Ecological Applications, 18(2) Supplement, 2008, pp. S56–S76

CLIMATE CHANGE AND THE MOLECULAR ECOLOGY OF ARCTIC MARINE MAMMALS

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Abstract. Key to predicting likely consequences of future climate change for Arctic marine mammals is developing a detailed understanding of how these species use their environment today and how they were affected by past climate-induced environmental change. Genetic analyses are uniquely placed to address these types of questions. Molecular genetic approaches are being used to determine distribution and migration patterns, dispersal and breeding behavior, population structure and abundance over time, and the effects of past and present climate change in Arctic marine mammals. A review of published studies revealed that population subdivision, dispersal, and gene flow in Arctic marine mammals was shaped primarily by evolutionary history, geography, sea ice, and philopatry to predictable, seasonally available resources. A meta-analysis of data from 38 study units across seven species found significant relationships between neutral genetic diversity and population size and climate region, revealing that small, isolated subarctic populations tend to harbor lower diversity than larger Arctic populations. A few small populations had substantially lower diversity than others. By contrast, other small populations retain substantial neutral diversity despite extensive population declines in the 19th and 20th centuries. The evolutionary and contemporary perspectives gained from these studies can be used to model the consequences of different climate projections for individual behavior and population structure and ultimately individual fitness and population viability. Future research should focus on: (1) the use of ancient-DNA techniques to directly reconstruct population histories through the analysis of historical and prehistorical material, (2) the use of genomic technologies to identify, map, and survey genes that directly influence fitness, (3) long-term studies to monitor populations and investigate evolution in contemporary time, (4) further Arctic-wide, multispecies analyses, preferably across different taxa and trophic levels, and (5) the use of genetic parameters in population and species risk analyses.

Key words: Arctic; climate change; DNA; marine mammals; molecular ecology.

Introduction

Recent warming of the earth's lower atmosphere has been linked to dramatic environmental changes, particularly in polar marine environments, where the warming trend has been connected to changes in sea ice cover, sea level, water temperature, and ocean currents (Rothrock et al. 1999, Parkinson and Cavalieri 2002, Comiso and Parkinson 2004, Walsh 2008), which in turn are believed to affect productivity and the entire web of life in polar and subpolar waters (Smetacek and Nicol 2005). Current climate models project a continuing warming trend in the near future (Vinnikov et al. 1999, Intergovernmental Panel on Climate Change 2007, but see Hansen et al. 2000), which spells continued decreases in sea ice, especially in the Arctic (Comiso 2000).

Changes in the environment can affect the behavior and fitness of individual organisms and the viability of populations. As such, climate-related environmental change can precipitate population extinctions and range expansions and contractions and be a major driving force behind evolution in natural populations. Such changes create new opportunities for natural selection to act on quantitative traits, resulting in evolutionary change. Changing resources and habitats can also influence population sizes and breeding and dispersal patterns and thus affect evolution via genetic drift and gene flow. Past shifts in the earth's climate have led to the alteration or loss of existing environments and the creation of new ones. These changes have been associated with speciation events, adaptive radiations and extinctions, population expansions and contractions, and changes in individual dispersal and breeding behavior (Hewitt 2000, Schluter 2000, Weider and Hobæk 2000), all of which have had profound effects on the genetic composition and structure of populations, species, and communities (Avise 1998, Hewitt 2000).

Oscillations in the earth's climate over the past few million years have been attributed to cyclical variation in aspects of the earth's orbit that control the seasonal

Manuscript received 12 May 2006; revised 1 February 2007; accepted 2 February 2007; final version received 27 March 2007. Corresponding Editor (ad hoc): A. Berta. For reprints of this Special Issue, see footnote 1, p. S1.

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distribution of the sun's radiation, modulated by ice sheet dynamics (Hays et al. 1976, Imbrie and Imbrie 1980, Clark et al. 1999). At higher latitudes the environmental effects of these recurrent climatic changes have been most extreme, characterized by dramatic changes in ice cover, precipitation, temperature, sea level, and ocean currents (Clark et al. 1999). Sequential cold and warm periods have also been characterized by range expansions and contractions in polar and subpolar species, including marine mammals (O'Corry-Crowe et al. 1997, Palsbøll et al. 1997*a*, Andersen et al. 1998, Palo 2003), and have presumably resulted in unique adaptations by polar species to an extreme and dynamic environment. Abrupt environmental change, however, is particularly challenging to organisms, populations, and entire ecosystems, even those most adept at surviving in environments that regularly experience substantial change on millennial or orbital timescales.

There is mounting evidence that the recent warming trend is driven, at least in part, by anthropogenic effects (Vinnikov et al. 1999, Intergovernmental Panel on Climate Change 2007), raising concerns over the ecological, demographic, and evolutionary consequences of what may be atypical environmental changes on polar species. Because of their small population size, slow reproductive rates, reliance on sea ice for breeding, resting, foraging, and hunting and their position at the apex of food webs, Arctic marine mammals may be particularly vulnerable to such natural and anthropogenically induced environmental change (Stirling and Derocher 1993, Tynan and DeMaster 1997, Harwood 2001, Derocher et al. 2004). There are signs that current changes in the Arctic marine environment are already having an impact on marine mammals (e.g., Derocher et al. 2004, Ferguson et al. 2005). Furthermore, many Arctic marine mammal populations are already compromised by centuries of commercial harvest.

The question facing Arctic marine mammal scientists, managers, and users is how these apex predators will deal with current and future change in their environment. Key to answering this question is (1) understanding how Arctic marine mammals dealt with past climate change, (2) determining the impact of changing climate on Arctic marine mammals over contemporary timescales, and (3) using these insights along with future climate projections to model future outcomes and make informed predictions.

The challenge is, and has been, how to conduct long-term research on such highly mobile, often elusive species that inhabit such an extreme environment. Molecular genetic approaches can provide unique and detailed insights into movement patterns, breeding behavior, genetic diversity, fitness, population viability, and evolution over several temporal and spatial scales and has found wide application in studies of Arctic marine mammals over the past few decades (Tables 1 and 2). In this paper I investigate the role of molecular genetic analysis in the assessment of the impact of climate change on the ecology and evolution of Arctic marine mammals. The paper begins with an overview of molecular ecology, including the markers and methods used, followed by a review of the primary areas of recent research and a synthesis of the collective findings into a unified model of population histories in relation to long-term climate cycles. For each area of research, the most recent information on Arctic marine mammals is reviewed, predictions of the effects of future climate change are made, and future research directions suggested. A brief treatise of ancient-DNA techniques is given. The paper concludes with a discussion of conservation issues and recommendations for new areas of research. Meta-analyses are conducted on multiple published data sets. All statistical analyses were performed in S-Plus 7 (Insightful Corporation, Seattle, Washington, USA), and all maps were created in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California, USA). Regions are defined by climate according to the Köppen climate classification system. The demarcation between Arctic and subarctic (boreal) regions is the location of the 10°C (50°F) isotherm for the warmest month.

THE PROMISE OF MOLECULAR ECOLOGY

With the development of modern molecular genetic techniques the ability to mine information about the evolution and biology of organisms from their DNA appears limitless. This paper will focus on the use of molecular genetic techniques in the study of the links between the ecology of Arctic marine mammals and climate change. Before we proceed, we must first clarify what we mean by molecular ecology in this paper. A combination of population genetics, molecular biology, and ecology, molecular ecology is the study of organismal ecology through the analysis of patterns of variation within genetic markers, typically the DNA itself. In the classical sense genetics is the study of heredity and the variation of inherited characteristics. It touches every intrinsic process in an organism and, by extension, in a population and all higher taxa. Patterns of variation within genetic loci are determined by four primary factors: (1) mutation, the process by which new variation is produced, (2) genetic drift, which is the loss of variation (over time) due primarily to random differences in survival and reproductive success among individuals, (3) gene flow, the rate of exchange of variants among groups of organisms, and (4) selection, a deterministic relationship between how free a genetic locus is allowed to vary and how essential its function is to an individual's fitness (Wright 1950, Nei 1987, Maynard Smith 1989). While the direction and extent of selective pressure is often difficult to quantify, the other three factors are theoretically measurable.

It is the properties of inheritance and variability in genetic markers and an understanding of the processes that influence them, in combination with the advent of more efficient methods to collect and analyze samples

TABLE 1. Populations of Arctic marine mammals with published information on abundance and trend that have also been the subject of molecular genetic analysis (see Table 2).

