and appears to provide a partial explanation for population genetic structure in seabirds: Estimates of Φ_{ST} or F_{ST} were lower in the population with the higher census size in 7 of 10 paired comparisons (Tables 4 and 6; although in two comparisons, estimates of Φ_{ST} differed by only 0.01). And, in the meta-analysis, population genetic and phylogeographic structure tended to be less frequent, and population genetic structure tended to be weaker, in species with total populations of 10^6 or more breeding pairs than in those with smaller total population sizes (although none of these effects attained statistical significance; Table 5). Thus, population size may have a weak effect on population genetic structure, possibly by its relationship to retained ancestral variation.

Range expansion. Following a range expansion, population genetic structure will be low until populations lose their ancestral variation (as above, in ~ $4N_f$ generations in the absence of subsequent gene flow). To date, 10 studies of mtDNA variation in seabirds have found evidence of a range expansion (Table 3). As predicted, most of these populations showed little if any genetic structure, and only one exhibited phylogeographic structure (band-rumped storm-petrels in the Atlantic). Similarly, post-Pleistocene range expansions appear to be erasing historical phylogeographic structure in Adelie penguins (Ritchie *et al*. 2004) and lesser black-backed gulls (Liebers & Helbig 2002) due to secondary contact between historically isolated lineages. However, too few studies have tested for and rejected range expansions to determine their effect on population differentiation in seabirds.

Climate zone. Several researchers have argued that population differentiation should be weaker in temperate and polar regions, which were only recently repopulated following deglaciation, than in tropical/subtropical regions, which were less influenced by the glaciers (e.g. Liebers & Helbig 2002). Climate zone was strongly related to variation in population genetic structure in the present study: In three of four paired comparisons, population genetic structure was greater in tropical/subtropical than in temperate/polar populations or species (Tables 4 and 6). In the meta-analysis, all 12 populations with tropical/subtropical components to their distributions ('TR' and 'TR/NT' in Table 1) had significant population genetic structure and seven also had phylogeographic structure, whereas only 3 of 25 populations with temperate to polar distributions ('ST', 'NT', 'NT/NP' and 'NP' in Table 1) had phylogeographic structure (Table 5). And mean Φ_{ST} or F_{ST} for populations with tropical/subtropical components to their distributions also was significantly higher than for those with temperate to polar distributions (Table 5). Interestingly, in species with tropical to temperate distributions, the greatest genetic differences involve the tropical populations, and in a paper that was published as the present review was being sent to press, Jouventin *et al*. (2006) found that rockhopper penguins (*Eudyptes moseleyi*) on subtropical islands are highly divergent from their subpolar conspecifics, despite smaller geographic distances from the subtropical to subpolar colonies than among the subpolar colonies. Thus, climate zone appears to provide a strong predictor of the extent of population genetic structure in seabirds, possibly because of an influence on lineage sorting via population stability. Alternatively, selective differences between tropical/subtropical and temperate/polar regions may promote population differentiation (Jouventin *et al*. 2006).

While not definitive, these tests together suggest that retained ancestral variation may be masking potential barriers to gene flow in seabirds, especially at high latitudes.

Cryptic physical barriers

Comparative phylogeography can sometimes reveal barriers to gene flow that are not otherwise obvious to researchers (Avise 2000). We used a comparative approach to identify geographic locations of population genetic and phylogeographic breaks common to two or more species. Several such sites were revealed (Table 8). Most of these sites also have endemic species or subspecies of seabirds, and some are hotspots of diversity (del Hoyo *et al*. 1992, 1996). For example, the Strait of Gibraltar appears to inhibit gene flow in several species of seabirds. It also has been identified as a biogeographic barrier in many nonseabird species (Fredj *et al*. 1992). (Gómez-Díaz *et al*. 2006 argue however, that the Almeria-Oran Oceanographic Front within the western Mediterranean, rather than the Strait of Gibraltar itself, provides the barrier to gene flow between Atlantic and Mediterranean populations of Cory's shearwaters.) Large expanses of low-productivity ocean, such as in the western and eastern equatorial Pacific Ocean and areas around many oceanic islands, also appear to restrict gene flow. Finally, several high arctic species exhibit partially overlapping, genetically differentiated populations,

