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Population genetic investigations of marine mammals date back several decades. The earliest studies examined patterns of phenotypic variation in blood proteins and enzymes to estimate the level of gene flow among spatially discrete groupings of animals (e.g., Shaughnessy 1969; McClanaghan and O'Shea 1988; Gales et al. 1989; Danielsdóttir et al. 1992), to assess the genetic consequences of population bottlenecks and founder events (Bonnell and Selander 1974), and to test theories about the relationship between life history strategies and genetic diversity (Allendorf et al. 1979). These studies launched a new field of inquiry into the evolution, ecology, and behavior of marine mammals that quickly developed from surveys of phenotypic variation in gene products to assessments of variation within the genetic material, the DNA, itself. Over the next 30 years, genetic investigation of marine mammal populations was revolutionized by the advent of cloning technology and the development of the Polymerase Chain Reaction, by remote biopsy methods of sample collection and more efficient methods of sample preservation, and by the development of new approaches to analyzing and interpreting molecular genetic data.

This chapter reviews population genetic studies on marine mammals, with particular emphasis on the molecular genetic analysis of selectively neutral markers. The chapter begins with a brief history of population genetics as a scientific discipline, and a summary of the evolutionary forces that determine patterns of variation within genetic loci. The following sections review population genetic investigation in marine mammals, and center on four main subjects: (1) genetic relatedness among individuals, (2) gene flow and dispersal on contemporary timescales (3) patterns of genetic diversity within populations over time, and (4) gene flow and dispersal over evolutionary timescales. I conclude with a brief summary of current limitations and future research.
challenges. Space limitations prevented a review of a number of aspects of marine mammal population genetic studies, including a summary of genetic markers and molecular methods, and an assessment of the role of population genetic study in marine mammal conservation and management. Fortunately, these subjects have recently been dealt with at length elsewhere and the reader is directed to the following volumes and relevant chapters therein (Dizon et al. 1997; Hoelzel 2002; Perrin et al. 2002).

15.1.1 Population Genetics: Principles and Definitions

Population genetics is a long established field that traces its origins to Darwin's (1859) theory of evolution by natural selection, and Mendel's (1866) elegant breeding experiments on the garden pea that demonstrated the predictable patterns of inheritance of dominant and recessive traits, and to the modern evolutionary synthesis and mathematical models of Wright, Haldane, Fisher and others in the early 20th century that bridged these two traditions. Population genetics is the study of inheritance and the patterns of genetic variation within and between populations, and of the evolutionary forces that determine these patterns: mutation, genetic drift, gene flow, and selection (Wright 1931; Nei 1987; Maynard Smith 1989; Hartl and Clark 1990). A thorough understanding of how these forces interact to shape patterns of genetic variation provides insight into the mechanisms of evolution, and enables inference on the demographic histories of natural populations and the behavior of individuals within and among these populations over time. Thus, before I proceed to an assessment of marine mammal population genetic investigation, I feel it is important to review them briefly here. Box 1 provides a simple schematic representation of how these forces might shape genetic patterns within and between two populations.

**Box 1** Heredity and the evolutionary forces that shape genetic differentiation within and among populations.

The schematic representation in Fig. 15.1 demonstrates heredity and three major influences on variation in a genetic marker within two populations over time: mutation, genetic drift, and natural selection. For clarity, gene flow, perhaps the easiest to conceptualize, is not included. A haploid marker (e.g., mtDNA) is used for simplicity and both populations pass through six phases in their history prior to being studied.

Phase 1, the point of population divergence, the pattern of genetic variation is similar for both populations. Here, both possess the same variant or haplotype, Hap A, a probable scenario if the ancestral population or the founding group was small.

In Phases 2 and 3 both populations experience a period of growth, as, for example, in species (re)colonizing new habitat following an ice age, and the genetic variant is passed from one generation to the next through reproduction. In Population 1, a mutation occurs in one individual, giving rise to a new haplotype, Hap B. Likewise, a mutation also occurs in an individual in Population 2, resulting in a second unique haplotype, Hap C. Through variation in reproductive success and survival among individuals within populations both new haplotypes become established by chance in their populations of origin.

![Fig. 15.1 Heredity and the mechanisms of population populations. Circles denote individuals; reproductive success is denoted by a number lost due to a population bottleneck or mutation.](image)

By Phase 4, the genetic composition of the two populations is substantially different, with Hap B greatly reduced in frequency and Hap C having increased. Additionally, some selective advantage to those individuals carrying Hap D may reflect a deleterious mutation in a second population. In Phase 6, Population 1 has reached a new equilibrium and homogenizing effects of drift and gene flow are once again present. The most common haplotype pre-bottleneck is Hap E, but the advantage on its hosts that increased the frequency of Hap D, and it is easy to see what would happen if this mutation were to occur early on in the history of the two populations, given the little discernible effect. If it occurred later, the deleterious mutation would be slowed, to what extent is difficult to determine.

It is at this point that we have decided to incorporate the two populations into one, and the question of whether they differ in population size, they show that the genetic diversity is higher in Population 1 than in Population 2. To establish the contemporary relationships among their respective histories from these data.
a number of aspects of taking a summary of genetic influences of the role of population genetic management. Fortunately, elsewhere and the reader others therein (Dizon et al.

Definitions

It traces its origins to beginning, and Mendel’s (1866) work demonstrated the dominance of recessive traits, and to the principles of Wright, Haldane, and Fisher who developed these two traditions. Many of the patterns of genetic variation and the evolutionary forces that influence them have been discussed elsewhere (e.g., Clark 1990). A central fact is that the patterns of evolution, and especially the patterns of evolution, and especially the evolution of populations and the evolutionary processes over time. Thus, the analysis of population genetic differentiation within and among populations is of interest here. Box 1 provides an overview of how differentiation might shape genetic diversity.

Fig. 15.1 Heredity and the mechanisms that influence genetic variation within populations. Circles denote individuals, letters denote unique haplotypes, and reproductive success is denoted by arrows from parents to offspring. Individuals lost due to a population bottleneck are indicated by dotted circles. Original.