			Population size			
Species and population†	Climate region	Geographic isolation‡	Estimated historical	Time frame	Lowest estimated	Time frame
Beluga whale						
1 Cook Inlet	Subarctic	strong	1300	1979	278	(in 2005)
2 Bristol Bay	Subarctic	moderate	···	···	1555	(in 1994)
3 East Bering Sea	Subarctic	weak	···	···	···	···
4 Chukchi Sea	Arctic	weak	···	···	···	···
5 Beaufort Sea	Arctic	weak	···	···	···	···
6 St. Lawrence	Subarctic	strong	10 100	1800s	836	1984
7 Southeast Baffin Island	Arctic	moderate	8465	···	"low" hundreds	1980s
8 Eastern Hudson Bay	Arctic	weak	12 500	1854	···	···
9 High Arctic - Baffin Bay	Arctic	weak	···	···	···	···
5 Beaufort Sea	Arctic	weak	···	···	···	···
Bowhead whale						
10 Okhotsk Sea	Subarctic	strong	>3000	mid-1800s	···	···
11 Western Arctic	Arctic	strong	10 400–23 000	1848	3000	1914
Narwhal						
12 Eastern Greenland	Arctic	weak	···	···	···	···
13 Western Greenland	Arctic	weak	···	···	···	···
14 Northern Baffin Bay	Arctic	weak	···	···	···	···
Ringed seal						
15 Saimaa	Subarctic	strong	1000–2500	1893	100	early 1980s
16 Baltic Sea	Subarctic	moderate	100 000–300 000	1900	5000	mid-1980s
17 Arctic - Svalbard	Arctic	weak	···	···	···	···
Polar bear						
18 Viscount Melville Sound	Arctic	weak	···	···	···	···
19 Kane Basin	Arctic	weak	···	···	···	···
20 Norwegian Bay	Arctic	moderate	···	···	···	···
21 West Hudson Bay	Subarctic	weak	···	···	···	···
22 North Beaufort	Arctic	weak	···	···	···	···
23 South Beaufort	Arctic	weak	···	···	···	···
24 Gulf of Boothia	Arctic	moderate	···	···	···	···
25 Davis St.	Arctic	weak	···	···	···	···
26 Chukchi Sea	Arctic	weak	···	···	···	···
27 Baffin Bay	Arctic	weak	···	···	···	···
28 Foxe Basin	Arctic	weak	···	···	···	···
29 Lancaster Sound	Arctic	weak	···	···	···	···
30 Franz Josef Land	Arctic	weak	···	···	···	···
31 Svalbard	Arctic	weak	···	···	···	···
32 East Greenland	Arctic	weak	···	···	···	···
Walrus						
33 East Greenland	Arctic	···	1600	1889	···	···
34 Svalbard–Franz Josef Land	Arctic	···	···	···	few hundred	mid-1960s
35 Northwest Greenland	Arctic	···	15 000	1900	···	···
36 West Greenland	Arctic	···	16 000	1900	···	···
35 Northwest Greenland	Arctic	···	15 000	1900	···	···
Gray whale§						
37 Western North Pacific	Subarctic	strong	···	···	···	···
38 Eastern North Pacific	Arctic	strong	15 000–30 000	1846	1500–5000	1900

Note: The population numbering scheme corresponds to numbering in Table 2 and Fig. 2.

† Primarily summering grounds in the case of beluga and narwhal.

‡ A relative measure for that study of the degree of geographic isolation from the nearest neighboring population or subpopulation.

§ Seasonally subarctic or Arctic.

from wild organisms, that have propelled molecular genetic analysis to the forefront of ecological studies in recent years (Avise 1994, Dizon et al. 1997, Hanski and Gaggiotti 2004). Genetic loci can be used as markers or tags that reveal some aspect of the behavior or ecology of individuals and populations without necessarily being directly linked to or responsible for the particular trait. By examining variation within these markers, we can learn much about movement, dispersal and breeding behavior, kinship, and group structure. Furthermore, through the predictable process of inheritance, and the somewhat predictable processes of mutation and drift,

TABLE 1. Extended.

Current population size	Observed or predicted trend	Abundance/trends references
278	declining	Calkins (1986), Hobbs et al. (2000, 2006)
1642	stable	Frost and Lowry (1995), Angliss and Lodge (2004)
7986	···	Angliss and Lodge (2004)
≫3710	···	Angliss and Lodge (2004)
39 258	···	Harwood et al. (1996), Angliss and Lodge (2004)
1100	0–1%	Kingsley (2002), DFO (2005)
2018	increasing	DFO (2005)
3100	···	DFO (2005)
21 213	···	Innis et al. (2002)
39 258	···	DFO (2000)
~250	···	Woodby and Botkin (1993), MacLean (2002)
10 470	3.40%	Woodby and Botkin (1993), George et al. (2004)
>300	···	Larsen et al. (1994)
>3000	···	Heide-Jørgensen (2002)
>22 000	···	Richard et al. (1994), Born et al. (1994)
250	increasing	Kokko et al. (1999), Hyvärinen and Sipilä (1992)
5500	stable to increasing	Kokko et al. (1999)
~7 000 000	···	Reeves (1998)
161	increasing	Aars et al. (2006)
164	declining	Aars et al. (2006)
190	declining	Aars et al. (2006)
935	declining	Aars et al. (2006)
1200	stable	Aars et al. (2006)
1500	declining	Aars et al. (2006)
1523	stable	Aars et al. (2006)
1650	···	Aars et al. (2006)
2000	···	Lunn et al. (2002), Aars et al. (2006)
2074	declining	Aars et al. (2006)
2197	stable	Aars et al. (2006)
2541	stable	Aars et al. (2006)
}2997	···	Aars et al. (2006)
	···	Aars et al. (2006)
	···	Aars et al. (2006)
500–1000	stable to increasing	Born et al. (1995), NAMMCO (2004)
<2000	increasing	Gjertz and Wiig (1995)
3000	declining	Born et al. (1995), NAMMCO (2004)
500	declining	Born et al. (1995), NAMMCO (2004)
3000	declining	Born et al. (1995), NAMMCO (2004)
100	stable	Weller et al. (2002)
18 178	stable	Rugh et al. (2005), Swartz et al. (2006)

events in the history of taxa, such as speciation, population bottlenecks, colonizations, and range expansions, can leave distinctive signatures or "footprints" in the patterns of variation within these types of markers that can be detected long afterwards (Nei et al. 1975, Slatkin and Hudson 1991, Rogers and Harpending 1992, Cornuet and Luikart 1996, Hewitt 2000). Thus, the analysis of contemporary variation within genetic markers enables us to reconstruct the evolutionary and demographic history of groups of organisms including reconstruction of phylogenetic relationships and estimation of historical population size (Nei 1987, Templeton 1998, Roman and Palumbi 2003, Drummond et al. 2005). Such reconstructions are still hypotheses, however, based on models of evolution and demography that make several assumptions, some overly simplistic, many unverifiable. Developments in the field of molecular biology and protein chemistry now enable us to actually revisit past worlds. So-called "ancient-DNA" methods, in combination with zooarchaeological investigations

TABLE 2. Populations of Arctic marine mammals that have been the subject of molecular genetic investigations of genetic diversity and population subdivision and for which there is good information on abundance and trend.

			mtDNA diversity	
Species and population†	mtDNA differentiation‡	Microsatellite differentiation‡	No. base pairs	H_{M}
Beluga whale				
1 Cook Inlet	high	high	410	0.52
2 Bristol Bay	low	intermediate	410	0.16
3 East Bering Sea	low	intermediate	410	0.49
4 Chukchi Sea	intermediate	low	410	0.74
5 Beaufort Sea	intermediate	low	410	0.70
6 St. Lawrence	high	high	234	0.51
7 Southeast Baffin Island	intermediate	low	234	0.69
8 Eastern Hudson Bay	intermediate	low	234	0.68, 0.57
9 High Arctic–Baffin Bay	high	low	234	0.78
5 Beaufort Sea	high	low	234	0.73
Bowhead whale				
10 Okhotsk Sea	intermediate	intermediate	397	0.61
11 Western Arctic	intermediate	intermediate	397	0.93
Narwhal				
12 Eastern Greenland	high	···	287, RFLP	0.00
13 Western Greenland	intermediate	···	287, RFLP	0.50
14 Northern Baffin Bay	intermediate	···	287, RFLP	0.41
Ringed seal				
15 Saimaa	···	···	416	0.62
16 Baltic Sea	···	low	416	0.98
17 Arctic Svalbard	···	low	416	1.00
Polar bear				
18 Viscount Melville Sound	···	low	···	···
19 Kane Basin	···	low	···	···
20 Norwegian Bay	···	intermediate–high	···	···
21 West Hudson Bay	···	low	···	···
22 North Beaufort	···	low	···	···
23 South Beaufort	···	low	···	···
24 Gulf of Boothia	···	low	···	···
25 Davis St.	···	low	···	···
26 Chukchi Sea	···	low	···	···
27 Baffin Bay	···	low	···	···
28 Foxe Basin	···	low	···	···
29 Lancaster Sound	···	low	···	···
30 Franz Josef Land	···	low	···	···
31 Svalbard	···	low	···	···
32 East Greenland	···	low	···	···
Walrus				
33 East Greenland	zero–low	intermediate	RFLP	0.19
34 Svalbard–Franz Josef Land	zero–low	low–intermediate	RFLP	0.28
35 Northwest Greenland	high	high	RFLP	0.19
36 West Greenland	high	intermediate	RFLP	0.68
35 Northwest Greenland	high	intermediate	RFLP	0.37
Gray whale§				
37 Western North Pacific	high	intermediate	523	0.77
38 Eastern North Pacific	high	intermediate	523	0.95

Notes: Only populations with ≥ 20 samples are included. The population numbering scheme corresponds to numbering in Table 1 and Fig. 2. RFLP stands for restriction fragment length polymorphism. When combined with a value, e.g., 287, this means that this study used both sequence analysis (examined 287 base pairs) and RFLP analysis.

† Primarily summering grounds in the case of beluga and narwhal.

‡ A relative categorization for that study of the lowest level of differentiation from a neighboring population or subpopulation. Parameter estimates (e.g., F_{st}, ϕ_{st}, H_{st}) were used when possible; otherwise, P values were used. Categorizations were more subjective in studies in which few populations were compared.

§ Seasonally subarctic or Arctic.

(Murray 2008) and reconstructions of past climatic and environmental conditions (e.g., Clark et al. 1999) offer fantastic opportunities to reconstruct species distributions, population histories, and movement patterns at different times in the Arctic's history.

