

NEW ROLES FOR MOLECULAR GENETICS IN UNDERSTANDING SEABIRD EVOLUTION, ECOLOGY AND CONSERVATION

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SUMMARY

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The potential for molecular markers to aid seabird research is continually expanding. Currently, sequencing has become very rapid and cost-effective, and methods for interpreting sequence variation have expanded exponentially, with the result that molecular genetics now provides powerful tools for many fields of study. Here, I provide examples of how molecular markers can advance our understanding of seabird evolution and ecology and aid conservation. Specifically, molecular tools provide insights into mechanisms of speciation, barriers to gene flow and dispersal, and morphologic adaptation. They can aid in the inference of metapopulation dynamics, help to census species that are difficult to observe, and provide insight into the extent of hybridization between species. Finally, modern molecular methods can benefit conservation by helping to delimit appropriate population units for management, indicating geographic regions that should be given high priority for protection, and helping with impact assessment. Potential applications of molecular markers will almost certainly continue to increase and improve in future.

Key words: Census methods, hybridization, impact assessment, metapopulation dynamics, morphologic evolution, population differentiation, speciation

INTRODUCTION

Information about an organism's evolution and ecology is retained as molecular "fossils" in its DNA, and recent analytical methods, especially those based on coalescent theory, are enabling this information to be extracted. In particular, neutral molecular markers (those that are not affected by selection—e.g. segments of DNA that do not code for proteins) contain information about an individual's relationships to other organisms, its population's present and historical size, and relationships among populations. Methods of DNA analysis are advancing so rapidly that entire genomes can now be sequenced within a few months, and approaches for extracting evolutionary and ecologic information from sequences are becoming increasingly sophisticated. In this paper, I provide examples of insights into seabird evolution, ecology and conservation provided by recent advances in genetic analyses.

EVOLUTION

Speciation

"Speciation" may be defined as the evolution of reproductive isolation between populations (Coyne & Orr 2004). Understanding speciation is fundamental for understanding many aspects of ecology and evolution because populations that are reproductively isolated can adapt and evolve independently. Furthermore, many aspects of morphology and behaviour are adaptations for species recognition, primarily for mate choice. Understanding speciation is also important for conserving biodiversity, because the maintenance of biodiversity ultimately requires conservation of the diversification process.

According to the classical *allopatric model* of speciation, a parental species initially becomes subdivided into two large populations by an extrinsic (geographic) barrier to dispersal. The populations diverge gradually through selection or genetic drift (or both) until they are no longer reproductively compatible because either of pre-mating barriers (e.g. failure to recognize one another as potential mates) or post-mating barriers (e.g. genetic incompatibilities resulting in inviable or infertile offspring).

The foregoing model appears to apply to many speciation events, but it does not provide a satisfactory explanation for several biogeographic patterns such as the coexistence of sympatric sister species. Several alternative models have therefore been proposed (reviewed in Coyne & Orr 2004; Gavrillets 2004).

The *peripatric model* of speciation is similar to the allopatric model, except that it involves the evolution of reproductive isolation in a small population on the periphery of the parental range. According to the parapatric model, reproductive isolation can develop between organisms at the extremes of the range of a continuously distributed species either because of isolation by distance (restrictions in gene flow attributable to distance) or because of strong selective differences.

Finally, according to the *sympatric model*, reproductive isolation can evolve between organisms that are co-distributed in time and space. This latter model requires special conditions such as a chromosomal rearrangement (e.g. polyploidization, as has been documented in plants) or divergence in breeding time (allochryony, as in periodical cicadas; reviewed in Coyne & Orr 2004). Although

theoretical support exists for all of these alternatives (but see Coyne & Orr 2004; Gavrilets 2004), little empiric evidence is available—especially for birds or mammals. However, seabirds provide potential examples of each model.

Sympatric speciation

The Band-rumped Storm-Petrel (also called the Madeiran Storm-Petrel) *Oceanodroma castro* breeds on tropical and subtropical islands throughout the Atlantic and Pacific Oceans (Fig. 1; Brooke 2004). In several archipelagos, different individuals nest on the same islands—even the same burrows—at different times of year (reviewed in Friesen *et al.* 2007b). In the Azores and Madeira, seasonally segregated populations differ in morphology, moult chronology and vocalizations. They are considered to represent sympatric species in the Azores (Bolton *et al.* in press), and Monteiro and Furness (1998) proposed that the hot season population arose sympatrically from the cool season population within the Azores.

