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Population Genetics of the Monk Seals (Genus *Monachus*): A Review

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Summary

Monk seals (genus *Monachus*) are among the most endangered mammals in the world, with all species sharing a similar history of anthropogenic overexploitation. Reductions in population abundance have been accompanied by the loss of genetic diversity in Mediterranean (*M. monachus*) and Hawaiian (*M. schauinslandi*) monk seals. Both species are characterized by extremely low variability at all genetic markers tested to date, including microsatellite loci, the mitochondrial control region, and major histocompatibility complex class I genes. Genetic variation is partitioned differently in the two species. The Hawaiian monk seal does not exhibit spatial population structure throughout its range in the Hawaiian Archipelago ($F_{ST} = 0.00$); therefore, it is unlikely that the translocation of monk seals will result in genetic incompatibilities. In contrast, Eastern Mediterranean and Western Saharan *M. monachus* populations are reproductively isolated ($F_{ST} = 0.56$), though the distribution of alleles likely signifies a once contiguous range sundered by the extirpation of geographically intermediate subpopulations. Given the magnitude of genetic differentiation, moving Mediterranean monk seals between eastern and western populations could result in reduced overall fitness; additional data is required to assess the risk of moving monk seals within a population (e.g., the Eastern Mediterranean). Recent advances in genomics will facilitate future investigation into the reproductive success of both species and guide managers in their quest to recover Mediterranean and Hawaiian monk seal populations.

Key Words: monk seal, conservation, DNA, genetic diversity, pinniped, stock structure

Introduction

The genus *Monachus* is comprised of three species: Caribbean (*M. tropicalis*), Mediterranean (*M. monachus*), and Hawaiian (*M. schauinslandi*) monk seals. There are few distinguishing morphological characters among the species (Scheffer, 1958), and the genus appears to be monophyletic. Phylogenetic analyses of the two extant species (*M. monachus* and *M. schauinslandi*) at mitochondrial DNA loci indicated deep divergence between Mediterranean and Hawaiian monk seals and a mid-late Miocene origin of the lineage (Davis et al., 2004). Sequencing one nuclear and three mitochondrial genes, Fyler et al. (2005) estimated the date of divergence to be 10.6 to 11.6 million years ago (MYA). Citing the occurrence of *Monachus* fossil representatives in southern Europe, Fyler et al. described a Tethys origin of the genus with initial dispersal to the Caribbean via the North Equatorial Current. Subsequent dispersal to the tropical Pacific occurred through the Central American Seaway, prior to the emergence of the Isthmus of Panama (de Muizon, 1982). Higdon et al. (2007) supported this hypothesis, citing greater morphological similarity between the Hawaiian and Caribbean species. They also analyzed a large, multi-gene dataset to date the origin of the genus at 11.3 MYA. Arnason et al. (2006) proposed an alternative phylogeographic hypothesis. Sequencing the whole mitochondrial genome of the Hawaiian monk seal and select genes of the Mediterranean monk seal, they estimated interspecific divergence at ~13 MYA. Because the earliest monachine fossil (~14.5 MYA) was found in southeastern North America, they postulated that the origin of the genus occurred in the western Atlantic, followed by dispersal to the Mediterranean and Hawaii (Arnason et al., 2006). Regardless of which hypothesis best represents *Monachus* evolution, the species have occupied their respective ranges for millions of years.

The now extinct Caribbean monk seal once occupied a large range throughout the Caribbean Sea and Gulf of Mexico. Historically, the Mediterranean monk seal ranged throughout the Mediterranean and Black Seas and into the subtropical East Atlantic Ocean (Johnson & Lavigne, 1999). Its range is now restricted to pockets of the northeastern Mediterranean and eastern Atlantic. Hawaiian monk seals are endemic to the Hawaiian Archipelago and are occasionally observed at Johnston Atoll, ~1,400 km west of Hawaii (Antonelis et al., 2006).