Theoretical and empirical studies on the importance of allelic diversity in reproductive success, survival, and natural selection (e.g., Lacy 1993, Westemeier et al. 1998) indicate that estimating levels of diversity at multiple markers can also be useful in assessing individual fitness

Table 2. Extended.

Microsatellite diversity		
No. loci	H_E	Genetics references
8	0.73	O'Corry-Crowe et al. (1997); G. O'Corry-Crowe (*unpublished data*)
8	0.74	O'Corry-Crowe et al. (1997); G. O'Corry-Crowe (*unpublished data*)
8	0.77	O'Corry-Crowe et al. (1997); G. O'Corry-Crowe (*unpublished data*)
8	0.79	O'Corry-Crowe et al. (1997); G. O'Corry-Crowe (*unpublished data*)
8	0.80	O'Corry-Crowe et al. (1997); G. O'Corry-Crowe (*unpublished data*)
5, 15	0.58	Brown-Gladden et al. (1997, 1999), deMarch and Postma (2003)
5	0.71	Brown-Gladden et al. (1997, 1999)
5, 15	0.76, 0.66	Brown-Gladden et al. (1997, 1999), deMarch and Postma (2003)
5	0.72	Brown-Gladden et al. (1997, 1999)
5	0.70	Brown-Gladden et al. (1997, 1999)
3	0.75	LeDuc et al. (2005)
3	0.80	LeDuc et al. (2005)
...	...	Palsbøll et al. (1997*a*)
...	...	Palsbøll et al. (1997*a*)
...	...	Palsbøll et al. (1997*a*)
8	0.25	Palo (2003), Palo et al. (2003)
8	0.80	Palo et al. (2001), Palo (2003)
8	0.82	Palo et al. (2001), Palo (2003)
16	0.66	Paetkau et al. (1999)
16	0.71	Paetkau et al. (1999)
16	0.67	Paetkau et al. (1999)
16	0.67	Paetkau et al. (1999)
16	0.70	Paetkau et al. (1999)
16	0.69	Paetkau et al. (1999)
16	0.72	Paetkau et al. (1999)
16	0.63	Paetkau et al. (1999)
16	0.70	Paetkau et al. (1999)
16	0.68	Paetkau et al. (1999)
16	0.66	Paetkau et al. (1999)
16	0.70	Paetkau et al. (1999)
16	0.66	Paetkau et al. (1999)
16	0.69	Paetkau et al. (1999)
16	0.69	Paetkau et al. (1999)
11	0.61	Andersen et al. (1998), Born et al. (2001)
11	0.64	Andersen et al. (1998), Born et al. (2001)
11	0.65	Andersen et al. (1998), Born et al. (2001)
12	0.60	Andersen and Born (2000), Born et al. (2001)
12	0.63	Andersen and Born (2000), Born et al. (2001)
6	0.72	LeDuc et al. (2002), Lang et al. (2005); A. Lang (*unpublished data*)
6	0.76	LeDuc et al. (2002), Lang et al. (2005); A. Lang (*unpublished data*)

and the evolutionary potential of populations, sometimes without the need to invoke the function of individual genes (Slate and Pemberton 2002, but see Coltman and Slate 2003). More direct assessments of the genetic component of fitness and population viability require the mapping of individual genes or groups of genes that underlie variation in specific qualitative traits and more complex, quantitative traits (Mackay 2001).

By examining variation within genetic markers we can thus potentially establish how Arctic marine mammal species emerged and how past climate change shaped their population histories. We can also describe many aspects of the ecology of extant populations and detect behavioral and ecological change in these populations as it occurs. To do this, we must be able to access the DNA molecule and decipher the patterns of variation within.

Marker choice

The rate at which different regions of the genome mutate, their mode of inheritance, and whether they are under selection or not provide a potentially endless supply of genetic tools applicable to a wide range of questions in wildlife ecology. This paper will focus on studies that used markers that are believed to be under weak or no selection. By excluding the confounding influence of selection, variation within these selectively neutral makers in populations is shaped by the forces of mutation, genetic drift, and gene flow. Accounting for two enables the estimation of the third. Highly variable nuclear markers, such as mini- and microsatellite loci, enable genetic "fingerprinting" of individuals that can aid in the analysis of kinship and parentage and in the estimation of population and group size through genetic mark–recapture (Amos et al. 1993, Palsbøll et al. 1997*b*). These biparentally inherited markers, as well as other loci with more moderate levels of variability, can also be used in assessing dispersal and gene flow among groups of organisms. Examples include the control region of the maternally inherited mitochondrial genome (mtDNA), gene introns, and individual polymorphic sites (e.g., single nucleotide polymorphisms [SNPs], amplified fragment length polymorphisms [AFLPs]) on the nuclear genome (Palumbi and Baker 1994, Baker and Medrano-González 2002, Morin et al. 2007). More slowly evolving regions retain historical signatures better. These tend to be conserved coding regions of genes and allow the reconstruction of phylogenetic relationships among populations and higher taxa and include the more conserved regions of mtDNA, the paternally inherited Y chromosome, and slowly mutating individual sites across the entire genome (e.g., AFLPs) (LeDuc et al. 1999, Kingston and Rosel 2004).

Molecular genetic techniques

Advances in the fields of molecular biology over the past few decades have enabled us to proceed from the assessment of variation within gene products, such as enzymes and blood proteins (e.g., Allendorf et al. 1979, Simonsen et al. 1982), to screen for variation within both the coding and noncoding regions of the genetic material itself, the DNA. Polymerase chain reaction (PCR) (Saiki et al. 1988) revolutionized the screening of DNA polymorphism, such that only small pieces of tissue, including hair and skin, are now required for genetic analysis. This technology, plus the development of remote biopsy sampling and more efficient tissue preservation methods (e.g., Amos and Hoelzel 1991), has been a particular boon to the study of marine mammals, especially relatively inaccessible polar species. Continued developments in protein chemistry and molecular biology enable us to extract DNA from baleen (Rosenbaum et al. 1997) and of both the predator and its prey from scat (Reed et al. 1997, Deagle et al. 2005) and to retrieve DNA from ancient material, including extinct and subfossil organisms (Höss and Pääbo 1993, Poinar 2002). Increasingly automated systems allow high sample throughput, while continuing software development in conjunction with ever-developing theoretical and quantitative approaches enable more efficient data handling and analysis. The full power of these methods has yet to be brought to bear on ecological investigations of the most remote organisms, including Arctic marine mammals. In the subsequent sections, recent and future applications of molecular genetic techniques to Arctic marine mammal ecology and evolution are reviewed and discussed.

POPULATION SUBDIVISION, DISPERSAL, AND GENE FLOW

Initial responses by Arctic marine mammals to climate change will likely be behavioral and physiological, followed by ecological and phenotypic (e.g., morphology, life history). While physical limitations and energetic demands set an upper bound on dispersal distance such that groups of Arctic marine mammals separated by very long distances experience limited genetic exchange, molecular studies are revealing that population structure in these highly vagile species is also shaped by behavioral and other environmental parameters, including natal homing and sea ice.

Although telemetry studies indicate that Arctic cetaceans possess long-distance dispersive capabilities (Suydam et al. 2001, Laidre et al. 2008), analyses of patterns of variation within mtDNA have demonstrated strong maternally directed philopatry to traditional summering grounds in beluga whales, *Delphinapterus leucas* (see Plate 1) (Brennin et al. 1997, Brown Gladden et al. 1997, O'Corry-Crowe et al. 1997, 2002, deMarch and Postma 2003; Table 2) and narwhals, *Monodon monoceros* (Palsbøll et al. 1997*a*). This tendency to return to the same locations generation after generation is likely driven by the predictable availability of resources, with the result that these summering concentrations eventually become demographically discrete populations. A number of studies found levels of differentiation within several microsatellite markers in beluga whales that were much lower than levels in mtDNA, suggesting more extensive male-mediated gene flow, possibly occurring on common wintering areas (Brown Gladden et al. 1999, deMarch et al. 2002, deMarch and Postma 2003). Lower heterogeneity in nuclear markers may also be the result of limited divergence through genetic drift because of the larger effective population size (N_e) of nuclear compared to haploid markers. Using mtDNA and microsatellites, Palsbøll et al. (2002) suggested that matrifocal group structure exists in beluga whales and cautioned that unwittingly sampling kin groups could bias studies of population genetic structure.

Sea ice acts as both a substrate and a vehicle for travel and gene flow in polar bears, *Ursus maritimus* (Stirling and Derocher 1993, Patkeau et al. 1995, 1999, Mauritzen et al. 2002). Despite the long-distance movements that have been recorded for individual bears (e.g., Mauritzen et al. 2002), analysis of variation within nuclear markers revealed restricted gene flow among several local populations of this species (Paetkau et al. 1995, 1999; Table 2). A hierarchical analysis of subdivision revealed that dispersal, when it occurs, is influenced by major landscape features. The enclosed insular environment of the Canadian High Arctic archipelago was characterized by subdivision over relatively small spatial scales, indicating short-range dispersal. By contrast, limited structure observed throughout the Palaearctic and western Nearctic suggests that the more open marine environment of the Alaskan, Russian, and European Arctic facilitates long-range dispersal (Paetkau et al. 1999). This was confirmed in a recent study of Beaufort and Chukchi Sea bears (Cronin et al. 2006). Interestingly, a recent study on a seasonally marine Arctic mammal, the Arctic fox, *Alopex lagopus*, revealed limited genetic subdivision over large spatial scales (>1000 km), indicating extensive movements and dispersal (Dalén et al. 2005). This raises the intriguing possibility that dispersal in some Arctic fox populations may be facilitated by sea ice, perhaps in association with polar bears.