If seasonal populations arose sympatrically, then populations from the same archipelago should be more closely related to one another than to populations from the same season from other archipelagos [Fig. 2(A)]; otherwise, if they arose allopatrically, populations from the same season from different archipelagos should be more closely

related to one another than to sympatric populations from the other season [Fig. 2(B)].

Friesen *et al.* (2007b) compared variation in mitochondrial DNA (mtDNA) and five microsatellite loci among 562 breeding adults sampled from 17 populations, including sympatric seasonal populations from four archipelagos and populations from two seasons from Cape Verde, where breeding occurs throughout the year. Those authors found that seasonal populations differ genetically in all five archipelagos (although only weakly in the Galapagos) and do not appear to exchange genes in either the Azores or Cape Verde (i.e. estimates of gene flow do not differ from 0), suggesting that they are reproductively isolated. Furthermore, seasonal populations from the Galapagos form sister taxa on the population trees, as do seasonal populations from Cape Verde. Although relationships between populations in the northeast Atlantic (coastal Portugal, the Azores, Madeira and the Canaries) could not be resolved unambiguously, seasonal populations from Madeira were part of the northeast Atlantic cluster, and hot-season populations from the Azores were a sister taxon to it [Fig. 2(C)]. Thus, although the evolution of seasonal populations is not simple, those populations appear to have arisen sympatrically at least four times (Friesen *et al.* 2007b). Furthermore, they appear to be at different stages of speciation, from initial