All three species have been hunted throughout their respective ranges for meat, oil, and skins such that *Monachus* seals are among the most endangered of all marine mammals. McClenachan & Cooper (2008) estimated that 233,000 to 338,000 Caribbean monk seals were distributed among 13 colonies prior to discovery and exploitation by Westerners, beginning with Christopher Columbus in 1494. The last monk seal was observed in 1952, and the species has since been declared extinct (Le Boeuf, 1986).

The Mediterranean species has a long history of exploitation. Monk seal remains found in caves occupied by Neanderthals exhibit anthropogenic damage (Stringer et al., 2008). Prehistorical drawings and historical accounts document exploitation of the once abundant species since the Stone Age, through the Greek, Roman, and Byzantine periods, and into modern times (Johnson & Lavigne, 1999; www.monachus-guardian.org). Extirpation along most mainland Mediterranean coasts has left only three small and isolated populations in remote locations: Desertas Islands of Madeira, Cap Blanc Peninsula in the Western Sahara, and in caves throughout the northeastern Mediterranean (i.e., Greece and Turkey). The Western Saharan population was reduced from an estimated 317 monk seals in 1996 to 109 individuals in 1997 after a mass mortality event (Forcada et al., 1999). Only 20 to 30 adults reside in the Madeira Archipelago (Pires et al., 2008). The largest population consists of 250 to 350 individuals in the eastern Mediterranean Sea (Dendrinos et al., 2008).

Little is known regarding the first human interactions with the Hawaiian monk seal. Remains found at an archaeological site in the main Hawaiian Islands, radiocarbon dated to 1400 to 1750 AD, suggest that early Hawaiians harvested monk seals (Rosendahl, 1994). Monk seals had been extirpated from the main Hawaiian Islands prior to the arrival of the first Western explorers in the 18th century. Western exploration of the uninhabited Northwestern Hawaiian Islands beginning in 1805 led to the discovery and exploitation of the species (Ragen, 1999). A minimum of 23 individuals survived at the nadir of the hunting-induced bottleneck (c. 1893; Schultz et al., 2009). Despite a partial recovery by the mid-20th century, population abundance is currently in decline. At present, less than 1,200 Hawaiian monk seals remain (Carretta et al., 2009). The majority of the monk seals reside in the Northwestern Hawaiian Islands, where their habitat is protected as the Papahanaumokuakea Marine National Monument. Since the 1990s, monk seals have also recolonized the main Hawaiian Islands (N = ~152 monk seals; Baker et al., 2011).

Such extreme population reductions have impacted the diversity and distribution of genetic variation within the extant species. The following is a review of published literature on population genetics of the Mediterranean and Hawaiian monk seals, focusing on genetic diversity, population bottlenecks, and stock structure. Implications for conservation and future directions are also addressed.

Genetic Diversity

Genetic diversity refers to the extent of variation found throughout the genome of a species or population. It is the raw material upon which natural selection acts and is essential to population persistence. Genetic diversity is often assessed at both nuclear and mitochondrial loci (i.e., location of a coding gene or non-coding DNA sequence). Each individual possesses two alleles at a single nuclear locus; the individual is heterozygous at that locus if the alleles differ. Mitochondrial loci are maternally inherited, and each individual generally possesses only one form or haplotype. Measures of genetic diversity include polymorphism (P), the proportion of genetic markers (or loci) which exhibit more than a single form (or allele); allelism (k), the number of alleles at a given locus; and heterozygosity (H), the percentage of individuals in a population or species that possess two different alleles at a given locus or averaged over all loci. While polymorphism and allelism reflect raw genetic variability, heterozygosity is a measure of how existing diversity is partitioned among individuals.