By Phase 4, the genetic composition of Populations 1 and 2 differ from their ancestral state and from each other substantially, due to the combined effects of genetic drift and mutation. As time goes by, these two isolated populations continue to diverge. Phase 5, Hap C becomes the dominant haplotype in Population 2 and gives rise to a new variant, Hap D. However, this haplotype drifts to extinction by chance. The emergence of Hap C in Population 2 may simply be the cumulative result of random lineage sorting over many generations. Alternatively, if we view our schematic as a model for a locus under some selective pressure, the relatively rapid rise of Hap C may indicate that this variant confers some selective advantage to those individuals who possess it. Similarly, the rapid loss of Hap D may reflect a deleterious mutation that compromised the fitness of its host.

In Phase 6, Population 1 has reached equilibrium between the diversifying process of mutation and the homogenizing effects of drift. By contrast, Population 2 has just witnessed a severe population bottleneck that resulted in the loss of much genetic variation. By chance, the most common haplotype pre-bottleneck, Hap C, is the only one that survived. Under our alternative model of a marker under selection, Hap C may have conferred a selective advantage on its hosts that increased their probability of surviving the bottleneck.

It is easy to see what would happen if gene flow was included in this scheme. If it occurred early on in the history of the two populations, say during Phase 2, it may have little discernible effect. If it occurred later, the rate of genetic divergence through drift and mutation would be slowed, to what extent depends on the level of genetic exchange.

It is at this point that we have decided to study these two populations, and observe that they differ in population size, they share no haplotypes in common and the diversity is higher in Population 1 than in Population 2. The challenge for the population geneticist is to establish the contemporary relationship among these populations and to reconstruct their respective histories from these data.
Mutation is the process by which new variation is produced. It occurs predominantly through errors in the replication of the genome during meiosis. Rates of mutation differ among regions of the genome and are influenced by the primary sequence of the genetic code itself, generation time, and by intrinsic and extrinsic mutagens. The establishment of a new mutant allele within a population depends in large part on the reproductive success of the carrier relative to others within the population (genetic drift), the breeding and dispersal behavior of the carrier (gene flow) and whether the site is under selection or not. Mutations are usually rare events that typically give rise to a new variant or allele. An understanding of the mode and rate of mutation at a particular genetic marker facilitates the reconstruction of phylogenetic relationships among alleles and the timing of lineage divergences, thus providing unique insights into the evolutionary history of taxa (see below).

Gene flow is the exchange of variants among groups of organisms via dispersal and interbreeding, such that close relatives share more alleles by descent than unrelated animals, and populations experiencing high levels of gene flow have fewer differences in genetic composition than do isolated populations. Genetic exchange is the primary force limiting differentiation among populations (Slatkin 1987) and its influence on the genetic landscape depends on who successfully disperses, when and how. Sex-biased versus non-biased dispersal, the emigration of close kin versus random dispersal, periodic versus continuous dispersal, all leave distinctive signatures in patterns of variation at genetic markers. Understanding gene flow can thus provide insight into mating systems, dispersal, social structure and population subdivision.

Genetic drift is the loss of variation over time due primarily to differences in survival and reproductive success among individuals within a population. In the absence of the introduction of new variants via gene flow or mutation, discrete populations will ultimately drift to fixation for alternative alleles such that among-population heterogeneity is maximized and within-population heterozygosity is minimized. The rate of drift is determined by the effective population size, \( N_e \), and the generation time (Frankham 1995). In a random mating population with equal sex ratio, where all mature individuals have an equal likelihood of breeding successfully, \( N_e = N \), the number of mature individuals. In species with kin-based social groupings and in species with highly skewed reproductive success, as for example in polygynous species, \( N_e \) can be much smaller than \( N \) and genetic drift can be a potent force in shaping patterns of genetic variation. Changes in \( N_e \) over time have lasting effects on the pattern of genetic diversity within populations. Substantial reductions in abundance and population bottlenecks can result in severe losses of genetic diversity through drift (Nei et al. 1975; O’Brien et al. 1987), with potentially dramatic consequences for population viability. Because of the slow rate of mutation, these effects can be detectable long after the event. Thus, levels of genetic diversity can reveal much about mating systems and the evolutionary history of populations.

The final factor influencing population demography is the underpinning of a deterministic relationship between the strength and extent of selective pressure is often changing environmental conditions and the response of populations to such changes. Natural selection is the underlying mechanism that drives the evolution of species, and its effects on population genetic structure are often preferred in the context of managing and conserving wildlife. Population genetic structure through drift limits the variation that can be used to inform conservation and management strategies.

15.2 POPULATION GENETIC STUDIES

Direct assessment of the mechanisms underlying population genetic structure in long-lived, relatively inaccessible species is limited. Some studies have assessed patterns of genetic diversity in wild populations of marine mammals (e.g., Tursiops truncatus, Tursiops aduncus, 1998; Hoelzel et al. 1999a), the interplay of natural selection acting on a genetic locus and population demography of these species, as well as on neutral genetic markers, such as microsatellites, and life histories, as well as a set of demographic parameters. These studies show that genetic diversity can be maintained at levels that are comparable to those observed in captive populations. Conversely, the past few decades have seen an increase in the collection of samples from wild populations, and these data provide insights into the genetic structure of wild populations. Genetic diversity in wild populations can be used to inform conservation and management strategies.

15.2.1 Population Subdivision

Two of the most fundamental questions in the study of population genetic structure are whether populations are discrete units or if they are part of a larger genetic network. The term "population" as used in population genetics refers to a group of individuals that are reproductively isolated from other groups and are subject to genetic drift and selection. The concept of genetic subdivision is important in understanding the distribution of genetic diversity within and among populations. Subdivision occurs when populations are isolated from each other and do not exchange genetic material. Subdivision can occur due to geographic barriers, habitat heterogeneity, or other factors. The study of population subdivision is important in understanding the evolutionary history of species and in developing conservation strategies.
The final factor influencing patterns of genetic variation is selection. Natural selection is the underpinning of Darwin’s theory on evolution and is a deterministic relationship between how freely a genetic locus is allowed to vary and how essential its function is to an individual’s fitness. The direction and extent of selective pressure is often difficult to quantify, and may change with changing environmental conditions, such that loci under weak or no selection are often preferred in population genetic studies of behavior, demography and population history. The rapid loss of diversity at genetic loci through drift limits the variation upon which selection can act, and thus may compromise the evolutionary potential of a population.