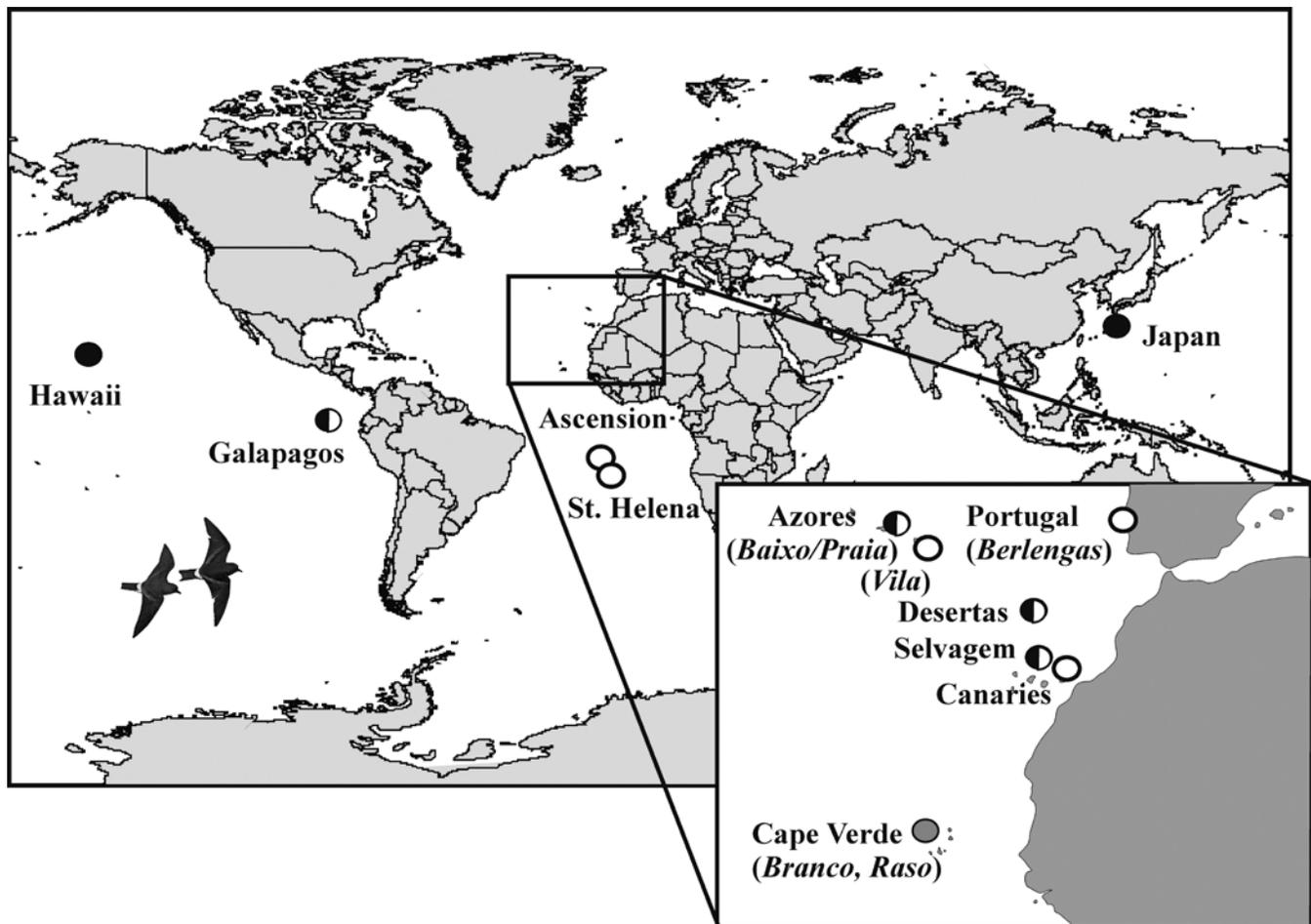


Fig. 1. Breeding range of the Band-rumped Storm-Petrel *Oceanodroma castro*, and sites sampled for genetic analyses (from Friesen *et al.* 2007b). Black symbols represent locations with breeding during the Northern Hemisphere hot season; white symbols represent locations with breeding during the Northern Hemisphere cool season; black and white symbols represent locations with sympatric seasonal populations; grey symbol represents protracted (aseasonal) breeding with two seasonal peaks. Archipelago names are in regular type; specific islands that were sampled are in italics.

population divergence (Galapagos) to reproductively isolated species (Azores), and so they provide one of the best examples of sympatric evolution in a tetrapod.

This speciation mode does not appear to be unique to Band-rumped Storm-Petrels. Leach's Storm-Petrels *O. leucorhoa* on Guadalupe, Mexico, also have seasonally segregated populations that appear to have arisen within the island (Friesen *et al.* unpubl. data).

Peripatric speciation

Variation in mtDNA and microsatellites suggests that the Armenian Gull *Larus armenicus* and Shy Albatross *Thalassarche cauta* arose through long-range colonization by small founder populations from Yellow-legged Gulls *Larus* spp. and White-capped Albatrosses *T. steadi*, respectively (Liebers *et al.* 2001, Abbott & Double 2003), suggestive of peripatric speciation.

Parapatric speciation

The Nazca Booby *Sula granti* breeds only on the Galapagos islands and Malpelo Island, Columbia (Pitman & Jehl 1998), and is a sister species to the Masked Booby *S. dactylatra*, which breeds throughout the tropical and subtropical Pacific, Atlantic and Indian Oceans (Nelson 1978). The Nazca Booby appears to have arisen from the Masked Booby without any physical barriers to gene flow (Friesen *et al.* 2002); rather, the unique ecologic conditions around the Galapagos probably provided strong selection, potentially promoting speciation.

Population differentiation

Understanding the mechanisms by which populations diverge genetically helps in gaining an understanding of the mechanisms of local adaptation and speciation, and aids conservation (discussed later in its own subsection).

In theory, the extent to which local populations differ genetically is inversely related to the amount of gene flow between them (Wright 1931). However, in practice, the barriers that prevent gene flow are not always evident. For example, most seabirds will not fly across land, but many are blown across land during storms, and so the extent to which land restricts gene flow is unclear.

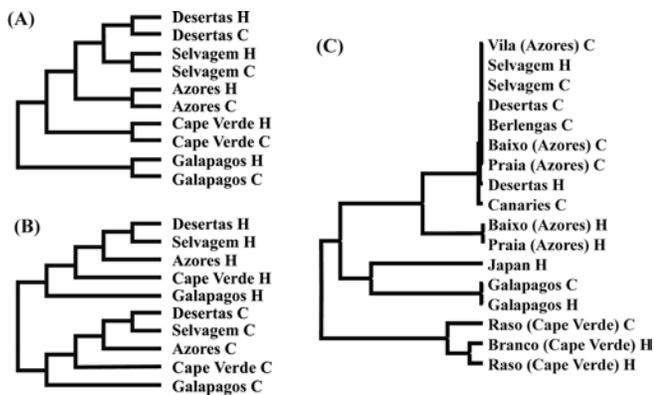


Fig. 2. Hypothetical relationships between populations of Band-rumped Storm-Petrels (A) if seasonal populations arose sympatrically within archipelagos, and (B) if seasonal populations arose allopatrically. (C) Relationships inferred from mitochondrial DNA sequences. See Fig. 1 for sampling locations. H = hot-season population; C = cold-season population.