Table 8 Locations of population genetic or phylogeographic breaks identified by comparative phylogeography, species affected, and possible reasons that gene flow is interrupted

Island, or location of barrier	Species affected	Potential reason
Strait of Gibraltar	Cory's shearwater; European storm-petrel; yellow-legged gull	Narrow passage or oceanographic front
Cape Verde	Band-rumped storm-petrel	Distance
Iceland	Razorbill; black guillemot	Distance
Norwegian Sea	Black-legged kittiwake; common murre	Polynya*
Baffin Bay	Black-legged kittiwake; thick-billed murre	Polynya
Chukchi Sea/Arctic Ocean	Thick-billed murre; black guillemot	Polynya
western/central Aleutian islands	Red-legged kittiwake; thick-billed murre; marbled murrelet	Distance
Aleutian islands/Alaska Peninsula	Pigeon guillemot; marbled murrelet; Kittlitz's murrelet	Distance
Guadalupe Island	Leach's storm-petrel; Xantus's murrelet	
Western/central Pacific Ocean	Black-footed albatross; band-rumped storm-petrel; masked booby	Distance
Central/eastern Pacific Ocean	Masked booby; brown booby	Distance
Galapagos islands	Band-rumped storm-petrel	Distance

*regions of open water surrounded by sea-ice or glaciers.

and these often occur in the vicinity of putative Pleistocene polynyas (regions of open water surrounded by sea-ice or glaciers; e.g. Chukchi Sea, Svalbard; Dyke & Prest 1987). These divergent populations are often associated with evidence of historical fragmentation (Table 3), suggesting long-term isolation.

Discussion

Mechanisms of population differentiation

Although factors promoting population differentiation may be obscured by retained ancestral variation in some species, the present review identified several potential barriers to gene flow in seabirds. Populations separated by contemporary or historical land consistently exhibited genetic differences, and most of these populations were also phylogeographically structured. Thus, gene flow in seabirds appears to be strongly limited by land. The effectiveness of land as a barrier probably results from the inability of most species of seabirds to find food and/or take flight from land. The degree of population segregation during the nonbreeding season also correlated strongly with the extent of population genetic and phylogeographic structure. Given that populations that are separated by contemporary or historical land also have separate nonbreeding distributions, nonbreeding distribution alone seems to be an excellent predictor of phylogeographic structure: all species with multiple nonbreeding areas or seasons except one (Leach's storm petrels in the Atlantic vs. Pacific) were phylogeographically structured, and all species but one with phylogeographic structure (Kittlitz's murrelet) had multiple population-specific nonbreeding areas or seasons. Furthermore, all populations that remain at or near their breeding colonies year-round had strong population genetic structure. Thus, separation during the nonbreeding season appears to provide a strong barrier to gene flow in seabirds. Correlations between nonbreeding distributions and population genetic structure, at least on a coarse scale, have also been reported in songbirds (e.g. Milot *et al*. 2000; Kimura *et al*. 2002; Lovette *et al*. 2004; but see, for example, Davis *et al*. 2006), shorebirds (e.g. Wenink & Baker 1996) and waterfowl (e.g. van Wagner & Baker 1990; Tiedemann *et al*. 2004; but see, for example, Pearce *et al*. 2004). Population genetic structure also tends to be greater in sedentary vs. migratory passerines (e.g. Burg *et al*. 2005, 2006). The effectiveness of segregation during the nonbreeding season in preventing gene flow may result simply from infrequent encounters of birds with different spatial distributions. Instead or in addition, migratory routes may be genetically programmed and the offspring of hybrids may have low fitness, as evidenced in some landbirds (Helbig 1991). Geographic distance between colonies, colony dispersion and foraging range appear to have a weak influence on population genetic structure, possibly operating through the same mechanisms as land barriers and nonbreeding distribution.