Microsatellite DNA

Mediterranean and Hawaiian monk seals exhibit low diversity at all genetic markers tested to date, including microsatellite loci—that is, tandemly repeated regions of nuclear DNA that are generally characterized by high variability. Gemmell et al. (1997) surveyed the utility of 20 microsatellite loci across 18 pinniped species (Table 1). Twelve of the 20 loci were polymorphic in the Mediterranean monk seal ($P = 0.60$), and allelism was low ($k = 1$ to 6, $k_{ave} = 2$). Only three of the 20 loci were polymorphic in the Hawaiian monk seal ($P = 0.15$); allelism was also low ($k = 1$ to 4, $k_{ave} = 1.25$). Though limited in scope (only four and five Mediterranean and Hawaiian monk seals were analyzed, respectively), the study is important because

Table 1. Comparisons of genetic diversity among seal species: for mitochondrial markers, haplotype diversity (*h*) and nucleotide diversity (α); for microsatellite loci, proportion polymorphic at a common set of 20 pinniped loci (P_1; Gemmell et al., 1997), proportion polymorphic in independent studies (P_2), average number of alleles (*k*) for all loci/for polymorphic loci (for *Monachus* spp.), and heterozygosity (H_e) for all loci/for polymorphic loci (for *Monachus* spp.).

	N	*N*	Mitochondrial loci		Microsatellite loci				
	census*	sample	*h*	α	P_1	P_2	*k*	H_e	Reference
Hawaiian monk seal	<1,200	50	0.24	0.006	3				Kretzmann et al., 1997
(*Monachus schauinslandi*)		2,423				17/163	1/3	0.05/0.46	Schultz et al., 2010
Mediterranean monk seal					12				
(*M. monachus*)	~500	52				15/39	2/2	0.16/0.41	Pastor et al., 2004
Eastern Mediterranean	150-300	12				11/24	2/3	/0.23	Pastor et al., 2007
Western Saharan	100-130	98				13/24	2/2	/0.35	Pastor et al., 2007
Northern elephant seal	171,000	80-160			9	14/41	2	0.40	Garza & Williamson, 2001
(*Mirounga angustirostris*)						6/20	1		Davis et al., 2002
Hooded seal	592,000	5			16	14/17	4		Davis et al., 2002
(*Cystophora cristata*)		300	1.0	0.021		21/21	12	0.73	Coltman et al., 2007
Ringed seal	>1 million	5			14	17/19	5		Davis et al., 2002
(*Phoca hispida*)		303					25	0.84-0.89	Davis et al., 2008
Bearded seal	500,000	5			8	17/19	4		Davis et al., 2002
(*Erignathus barbatus*)		119					9	0.59-9.69	Davis et al., 2008
Weddell seal	500,000	17				24/24	9		Davis et al., 2002
(*Leptonychotes weddellii*)		893					16	0.55-0.76	Davis et al., 2008
Leopard seal	300,000	20			5	24/24	6		Davis et al., 2002
(*Hydrurga leptonyx*)		150					13	0.72-0.76	Davis et al., 2008
Ross seal	130,000	5				22/22	5		Davis et al., 2002
(*Ommatophoca rossii*)		90					14	0.70-0.74	Davis et al., 2008
Crabeater seal	950,000	16				24/24	12		Davis et al., 2002
(*Lobodon carcinophagus*)		303					21	0.85	Davis et al., 2008

*Rough estimates of total population size (www.iucnredlist.org) it compares the genetic diversity of the two species at a common suite of markers, allowing for direct comparison (Gemmell et al., 1997). The results are surprising given that the less abundant species (Mediterranean monk seal, N = ~500) has higher genetic diversity than the more abundant species (Hawaiian monk seal, N < 1,200). Possible reasons for this discrepancy are discussed below.

