MOLECULAR ECOLOGY

Dispersal provided resilience to range collapse in a marine mammal: insights from the past to inform conservation biology

Journal:	*Molecular Ecology*
Manuscript ID:	MEC-09-1238.R2
Manuscript Type:	Original Article
Date Submitted by the Author:	
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Keywords:	Conservation Biology, Mammals, Population Dynamics, Population Genetics - Empirical, Wildlife Management

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Running Head: Dispersal and resilience to range collapse

Keywords: *Callorhinus ursinus*, Northern fur seal, ancient DNA, Approximate Bayesian Computation

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Data deposition: The sequences reported in this study have been deposited in GenBank under Accession numbers GU989644-GU990048 (control region) and GU990049-GU990076 (cytochrome *b*).

Abstract

Population loss is often a harbinger of species extinction, but few opportunities exist to follow a species' demography and genetics through both time and space while this occurs. Previous research has shown that the northern fur seal (*Callorhinus ursinus*) was extirpated from most of its range over the past 200-800 years and that some of the extirpated populations had unique life history strategies. In this study, widespread availability of subfossils in the eastern Pacific allowed us to examine temporal changes in spatial genetic structure during massive population range contraction and partial recovery. We sequenced the mitochondrial control region from 40 ancient and 365 modern samples and analyzed them through extensive simulations within a serial Approximate Bayesian Computation framework. These analyses suggest that the species maintained a high abundance, probably in Arctic refugia, that dispersal rates are likely 85% per generation into new breeding colonies, and that population structure was not higher in the past. Despite substantial loss of breeding range, this species' high dispersal rates and refugia appear to have prevented a loss of genetic diversity. High dispersal rates also suggest that previous evidence for divergent life history strategies in ancient populations likely resulted from behavioral plasticity. Our results support the proposal that panmictic, or nearly panmictic, species with large ranges will be more resilient to future disturbance and environmental change. When appropriately verified, evidence of low population structure can be powerful information for conservation decisionmaking.

Introduction

The population is a basic unit of evolution and ecology (Krebs 1994; Wright 1931), and around the world, loss of populations is seen as a harbinger of extinction (Ceballos & Ehrlich 2002). In addition, population boundaries are commonly used for making management decisions for exploitation and conservation (Palsbøll *et al.* 2006). However, while population boundaries are typically assumed to be static, accumulating evidence suggests that these boundaries change through time (Hofreiter *et al.* 2004). In fact, species can respond to environmental change with gene flow among populations (Hadly *et al.* 2004). This process redistributes genetic diversity and reshapes populations, which can make current population boundaries misleading (Valdiosera *et al.* 2008). Finally, understanding how dispersal and gene flow affected species responses to past disturbance is important for predicting future changes. Much of the debate about species response to climate change centers on the ability of populations to migrate (McLachlan *et al.* 2005), the tension between local adaptation and dispersal (Davis & Shaw 2001), and the wisdom of human-assisted relocation (Hoegh-Guldberg *et al.* 2008).

Insights into dynamics of population structure are beginning to emerge from ancient DNA (aDNA) studies that directly reconstruct genetic and demographic changes accompanying long-term disturbance (Hadly *et al.* 2004; Hofreiter *et al.* 2004; Valdiosera *et al.* 2008). For example, populations that were once connected can become isolated (Valdiosera *et al.* 2008), and vice versa (Wakeley 1999). When isolated populations go extinct, genetic lineages may be permanently removed from a species (Pannell & Charlesworth 2000). The opportunities for research into these processes, however, are greatly limited by the availability of aDNA samples through both space and time. Analyses are also complicated by small sample sizes

(Ramakrishnan & Hadly 2009) and fragmentary historical information that is difficult to analyze quantitatively (Baker & Clapham 2004).

When samples are available, new analytical approaches may address these concerns. The use of the Approximate Bayesian Computation framework (ABC, Beaumont *et al.* 2002) with temporal genetic data (Chan *et al.* 2006) allows researchers to consider the realities of aDNA sample sizes, the power of the analyses, the temporal nature of the data, and prior information from historical accounts. ABC methods are highly flexible because they simulate a wide range of demographic histories and select the histories most consistent with observed data. Bayesian priors determine the range of parameters explored by the simulations, and they can be tailored to incorporate historical information. By selecting and weighting the simulations that best match summary statistics computed on the observed data, one can then calculate posterior probability distributions for the demographic parameters (Beaumont *et al.* 2002). In this way, more explicit connections between genetics and demography can be explored than are available from summary statistics (Ramakrishnan & Hadly 2009).