Barriers to gene flow were not obvious in a few species that exhibit population genetic structure, such as Xantus's murrelets and Galapagos petrels. Thus, factors other than land and nonbreeding distribution may be promoting population differentiation in seabirds. For example, philopatry (the tendency of individuals to breed in their natal area) can reduce gene flow, and appears to have lead to population differentiation in organisms such as salmon (e.g. Quinn & Dittman 1990). Seabirds are well known for their generally

strong philopatry, with banding studies of numerous species indicating little intercolony dispersal (although there are also many exceptions; Coulson 2002; Gaston 2004). Philopatry may evolve from the many benefits of coloniality (Coulson 2002): defence against predation, social stimulation, conspecific facilitation of location and capture of prey, and possibly mate choice. The best information that a young bird may have about a suitable place to breed is its own survival at its natal colony. Local factors also could limit effective dispersal among colonies via selection, thereby increasing genetic structure. For example, the roles of adaptations for parasite resistence or other local habitat conditions in structuring seabird populations have yet to be examined (McCoy *et al*. 2005).

Seabird colonies have many features conducive to metapopulation dynamics: physically discrete populations of varying size, strong temporal dynamics, philopatry, sporadic dispersal, and the potential for long-range dispersal and colonization (Hanski 1999). The mechanisms by which recruits chose a breeding colony are generally unknown, but are thought to be related to information gathered from conspecifics while young birds are prospecting for a breeding site (Boulinier *et al*. 1996; Danchin *et al*. 1998, 2004). If local conditions are poor such that reproductive success is limited, young birds and failed breeders may disperse. In this sense, the amount and distance of gene flow may be directly dependant on the quality of the local environment (e.g. food availability, predators, parasites) and the spatial scale of environmental heterogeneity. Dispersal among colonies may then be asymmetric, with some colonies sending or receiving a disproportionate number of recruits compared to others, setting up a source–sink dynamic. Evidence for a meta-population structure and asymmetric gene flow among patches has already been suggested for several species where local population dynamics could not be explained by philopatry alone (e.g., Frederiksen & Petersen 2000; Breton *et al*. 2006; Peery *et al*. 2006). The general importance of metapopulation dynamics in shaping the genetic structure of these species should become more apparent as more long-term data sets on local population dynamics become available and are integrated with genetic approaches.

Speciation

Under the allopatric model of speciation, population differentiation is the first stage in the evolution of reproductive isolation (e.g. Mayr 1963; Turelli *et al*. 2001; Coyne & Orr 2004). Although widely accepted, this model is not satisfactory for many natural phenomena, such as adaptive radiations and sympatric sibling species. Several alternative models have been proposed (reviewed in Coyne & Orr 2004), but the prevalence of these alternatives in the natural world, and their exact mechanisms (e.g. the roles of physical barriers to gene flow, genetic bottlenecks, hybridization, and sexual selection, and the genetic basis of reproductive isolation), are unclear (e.g. Chesser & Zink 1994; Barraclough & Nee 2001; Orr 2001; Turelli *et al*. 2001; Gavrilets 2003; Rundle & Nosil 2005). The apparent importance of land as a barrier to gene flow in seabirds suggests that allopatric speciation is probably common in this group; for example, Pleistocene glaciations are thought to have driven the origin of several species within the herring and yellow-legged gull complexes (Liebers *et al*. 2001, 2004; Liebers & Helbig 2002), and several sister species are separated by contemporary or historical land barriers (e.g. Atlantic and horned puffins, *Fratercula arctica* and *F. corniculata*, respectively; Friesen *et al*. 1996c). However, reproductive isolation between the Armenian and other yellow-legged gulls, and between shy and white-capped albatrosses was apparently associated with long-range colonization events and severe population bottlenecks (Liebers *et al*. 2001; Abbott & Double 2003), and so these species represent potential examples of founder-induced peripatric speciation (Slatkin 1996; Templeton 1996). Furthermore, the existence of genetic structure in the absence of either contemporary or historical physical barriers to gene flow in a large number of populations suggests that parapatric and sympatric speciation also are possible in seabirds. Notably, population differentiation and speciation appear to be occurring in sympatric seasonal populations of band-rumped storm-petrels in at least three archipelagos (Monteiro & Furness 1998; Smith & Friesen 2007; Smith *et al*. 2007), and in Leach's storm-petrels on Guadalupe Island (P. Gulavita unpublished), and many sister species are not separated by any known contemporary or historical land barrier (e.g. *Aethia* auklets). The potential for nonallopatric divergence requires further investigation.