Additional studies of microsatellite diversity have been completed for both species (Table 1). Pastor et al. (2004) analyzed 39 pinniped microsatellite loci (including those already mentioned) in 52 pups at Cap Blanc, Western Sahara, and found 15 to be polymorphic ($P = 0.39$, $k = 1$ to 3, $k_{ave} = 1.5$). Mean expected heterozygosity was $H_e = 0.16$ for all loci and $H_e = 0.41$ for polymorphic loci only. In a later study, Pastor et al. (2007) compared the genetic diversity of 98 Western Saharan monk seals to 12 monk seals from the Eastern Mediterranean. Analyzing a panel of 24 pinniped microsatellite loci, 13 were found to be polymorphic in Western Saharan monk seals ($P = 0.55$, $k = 1$ to 5, $k_{ave} = 2$), while 11 were polymorphic in Eastern Mediterranean monk seals ($P = 0.45$, $k = 1$ to 5, $k_{ave} = 1.88$). Only 52% of all alleles were shared by both populations: 18 private alleles were found in the Western Saharan and 14 private alleles were found in the Eastern Mediterranean. Mean expected heterozygosity at the polymorphic loci was similarly low in Western Saharan ($H_e = 0.38$) and Eastern Mediterranean ($H_e = 0.32$) populations.

The Hawaiian monk seal has also been the subject of more in-depth analyses of genetic diversity (Table 1). The species was surveyed at an additional 10 microsatellite loci isolated from Antarctic seals (Davis et al., 2002), but none were found to be polymorphic (Schultz et al., 2009). Because loci isolated in one species are often invariant in distantly related taxa, microsatellite loci were isolated from the Hawaiian monk seal genome (Schultz et al., 2009). Of 143 loci isolated in the first round of microsatellite development, only seven were found to be polymorphic. A second round of development, using more stringent requirements for microsatellite selection, resulted in the isolation of an additional 10 polymorphic loci (Schultz et al., 2010). Overall, the Hawaiian monk seal exhibits extremely low genetic diversity ($P = 0.10$, $k_{ave} = 1.1$, $H_e = 0.05$) compared to other similarly exploited pinniped species (Table 1). Diversity is low, even when only polymorphic loci are considered ($k_{ave} = 3.4$, $H_e = 0.46$).

Mitochondrial DNA

Mediterranean and Hawaiian monk seals also exhibit low genetic diversity at the mitochondrial control region, which does not code for proteins and thus may accumulate mutations more quickly than other regions (Table 1). Harwood et al. (1996) found only two mitochondrial haplotypes in seven Mediterranean monk seals: one haplotype was shared by four monk seals from the Eastern Mediterranean population, and another was shared by three monk seals from the Western Saharan population. Kretzmann et al. (1997) found only three mitochondrial haplotypes in 50 Hawaiian monk seals: 43 monk seals shared a common haplotype, six monk seals shared a rare haplotype, and one individual exhibited a unique haplotype.

Major Histocompatibility Complex

Genetic variation at neutral (or nearly neutral) markers, such as microsatellites and the mitochondrial control region, is expected to be high. Coding genes may also exhibit high levels of variability if polymorphism is linked with greater fitness. One example of this is the major histocompatibility complex (MHC), which plays an important role in the immune response of vertebrates. The high allelic diversity of MHC loci provides resistance to a broad variety of pathogens; when MHC diversity is low, populations may be more susceptible to infectious disease epidemics (Gaggiotti, 2003). Aldridge et al. (2006) found unprecedented uniformity in MHC class I genes in a survey of 80 Hawaiian monk seals. Though MHC studies have yet to be performed in the Mediterranean monk seal, the species may be prone to disease epidemics. In 1997, the Western Saharan population suffered a mass mortality event as the result of a morbillivirus outbreak or a dinoflagellate bloom (Osterhaus et al., 1997; Harwood, 1998).

Inferring Demographic Events

Low genetic diversity may threaten the future of a species, but it also reflects past demographic events. The various measures of genetic diversity provide insight into the cause, duration, and severity of population reductions. For example, a severe disease epidemic may result in a selective sweep (i.e., the loss of variation at loci located near a gene under strong, positive selection; Smith & Haigh, 1974). Selective sweeps result in localized loss of genetic diversity at a specific area on a single chromosome. Mapping 110 of 163 Hawaiian monk seal loci to the dog genome revealed broad distribution of polymorphic and monomorphic loci, likely reflecting genome-wide rather than localized loss of genetic diversity (Schultz et al., 2010). Therefore, extremely low genetic diversity in the Hawaiian monk seal is probably not the result of a selective sweep resulting from a disease epidemic.