Genetic studies are revealing that long-distance dispersal and interbreeding may be extensive in many ice-breeding pinnipeds and that sea ice may act as both a vehicle for and barrier to exchange. High genetic diversity and limited structure over broad geographic scales have characterized recent molecular genetic studies on a number of ice seals, including ringed seals, *Phoca hispida* (Palo et al. 2001, Davis 2004; Table 2); harp seals, *Pagophilus groenlandicus* (Perry et al. 2000); and spotted seals, *Phoca largha* (O'Corry-Crowe and Westlake 1997, Mizuno et al. 2003). These findings imply recurrent exchange over long distances, a pattern consistent with the long-distance movements of these species recently recorded by satellite telemetry (Lowry et al. 1998, Teilmann et al. 1999). Gene flow among geographically discrete breeding concentrations in these ice seals is likely facilitated by the annual movements of sea ice. The ability to haul out on a mobile substrate can result in passive movements over long distances. In some studies, however, marker choice and small sample sizes in conjunction with very large population sizes (e.g., Perry et al. 2000) may have contributed to the failure to detect subdivision. Significant subdivision was recently observed in bearded seals, *Erignathus barbatus*, suggesting that this ice-breeding phocid does not move extensively between breeding sites and that multiyear ice is an effective barrier to gene flow (Davis 2004). Finally, limited differentiation at mitochondrial and nuclear loci in eastern north Atlantic (Franz Joseph Land and Svalbard) walruses, *Odobenus rosmarus*, may reflect substantial individual exchange and recent founder events associated with recovery from large-scale commercial hunting in the early 20th century (Andersen et al. 1998; Tables 1 and 2). Conversely, significant genetic differences between northwestern and eastern Greenland walrus indicate that dense polar pack ice in the polar basin is an effective barrier to gene flow, while differentiation between western and northwestern Greenland animals indicate strong behavioral philopatry to local concentration areas (Cronin et al. 1994, Andersen et al. 1998, Andersen and Born 2000).

Reconstructing the phylogenetic relationships among genetic lineages and mapping their contemporary geographic distributions adds a temporal dimension to the interpretation of genetic differentiation. Over the past two decades this phylogeographic approach (sensu Avise et al. 1987) has illuminated the species and population histories of many high-latitude organisms (e.g., Bernatchez and Wilson 1998, Weider and Hobæk 2000, Stamford and Taylor 2004), including marine mammals. The star-like phylogenies of mtDNA lineages observed in beluga whales and the substantial phylogeographic partitioning of these lineages today argue that the origins of separate summering concentrations date back to postglacial expansion from refugial populations and indicate limited dispersal among these summering groups for long periods (Brennin et al. 1997, Brown Gladden et al. 1997, O'Corry-Crowe et al. 1997, 2002). In some cases (e.g., Cook Inlet, Gulf of St. Lawrence) the genetic evidence indicated isolation of populations over evolutionary timescales. Similarly, the phylogeography of mtDNA variation in walruses 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 (Cronin et al. 1994, Andersen et al. 1998).

Conclusion

While phenotypic, behavioral, and ecological differences among Arctic marine mammals indicate that environmental change will affect each species in a unique way, sea ice is a dominant variable in all. Sea ice can act as a barrier to movement, dispersal, and gene flow or as a platform and vehicle for active and passive movement, dispersal, and genetic exchange in marine mammals. Changes in sea ice will affect these behaviors. Molecular genetic tools enable the rapid analysis of dispersal and gene flow in Arctic species that facilitate the assessment of demographic and ecological differences among populations and the detection of responses to environmental change.

Future directions

Considering their population histories, future molecular genetic studies must focus on nonequilibrium approaches (e.g., Paetkau et al. 1995, Pritchard et al. 2000, Gaggiotti et al. 2002, Wilson and Rannala 2003) to the genetic estimation of dispersal and interbreeding rates, past and present, in Arctic marine mammals. While geographic isolation and behavioral philopatry appear to be the dominant diversifying forces over long temporal scales, future climate-related changes in the Arctic may promote more dynamic relationships among local breeding groups and feeding aggregations, highlighting the need for alternative models of subdivision and dynamics, including meta-population models (Hanski and Gaggiotti 2004), for individual-based approaches to resolving population structure (Strand 2002) and for closer collaboration among geneticists, field biologists, oceanographers, and climatologists to measure, monitor, and explain dispersal and gene flow in these apex predators in real time.

Research to date has been characterized by single-species investigations, often conducted within a single region (Table 1). To better understand system-wide forcing on decadal as well as millennial time scales, regional and basin-wide comparative phylogeographic studies (Avise 1998, Bermingham and Moritz 1998, Hewitt 2000, Weider and Hobæk 2000) are necessary and meta-analyses of population subdivision across many species at multiple trophic levels are required, in combination with more studies of dispersal and subdivision within and among historic and prehistoric populations using ancient-DNA technology.

Prediction

Changes in biological productivity and the seasonal distribution and abundance of sea ice will likely affect movement patterns, hunting and foraging strategies, and breeding behavior of Arctic marine mammals. These in turn could affect gene flow and dispersal and group and population structure.

Ancient-DNA Studies of Arctic Marine Mammals

Arctic and boreal marine mammals are ideal subjects for so-called ancient-DNA analyses for several reasons. First, some species, such as Arctic spotted seals and boreal harbor seals (*P. vitulina*), Steller sea lions (*Eumetopias jubatus*), and fur seals (*Callorhinus ursinus*), congregate at discrete terrestrial sites to breed, rest, or molt. Traditional return to these sites over generations is common, leading to a build-up of osteological material, conveniently preserved in stratified form that allows the collection of entire time series. Secondly, all Arctic and boreal marine mammals have been hunted by man, some, such as the Steller sea cow (*Hydrodamalis gigas*), to extinction. Their size often required bringing the carcass to shore to be butchered. Furthermore, their bones were themselves of great use in an environment short on malleable materials (Murray 2008). This led to the accumulation of bones and teeth of marine mammals at discrete coastal sites (Storå and Ericson 2004), further facilitating sample collection. Finally, the large size and high density of many marine mammal bones combined with the Arctic's cold, dry environment improve preservation of the fragile DNA molecule (Smith et al. 2001, Poinar 2002) and increase the likelihood of finding material.

An ongoing ancient-DNA investigation of bowhead whale bones from Svalbard is revealing levels of mtDNA diversity in this population throughout the Holocene that are similar to the high levels found in the western Arctic population today (T. Borge, L. Bachmann, and Ø. Wigg, *unpublished data*). These findings suggest the maintenance of large populations in the northeast Atlantic prior to 19th century commercial whaling that almost extirpated this species. Crossing to the northwest Atlantic, genetic analysis of whale bones recovered from a sunken Basque galleon off Canada's Labrador coast revealed that 16th century Basque whalers were mainly hunting bowhead whales and not right whales (*Eubalaena glacialis*), as was earlier inferred from osteological studies of the same material (Rastogi et al. 2004). These findings have prompted a revision of the impact of Basque whaling on both species. In the North Pacific a recent genetic study of marine mammal bones recovered from an ancient village site documented the presence of a number of Arctic marine mammals much farther south than their current ranges: beluga whales and spotted seal bones were identified in a 3000-year-old midden in the Aleutian Islands, in Alaska, USA (A. Frey, *unpublished data*).

Evolutionary History, Population Dynamics, and Population Viability

As well as influencing dispersal patterns and gene flow, climate change and the associated environmental changes in the Arctic and subarctic will likely affect population size and range and reproduction and survival in marine mammals with potentially dramatic consequences for individual fitness and population viability. As well as providing unique perspectives on the evolutionary and demographic history of populations, molecular genetic investigation can provide insight into the genetic consequences of this history, insight integral to assessing extinction risk and modeling the future demography and genetics of populations and ultimately to designing effective conservation strategies.

Climate warming will likely further isolate small, geographically distinct populations of Arctic marine mammals at the southern margins of species ranges (Fig. 1C), with consequences for diversity loss and adaptive potential. Populations lose genetic diversity at a rate inversely proportional to population size (Frankham 1996), while peripheral populations in marginal habitats are typically genetically impoverished (Johannesson and André 2006). This paucity of genetic variability in turn may compromise a population's ability to deal with new challenges, including environmental change, disease, and an array of human impacts on the environment. Furthermore, through increased inbreeding, deleterious and even lethal recessive alleles may be expressed at higher frequencies in small populations, thus reducing individual viability and fitness and in turn further compromising a population's viability (Lande and Barrowclough 1987, Lacy 1997, Westemeier et al. 1998). How a population becomes small is also critical to genetic viability issues. Naturally small populations, for example, may no longer suffer from increased homozygosity for lethal or sublethal recessives as the reduced fitness of their genotypes increase the likelihood that these deleterious alleles will eventually be purged from the population, resulting in a highly inbred population that does not exhibit inbreeding depression (Lacy 1997). Such populations are, however, still at risk from a limited ability to adapt to environmental change because they have low levels of genetic variability. Conversely, a large population that suffers a dramatic decline in numbers may go through a genetic "bottleneck" in which much adaptive as well as neutral genetic variation is lost relatively rapidly (Nei et al. 1975, Cornuet and Luikart 1996, Miller and Hedrick 2001). Such populations are simultaneously at risk for both inbreeding depression and reduced evolutionary potential.