Conservation implications

Results of the present study have direct implications for conservation in that the extent of population genetic structure in seabirds is highly variable, and potentially very strong. Twenty-one of the 53 species studied to date exhibit phylogenetic structure at some geographic scale, and so represent multiple evolutionary significant units (Moritz 1994; Crandall *et al*. 2000). These species will therefore lose a high proportion of their genetic variation if local populations are lost or reduced, and will probably be slow to recover through natural dispersal (e.g. in the event of an oil spill). Nine additional species have haplotype frequency differences between populations, and so may represent multiple genetic management units (*sensu* Moritz 1994). Results of this study also may help us predict the extent of population genetic structure in the approximately 260 seabird species that have not yet been analysed, to

guide conservation priorities and actions. Most notably, conspecific populations separated by land (e.g. Atlantic vs. Pacific populations of Holarctic and pantropical species such as roseate terns *Sterna dougallii*) are almost certainly genetically and probably also phylogeographically distinct. Within ocean basins, populations of year-round residents or those with separate nonbreeding distributions (or seasons) (e.g. common diving-petrels, *Pelecanoides urinatrix*) are also almost certainly genetically and probably phylogeographically differentiated. Furthermore, tropical species (e.g. red-tailed tropicbirds, *Phaethon aethereus*) and inshore foragers (e.g. brown boobies) probably possess population genetic structure and should be investigated for the existence of multiple management units. Species that disperse from their colonies when not breeding, migrate to a single common nonbreeding ground, breed at high latitudes and/or have large foraging ranges are least likely to include multiple evolutionary significant units or management units.

Future directions

Results of the present review highlight several immediate research needs. (i) More surveys are needed on sphenisciform and pelecaniform species to determine if the present results can be generalized to these taxa. (ii) The extent to which retained ancestral variation is masking barriers to gene flow needs to be tested explicitly in a variety of species, e.g. using coalescent-based methods of estimating contemporary gene flow (e.g. Nielsen & Wakeley 2001). (iii) The potential role of population bottlenecks in shaping genetic structure needs to be tested. (iv) Comparisons of results from long-term banding data and/or assignment tests to results from molecular studies would provide insight into the relationship between population genetic structure and contemporary gene flow, especially for populations that may retain ancestral variation and/or represent metapopulations. (v) Satellite tracking may help to identify nonbreeding distributions more precisely, and, thus, test the extent of the effect of nonbreeding distributions on population genetic structure. (vi) The general importance of the Almeria-Oran Oceanographic Front, large expanses of open ocean, and Pleistocene polynyas as barriers to dispersal in seabirds should be tested. (vii) Finally, results of the present review need to be addressed using other types of organisms, and nuclear markers. It will be especially useful to test the present conclusions with studies of nuclear variation given that mtDNA reflects female-mediated gene flow only, and may be subject to periodic selective sweeps (e.g. Bazin *et al*. 2006). Ultimately, as studies of population structure in seabirds and other organisms accumulate, formal multifactorial analyses will be possible and will enable us to predict accurately the extent of population genetic structure in species that have not been studied using molecular markers. By understanding the general factors linked to population differentiation, and ultimately speciation, we may be better prepared to deal with the effects of human disturbance on the natural processes of diversification and extinction.

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Vicki Friesen uses molecular markers to study mechanisms of population differentiation in vertebrates, primarily seabirds. Much of her work has applications to conservation. Theresa Burg studies the role of intrinsic and extrinsic barriers to gene flow in high-latitude vertebrate species. Karen McCoy's research focuses on host–parasite interactions and, more specifically, considers how the interaction between seabirds and their obligate parasites has affected their ecology and evolution.