Sudden, dramatic reductions in effective population size (N_e) result in the loss of rare alleles with little impact on heterozygosity (Nei et al., 1975). Bottlenecked populations often will exhibit temporary heterozygosity excess relative to expectations given the number of alleles (i.e., alleles have been lost from the population but average heterozygosity remains relatively unchanged; Cornuet & Luikart, 1996). There is genetic evidence for a recent bottleneck in both the Mediterranean and Hawaiian monk seal species. Pastor et al. (2004) reported a deficit of rare alleles and an excess of heterozygosity in the Mediterranean monk seal, which were attributed to recent reductions in effective population size. Schultz et al. (2009) described a similar loss of alleles and heterozygosity excess, likely caused by the extreme reduction of effective population size as a result of 19th-century hunting in the Northwestern Hawaiian Islands.

Recent declines in the Mediterranean and Hawaiian species are not sufficient to explain the low levels of heterozygosity exhibited by both species. Heterozygosity is lost only when the effective population size remains small for long periods of time. Thousands of years of hunting of the Mediterranean monk seal resulted in severe population reductions and likely explain the species' low heterozygosity. Compared with less-exploited pinniped species, the Mediterranean monk seal has lost ~53% of its expected heterozygosity (Pastor et al., 2004). Heterozygosity is similarly low in the Hawaiian monk seal. It is unlikely that the 19th-century hunting (which lasted less than eight monk seal generations) could reduce heterozygosity so dramatically. A more likely explanation is long-term population size restriction as a result of earlier, undocumented hunting (i.e., the species may have been extirpated in the main Hawaiian Islands by early Polynesian colonizers) or natural mechanisms (i.e., the abundance of a large, insular carnivore population may be restricted due to habitat availability or prey abundance).

Genetic Stock Structure

Genetic stock or population structure refers to the spatial partitioning of genetic variation within a species. It provides an important tool for wildlife managers tasked with delineating stocks (i.e., a group of potentially interbreeding individuals that are exposed to common threats) and understanding how those stocks are connected via migration. If a stock is reproductively isolated from other stocks, it may accumulate unique alleles through mutation. In addition, allele frequencies will randomly change over time, relative to other stocks. This mechanism is called genetic drift, and it results in genetic differences, or structure, among isolated stocks. Effective migration or gene flow (i.e., mating among stocks) diminishes the magnitude of these genetic differences.

The two largest Mediterranean monk seal populations (Eastern Mediterranean and Western Saharan) are separated by 4,000 km. Though only a limited number of samples have been analyzed, Eastern Mediterranean (N = 4) and Western Saharan (N = 3) populations appear to be fixed at different haplotypes as determined by comparing partial mitochondrial sequences (Harwood et al., 1996). Though such results may reflect reproductive isolation, the maternal inheritance of mitochondrial genes allows for the possibility of male-mediated gene flow. Therefore, Pastor et al. (2007) analyzed Eastern Mediterranean (N = 12) and Western Saharan (N = 98) monk seals at 13 nuclear microsatellite loci. Each population had several private alleles (14 and 18, respectively). There was substantial genetic differentiation (F_{ST} = 0.58) and virtually no gene flow (0.47 effective migrants per generation) between the populations (Table 2; Pastor et al., 2007). These results confirm that the two populations are reproductively isolated and should be managed as independent stocks. The Western Saharan population inhabits a relatively small area at the peninsula of Cap Blanc and is assumed to be a single stock. The Eastern Mediterranean population, however, consists of monk seals scattered throughout the Ionian and Aegean Seas and in remote locations along the Turkish coast; it remains to be determined whether this population is comprised of one or several stocks (Pastor et al., 2007).

Reproductive isolation among geographically distant populations may reflect extirpation of geographically intermediate subpopulations as is true of the Mediterranean monk seal, which was once found throughout the Mediterranean Sea. In the past, it was likely comprised of a single large and interbreeding population. The two remaining populations exhibit a similar size range for most loci, with the intermediate-sized microsatellite alleles missing in one population present in the other. Furthermore, when data from both populations are combined, there is a continuous distribution of alleles, indicative of a once contiguous population (Pastor et al., 2007).