Friesen *et al.* (2007a) reviewed population genetic studies of mtDNA variation in seabirds to identify barriers to gene flow. They discovered that major landmasses (including ice) constitute an important barrier. Of 12 species whose distributions are fragmented by contemporary or historical land (primarily species that breed in both the Atlantic and the Pacific oceans—e.g. murre *Uria* spp.), all exhibit major genetic differences between the fragmented populations [Fig. 3(A)]. However, 22 species also exhibit population genetic structure in the absence of obvious physical barriers to gene flow [Fig. 3(A)]. For example, Galapagos Petrels *Pterodroma phaeopygia* from different islands within the Galapagos differ genetically.

Friesen *et al.* 2007a found that the extent of population genetic structure in seabirds can be explained in part by nonbreeding distribution: conspecific populations with different nonbreeding distributions and those that are resident at colonies year-round tend to differ genetically [Fig. 3(B)]. Thus, philopatry to nonbreeding areas appears to reduce or prevent gene flow between seabird populations.

Results of the foregoing meta-analysis are preliminary and need to be confirmed when more mtDNA studies are published and when a similar analysis of variation in nuclear DNA is carried out.

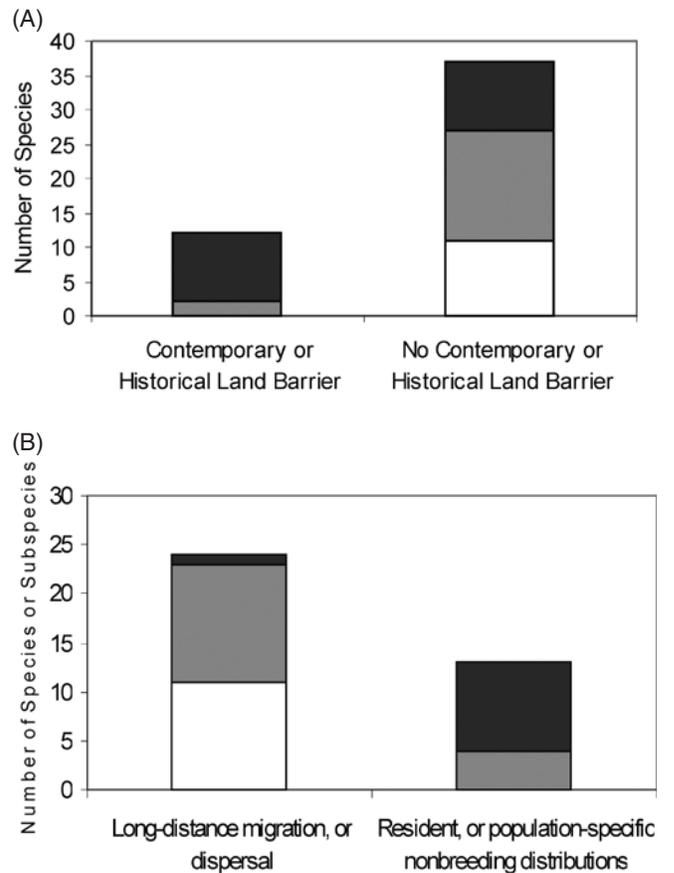


Fig. 3. Number of seabird species with population genetic structure (grey) or phylogeographic structure (population genetic structure that includes population-specific genealogical lineages; black) (A) in the presence or absence of a land or ice barrier within the species' range, and (B) under different non-breeding distributions.

Adaptation

Molecular analyses can complement traditional studies of morphologic and behavioural evolution, providing important insights into adaptation. For example, Red-footed Boobies *S. sula* display several plumage types, varying from almost completely white to completely brown (del Hoyo *et al.* 1992). These morphs vary in frequency between colonies.

Baião *et al.* (2007) analyzed sequence variation in the melanocortin receptor gene among Red-footed Boobies with different plumage types, and found that plumage variation is determined largely by two mutations, which also vary in frequency geographically. These mutations appear to have occurred independently in Snow Geese *Chen caerulescens*, which exhibit similar plumage variation. The fact that Red-footed Boobies exhibit geographic variation in the melanocortin gene but not in mtDNA within the Pacific (Steeves *et al.* 2003) suggests that plumage variation is under natural or sexual selection (Baião *et al.* 2007). Although identification of the mutations underlying variation in behaviour or morphology is difficult, it has largely untapped potential for providing insights into adaptation.