15.2 POPULATION GENETIC STUDIES OF MARINE MAMMALS

Direct assessment of the mechanisms of evolution is particularly challenging in long-lived, relatively inaccessible species such as marine mammals. While some studies have assessed patterns of variation in markers under selection in wild populations of marine mammals (e.g., Slade 1992; Murray and White 1998; Hoelzel et al. 1999a), the investigation of the direction and extent of selection acting on a genetic locus or suite of loci requires detailed pedigrees and life histories, as well as a sound understanding of the link between phenotype and genotype, a tall order as yet for most marine mammal species. Conversely, the past few decades have seen a dramatic increase in the collection of samples from several species that have facilitated surveys of variation within selectively neutral markers that reflect the accumulated effects of mutation, genetic drift and gene flow across time. These investigations span the gamut of population genetic study and have provided unique perspectives on the evolution, ecology and behavior of marine mammal populations. The following two sections elaborate on four areas of enquiry.

15.2.1 Population Subdivision and Gene Flow in Marine Mammals

Two of the most fundamental questions in population biology are: what defines a population or smaller grouping of individuals, and how do these groupings relate to one another (Mayr 1970)? The key to answering these questions is an understanding of the level and form of dispersal and interbreeding within and between them (Shields 1987). While population dynamics models are typically developed for closed populations (Turchin 2003) more realistic models must take dispersal, termed migration in genetic parlance, into account. Further, management and conservation are often concerned with resolving the demographic and reproductive connectedness among groups of organisms. Something so fundamental as dispersal, however, is difficult to estimate directly in natural populations, especially in marine mammals. This is where population genetic analysis comes in.
The theoretical relationships between the forces shaping patterns of genetic diversity within and between populations were established by Wright (1931, 1943, 1951), Kimura and Weiss (1964) and others (see Box 2), and subsequently confirmed through captive breeding and simulation studies (e.g., Slatkin and Barton 1989). This enabled the indirect estimation of various population parameters, including the rate of dispersal (m) and the number of dispersers per generation \( N_m \) among populations, from genetic data. Alternatively, a statistical approach can be used to assess dispersal and genetic exchange. For example, allele frequencies can be used to test a specific hypothesis, e.g., random mating (diploid markers) or mixing (haploid markers) among groups of animals, where the resultant estimate of statistical significance of the measure of genetic differentiation (e.g., \( F_{st} \), \( X^2 \)) tells you something about the degree of population subdivision. A third approach to resolving patterns of dispersal and gene flow is to assign individuals to populations of origin based on the likelihood of their genotype or haplotype occurring in each sampled population, high levels of 'misassignment' indicating extensive mixing (e.g., Paetkau et al. 1995).

### 15.2.1.1 Kinship, mating systems and social organization

To fully understand dispersal and gene flow among natural populations, and to calculate meaningful estimates of \( N_e \) within populations, knowledge of mating systems and social organization within populations is required (Shields 1987; Frankham 1995; Storz 1999). For example, mating systems where reproductive success can vary widely among individuals will reduce \( N_e \), while kin-based societies can also affect \( N_e \) as well as violate random mating expectations assumed in most genetic methods of dispersal estimation. Such information, however, is difficult to obtain through direct observation in most marine mammals, particularly cetaceans and aquatic mating pinnipeds (Amos et al. 1993; Coltman et al. 1998). Fortunately, genetic markers can be used to resolve pedigree relationships thereby providing detailed information on parentage and kinship which, in turn, can be used in studies of mating systems, social structure, sexual selection and kin selection. By using several diploid markers which are polymorphic enough such that closely related individuals have a high likelihood of possessing different alleles, pedigree relationships can be estimated based on the allelic frequencies at these loci within the population (Queller et al. 1993; Goodnight and Queller 1999).

Genetic profiling revealed that Globicephala melas (Long finned pilot whales) form stable, kin-based social groups or pods, where both females and males remain within their natal pod but mate with unrelated whales from other pods, most likely when different pods temporarily consort with each other (Amos et al. 1993). A similar genetic analysis of cow-calf pairs revealed a promiscuous mating system in female Megaptera novaeangliae (Humpback whales), which is consistent with field observations of females associating with several males (Clapham and Palsbøll 1997).

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**Box 2 Population structure and gene flow**

Observed differences in allele frequencies and gene flow between natural populations in equilibria where differences in the frequency of a marker (e.g., mtDNA control region, sex) and genetic drift.

**Fig. 15.2** Gene flow and genetic diversity

Wright's island model of population structure

(Wright's model of population structure) to indirectly estimate gene flow in a given model of gene flow (E) ranges from 0, where mixing population, to 1, when the two loci consist for alternate alleles.

Here, Wright's model is modified slightly.

In pinnipeds, genetic analyses and studies of mating behavior and association, the highly polygynous Mirounga angustirostris, fingerprinting and microsatellite analysis observed mating success and actual mating (Hoelzel et al. 1999b). In the case of the California sea lion, microsatellite analysis revealed a high level of breeding-colony kin selection in the evolution of fossa (1999). In Halichoerus grypus (Gray seal)
Box 2 Population structure and gene flow.

Observed differences in allele frequencies can be used to estimate average levels of gene flow between natural populations. Figure 15.2 represents two populations at equilibrium where differences in the frequencies of alleles at a selectively neutral haploid marker (e.g., mtDNA control region, see Box 1) reflect the relative strengths of gene flow and genetic drift.

![Population diagrams](image)

Wright's island model of population structure uses the extent of genetic differentiation ($F_{st}$) to indirectly estimate gene flow in terms of the average number of dispersers per generation ($N_e m$). $F_{st}$ ranges from 0, when the two locations are part of a single random mixing population, to 1, when the two locations represent two populations that are fixed for alternate alleles.

Here, Wright's model is modified slightly for a haploid marker.