The Hawaiian monk seal is found throughout the Hawaiian Archipelago, a range of ~2,000 km. Parturition and nursing occur primarily at six locations in the uninhabited Northwestern Hawaiian Islands and throughout the main Hawaiian Islands. Using mitochondrial analyses, Kretzmann et al. (1997) found no evidence for population differentiation, comparing 10 individuals each from five locations in the Northwestern Hawaiian Islands. However, preliminary analyses of multilocus DNA

Table 2. Recent studies of seal population differentiation based on microsatellite analyses of stock structure, including F_{ST} or Weir & Cockerham's θ (1984), an exact test of differentiation, the number of populations (K) as determined in the software *Structure* (Pritchard et al., 2000), and isolation by distance (IBD)

Species	N sample	# sites	θ or F_{ST}	Exact (P)	K	IBD	Reference
Hawaiian monk seal	1,897	7	-0.01	1	1	0.0001	Schultz et al., 2010
Mediterranean monk seal	110	2	0.58				Pastor et al., 2007
Hooded seal	300	4	-0.003	0.13	1		Coltman et al., 2007
Ringed seal	303	8	0.005	0	1	0.52	Davis et al., 2008
Bearded seal	119	6	0.064	0	2	0.46	Davis et al., 2008
Weddell seal	893	23	0.03	0	3	0.16	Davis et al., 2008
Leopard seal	150	6	0.001	0.001	1	0.14	Davis et al., 2008
Ross seal	90	4	0.006	0.221	1	0.33	Davis et al., 2008
Crabeater seal	303	4	0.003	0.045	1		Davis et al., 2008

fingerprinting (Kretzmann et al., 1997) and a single microsatellite locus (Kretzmann et al., 2001) indicated significant genetic structure. To resolve this discrepancy, Schultz et al. (2010) genotyped ~85% of the entire species living over the past 14 y (N = 1,897) at 18 microsatellite loci. They did not find evidence for reproductive isolation among any of the locations ($F_{ST} = 0$; Table 2). A Bayesian clustering method indicated that the species is comprised of one population ($K = 1$), and genetic results support the current management of the species as a single stock. One possible caveat is that the lack of population structure might be a result of recent population expansion (since the 19th-century bottleneck) or anthropogenic translocation. This is unlikely, however, given the extremely small population sizes (in which genetic drift should act quickly) and the high rate of inter-island movement (10 to 15%), which provides the potential for substantial gene flow.

Conservation Implications

Though the Mediterranean and Hawaiian monk seals share a common history of evolutionary origins and anthropogenic exploitation, their management needs are quite different. These differences can be explained in the context of the single large or several small (SLOSS) paradigm. Managers of captive populations and protected areas have long debated the relative merits and concerns associated with a single large population or alternatively several small populations (Simberloff & Abele, 1982). A single large population has the demographic advantage: its overall risk of extinction is lower than that of smaller populations. Several small populations, however, may have a genetic advantage. As observed in the Mediterranean monk seal, several small isolated populations preserve a greater wealth of genetic variation than would a single population of the same total size.

Both monk seal species exhibit extremely low genetic diversity, which is required to adapt to a changing environment and mount an effective immune response (Frankham et al., 1999; Gaggiotti, 2003). Infectious disease epidemics are an emerging threat to the future of both species. The Mediterranean monk seal is comprised of two small but genetically differentiated populations separated by 4,000 km (Pastor et al., 2007). Thus, it is unlikely that an infectious disease would be transmitted between populations. In the Western Saharan population, however, monk seals breed and haul out in two main caves (Gazo et al., 2000); such close proximity of individuals increases the risk of disease transmission. Hawaiian monk seals do not form large breeding colonies. They do, however, appear to move and mate freely throughout their range, providing a greater chance for transmission throughout the entire species. As the number of Hawaiian monk seals increases in areas of dense human population (i.e., the main Hawaiian Islands), there is increased potential for exposure to infectious diseases carried by humans, dogs, cats, and rodents (Littnan et al., 2006). Given the differences in the proportion of polymorphic loci, the Hawaiian species is also more likely to be monomorphic at genes conferring immunity. To prevent an epidemic in either species, management may strive to limit exposure, vaccinate, develop early detection systems, and quarantine symptomatic monk seals.