CONTEMPORARY ECOLOGY

Recent analytic methods, especially molecular assignments, can provide insight into contemporary ecology with minimal disturbance to individuals. Molecular assignments involve using an individual's "multilocus genotype" to infer its origin (Fig. 4): A large number of individuals (20 or more each) from a number of sites from throughout the species' range are typed for several loci [typically six or more—e.g. microsatellites, introns or amplified fragment length polymorphisms (Baker 2000)], generating a baseline of the geographic distribution of alleles. An "unknown" individual (e.g. a beached bird) is typed for the same loci, and any of several computer programs (reviewed in Excoffier & Heckel 2006) is used to compare its genotype to the baseline. The program then assigns a probability to the unknown individual's membership in each of the baseline populations. If the genetic structure of the population is strong or if a large number of loci and individuals have been characterized, migrant individuals can be identified within the baseline samples, because

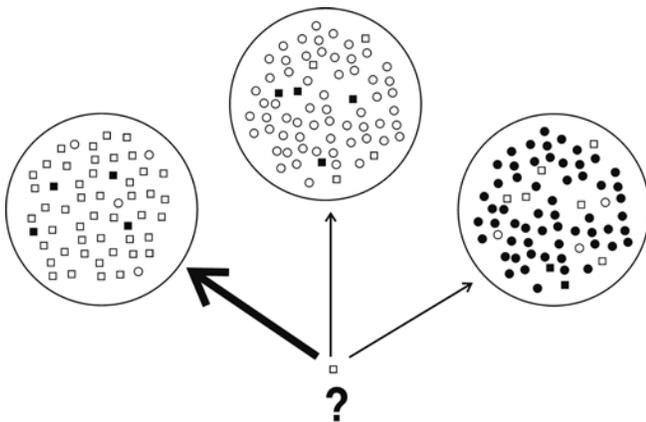


Fig. 4. General principle of molecular assignments. A sample of individuals (small symbols) from different populations (large circles) are typed for allelic variation at several loci [shape (square or circle) and colour (white or black)]. An individual from an unknown population is then assigned a probability of belonging to each population depending on its genotype at the typed loci.

their probability of belonging to the population from which they were sampled is very low (Berry *et al.* 2004).

Three examples of applications of such an analysis follow.

Metapopulation dynamics

A metapopulation is a group of physically discrete populations connected by dispersal (Thrall *et al.* 2000). One type of metapopulation is the source–sink system. Source populations have high productivity and so can export recruits to, and potentially sustain, sink populations (those with low productivity; Dias 1996). From a conservation perspective, protection of source populations may be critical to a species' survival, but protection of sinks may be a waste of resources and may even accelerate a species' extinction (Dias 1996).

Molecular assignments can aid in the identification of metapopulation dynamics, because sink populations will have a high number of immigrants and source populations will have a large number of emigrants. For example, Friesen *et al.* (2005) used molecular assignments to identify three genetic population units (geographic regions between which gene flow is low; Fig. 5) for Marbled Murrelets (*Brachyramphus marmoratus*):

- The central and western Aleutian Islands
- The eastern Aleutian Islands to northern California
- Central California

Assignments suggested that five individuals may be migrants (identified with arrows in Fig. 5), but none of the regions appeared to have an especially high number of either immigrants or emigrants.

Successful use of molecular assignment requires either strong population genetic structure or characterization of a large number of loci and individuals, and so may be expensive. Also, results of assignment tests must be combined with data on productivity to confirm source–sink status.

Population size

Some species are notoriously difficult to census, especially during the non-breeding season. Molecular assignments can aid in overcoming this problem by permitting individuals to be identified using non-invasive "mark and recapture." Although no examples are available currently for seabirds, a recent study of Imperial Eagles (*Aquila heliaca*) provides a useful illustration.

The Naurzum Zapovednik national park in Kazakhstan is an important breeding and non-breeding site for raptors. The number of non-breeding Imperial Eagles that use the park is unknown, but the maximum number during direct counts is 32 (Rudnick *et al.* 2008). Rudnick *et al.* collected moulted feathers from four roost sites on four occasions in July 2004 and screened the feathers for variation in seven microsatellite loci. Analysis of probabilities of identity (the probability that two individuals share the same multilocus genotype) revealed that these feathers represented 287 birds, and capture–recapture analysis of feathers from various collection periods with the program Mark (White & Burnham 1999) indicated that 308 ± 8 non-breeding Imperial Eagles used the site during the study period.