Appendix

Studies of population level variation in mtDNA in seabirds. Only studies including two or more sampling sites are included

Species*	Common name	Sampling range	Number of sites sampled	Number of sub-species sampled	Compre-hensive sampling†	Number of individuals sampled	DNA region‡	Number of base pairs sampled	Number of haplo-types	Reference
Sphenisciformes										
Spheniscidae										
Pygoscelis adeliae	Adelie penguin	circum-Southern Ocean	24	1	Y	653	CRI	352+	440	Ritchie *et al.* 2004
Procellariiformes										
Diomedeidae										
Diomedea exulans	Wandering albatross	circum-Southern Ocean	4	1	Y	38	CRI	234	23	Burg & Croxall 2004
Diomedea dabbenena	Tristan albatross	Tristan I.	1	1	Y	3	CRI	234	2	Burg & Croxall 2004
Diomedea antipodensis	Antipodean albatross	New Zealand	2	1	Y	23	CRI	234	17	Burg & Croxall 2004
Diomedea gibsoni	Gibson's albatross	New Zealand	1	1	Y	20	CRI	234	8	Burg & Croxall 2004
Phoesbastria nigripes	Black-footed albatross	Central Pacific	4	1	Y	140	Cyt *b*	609	6	Walsh & Edwards 2005
Thalassarche melanophris	Black-browed albatross	Southern Ocean	5	1	Y	58	CRI	219	36	Burg & Croxall 2001
Thalassarche impavida	Campbell Island albatross	Campbell I.	1	1	Y	15	CRI	219	15	Burg & Croxall 2001
Thalassarche cauta	Shy albatross	Tasmania	3	1	Y	30	CRI	299	15	Abbott & Double 2003
Thalassarche steadi	White-capped albatross	New Zealand	3	1	Y	29	CRI	299	22	Abbott & Double 2003
Thalassarche eremita	Chatham albatross	New Zealand	1	1	Y	3	CRI	299	2	Abbott & Double 2003
Thalassarche salvini	Salvin's albatross	New Zealand, Crozet I.	1	1	Y	3	CRI	299	3	Abbott & Double 2003
Thalassarche chrysostoma	Grey-headed albatross	circum-Southern Ocean	5	1	Y	50	CRI	220	39	Burg & Croxall 2001
Procellariidae										
Fulmarus glacialis	Northern fulmar	Eastern North Atlantic	7	1	N	115	CRI	299	42	Burg *et al.* 2003
Pterodroma phaeopygia	Galapagos petrel	Galapagos Is.	5	1	Y	206	ATPase	650	2	Friesen *et al.* 2006
Pachyptila turtur	Fairy prion	Tasmania	3	1	N	61	RFLP	?	10	Ovenden *et al.* 1991
Pachyptila belcheri	Slender-billed prion	Southern Ocean	2	1	N	22	CRI, II	685	?	M. Silva & S.V. Edwards, unpublished
Calonectris diomedea	Cory's shearwater	Atlantic, Mediterranean	26	2	Y	57	Cyt *b*, CRI	1269	49	Gómez-Díaz *et al.* 2006
Puffinus griseus	Sooty shearwater	South Pacific	8	1	Y	200	Cyt *b*, CRII	695	78	C. Baduini & K. Warheit, unpublished
Puffinus tenuirostris	Short-tailed shearwater	Tasmania	11	1	Y	335	RFLP	11 6/5.33-cutters; 4 4-cutters	25,48	Austin *et al.* 1994
Puffinus yelkouan	Yelkouan shearwater	Mediterranean	4	2	Y	30	Cyt *b*	1100	4	Heidrich *et al.* 1998
Hydrobatidae										
Hydrobates pelagicus	European storm-petrel	North Atlantic	5	2	Y	65	Cyt *b*	910	8	Cagnon *et al.* 2004
Oceanodroma castro	Band-rumped storm-petrel	Circumtropical	10	1	Y	389	CRI	448	17	Smith *et al.* 2007
Oceanodroma leucorhoa	Leach's storm-petrel	Atlantic & Pacific	10	3	Y	198	Cyt *b*, CRI	682	32	M. Atkey & P. Gulavita, unpublished