Fig. 15.2 Gene flow and genetic drift among populations in equilibrium. Circles denote individuals, letters denote unique haplotypes. Original.

In pinnipeds, genetic analyses are complementing more traditional field studies of mating behavior and association patterns on breeding colonies. In the highly polygynous Mirounga angustirostris (Northern elephant seal), DNA fingerprinting and microsatellite analysis found discrepancies between observed mating success and actual reproductive success in some dominant males (Hoelzel et al. 1999b). In the aquatically mating Phoca vitulina (harbor seal), microsatellite analysis revealed low variance in male reproductive success (Coltman et al. 1998) while a multilocus DNA fingerprinting study found high levels of breeding-colony site fidelity in females but no evidence of kin selection in the evolution of fostering behavior by females (Schaefer et al. 1999). In Halichoerus grypus (Gray seal), molecular genetic studies documented...
polygyny and inter-year mate fidelity simultaneously occurring within the same breeding colony (Amos et al. 1995). A subsequent study, confirmed that male-reproductive success is highly skewed but also found that, a high proportion of pups were not fathered by known males, suggesting that aquatic mating involving males that seldom haul out on shore occurs more frequently than previously thought (Worthington Wilmer et al. 1999).

Conclusion. These types of studies of relatedness and parentage are revealing that random mating is probably atypical in marine mammals, that \( N_e \) is less than the census population size, that there is a strong tendency to remain in your group of birth or return to your site of birth, and that marine mammals employ a variety of strategies to maximize reproductive success and avoid consanguineous matings.

15.2.1.2 Gene flow and dispersal on contemporary timescales

The vast majority of population genetic studies on marine mammals to date have been concerned with elucidating patterns of population subdivision, dispersal and gene flow. In this section genetic exchange on ecological time scales are discussed. Differentiation on evolutionary timescales is dealt with in Section 15.2.2.2 (see below).

The first studies of population genetic structure in cetaceans screened for variation at enzyme loci and detected restricted gene flow across ocean basins in several baleen whales (e.g., Danielsdóttir et al. 1991, 1992; Wada and Numachi 1991) as well as subdivision on smaller spatial scales in smaller species (Anderson 1993). Though informative, many of these electrophoretic studies were limited by sample size and distribution, and by the redundancy of the genetic code.

Subsequent studies of mtDNA variation demonstrated population subdivision in several whale, dolphin and porpoise species (e.g., Pastene et al. 1993; Secchi et al. 1998; Escorza-Treviño and Dizon 2000; Yoshida et al. 2001), and found strong female-directed philopatry to geographically discrete feeding and breeding areas in a number of highly migratory species including *Delphinapterus leucas* (beluga whale), *M. novaeangliae* and *Eubalaena glacialis* (right whale) (Baker et al. 1993; Schaef et al. 1993; Palsbøll et al. 1995; Brown-Gladden et al. 1997; O'Corry-Crowe et al. 1997, 2002; Baker and Medrano-González 2002). This tendency to return to the same locations generation after generation is presumably mediated by the cultural transmission of migration destinations from mother to offspring facilitated by the relatively long period of maternal care in these species, and is likely driven by the predictable availability of seasonal resources with the result that these groupings eventually become demographically discrete populations.

Recent investigations have returned to examining bi-parentally inherited markers, this time screening for variation within the DNA itself as opposed to within gene products. Significant heterogeneity in nuclear DNA variation, indicating restricted gene flow, has been documented at global, regional and local scales in several cetacean species (e.g., van Pijlen et al. 1995; Andersen et al. 1997; Chivers et al. 2002; 2003) different levels of differentiation within populations that differ, than levels recorded within mtDNA (deMarsh and Postma 2003). Differing patterns suggest more may occur on common breeding grounds characteristic of many mammals (Hoelzer 1991). Mixing on common genetic mark-recapture studies (1997). Caution, however, is needed since differentiation in other species may also be the result of limited gene flow and the larger effective populations sizes.

Population differentiation has been found in pinnipeds. Heterogeneity in markers in *P. vitulina*, indicating regional populations as well as sex differences (e.g., Macdonald et al. 1996; Goodman 1998; Benvenuto and Born 2000). Genetic studies have also been done in *Eumetopias jubatus* (Steller seal) (Gales et al. 1997), and have shown behavioral philopatry are stronger in *Odobenus rosmarus* (Walrus) (Chivers and Born 2000). Conversely, the number of ice breeding seals, *O. corrie Westlake 1997; Miura et al. 1998; findings), *Phoca hispida* (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), *Phoca hispida* (Ringed seal), *Pagophilus groenlandicus* (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger seal) (findings), Phoca hispida (Ringed seal), Pagophilus groenlandicus (Harbinger se
et al. 1997; Chivers et al. 2002; LeDuc et al. 2005). A number of studies found levels of differentiation within microsatellite markers that were much lower than levels recorded within mtDNA (Larsen et al. 1996; Brown-Gladden et al. 1999; deMarsh and Postma 2003; G. O’Corry-Crowe, unpublished data). These differing patterns suggest more extensive male-mediated gene flow, which may occur on common breeding areas or via male-biased dispersal, a characteristic of many mammalian species (Greenwood 1980; Melnick and Hoelzer 1992). Mixing on common breeding grounds has been confirmed by genetic mark-recapture studies in the case of *M. novaengliae* (Falsbøll et al. 1997). Caution, however, is required when interpreting these differing levels of differentiation in other species as lower heterogeneity in nuclear markers may also be the result of limited divergence through genetic drift because of the larger effective population size (*N*<sub>e</sub>) of nuclear compared to haploid markers.