Although this type of analysis does not require as many individuals and loci as most assignment studies do, it requires a source of DNA such as feathers, pellets or faeces.

Hybridization

Hybridization can have both positive and negative effects on the hybridizing species. It can provide an infusion of new genetic variation into a species, and so increase both individual and population fitness. However, it can also reduce the fitness of individuals and populations, and it can even promote extinction (reviewed in Avise 2004). Studies of hybrids also can provide useful insights into such aspects of ecology and evolution as mate choice and mechanisms of reproductive isolation.

Molecular assignments permit identification of hybrid individuals and their descendants, including those that are morphologically indistinguishable from one of the parental species, because such individuals have a low probability of assignment to the species that they resemble.

A study of hybridization between Herring (*L. argentatus*) and Caspian Gulls (*L. cachinnans*) by Gay *et al.* (2007) provides a useful illustration. Those authors compared variation in neutral molecular markers (microsatellites and mtDNA) and several phenotypic traits across a secondary contact zone in Europe. Neutral markers appeared to be transmitted between the species, but introgression of some phenotypic traits was low, suggesting that those traits, especially orbital ring colour, act as a pre-mating barrier to hybridization but that the barrier is incomplete.

The foregoing study underlines the power of combining molecular and phenotypic data. Such studies also require fewer samples and loci than other types of molecular assignments, because individuals are more easily assigned to species than to populations. However, the more ancient the hybridization event, the more loci are required for detection.

CONSERVATION

Molecular markers can aid conservation both by improving the general understanding of ecology and evolution (as in the examples mentioned earlier), and by providing tools to aid specific problems.

Prioritizing populations for conservation

If local populations differ genetically, then loss of a population may result in loss of some of the species' genetic variation, including local adaptations (e.g. timing of breeding), cryptic species (species that are difficult for humans to differentiate), and the species' ability to adapt, evolve and speciate. In addition, because the degree of genetic divergence between populations is inversely related to the amount of gene flow (Wright 1931), populations that differ genetically may not recolonize naturally following a local decline or extirpation. Evolutionarily significant units (ESUs) are populations that do not exchange genes and so are evolutionarily (and demographically) independent (Moritz 1994). They form important units for conservation and accordingly are recognized by many conservation policies (e.g. the U.S. Endangered Species Act). They equate with "species" by many definitions and may be cryptic, but they can be identified by population-specific alleles or groups of alleles (e.g. Moritz 1994).

For example, no mtDNA haplotypes are shared between Band-rumped Storm-Petrels from the Galapagos and from Japan, and haplotypes from those two regions form separate branches on the mtDNA tree (Smith *et al.* 2007). These haplotypes also significantly differ in their nuclear DNA (Friesen *et al.* 2007b), and so constitute separate ESUs.