Continued warming may also result in secondary contact between large, allopatrically divergent High Arctic populations (Fig. 1C). In contrast to the genetic consequences of isolation and small size, such contact between genetically divergent populations will increase heterozygosity. This may increase vigor (heterosis) at the individual level and evolutionary potential at the population level, particularly in new or altered environments, but in certain circumstances may result in outbreeding depression in which coadapted gene complexes are broken apart (Barton 2001).

Recurrent glaciations in combination with a more recent history of overharvesting indicate that many of these scenarios have likely occurred in Arctic marine mammal species. Today, several populations are depleted, and many are small and geographically isolated (Table 1, Fig. 2). Most molecular studies of Arctic marine mammals to date have measured diversity in (nearly) neutral markers, primarily the mtDNA control region and microsatellites (Table 2). These markers are ideally suited to reconstructing the demographic and evolutionary histories of populations and in some cases may be correlated with fitness and evolutionary potential (Coltman et al. 1998, Slate and Pemberton 2002, but see Reed and Frankham 2001, Coltman and Slate 2003, Hoffman et al. 2006). Tables 1 and 2 summarize published studies on Arctic marine mammals in which estimates of genetic subdivision and neutral diversity can be viewed in relation to population location, size, and trend. A meta-analysis was conducted on these data to test whether there was a significant relationship between neutral diversity (mtDNA control region sequence haplotypic diversity [H_M] and microsatellite expected heterozygosity [H_E]) and population size, climate region, and study unit (i.e., study design and species). Only populations ($n = 38$) with $\geq$20 samples were included in the analysis, multiple regressions were performed to determine whether choice of study or geographic region contributed substantially to the variance in genetic diversity, and outliers were identified by plotting the square root of the residuals against the fitted values.

A significant relationship was found between current population size and both nuclear (H_E, $r^2 = 0.19$, $P = 0.011$) and mtDNA (H_M, $r^2 = 0.24$, $P = 0.044$) diversity (Fig. 3A, B). No significant relationship was found between historical (i.e., pre-decline or early-decline) population size and nuclear diversity (H_E, $r^2 = 0.24$, $P = 0.122$; Fig. 3C). By contrast, a strong relationship was found between historical population size and mtDNA diversity (H_M, $r^2 = 0.62$, $P = 0.012$; Fig. 3D). A significant relationship was also found between climate region and mtDNA diversity (H_M, $r^2 = 0.29$, $P = 0.029$), with lower diversity in the subarctic compared to the Arctic, but not between climate region and nuclear diversity (H_E, $r^2 = 0.03$, $P = 0.32$). Study design also appeared to contribute to the variance in genetic diversity. This was most evident in multiple regressions in which the independent variables (study, climate region, and current or historic population size) explained most of the variance observed in neutral genetic diversity, especially in the case of mtDNA diversity in which more than 99% of haplotypic diversity could be explained by historic population size, climate region, and differences among the individual studies (H_M, $r^2 = 0.997$, $P = 0.009$). Scrutiny of these linear models, including the significant outliers (Fig. 3), bares some discussion.

High genetic diversity is a feature of many ice seal species (O'Corry-Crowe and Westlake 1997, Perry et al. 2000, Palo et al. 2001, Mizuno et al. 2003) and suggests historically large population sizes. Palo et al. (2003) concluded that the much lower (69% less) microsatellite diversity found in the Lake Saimaa ringed seal (*Phoca hispida saimensis*) compared to marine populations most likely reflected a gradual loss of diversity since postglacial isolation more than 9500 years ago in what was probably never a large population. That this lacustrine seal possesses unusually low heterozygosity relative to historical (Fig. 3C) as well as current population size (Fig. 3A) suggests that some of the loss is due to the current population bottleneck this species is experiencing as a result of a human-induced, 20th century crash.

Low mtDNA diversity in narwhals has been ascribed to small refugial populations during a previous glacial maximum (Palsbøll et al. 1997*a*). Similarly, the lower diversity found within Okhotsk Sea bowhead whales compared to the western Arctic population might reflect relatively small population size throughout the Holocene or perhaps a 19th century population bottleneck due to commercial whaling (LeDuc et al. 2005). By contrast, the much higher diversity observed within the larger western Arctic population indicates that this population most likely did not experience a genetic bottleneck due to commercial hunting (Rooney et al. 1999, 2001, LeDuc et al. 2005) and underwent an expansion initiated in the middle to late Pleistocene (Rooney et al. 2001). The Pacific gray whale (*Eschrichtius robustus*), although only a seasonal visitor to Arctic and subarctic waters, I believe deserves mention here. Similar to bowheads, the western Pacific population experienced a dramatic decline and now numbers approximately 100 individuals, while the eastern Pacific population recovered from declines wrought by commercial whaling and has stabilized at approximately

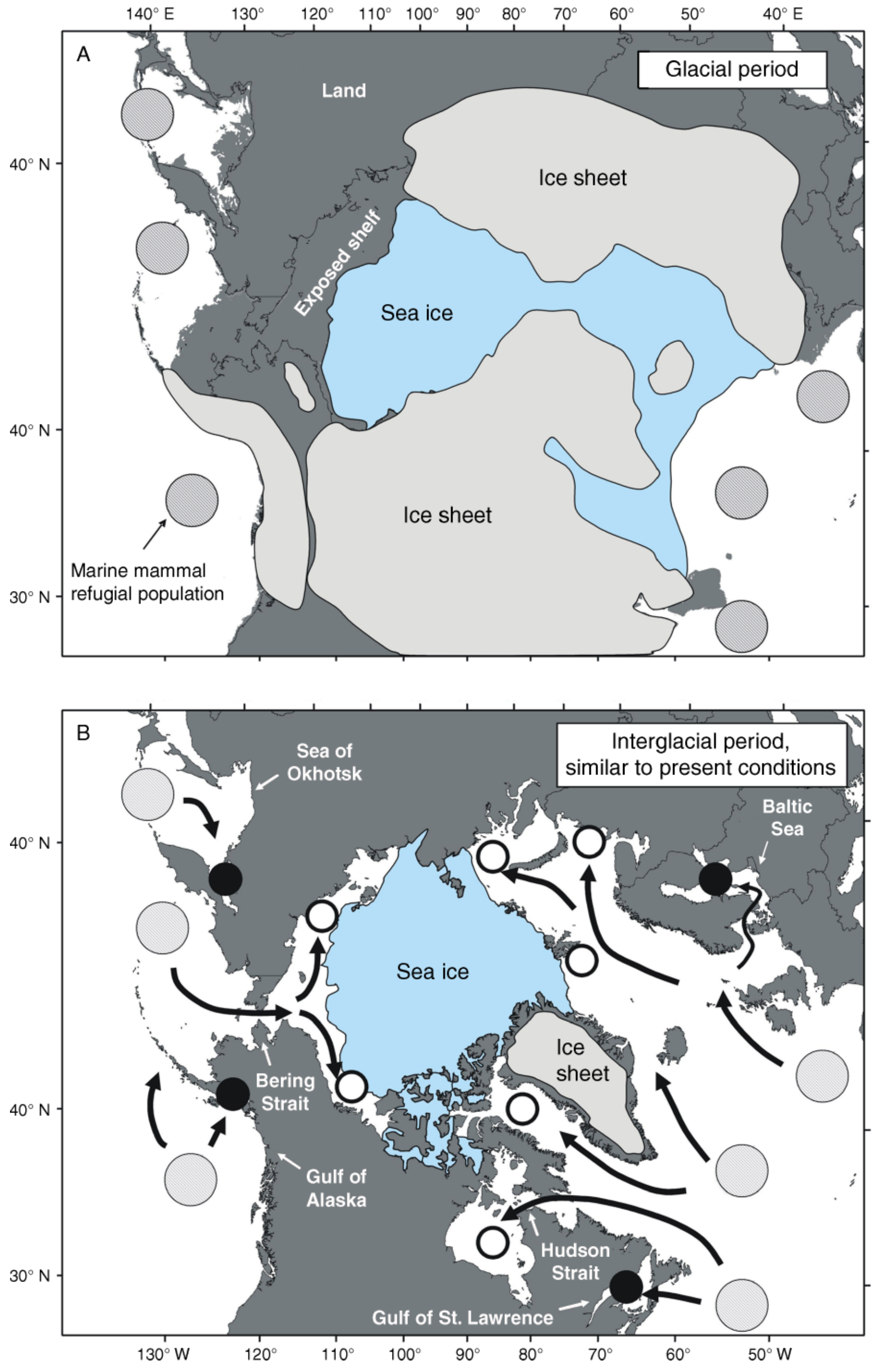

FIG. 1. (A) The Arctic during a glacial period and hypothesized locations of marine mammal populations. Conditions presented reflect the last glacial maximum (16 000–22 000 yr BP). Sea levels were 120 m below current levels, exposing extensive areas of the continental shelf (dark gray), ice sheets (light gray) covered much of the Nearctic and extensive parts of the Palearctic (Pielou 1991, Mann and Hamilton 1995), and summer sea ice (blue) extended far south into the North Atlantic (NOAA, paleoclimatology program). The location of six hypothetical refugial populations, three in the North Pacific and three in the North Atlantic, are indicated (gray shaded circles). (B) The Arctic during an interglacial in which climate matches contemporary conditions. Postglacial expansion routes from refugial populations are indicated by black arrows; the location of populations geographically isolated by land masses are indicated by black circles. The locations of highly migratory High Arctic populations are indicated by open circles with thick outlines. Other geographical features and the locations of the refugial populations during glacial maxima are represented as in (A), with the refugial populations in lighter gray, to indicate that they no longer exist. (C) The Arctic during an interglacial period, in which climate is warmer than contemporary conditions. The further reduction in sea ice facilitates dispersal and gene flow (black arrows) among High Arctic populations (open circles). Conversely, it may lead to the demise of Low Arctic or subarctic populations (black circles) isolated in small water masses. Geographical features are represented as in (A).