In this paper, we aim to understand the temporal dynamics of population structure and the role of dispersal in driving population responses to disturbance in a large marine vertebrate. The widespread availability of northern fur seal (*Callorhinus ursinus*) bones and teeth in archaeological middens along the west cost of North America (Newsome *et al.* 2007) presents a valuable opportunity for this research. The species experienced a serious disturbance from hunting and potentially climate changes in the late Holocene that resulted in a dramatic reduction in breeding range and population size over the last few hundred years (Busch 1985; Kennett 2005; Newsome *et al.* 2007). Population declines and range collapses from hunting, climate

change, and other disturbances are common in a wide range of species (Ceballos & Ehrlich 2002), including many pinnipeds (Busch 1985). Reduced genetic diversity characterizes some of these marine vertebrates, including the northern elephant seal (*Mirounga angustirostrus*) (Hoelzel *et al.* 1993), Hawaiian monk seal (*Monachus schauinlandi*) (Kretzmann *et al.* 1997), and Guadalupe fur seal (*Arctocephalus townsendi*) (Weber *et al.* 2004). However, other marine vertebrates show no reduction (e.g., Baker *et al.* 2005; Borge *et al.* 2007; Matthee *et al.* 2006), potentially because appropriate aDNA baselines were unavailable, bottlenecks were not severe, or gene flow offset local declines in abundance. Few of these studies had aDNA samples, and none had access to samples through space and time to study dispersal as a species responded to range collapse. Attempting to reconstruct past demographic dynamics without aDNA is often misleading (Hofreiter *et al.* 2004; Valdiosera *et al.* 2008).

North American explorers reported only two eastern Pacific breeding colonies of the northern fur seal: a large colony on the Pribilof Islands (57°N) and a much smaller one on the Farallon Islands (38°N) (Gentry 1998; Pyle *et al.* 2001). Fur seals from these colonies were intensively exploited for the fur trade starting in 1786, leading to near extinction by the late 1890s (Busch 1985). In the eastern Pacific, only the Pribilof colony survived into the 1900s, and even in this refuge, surveys indicated a 90% decline before 1910 (Gentry 1998).

Modern ecological study has focused on Bering Sea colonies. However, high *C. ursinus* prevalence in prehistoric middens demonstrates that they were once more widespread and presumably more common at temperate latitudes than they are today (Newsome *et al.* 2007). Furthermore, many of these sites contain skeletons of unweaned pups, strongly suggesting that the northern fur seal actively bred along the west coast of North America (Newsome *et al.* 2007).

Stable isotope profiles define ecologically distinct populations in the western Aleutians, Gulf of Alaska/Pacific Northwest, and California (Newsome *et al.* 2007). In addition, these isotope data suggest that prehistoric temperate populations nursed pups up to three times longer than do modern seals (Newsome *et al.* 2007). Taken together, these observations reveal that 200-800 ybp, the northern fur seal experienced a dramatic collapse in its breeding range, coincident with the apparent loss of a unique life history strategy when the temperate colonies were extirpated. More recently, a small number of breeding rookeries have been recolonized, including in Alaska and California (Peterson *et al.* 1968).

In this study, we investigate the following questions: 1) was genetic diversity lost when the northern fur seal range was extirpated from most of its range? 2) did spatial population structure change during the collapse and recolonization of its breeding range? and 2) how did abundance and dispersal change during this collapse and recovery?

Methods

Sample Collection

We obtained 49 pre-sealing bones identified as *C. ursinus* from archaeological middens as old as 2500 years before present (ybp) (Figure 1, Table 1). Sampling the same individual multiple times is a concern when samples come from archaeological sites (Larson *et al.* 2002). Therefore, we only selected samples from the same site that were either 1) the same diagnostic element (e.g., two left mandibles), 2) different sexes, 3) different ages, or 4) from different excavation units

within the site. We could not apply these criteria for our Chaluka site because excavation unit data were unavailable. To test whether duplicate individuals might still bias our results, we repeated our analyses after removing any duplicate haplotypes from the same site.

Carbon-14 dates for our samples (Table 1) were collected from the literature and represent either directly dated *C. ursinus* bones or associated material (Gifford-Gonzalez *et al.* 2005; Kennett 2005; Newsome *et al.* 2007). We calibrated these dates with OxCal 4.0 using the Marine 04 curve, 100% marine, with a Delta reservoir of 250+/-35 (Ramsey 2009).

In addition, we analyzed 365 tissue samples collected from unweaned pups during the 1993 to 1998 summer breeding seasons from all major eastern Pacific colonies: St. George Island (n = 92) and St. Paul Island (n = 91) in the Pribilofs, Bogoslof Island (n = 96) in the Aleutians, and San Miguel Island (n = 86) in California.