Population differentiation has also been documented at a number of spatial scales in pinnipeds. Heterogeneity has been found in nuclear and mtDNA markers in *P. vitulina*, indicating limited dispersal and interbreeding among regional populations as well as among subspecies (Lamont et al. 1996; Stanley et al. 1996; Goodman 1998; Burg et al. 1999; Westlake and O’Corry-Crowe 2002). Genetic studies have also revealed substantial population subdivision in *Eumetopias jubatus* (Steller sea lions) (Bickham et al. 1996; Hoffman et al. 2006; O’Corry-Crowe et al. 2006) and *Mirounga leonina* (Southern elephant seal) (Gales et al. 1989), and have determined that dense polar pack ice and behavioral philopatry are strong forces promoting population subdivision in *Odobenus rosmarus* (Walrus) (Cronin et al. 1994; Andersen et al. 1998; Andersen and Born 2000). Conversely, limited subdivision has been detected in a number of ice breeding seals, including *Phoca largha* (Spotted seal) (O’Corry-Crowe and Westlake 1997; Mizuno et al. 2003; G. O’Corry-Crowe, unpublished findings), *Phoca hispida* (Ringed seal) (Davis 2004; Palo et al. 2001) and *Pagophilus groenlandicus* (Harp seal) (Perry et al. 2000). Gene flow among geographically discrete breeding concentrations in these species is likely facilitated by the seasonal movements of sea-ice. The ability to haul out on a mobile substrate can result in passive movements over long distances.

Subdivision has also been documented in *Trichechus manatus* (Manatee) (McClenaghan and O’Shea 1988; Garcia-Rodriguez et al. 1998), *Enhydra lutris* (Sea otter) (Cronin et al. 1996) and *Ursus maritimus* (Polar bear) (Patkeau et al. 1995, 1999). Despite the extensive movements individual polar bears make across sea ice (Mauritzen et al. 2002), microsatellite analysis revealed restricted gene flow among several local populations of this species, particularly in the Canadian high Arctic archipelago, where the insular geography may restrict dispersal (Paetkau et al. 1995, 1999).

**Conclusion.** Genetic studies are revealing that dispersal, breeding behavior and population subdivision in marine mammals are influenced by a variety of factors, including the physical environment, life history and behavior. Global-
scale patterns tend to be shaped by the juxtaposition of continental land masses and the world’s oceans, by physical oceanography, including sea ice, water temperature and ocean currents, and by biological oceanography and prey distribution. Life history sets the requirements for survival which results in non-uniform distributions and population structure in heterogeneous environments. The need to haul out on remote islands close to a patchy food source, for example, greatly restricts the distribution of breeding colonies of several pinnipeds. It is the influence of individual behavior, however, that has been the most difficult to elucidate by traditional methods and where genetics is providing the greatest insight. Despite their capacity for long-distance movements, and the paucity of obvious physical barriers to movement within ocean basins, genetic studies are revealing high levels of population subdivision in many species of marine mammal. This often reflects behavioral philopatry to natal site or home range and limited interbreeding among geographically distinct groups.

Genetic investigations are thus not only documenting patterns of population subdivision in marine mammals but are also providing unique perspectives on the factors that shape this subdivision. For these reasons, population genetics has found wide application in the identification of units of management and conservation in marine mammals, and provides insights into population biology that inform managers on how best to attain their management goals.

15.2.2 Reconstructing the Past

Up to now, population genetic studies of marine mammals have typically involved sampling individuals at a number of locations at a single point in time. The observed patterns of genetic variation, however, reflect the recorded history of populations. As in human oral histories, new events are occurring all the time (mutation), some episodes have been lost (drift) but much is still there to be retold (inheritance). Through the predictable process of inheritance, and the somewhat predictable processes of mutation and drift, events in the history of populations, such as bottlenecks and divergences, colonizations and range expansions, can leave distinctive signatures in the patterns of variation within genetic markers that can be detected long afterwards. Thus, the analysis of variation within genetic markers enable us to reconstruct the evolutionary and demographic history of groups of organisms including the reconstruction of phylogenetic relationships (e.g., Swoford et al. 1996) and estimation of historical population dynamics (Nei 1987; Drummond et al. 2005). In Box 3, we return to our two populations from Box 1 to illustrate how the reconstruction of the phylogenetic relationships among extant haplotypes provides insight into the populations’ past. With the recent advent of ‘ancient DNA’ technologies it is now possible to actually revisit past populations, where direct comparisons with contemporary populations offer incredible opportunities to reconstruct population histories.

15.2.2.1 Genetic diversity

Large populations tend to harbor many haplotypes, so that different individuals of the same species will have unique haplotypes, reconstruct the evolutionary history of the species and map their geographic distribution and the history of their dispersal. They can also be used to determine the extent of population subdivision in many species of marine mammal. This often reflects behavioral philopatry to natal site or home range and limited interbreeding among geographically distinct groups.

Box 3 Phylogeography of a haptoparlable species

Returning to our two Populations 1 and 2, we can use the DNA sequence and haplotypes of the species to determine the phylogenetic relationships among the extant haplotypes. The phylogenetic reconstruction is based on the DNA sequence and haplotypes found in a particular population. The phylogenetic tree is constructed using the maximum likelihood method, which is based on the assumption that the DNA sequence is evolving at a constant rate.

The central position of Hap A on the phylogenetic tree, suggests that it is an ancestral haplotype and is found in both Populations 1 and 2. Conversely, Hap B is found only in Population 2 and is not found in Population 1. Comparing the two populations, it is clear that our inferences are, not surprising.
15.2.2.1 Genetic diversity, inbreeding and population history

Large populations tend to harbor high diversity. Such patterns are a feature of many seal (Mizuno et al. 2003; O’Corry-Crowe and Westlake 1997; Perry et al.

Box 3 Phylogeography of a haploid marker in two populations.

Returning to our two Populations from Box 1, here we display the sequences of the 5 unique haplotypes, reconstruct the phylogenetic relationships among the haplotypes and map their geographic distribution at the time of sampling, and thereby attempt to learn about the history of both Populations.

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>DNA sequence</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>CGTTAGATAGACC</td>
</tr>
<tr>
<td>B</td>
<td>CGTAACGATAGACC</td>
</tr>
<tr>
<td>C</td>
<td>CGTTACCATAGACC</td>
</tr>
<tr>
<td>D</td>
<td>CGTTAATAGACC</td>
</tr>
<tr>
<td>E</td>
<td>CGTTACGATAGACC</td>
</tr>
</tbody>
</table>

Fig. 15.3 DNA sequence and minimum spanning tree of haplotypes found in Population 1 and Population 2 and their contemporary distribution. Pre- and post-bottleneck trees are provided for Population 2. Original.