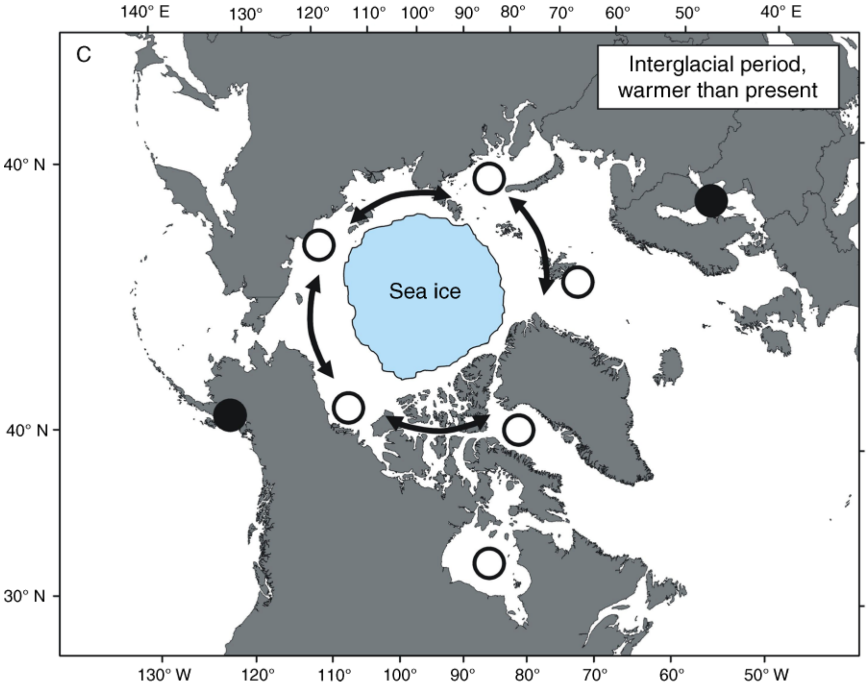

FIG. 1. Continued.

20 000 whales (Weller et al. 2002, Rugh et al. 2005). As with bowheads, the smaller western population has lower diversity than its Arctic counterpart (LeDuc et al. 2002; Tables 1 and 2). Although lower, the western population's contemporary mtDNA variation likely reflects a much larger historical population (Fig. 3B).

The majority of beluga whale populations studied to date maintain comparable levels of genetic diversity regardless of population size. A few western Alaska populations (e.g., Bristol Bay) have relatively low mtDNA diversity that may reflect small founding populations (Fig. 3B). There are two small isolated populations, however, that face an uncertain future with little hope of rescue from other populations. The population of beluga whales in Cook Inlet, Alaska, has witnessed a dramatic decline and a substantial reduction in its range in recent decades, has shown no signs of recovery since protection in 1999, is likely still declining, and today may number as few as 200 mature individuals (Hobbs et al. 2000, Rugh et al. 2000, Lowry et al. 2006). There is little evidence as yet, however, that the recent declines have precipitated a dramatic loss in neutral diversity (O'Corry-Crowe et al. 1997, 2002; Tables 1 and 2). Conversely, the small isolated beluga population in the St. Lawrence River estuary, Canada, possesses lower levels of mtDNA and microsatellite variation than other eastern Arctic beluga populations (Brown Gladden et al. 1997, 1999, deMarch and Postma 2003). Large population size prior to commercial whaling (DFO 2005; Table 1) suggests that these lower levels of neutral diversity are more a consequence of 19th and 20th century declines from overharvest than accumulated genetic drift in a naturally small population (Fig. 3D). It is unclear whether genetic factors are currently impeding recovery in either population. We can, however, predict that a prolonged period of small population size in the Cook Inlet population and the further decline of either population will likely result in the loss of additive genetic variation and increased inbreeding, which will likely hinder recovery and adaptation in a changing environment.

None of the 19 recognized polar bear populations can be considered large, few exceed 2000 individuals, and a number are currently in the low hundreds and in decline (Aars et al. 2006). These smaller subpopulations, however, appear to have retained levels of microsatellite diversity similar to those of much larger populations (Paetkau et al. 1999; Tables 1 and 2). In some, such as Kane Basin in the Canadian High Arctic, this is likely aided by continued gene flow with larger populations. In others, such as the Norwegian Bay population, which is differentiated from other polar bear populations, it may reflect larger historical population size. Continued decline in these populations, however, may result in increased inbreeding and a potentially rapid loss of adaptive as well as neutral polymorphism.

As with other Arctic marine mammals, Atlantic walrus (*Odobenus rosmarus rosmarus*) suffered dramatic declines in numbers and reductions in range from overharvest in the 19th and 20th centuries, with some populations near extinction in the middle of the last century (Born et al. 1995, Gjertz and Wiig 1995). Some

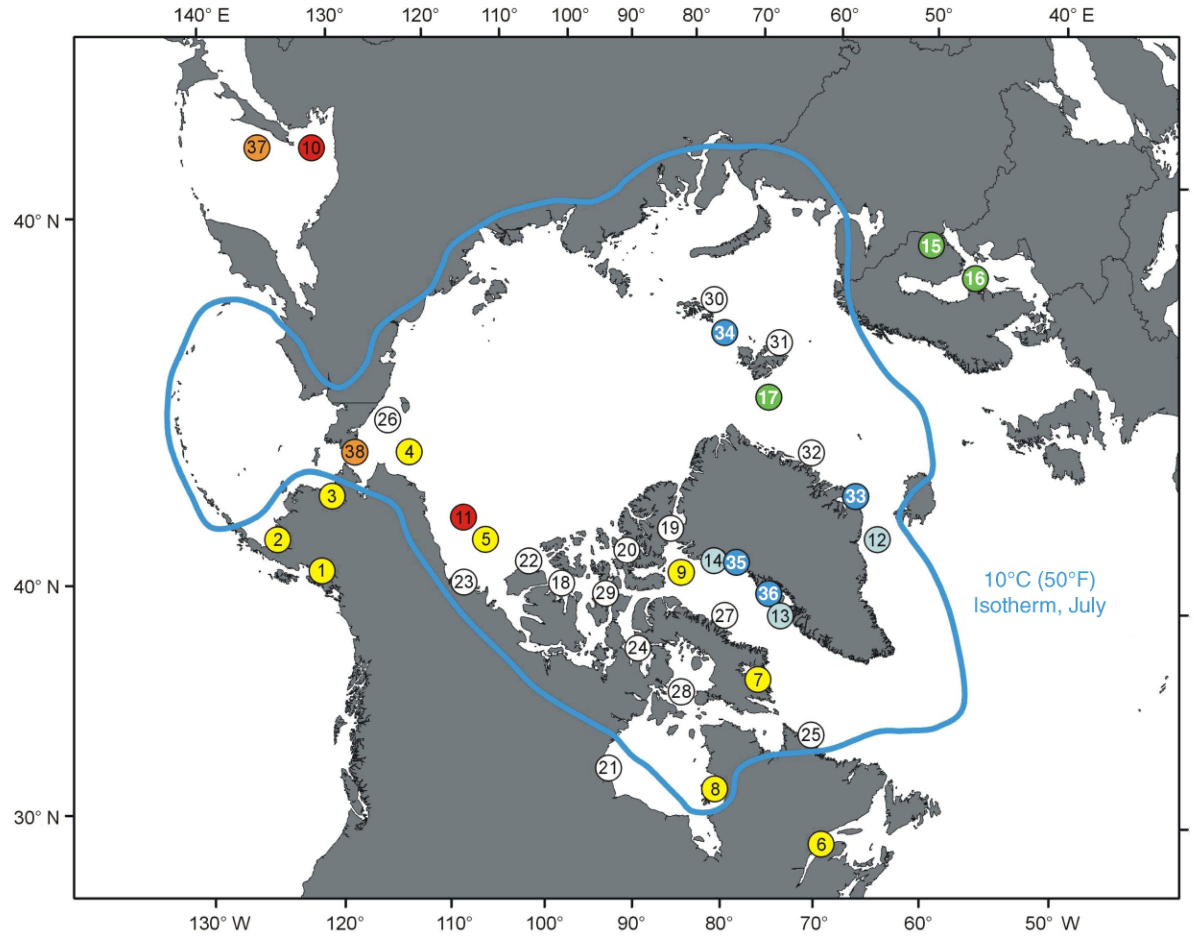

FIG. 2. The location of 38 Arctic marine mammal populations with published data on abundance, genetic differentiation, and genetic diversity. Beluga whale populations ($n = 9$) are in yellow, polar bear populations ($n = 15$) are in white, ringed seal populations ($n = 3$) are in green, narwhal populations ($n = 3$) are in light blue, walrus populations ($n = 4$) are in dark blue, bowhead whale populations ($n = 2$) are in red, and gray whale populations ($n = 2$) are in orange. Numbers correspond to populations listed in Tables 1 and 2. The 10°C isotherm, demarking the Arctic–subarctic boundary is highlighted.

populations are recovering, most likely aided by immigration from healthier populations. Others are still in decline. While molecular genetic investigations have revealed much about population subdivision, current estimates of neutral diversity provide little insight into the demographic and genetic history of individual populations (Andersen et al. 1998, Andersen and Born 2000, Born et al. 2001). Of note, the small, declining population in west Greenland harbors substantially more mtDNA haplotypic diversity than other, larger populations (Tables 1 and 2). Whether this reflects a much larger historical population size or continued gene flow with larger populations to the west is unclear (Andersen and Born 2000).