Appendix *Continued*

Species*	Common name	Sampling range	Number of sites sampled	Number of sub-species sampled	Compre-hensive sampling†	Number of individuals sampled	DNA region‡	Number of base pairs sampled	Number of haplo-types	Reference
Pelecaniformes										
Sulidae										
Sula dactylatra	Masked booby	Atlantic, Pacific	6	3	N	37	Cyt *b*	450	5	Friesen & Anderson 1997
		Atlantic, Pacific	4	2	Y	64	Cyt *b*	450	5	Steeves *et al*. 2003
		Atlantic, Indopacific	11	5	Y	288	CRI, II	500	106	Steeves *et al*. 2005
Sula granti	Nazca booby	Galapagos Is.	2	1	N	60	Cyt *b*	450	2	Friesen & Anderson 1997
Sula sula	Red-footed booby	Atlantic/Pacific	3	3	N	89	Cyt *b*	450	3	Steeves *et al*. 2003
Sula leucogaster	Brown booby	Atlantic/Pacific	5	3	N	78	Cyt *b*	450	5	Steeves *et al*. 2003
Phalacrocoracidae										
Phalacrocorax pelagicus	Pelagic cormorant	North Pacific	2	2	N	6	RFLP	12 enzymes	4	Zink *et al*. 1995
Charadriiformes										
Laridae										
Larus crassirostris	Black-tailed gull	Hokkaido	6	1	N	218	CRI	438	23	O. Hasegawa, unpublished
Larus canus§	Mew gull	North Pacific	2	2	N	4	RFLP	12 enzymes	2	Zink *et al*. 1995
Larus marinus	Great black-backed gull	Europe	7	1	N	74	Cyt *b*, CRII, III	280–891	4	Crochet *et al*. 2002, 2003
Larus hyperboreus	Glaucous gull	Circumarctic	4	2	N	40	CRI, cyt *b*	1573	40	Liebers *et al*. 2004
			2	2	N	43	Cyt *b*, CRII, III	280–891	2	Crochet *et al*. 2002, 2003
Larus argentatus§	Herring gull	France, Scandinavia	3	2	N	36	Cyt *b*, CRII, III	280–891	5	Crochet *et al*. 2002, 2003
		Circumarctic	16	4	Y	148	CRI, cyt *b*	1573	137	Liebers *et al*. 2004
Larus cachinnans§	Caspian gull	Western & Central Asia	11	3	Y	261	CRI	430	31	Liebers *et al*. 2001
		Western Asia	4	1	N	26	CRI, cyt *b*	1573	20	Liebers *et al*. 2004
Larus barabensis	Siberian gull	Western Russia	2	1	N	46	CRI	430	7	Liebers *et al*. 2001
Larus michahellis	Yellow-legged gull	Eastern North Atlantic & Mediterranean	6	2	Y	172	CRI	430	28	Liebers *et al*. 2001
		Europe	9	1	Y	78	Cyt *b*	280–891	4	Crochet *et al*. 2002, 2003
		Europe	5	1	Y	79	Cyt *b*	308	5	Pons *et al*. 2004
		Europe	10	2	Y	46	CRI, cyt *b*	1573	2	Liebers *et al*. 2004
Larus mongolicus	Mongolian gull	Mongolia	2	1	N	10	CRI, cyt *b*	1573	2	Liebers *et al*. 2004
Larus armenicus§	Armenian gull	Anatolia, Armenia, Iran	3	1	Y	81	CRI	430	10	Liebers *et al*. 2001
		Turkey	2	1	Y	10	CRI, cyt *b*	1573	22	Liebers *et al*. 2004
Larus schistisagus	Slaty-backed gull	Hokkaido	4	1	N	93	CRI	438	16	O. Hasegawa, unpublished
Larus fuscus	Lesser black-backed gull	N. Europe	5	3	N	147	CRI	430	?	Liebers *et al*. 2001
		N. Europe, Russia	10	5	Y	272	CRI	430	44	Liebers & Helbig 2002
		N. Europe	3	2	N	38	Cyt *b*, CRII, III	~920	4	Crochet *et al*. 2002, 2003
		N. Europe, Russia	8	5	Y	79	CRI, cyt *b*	1573	32	Liebers *et al*. 2004
Rissa tridactyla	Black-legged kittiwake	North Atlantic, Pacific	18	2	Y	404	CRI, II, III	773	155	Patirana 2000
Rissa brevirostris	Red-legged kittiwake	Bering Sea	3	1	Y	27	CRI	445	14	Patirana *et al*. 2002