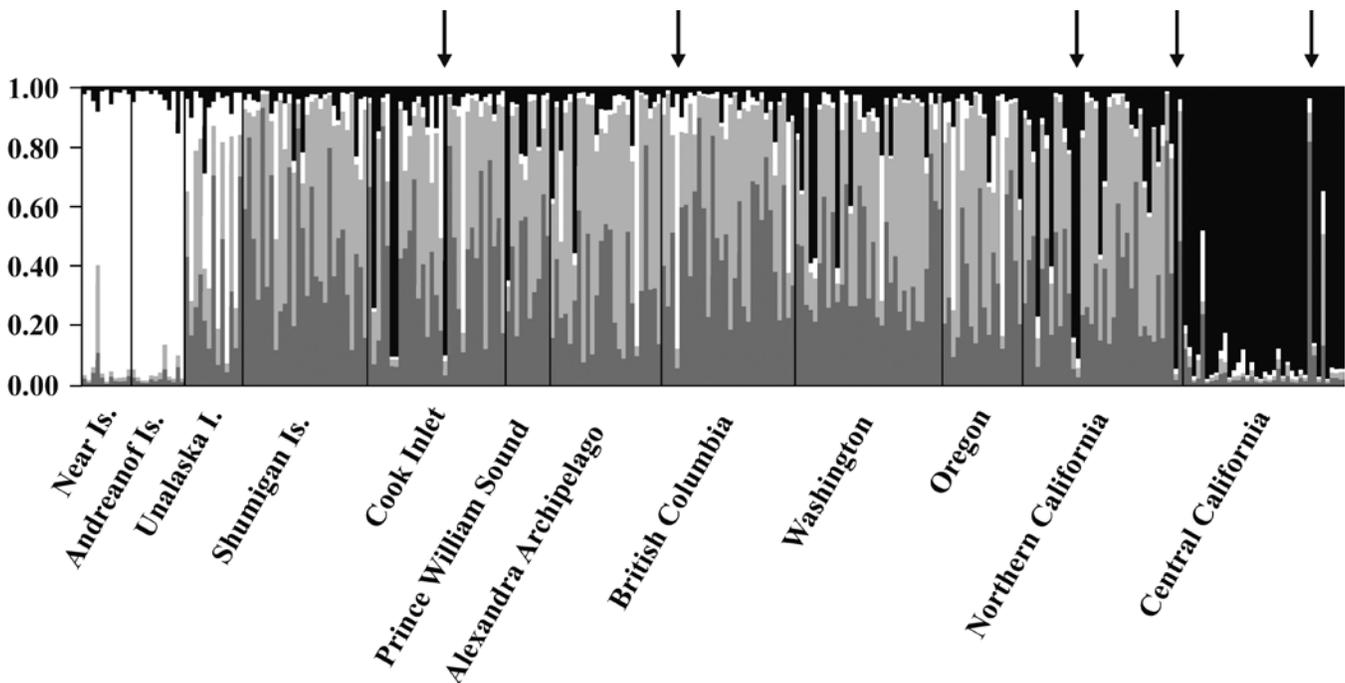


Fig. 5. Probability of assignment of individual Marbled Murrelets *Brachyramphus marmoratus* (vertical bars) to each of four genetic populations (represented by varying shades). Arrows indicate individuals with a high probability of belonging to a genetic population not otherwise found in their sampling site. Labels on the x axis are sampling sites (from Friesen *et al.* 2005).

Genetic management units (MUs) have low levels of genetic exchange, and so are not genetically independent; they are, however, demographically independent (Moritz 1994). They differ in allele frequencies and generally equate with “stocks” (e.g. salmon stocks).

The three genetic populations of Marbled Murrelets described earlier constitute genetic MUs: Gene flow among them is low such that allele frequencies and potentially also demographic parameters differ between them, but they lack defining alleles (Friesen *et al.* 2005).

The extent of population genetic structure and thus the importance of managing local populations independently varies widely across

seabird species that have been studied to date (Table 1). At one extreme, the Wandering Albatross *Diomedea exulans* (Burg & Croxall 2004) and Least Auklet *Aethia pusilla* (Walsh *et al.* 2005) appear to be genetically homogeneous throughout their range, but species such as the Black-browed Albatross *T. melanophris* (Burg & Croxall 2001) and Band-rumped Storm-Petrel (Smith *et al.* 2007) each appear to constitute multiple ESUs.

Meta-analyses of published studies of mtDNA variation in seabirds suggest that the extent of population genetic structure can be predicted from a species’ breeding and non-breeding distributions (see “Population differentiation,” earlier). As genetic studies

TABLE 1
Extent of population genetic and phylogeographic structure^a in mitochondrial DNA in various species of seabirds^b