The phylogenetic reconstruction is a minimum spanning network that links haplotypes with the smallest number of mutational differences together. Haplotype size reflects the frequency of the haplotype across all populations at the time of sampling, and those haplotypes found in a particular Population are highlighted for that population.

The central position of Hap A in the network and its connection to several other haplotypes, suggests that it is an ancestral haplotype. The fact that it has a high frequency and is found in both Populations also argues for its ancient origins.

Conversely, Hap D is on a branch tip and connected to only one other, internal, haplotype, suggesting that it is a more recently derived haplotype. The fact that it is rare and has been found in only one Population may mean that it arose in that population relatively recently.

Comparing our reconstructions to actual population histories in Box 1 will demonstrate that our inferences are, not surprisingly, accurate.
2000; Palo et al. 2001; Westlake and O’Corry-Crowe 2002) and pelagic dolphin species (e.g., Dizon et al. 1994), and suggest the maintenance of large population sizes over time. Conversely, small populations typically retain low levels of diversity. This often raises concerns about inbreeding depression and the ability of these populations to deal with changing environmental conditions. Naturally small populations, however, may be uniquely adapted to high levels of inbreeding and low levels of genetic diversity (Lande 1988; Nei et al. 1975). The rare Phocoena sinus (Gulf of California porpoise, or Vaquita) is characterized by a complete lack of variability within mtDNA (Rosel and Rojas-Bracho 1999). This species may never have been very abundant and through the purging of deleterious recessive alleles may be adapted to high levels of consanguinity and low diversity (Taylor and Rojas-Bracho 1999). Nevertheless, limited genetic variation in combination with small current population size means P. sinus still faces an uncertain future in a changing world (Rojas-Bracho and Taylor 1999).

Population expansions and contractions over various time frames leave distinctive signatures or ‘footprints’ in the pattern of genetic variation within them (Slatkin and Hudson 1991; Rogers and Harpending 1992). Over evolutionary timescales, population expansions will be accompanied by the generation of new diversity, the new variants typically being one or two mutational steps from the original, ancestral ones. Populations that have undergone expansions in the distant past may retain both the ancestral and derived variants, such that their gene phylogenies are more akin to a well filled-out bush than a tree (Fig. 15.4). A number of species of marine mammal possess such star-like mtDNA phylogenies, including Monodon monoceros (Narwhal) (Palsbøll et al. 1997), Delphinapterus leucas (Fig. 15.4, O’Corry-Crowe et al. 1997, 2002; Brown-Gladden et al. 1997) and Phocoena phocoena (Rosel et al. 1995), which have been interpreted as evidence of population expansions associated with the (re)colonization of marine habitats following the retreat of the Pleistocene ice sheets.

Just as population expansions can generate new diversity, so population reductions can lead to a loss of diversity (Cornuet and Luikart 1996; Nei et al. 1975). In a landmark population genetic study on a marine mammal, Bonnell and Selander (1974) attributed the complete lack of electrophoretic variation observed in 24 protein loci in the Northern elephant seal to a 13th century population “bottleneck” caused by overhunting. Subsequent studies reaffirmed the absence of allozyme variation and detected low variability within mtDNA (Hoelzel et al. 1993) and minisatellite loci (Lehman et al. 1993), and similarly concluded that these low levels of genetic variation were consistent with a severe population bottleneck (Hoelzel et al. 1993). The consequences of the genetic bottleneck on individual fitness, however, appear to have been minimal. Although the species may have been reduced to as few as 20 individuals, it has achieved a spectacular recovery and now numbers in excess of 120,000 animals (Stewart et al. 1994). Commercial harvest in the 18th and 19th centuries also resulted in dramatic reductions in genetic diversity in

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Fig. 15.4 Minimum spanning network for Delphinapterus leucas (Beluga whale), with the number of the haplotype is denoted by an asterisk. Each asterisk is in the case of the link between mutations. Haplotypes are shown with the most parsimonious tree is indicated. Haplotypes 30, 31 and 32 are not represented in the study. From O’Corry-Crowe, G. and Westlake, J. 2002. Pp. 53-64 in C. J. Pfeiffer (ed.), North American Mammals. Krieger Publishing Co.
and pelagic dolphin populations typically retain low levels of genetic diversity. The maintenance of large populations may be uniquely adapted to pelagic life (Lande 1988; Hansen 1992). Over time, genetic variation within a population may be lost due to genetic drift and non-random mating. Reduced effective population sizes and the loss of rare alleles may reduce genetic variability (Taylor and Rojas-Bracho 1999). In addition, the introduction of management strategies that reduce population sizes may have significant effects on genetic diversity.

Fig. 15.4 Minimum spanning network of 31 unique mtDNA haplotypes found in *Delphinapterus leucas* (Beluga whale). The reconstructed consensus haplotype is denoted by an asterisk. Each link represents a unique mutational event, except in the case of the link between haplotypes 27 and 28 which represents two mutations. Haplotype sizes reflect their abundance in the total sample. A single-linkage parsimonious tree is indicated by the bold lines. (Note that haplotypes nos. 30, 31 and 32 are not represented in the network as they were found in a separate study.) From O’Corry-Crowe, G. M., Dizon, A. E., Suydam, R. S., and Lowry, L. F. 2002. Pp. 53-64 in C. J. Pfeiffer (ed.), *Molecular and Cell Biology of Marine Mammals*. Krieger Publishing Co., Malabar, Florida, USA, Fig. 6.2.
other species. Using ancient DNA techniques, Weber et al. (2004) documented much higher levels of mtDNA diversity in pre-exploitation Arctocephalus townsendi (Guadalupe fur seal) bones collected at archaeological middens than in samples collected from contemporary populations. Similarly, Larson et al. (2002) found higher levels of nuclear DNA variation (microsatellites) in Sea otter bones that pre-date the dramatic population reductions in this species wrought by the fur trade compared to samples from extant populations. In cetaceans, lower levels of nuclear and mtDNA variation have been found in Eubalaena glacialis (Southern right whale) compared to E. australis (South Atlantic right whale) (Schaeff et al. 1991, 1997). The authors interpret the lower diversity in the northern species as a consequence of a population bottleneck resulting from centuries of whaling, and suggest that the reduced fertility, fecundity and survival observed in the northwest Atlantic population may be evidence of inbreeding depression. By contrast, at least some populations of the closely related Balaena mysticetus (Bowhead whale), still retain substantial genetic diversity despite the depredations of commercial whaling (Rooney et al. 1999, 2001; LeDuc et al. 2005). Moderate to high diversity may be the case in most large whale species, where numbers were not reduced low enough for long enough by commercial whaling for substantial diversity to be lost (Amos 1996).