Conclusion

Differences in study design (marker number, sample size, etc.), unquantified species effects including differences in N_e/N, and potential publication bias complicate meta-analyses of genetic diversity (Coltman and Slate 2003, Rosenberg 2005). Nevertheless, the rudimentary analysis presented here is instructive. Neutral or near-neutral genetic diversity in Arctic marine mammals has been primarily shaped by the following four factors: (1) Quaternary history, including the size of refugial populations during glacial maxima and the size and composition of founding populations following the LGM; (2) long-term effective population size as smaller populations in general tend to harbor lower neutral diversity than larger ones; (3) geographic location, in that subarctic populations tend to be isolated in marginal seas and estuaries or landlocked in lakes and are small and harbor lower neutral diversity than Arctic populations; and (4) extent and timing of recent declines as a number of populations retained substantial diversity despite the depredations of man during the 19th and 20th centuries. Further, it emerged that some regions have small, depleted, and/or declining populations of a number of species. These include eastern Greenland (walrus, narwhal), Hudson Bay (beluga and

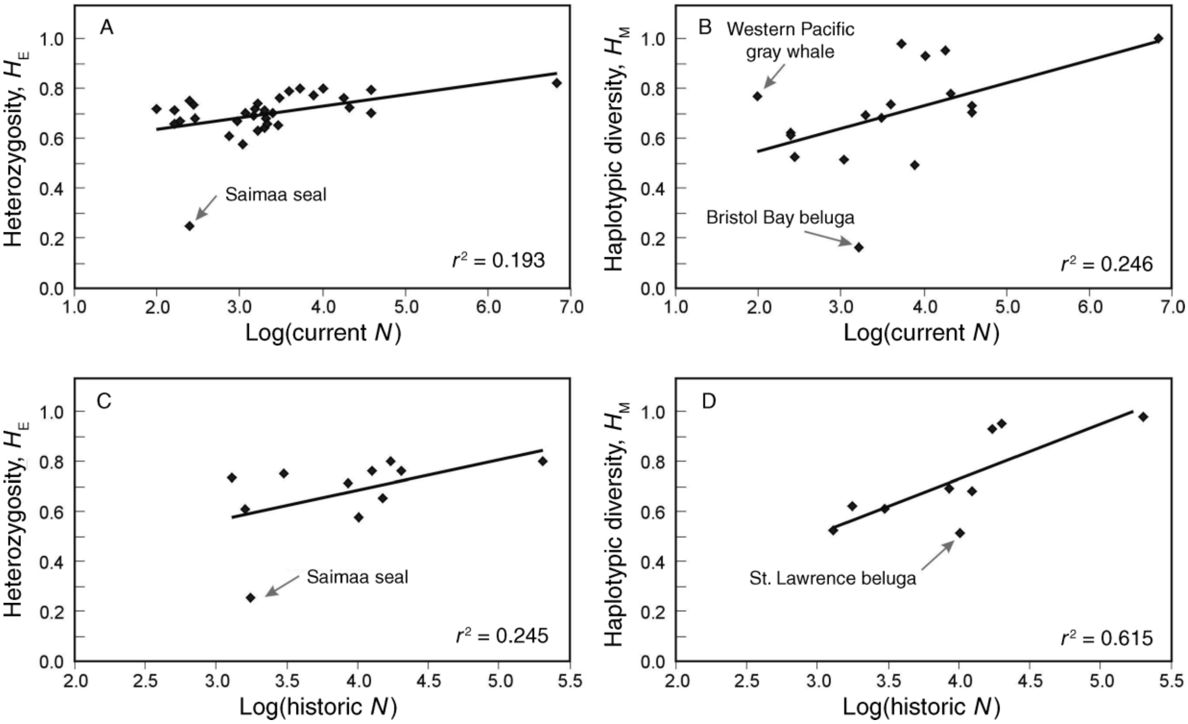

FIG. 3. The relationship between genetic diversity and population size. (A, C) Mean microsatellite expected heterozygosity and (B, D) mtDNA haplotypic diversity were regressed against log transformations of (A, B) current and (C, D) historic population size. The named species in the panels are outliers.

polar bear), and the Okhotsk Sea (bowhead whale and gray whale).

Future directions

Hypotheses need to be constructed and tested regarding the manner in which a continued warming trend will affect the demography, genetics, and viability of Arctic marine mammal populations. Future meta-analyses of the relationship between patterns of neutral diversity and population dynamics need to consider the levels of gene flow between populations, quantify the variance in the parameter estimates and the extent to which different variables covary, and explore other models and markers that more accurately capture diversity across the entire genome. Ancient-DNA technology can be used to directly measure changes in genetic parameters over time, including changes in population genetic diversity pre- and post-commercial exploitation. While neutral or near-neutral diversity may be correlated with fitness in some mammal species (Coltman et al. 1998, Coulson et al. 1998, Kretzmann et al. 2006), recent single-species studies and meta-analyses across multiple taxa indicate that, in general, diversity at these genetic markers is a poor indicator of fitness (Coltman and Slate 2003, Hoffman et al. 2006) or quantitative genetic variation (Reed and Frankham 2001). Systematic surveys of the association between neutral marker variation and phenotypic trait variation should be conducted to assess the utility of these markers in measuring inbreeding depression and fitness in Arctic marine mammals. The following general predictions can be made at this time.

Predictions

Small, closed populations of Arctic marine mammals, especially those at the southern extent of species ranges, will face the most immediate risks from a continued warming trend, including Allee effects, environmental stochasticity, human impacts, demographic stochasticity, predation, inbreeding, and loss of genetic diversity.

Loss of permanent ice plugs in the High Arctic may result in mixing of some genetically divergent populations. This will likely increase genetic diversity, resulting in increased vigor (heterosis) in some populations or possibly initial outbreeding depression in others.

SYNTHESIS

In reviewing these single-species genetic studies in relation to palaeoclimate and the ancient environments of the Arctic, a picture emerges of the relationship between climatic oscillations and Arctic marine mammal ecology and behavior over time that is instructive in predicting the effects of future climate change. During cold glacial periods, which typically persist for ~70 000–80 000 years (Clark et al. 1999), Arctic marine mammals are likely farther south than their contemporary ranges

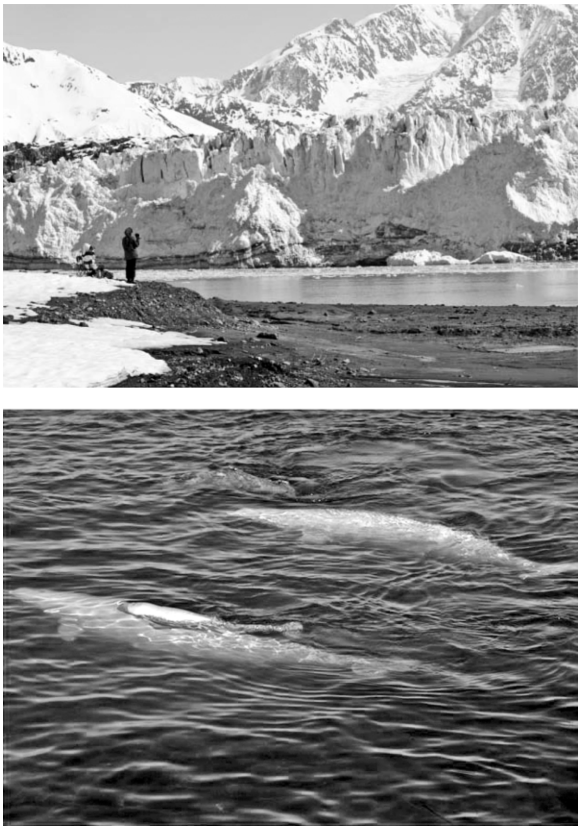

Plate 1. (Top) Beluga whale observation post in glacial fiord, Alaska, USA. (Bottom) Beluga whale nursery group: two cow–calf pairs in Cunningham Inlet, Canadian High Arctic. Photo credit: G. O'Corry-Crowe.

due to more extensive sea ice, coastal ice sheets, and the emergent land masses resulting from lower sea levels (Fig. 1A). While these conditions may isolate populations of some species in different ocean basins and some marginal seas, dispersal and gene flow may be promoted among some geographic regions (Fig. 1A). For example, contact between Arctic marine mammals currently in the Sea of Okhotsk and in the Bering, Chukchi, and Beaufort Seas may have been more prevalent during previous glacial maxima than today.