No population genetic structure		Population genetic structure but no phylogeographic structure		Population genetic and phylogeographic structure	
Wandering Albatross <i>Diomedea exulans</i>	Antipodean Albatross <i>D. antipodensis</i>	Adélie Penguin <i>Pygoscelis adeliae</i>	Yellow-legged Gull <i>Larus michahellis</i>	Black-browed Albatross <i>D. melanophris</i>	Cory’s Shearwater <i>Calonectris diomedea</i>
Shy Albatross <i>Thalassarche cauta</i>	White-capped Albatross <i>T. steadi</i>	Red-legged Kittiwake <i>Rissa brevirostris</i>	Razorbill <i>Alca torda</i>	Yelkouan Shearwater <i>Puffinus yelkouan</i>	European Storm-Petrel <i>Hydrobates pelagicus</i>
Grey-headed Albatross <i>T. chrysostoma</i>	Crested Auklet <i>Aethia cristatella</i>	Pigeon Guillemot <i>Cephus columba</i>	Marbled Murrelet <i>Brachyramphus marmoratus</i>	Band-rumped Storm-Petrel <i>Oceanodroma castro</i>	Leach’s Storm-Petrel <i>O. leucorhoa</i>
Least Auklet <i>Aethia pusilla</i>		Black-footed Albatross <i>Phoebastria nigripes</i>	Galapagos Petrel <i>Pterodroma phaeopygia</i>	Masked Booby <i>Sula dactylatra</i>	Red-footed Booby <i>Sula sula</i>
		Sooty Shearwater <i>Puffinus griseus</i>		Brown Booby <i>Sula leucogaster</i>	Glaucous Gull <i>L. hyperboreus</i>
				Lesser Black-backed Gull <i>L. fuscus</i>	Black-legged Kittiwake <i>R. tridactyla</i>
				Sooty Tern <i>Sterna fuscata</i>	Common Murre <i>Uria aalge</i>
				Thick-billed Murre <i>Uria lomvia</i>	Black Guillemot <i>Cephus grylle</i>
				Kittlitz’s Murrelet <i>Brachyramphus brevirostris</i>	Xantus’s Murrelet <i>Brachyramphus hypoleucus</i>

^a Population genetic structure that includes population-specific genealogic lineages.

^b From Friesen *et al.* 2007a.

TABLE 2
Assignment level and success for several species of seabirds studied using various molecular markers

Species	Anthropogenic mortality	Molecular marker	Assignment level	Assignment success (%)	Source
Marbled Murrelet <i>Brachyramphus marmoratus</i>	Oil, bycatch	Introns	Geographic region	75	Edwards <i>et al.</i> 2000
Cory’s Shearwater <i>Calonectris diomedea</i>	Bycatch	mtDNA	Subspecies	63	Gomez-Diaz <i>et al.</i> 2007
		Microsatellites	Subspecies	26	Gomez-Diaz <i>et al.</i> 2007
Common Murre <i>Uria aalge</i>	Oil	Microsatellites	Colony	6	Riffaut <i>et al.</i> 2005

accumulate, it should become possible to predict the existence and location of ESUs and MUs within species that have not been studied, reducing the time and expense required for molecular analyses for species in crisis situations.

Prioritizing regions

The existence of biodiversity “hotspots” is widely recognized; these geographic areas hold unusually large numbers of taxa. Several hotspots have been described for seabirds, especially various archipelagos in the Southern Ocean (reviewed in Gaston 2004). Molecular genetics can aid in the identification of biodiversity hotspots by revealing areas with ESUs in multiple species.

For example, in their review of geographic studies of mtDNA variation in seabirds, Friesen *et al.* (2007a) found endemic ESUs in several diversity hotspots, including the Mediterranean (endemic ESUs of European Storm-Petrel *Hydrobates pelagicus*, Cory’s Shearwater *C. diomedea* and Yellow-legged Gull *L. michahellis*, plus two endemic species), Guadalupe Island (Baja California; endemic ESUs of Leach’s Storm-Petrel and Xantus’s Murrelet *Synthliboramphus hypoleucus*, plus one essentially endemic species), the Galapagos (an endemic ESU of Band-rumped Storm-Petrel, plus four endemic species) and Cape Verde (mid-Atlantic Ocean; an endemic ESU of Band-rumped Storm-Petrel, plus one endemic species). Such areas should be given high conservation priority. In addition, the genetic uniqueness of populations of other species of seabirds in these areas should be checked.

Impact assessment

Anthropogenic mortality, such as fishery bycatch and hunting, often occurs during the non-breeding season. Molecular assignments can help to determine the effects of such mortality on breeding colonies. For example, Marbled Murrelets suffer mortality from oil pollution and fisheries bycatch. In test runs, Edwards *et al.* (2001) were able, with 75% success, to assign Marbled Murrelets to one of 11 regions on the basis of variation in nine nuclear introns. Few such studies have been conducted with seabirds, and success is variable (Table 2). However, combining data from molecular markers with data from other sources, such as stable isotopes, trace metals or morphometrics, may improve assignment success (Gómez-Díaz & González-Solís 2007).

CONCLUSIONS

In this review, I have provided nine examples of how molecular markers can provide insights into seabird evolution, ecology and conservation. Some of these methods have shortcomings, but as analysis of molecular markers becomes cheaper and faster, and as methods of data interpretation become more sophisticated, the scope, versatility and accuracy of these tools will certainly increase.

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