Appendix *Continued*

Species*	Common name	Sampling range	Number of sites sampled	Number of sub-species sampled	Compre-hensive sampling†	Number of individuals sampled	DNA region‡	Number of base pairs sampled	Number of haplo-types	Reference
Sternidae										
Sterna hirundo	Common tern	North Pacific	2	2	N	8	RFLP	12 enzymes	6	Zink *et al.* 1995
Sterna fuscata	Sooty tern	Atlantic, Indopacific	5	3	Y	55	RFLP, CRI	516, 343	12, 47	Avise *et al.* 2000
		SW Pacific	4	1	N	89	CRII, III	540	18	Peck & Congdon 2004
Alcidae										
Uria aalge	Common murre	Norway	4	2	N	51	RFLP	~410	13	Moum *et al.* 1991
		North Atlantic, Pacific	10	3	Y	160	Cyt *b*¶	204	11	Friesen *et al.* 1996a
		North Atlantic	4	2	N	79	CRI	266	29	Moum & Arnason 2001
		North Atlantic	12	3	Y	248	CRI, II, III	705	?	M. Damus, unpublished
		North Pacific	17	2	Y	328	CRI, II, III	760	74	T. Birt, unpublished
Uria lomvia	Thick-billed murre	North Atlantic	5	1	N	215	Cyt *b*	253	15	Friesen *et al.* 1996a
		Circumarctic	19	4	Y	420	CRI, II, III	743	149	M. Damus, unpublished
Alca torda	Razorbill	North Atlantic	5	2	Y	123	CRI	300	43	Moum & Arnason 2001
Cepphus grylle	Black guillemot	North Atlantic	5	5	Y	65	CRII, III	504	16	Kidd & Friesen 1998a
Cepphus columba	Pigeon guillemot	Eastern North Pacific	3	2	N	52	CRII, III	504	6	Kidd & Friesen 1998a
		Eastern North Pacific	8	3	Y	186	CRI, II, III	721	73	V. Poland, unpublished
Brachyramphus marmoratus	Marbled murrelet	Eastern North Pacific	8	1	N	30	Cyt *b*	1045	13	Friesen *et al.* 1996b
		Eastern North Pacific	11	1	Y	146	CRI	547	76	Friesen *et al.* 2005
Brachyramphus brevirostris	Kittlitz's murrelet	Eastern North Pacific	2	1	N	77	Cyt *b*	1045	4	Friesen *et al.* 1996b
		North Pacific	3	1	Y		CRI	330	13	D. MacKinnon, unpublished
Synthliboramphus hypoleucus	Xantus's murrelet		3	2	Y	100	CRI	412	27	A. McDonald, unpublished
Synthliboramphus antiquus	Ancient murrelet	North Pacific	3	1	N	58	CRI, II, III, cyt *b*	1132	20	Pearce *et al.* 2002
Aethia cristatella	Crested auklet	North Pacific	7	1	Y	81	Cyt *b*	306	8	Walsh *et al.* 2005
Aethia pusilla	Least auklet	North Pacific	8	1	Y	89	Cyt *b*	306	5	Walsh *et al.* 2005

? = not given.

*Scientific names are from del Hoyo *et al.* (1992, 1996), Schreiber & Burger (2002) or the reference cited.

†Y, sampling involved comprehensive coverage of the species' breeding range; N, a significant portion of the species' range not sampled.

‡CR, mitochondrial control region; I, Domain I; II, Domain II; III, Domain III; cyt *b*, cytochrome *b* gene; RFLP, analysis of restriction fragment length polymorphisms of the complete mitochondrial genome.

§Breeding distribution primarily inland and/or freshwater.

¶Results of this study were probably complicated by the presence of a nuclear copy of cytochrome *b*, so were excluded from further analyses.