As the climate returns to a relatively short (∼10 000–20 000 year), warm interglacial, the ice sheets recede, the polar pack retreats, and low-elevation land masses (e.g., Beringia) are flooded by rising sea levels (Fig. 1B). Ice-adapted species move north from their southerly glacial refugia and (re)colonize newly created marine habitats. Some populations may colonize geographically isolated water masses such as the Gulf of Alaska, the Sea of Okhotsk, the Gulf of St. Lawrence, and the Baltic Sea (Fig. 1B). Over time, these isolated populations may evolve unique ecologies, life histories, and behaviors, a process enhanced by behavioral philopatry, small population size, and unique habitat. Meanwhile, other populations push farther north, migrating through newly opened seaways, such as Bering and Hudson Straits, into the High Arctic. Here too, distinct ecologies emerge. Still subject to the seasonal advance and retreat of the polar pack, many populations evolve extensive annual migrations between breeding and feeding areas.

If the climate continues to warm, further reductions in sea ice and ice caps along with rising sea levels may bring geographically discrete High Arctic populations of many marine mammals into contact with one another (Fig. 1C). Such contact between allopatrically divergent populations may have both deleterious and advantageous effects. Increased dispersal and gene flow can confer genetic advantages (e.g., heterosis) that enhance fitness and can help rescue small, isolated populations from extinction. Secondary contact, however, may also initially increase the opportunities for disease transmission and result in the loss of unique local adaptations, ecologies, and behaviors. As smaller populations mix with larger populations, local adaptations, including unique natural histories, ecologies, and social structures, may be diluted and lost. Furthermore, the already isolated populations at the southern margins of species' ranges must deal with the effects of greater isolation from conspecifics and the further erosion and ultimate loss of an already finite habitat. During previous warm periods, some of these populations may have adapted to their changing environment, others most likely went extinct (Fig. 1C). As the world inexorably moves to the next cold period, so the cycle of population expansion and contraction, of founder and extinction events, and of local adaptation and genetic mixing begins again.

The distribution and migration patterns of many Arctic marine mammals today are similar to the scenario presented in Fig. 1B. Several species have small, geographically isolated populations in subarctic waters as well as large, highly migratory populations that seasonally occupy the waters of the Arctic basin (Fig. 2). The numerous genetic reconstructions of population histories recounted here are dominated by how these species recolonized Arctic and subarctic waters following the LGM. A continuing warming trend in the earth's climate, however, may result in a scenario for many species similar to that presented in Fig. 1C. While instructive in reminding us that Arctic marine mammals have survived warm interglacial periods in the past and that the earth will ultimately return to an ice age, such reconstructions are also overly simplistic. The unique aspects of the current warming trend appear to be its speed and the substantial anthropogenic contribution to this trend (Vinnikov et al. 1999, Intergovernmental Panel on Climate Change 2007), as many of the papers in this Special Issue attest. Furthermore, the presence of six billion people on the planet has other unprecedented consequences for Arctic marine mammals (Hovelsrud et al. 2008, Ragen et al. 2008). An efficient predator and successful competitor, man can effect large changes on these species' environments.

Conservation and management

Molecular genetic studies currently provide guidance to marine mammal conservation and management and will provide unique perspectives for effective conservation and management of Arctic species in a changing environment. As mentioned earlier, genetic analyses determined that many summer and breeding concentrations of Arctic marine mammals are demographically discrete populations. This raises the possibility that local and even regional declines may not be reversed by external recruitment. Evidence for this comes from a number of species of which local populations have not recovered from past commercial harvest (e.g., Reeves and Mitchell 1989). These findings argue that these demographically independent populations should be managed as separate stocks (Dizon et al. 1992, Moritz 1994, Avise 1995), and indeed many now are (e.g., O'Corry-Crowe et al. 1997, deMarch and Postma 2003). In cases in which genetic analyses reveal that a population has been effectively isolated for a long time, say since the Pleistocene, local adaptations and unique genetic compositions are likely such that these populations harbor an important part of the evolutionary legacy and potential of the species and should thus be accorded specific protection (Ryder 1986, Waples 1991, Moritz 1994). Some populations of Arctic marine mammals at the southern extent of the species range are small and geographically isolated and currently face the greatest threat of extinction (e.g., Lowry et al. 2006). The effects of climate change will first be felt here at the species' southern margins, effects that will be exacerbated by small population size and finite habitat. If these populations are found to possess unique genetic attributes, specific management actions may be required in order to preserve the evolutionary potential of the species.

While climate variability and associated environmental change has long been a feature of the Arctic, and Arctic marine mammals are presumably resilient to such change, two factors regarding the impact of the current warming trend on Arctic marine mammals appear unique: the speed of the trend and the declines Arctic marine mammals have suffered over the past few centuries at the hands of man. Commercial harvest wiped out many populations and reduced others to small, often isolated relicts. These reductions and range fragmentations have likely compromised the genetic health and potential of some remaining populations. Continued anthropogenic influences, including development, pollution, and competition for prey are certain and set to increase as the warming trend opens up more of the north to human activities (Stirling and Derocher 1993, Hovelsrud et al. 2008, Huntington and Moore 2008, Ragen et al. 2008). Genetic parameters and molecular genetic indices of population subdivision and demographic history must be included in quantitative risk analyses of individual species and regional species complexes. The analyses presented in this paper provide an initial framework for such assessments. Furthermore, molecular genetic monitoring of changes in the population dynamics and ecology of Arctic marine mammals and in the genetic health and potential of populations will be essential to the design of effective, forward-looking conservation and management strategies.

New directions and future challenges of molecular ecological investigations

As reviewed here, molecular genetic studies of Arctic marine mammals have primarily been concerned with the examination of neutral marker variation to resolve population subdivision and demography on many different timescales and the application of the findings to immediate stock identity issues. New initiatives, aided by genomic technology and detailed long-term population studies, are now required to efficiently survey fitness-influencing as well as neutral loci across the entire genome in order to address a host of new questions relating to foraging ecology, infectious disease, mating systems, quantitative genetic variation, and the adaptive potential of Arctic marine mammals in a changing environment.

Almost nothing is known about the genetic underpinnings of Arctic marine mammal mating systems and social organization. Molecular genetic investigations are needed to resolve pedigrees, determine the role of kinship in social structure, measure the incidence of inbreeding, and estimate variance in reproductive success, all parameters essential to estimating effective population size, understanding inbreeding depression, and establishing the heritability of phenotypic traits related to fitness.

With enough selective pressure, as with dramatic shifts in food supply, evolutionary change in natural populations can be remarkably rapid (e.g., Grant and Grant 2002). The scale and speed of projected climate change in the Arctic marine environment over the coming decades (Walsh 2008) highlight the need to consider evolution in Arctic marine mammal populations on contemporary timescales. As evolution follows as a response to natural selection acting on quantitative or polygenic traits (Falconer and Mackay 1996), determining the heritability (h^2) of a trait, i.e., the proportion of variation in the trait due to additive genetic variation, will enable investigation of natural selection and the evolutionary response in a changing environment. In the Arctic, predictions can be made as to the direction and extent of environmental change and hypotheses tested as to the likely evolutionary consequences of these predicted changes for various possible inherited traits (e.g., lifetime reproductive success, disease resistance, body size) in Arctic marine mammals. Such investigations require detailed study of multiple generations in small, finite populations, ideally in species that exhibit large levels of phenotypic variation and populations approaching equilibrium, in which detailed molecular genetic analyses of pedigrees can be conducted in conjunction with the systematic measurement of phenotypic traits (e.g., Kruuk et al. 2000, Keller et al. 2001, Grant and Grant 2002). Long-term studies of polar bears, Arctic foxes, and highly philopatric pinniped species with relatively short generation times may be the most tractable.

New genomic platforms are facilitating high-throughput analyses of a broader range of markers and hold tremendous promise for research on a variety of scientific questions in polar research (National Research Council 2003) and for management and conservation (Kohn et al. 2006). As well as improving the scope and efficiency of screening neutral marker variation, genomic technologies can be used to identify, map, and survey genetic loci directly related to fitness, in which patterns of allelic variation more accurately reflect the adaptive potential of populations and patterns of gene expression indicate how the individual responds to climate-induced environmental change. Investigating functional loci may also help resolve why some populations of Arctic marine mammals have failed to recover following protection. Research on Arctic marine mammals should begin with well-characterized genes or gene complexes such as the major histocompatability complex (MHC), a multigene family associated with the immune response (Murray and White 1998, Romano et al. 1999, 2002). Variation at these genes is essential to combating new and diverse arrays of pathogens. Loss of variation here could reduce individual viability and survival (Piertney and Oliver 2006).

Much of the genetic research on Arctic marine mammals to date can be viewed as establishing baseline data for comparison with data sets collected in the future as well as those mined from the past. The challenge now facing us is to collect and analyze sufficient quantities of the right data to be able to detect underlying temporal patterns that provide insight on time frames that allow effective action. Most molecular ecological studies of Arctic marine mammals up to now have been single-species, often single-population, investigations, typically conducted ancillary to, or in isolation from, other scientific research, and over very short time frames. Long-term, multispecies, and system-wide studies are now required. Fortunately, a number of long-term ecological studies exist. Understanding the impacts of climate change on regional and circumpolar marine mammal fauna ultimately requires more coordinated interdisciplinary research.

ACKNOWLEDGMENTS

This work was funded by grants from the U.S. National Marine Fisheries Service (NOAA Fisheries) and the Alaska Beluga Whale Committee. I thank Carolina Bonin, Amy Frey, and all members of the High Latitude Molecular Ecology Group for their help in conducting much of the research reported here, and I also thank colleagues at the Southwest Fisheries Science Center for their assistance in many aspects of that research. I am grateful to Henry Huntington and Sue Moore for their comments and support in this endeavor and to the two anonymous reviewers for their helpful comments. Finally, a word of thanks to Rich Cosgrove for his assistance with the GIS analysis.

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