Despite having greater raw genetic diversity, the Mediterranean monk seal exhibits lower heterozygosity at polymorphic loci. This is likely a result of long-term small population size. Small populations are often plagued with inbreeding and an accompanying loss of fitness (i.e., inbreeding depression). Similarly, there may be a positive correlation between heterozygosity and fitness. Translocation of Mediterranean monk seals between populations could restore lost genetic diversity, alleviate inbreeding depression, and boost heterozygosity; however, the large degree of genetic differentiation may signify long-term isolation of the two populations, providing ample time for local adaptation. Because translocated Mediterranean monk seals may be poorly adapted to their new habitat or have difficulty in finding mates, such initiatives are not encouraged without further investigation. In addition, future research is required to determine whether monk seals may be translocated within a population (e.g., Eastern Mediterranean).

The Hawaiian species has less raw genetic diversity but higher levels of heterozygosity. While its population size has been recently reduced, it does not appear to be inbred ($F_{IS} = 0.02$; Schultz et al., 2009). A possible explanation for both of these observations may be the apparently extensive movement of monk seals and alleles throughout their range. Given the lack of population structure, Hawaiian monk seals may be translocated to areas with higher survival rates with little concern for genetic incompatibilities; however, translocation will not improve the genetic diversity of the species.

Future Directions

Future areas for research include determining the extent of inbreeding in both species. Are inbred monk seals less likely to survive to maturity? Do they exhibit lower reproductive rates? To address these questions in the Hawaiian monk seal, a species-wide wild pedigree could be constructed by confirming maternity and elucidating paternity of nearly all pups born from 1994 to 2010. Such in-depth analysis is possible as a result of long-term, extensive monitoring of the species, of which ~85% of all pups have been genetically sampled over the past two decades. New advances in genome sequencing would allow the identification of an adequate number of variable markers; however, the costs associated with genotyping thousands of monk seals at all markers remains high. The elusive behavior of the Mediterranean monk seal prevents a similar study, but the Hawaiian monk seal data could be used as a model to interpret observations in the Mediterranean species, which may be more prone to inbreeding given its smaller population size. Heterozygosity-fitness correlations (HFC) may also provide an estimate of inbreeding (though the linkage has not been verified) or at least a genetic measure of potential fitness. Performing HFC analyses requires an abundance of polymorphic loci (Balloux et al., 2004), which is currently not available for either species.

New genomic techniques provide the opportunity to discover further genetic variation in both species. "Next-generation" sequencing technology is able to read and process millions of base pairs in parallel (Mardis, 2008). For species with low genetic diversity, such advances will provide a greater opportunity to identify variable loci, such as microsatellites or Single Nucleotide Polymorphisms (SNPs), in the pursuit of parentage and HFC studies. Next-generation sequencing technology has also proven to be an effective method for examining MHC variability (Balbik et al., 2009; Wegner, 2009), which should be further investigated in both species given the potential impact of an infectious disease epidemic. Sequence variation alone is not sufficient to measure the potential for an effective immune response. Therefore, functional genomics should also be an area of future research. The development of cell lines and advances in transcriptomics will allow the detection of gene expression in response to various pathogens *in vitro*.

In conclusion, population genetics has and will continue to inform managers of Mediterranean and Hawaiian monk seal stocks. Though these findings may not directly impact population persistence, they provide a wealth of knowledge regarding reproductive potential and epidemiological risks. Thus, studies of monk seal genetics can guide initiatives, which could promote population growth, restore genetic variation, and hopefully lead to the recovery of these critically endangered species.

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