Finally, using a number of simplifying assumptions, it is theoretically possible to estimate population parameters such as long-term effective population size from patterns of genetic variation (Nei 1987). In a recent study, Roman and Palumbi (2003) used contemporary estimates of mtDNA diversity to estimate pre-exploitation population sizes in a number of large whale species in the North Atlantic. Species estimates ranged from 240,000 to 360,000 whales far exceeding previous calculations and questioning the efficacy of current management goals. Caution, however, is required when evaluating these estimates of historic population size as considerable uncertainty remains over some of the assumptions made in Roman and Palumbi's calculations, including the ratio of effective to census population size, the rate of mtDNA substitution in baleen whales, and whether populations were in drift-mutation equilibrium (Clapham et al. 2004).

Conclusion. The level and pattern of genetic diversity within marine mammal populations provides insight into the demographic history of populations, the degree of inbreeding and its consequences on individual fitness, and, potentially, the extent and direction of natural selection. Assessments of genetic diversity can thus also give guidance as to the conservation status and evolutionary potential of a population.

15.2.2.2 Phylogeography
As the analysis of mtDNA haplotype and nuclear allele frequencies can reveal much about contemporary levels of gene flow and dispersal, so the reconstruction of the phylogenetic relationships among genetic lineages and the mapping of their present-day geographic distribution can provide unique insights into the evolutionary and the past two decades this "phylogeography" has illuminated the species' dispersal behavior of many marine mammals (Moritz et al. 1996; Westlake and O'Connell 2004). A particular application in phylogeography is the use of mitochondrial DNA (mtDNA) and absence of recombination in maternal pedigrees or matrilineage. If female dispersal among populations is limited, haplotype frequencies will eventually be different. Mapping the condition of maternal lineages can thus provide insights into relationships among populations' colonization and management practices (Moritz et al. 1992; Gladden et al. 1997; O'Corry-Crowe et al. 2006).

Substantial phylogeographic structure has been found in a number of highly mobile female-mediated philopatry to their natal home range is a long-established behavior. Mitochondrial DNA haplotypes has been found at discrete locations within and between ocean basins (Baker et al. 2004). A number of studies have observed in Delphinapterus leucas with the star-like phylogeography of summering concentrations of D. leucas within ocean basins (King et al. 2004; Allman et al. 2006) and the star-like phylogeography of summering concentrations of Delphinapterus leucas within and between ocean basins (Baker et al. 2004). A number of studies have observed in Delphinapterus leucas with the star-like phylogeography of summering concentrations of D. leucas within ocean basins (King et al. 2004; Allman et al. 2006) and the star-like phylogeography of summering concentrations of D. leucas within ocean basins (King et al. 2004; Allman et al. 2006) and the star-like phylogeography of summering concentrations of D. leucas within ocean basins (King et al. 2004; Allman et al. 2006) and the star-like phylogeography of summering concentrations of D. leucas within ocean basins (King et al. 2004; Allman et al. 2006).
insights into the evolutionary and demographic history of populations. Over the past two decades this "phylogeographic" approach (sensu Avise et al. 1987) has illuminated the species and population histories, migratory and dispersal behavior of many marine mammals (e.g., Rosel et al. 1995; Stanley et al. 1996; Westlake and O'Corry-Crowe 2002). One marker has found particular application in phylogeographic investigations of marine mammals: mitochondrial DNA (mtDNA). Because of its maternal mode of inheritance and absence of recombination, mtDNA phylogenies represent extended maternal pedigrees or matriline (Avise 1995; Brown 1983; Wilson et al. 1985). If female dispersal among populations is restricted, differences in mtDNA haplotype frequencies will emerge through the action of genetic drift. If dispersal is restricted for long enough, phylogeographic differences among the populations will eventually develop through the combined action of drift and mutation. Mapping the contemporary geographic distribution of these maternal lineages can thus provide a detailed account of the demographic relationships among populations over time (Avise 1995), and thus help guide conservation and management of natural populations (Avise 1995; Dizon et al. 1992; Moritz 1994; Vogler and DeSalle 1994).

Substantial phylogeographic partitioning of mtDNA lineages has been found in a number of highly migratory cetacean species indicating that the female-mediated philopatry to traditional migration routes and destinations is a long-established behavior. Extensive phylogeographic sorting of mtDNA haplotypes has been found among Megaptera novaeangliae populations in different ocean basins, and among geographically discrete feeding concentrations and similarly discrete wintering concentrations of this species within ocean basins (Baker et al. 1993; Baker and Medrano-González 2002). Substantial geographic partitioning of mtDNA lineages has also been observed in Delphinapterus leucas (Fig. 15.5). These patterns, in combination with the star-like phylogeny of this marker, argue that the origins of separate summering concentrations of D. leucas date back to postglacial expansion from refugial populations and indicate limited dispersal among these summering groups for long periods, in some cases over evolutionary time scales (Brown-Gladden et al. 1997; O'Corry-Crowe et al. 1997, 2002).

In pinnipeds, the phylogeography of mtDNA variation in Odobenus rosmarus may indicate an ancient divergence between Atlantic and Pacific subspecies (Cronin et al. 1994) and between populations of the Atlantic subspecies to the west and east of Greenland (Andersen et al. 1998; Cronin et al. 1994), while in Eumetopias jubatus strong phylogeographic partitioning of mtDNA between eastern and western North Pacific Ocean rookeries indicate at least two evolutionarily distinct populations that may have originated in separate glacial refugia (Bickham et al. 1996; Harlin-Cognato et al. 2006; O'Corry-Crowe et al. 2006).

Conclusion. Investigations of mtDNA phylogeography in marine mammals have revealed that present-day patterns of dispersal, philopatry and migration are in many cases long established behaviors such that populations
Advances in population genetic technology have played major roles in solving challenges, however, remain.

Fresh insights into the mechanisms and behaviors of populations and into the inherent variability and population viability will require specific traits (e.g., Mackay 2001). Genetic studies of reproductive dispersal are conducted in conjunction with population trend and physiological data. This is becoming increasingly apparent as metapopulations (e.g., Yoo et al. 2003). Populations linked via dispersal patterns, causes and consequences, can lead to a greater understanding across the metapopulation’s range.

Many population genetic studies suffer from limited statistical power to detect and population subdivision. The recent common ancestry within species is often minimal such that distinct populations are not or only can be detected by approach (Dizon et al. 1995; Taylor et al. 2001). However, most species and even populations that have been documented to have attained equilibrium after the effects of genetic flow at selectively neutral loci and the effect of changes in the ecosystem regime are likely to exhibit very similar population expansions and contractions in response to the environmental changes. They have also suffered dramatic population declines (e.g., recoveries) over the past few decades. The populations shown in Box 2-1 are candidates that have reached or attained equilibrium such that the frequencies of certain loci can be used to infer the average level of genetic diversity (e.g., haplotype frequencies match those in Fig. 15.5). The point here is that studies of these populations that are in equilibrium and are characterized by average measures of genetic diversity may be meaningful in populations that are

![Fig. 15.5 MiDNA haplotype diversity among summering concentrations of Delphinapterus leucas (Beluga whale) in Alaska and northwest Canada represented on an optimum minimum spanning tree. (Solid disks indicate the set of haplotypes in the tree that were found in each area.) Haplotype size reflects the overall frequency, not the frequency within each area (see Fig. 15.4 for more details). After O’Corry-Crowe et al. (1997, 2002).](image-url)

are evolutionarily as well as demographically distinct. This approach has facilitated the reconstruction of population histories, including identifying the likely location of refugial populations during previous ice ages and the routes of population expansion following ice retreat. The ability to assess marine mammal populations in a historical as well as contemporary context helps in the assessment of the importance of individual populations to species survival and to prioritize management objectives.

15.3 FUTURE CHALLENGES

Population genetic investigations have provided unique insights into the ultimate and proximate forces that shape subdivision and genetic diversity in marine mammal populations, and have thereby greatly improved our understanding of the demographic and evolutionary processes acting within and among marine mammal populations over time, as well as aided in the conservation and management of these highly mobile, often elusive animals.
Advances in population genetic theory, sampling methods and molecular technology have played major roles in the development of the field. Challenges, however, remain.

Fresh insights into the mechanisms of evolution within marine mammal populations and into the inherent genetic component of individual fitness and population viability will require the examination of markers that code for specific traits (e.g., Mackay 2001) and more interdisciplinary research where genetic studies of reproductive success, mating systems, kinship and dispersal are conducted in conjunction with studies of survival, health, population trend and physiological response. At the conceptual level, it is becoming increasingly apparent that many marine mammal populations behave as metapopulations (e.g., York et al. 1996) comprising discrete local populations linked via dispersal and gene flow, where elucidating the patterns, causes and consequences of dispersal through genetic investigation can lead to a greater understanding of population and evolutionary dynamics across the metapopulation's range (Hanski and Gaggiotti 2004).

Many population genetic studies on marine mammals to date have suffered from limited statistical power to elucidate the underlying patterns of gene flow and population subdivision. This is often the case in large populations with recent common ancestry where the diversifying power of genetic drift is minimal such that distinct populations may not have diverged much genetically. Failure to detect subdivision may also be a consequence of small sample sizes, uninformative markers or inappropriate statistical methods (Dizon et al. 1995; Taylor et al. 1997; Ryman et al. 2006). Thus, new sampling approaches, new genetic markers and alternative statistical techniques are required to improve statistical power.

On the analytical front, traditional methods of population genetic inference are based on idealized models of populations in equilibrium or undergoing deterministic expansion (e.g., Slatkin and Barton 1989; Beerli and Felsenstein 2001). However, most species of marine mammals are unlikely to comprise of populations that have been demographically stable enough for long enough to have attained equilibrium between the opposing forces of drift and gene flow at selectively neutral loci. Regular climatic oscillations and marine ecosystem regime changes have resulted in histories of population expansions and contractions in several marine mammals, while many species have also suffered dramatic declines (and in some cases spectacular recoveries) over the past few centuries from commercial harvest. The populations shown in Box 2 were represented as two populations that had attained equilibrium such that Wright’s idealized model could be used to infer the average level of gene flow. As may have already been noticed, the haplotype frequencies match those of Populations 1 and 2 from Box 1 (Phase 5). The point here is that similar haplotypic distributions could arise in populations that are in equilibrium, expanding or even declining, and that average measures of gene flow estimated in this way are essentially meaningless in populations not in equilibrium. New mathematical models
and methods of data analysis are emerging (e.g., Paetkau et al. 1995; Pritchard et al. 2000; Gaggiotti et al. 2002; Wilson and Rannala 2003) that are now facilitating genetic investigations of marine mammal populations that are not in equilibrium.

Key to successfully facing these and future challenges will be empirical studies that track the fortunes of individuals, and temporal analyses that put the traditional ‘snapshot’ studies of spatial variation in the proper context of dynamic ecosystems and of the ever evolving populations of marine mammals that inhabit them.

15.4 ACKNOWLEDGMENTS

I wish to thank my colleagues in the High Latitude Molecular Ecology Group and the Population Identity Group at the Southwest Fisheries Science Center for many stimulating discussions on, and insight into, the population genetics of marine mammals, including Andrew Dizon, Rick LeDuc, Barb Taylor, Eric Archer, and Bill Perrin.

15.5 LITERATURE CITED


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