Ancient DNA sequencing

A 0.05 to 0.2 g sample of bone or tooth was removed from each ancient specimen, ground to a powder with liquid nitrogen, and incubated overnight with lysis buffer (0.5 M EDTA pH 8, 0.5% SDS, and 100 µg/ml proteinase K) at 55°C on a shaker table. After centrifugation, 125 µl of supernatant was transferred to a Qiagen Qiaquick PCR purification column (Valencia, CA) to isolate DNA. Approximately 30 µl of DNA in buffer was eluted from the column for PCR amplification.

We used CalloCR1 (5'-CTCCCCCTATGTACTTCGTGCA-3') and CalloCR2 (5'-CAGCAACCCTTGTGAAAAGTGTAC-3') primers to amplify 157 base pairs (bp) of the

149 mitochondrial control region for each ancient specimen. Final PCR concentrations were
150 *AmpliTaq* Gold polymerase (0.025 U/µl), *Taq* Gold buffer (1x), $MgCl_2$ (5 mM), dNTPs (1 mM
151 each), primers (0.2 µM each), sterile water, spermidine (1 mM) or bovine serum albumin (1.3
152 mg/ml), and 2.5 µL of DNA template in a total volume of 50 µl. We used the following PCR
153 conditions: 95°C for 10 min followed by 45 cycles of 95°C for 30 s, 45°C for 30 s, and 72°C for
154 1 min. Sequencing was performed by Cogenics (Newton, MA) or on an ABI 3100 at Hopkins
155 Marine Station (Pacific Grove, CA). Fragments were sequenced in both directions.

156 In addition, we sequenced a 157 bp fragment of the cytochrome *b* gene from 28 ancient
157 samples. Final PCR concentrations were as for control region, except we used 0.02 U/µl *FirePol*
158 polymerase, 2 µM each primer, and 3 µl template. PCR conditions were also the same, except we
159 denatured at 94°C, annealed for 45 s, and used a final extension for 10 min at 72°. Primers were
160 CalloCB3F (5'-GACCAACATTCGAAAAGTTCA-3') and CalloCB200R (5'-
161 GGYGACTGATGAGAAGGCTGT-3').

162 *Modern DNA sequencing*

163 As part of a larger study of northern fur seals, a 385 bp fragment of mtDNA was
164 sequenced in the modern samples. Only the fragment of sequence matching the ancient samples
165 was used for analysis in this paper. For modern samples, DNA was extracted from flipper tissue
166 using Qiagen DNeasy kits (Valencia, CA). We used primers LGL 283 (5'-
167 TACACTGGTCTTGTAAACC-3') and PINN 1115 (5'-
168 ATGGCCCTGAAGTAAGAAGAACCAG-3'), the latter of which is a slight modification of
169 LGL 1115 (Bickham *et al.* 1996) for greater specificity. The PCR was conducted in a 10 µl

volume consisting of 10 mM Tris-HCL at pH 8.3, 50 mM KCL, 2.0 mM $MgCl_2$, 0.2 mM each dNTP, 0.1 units *Taq* DNA polymerase, 0.2 μM of each primer, and 100 ng DNA template. PCRs were performed under the following profile: 30 cycles of 93 ^{o}C for 20 s, 59 ^{o}C for 20 s, and 72^{o} C for 35 s. To purify the amplified PCR fragment the bands were excised from the gel, placed in 20μl of low TE buffer (10mM Tris, 0.1 mM EDTA, pH8.3), and stored overnight at 4^{o}C. We used Thermo Sequenase Primer Cycle Sequencing Kit (Amersham Biosciences) protocols in a MJ Research DNA engine (Waltham, MA) and performed sequencing on a Li-Cor 4200 automated sequencer (Lincoln, NE).

Contamination controls

All aDNA extractions were performed in the Hadly lab at Stanford University (Stanford, CA) in a dedicated, positive-pressure room that is regularly irradiated with ultraviolet light and cleaned with dilute bleach. All aDNA amplification occurred in a physically separate lab with no flow of genetic material back to the aDNA extraction room. Contamination controls were used throughout extraction, amplification, and sequencing. None of these laboratory facilities have a history of working with modern seal DNA. All modern DNA work took place at the National Marine Mammal Laboratory (Seattle, WA).

For corroboration of our results and to guard against PCR error, eight aDNA samples were re-amplified and re-sequenced in the van Tuinen aDNA lab at the University of North Carolina (Wilmington, NC). Three of the same samples were also cloned and sequenced at Hopkins Marine Station (Pacific Grove, CA). A single basepair error in one San Miguel sequence was discovered by the van Tuinen lab and confirmed at Hopkins Marine Station.

Analysis

Sequences were aligned in Sequencher 4.7 and compared against available sequences in GenBank using a BLAST search (blast.ncbi.nlm.nih.gov) to verify species identity. Analysis with jModeltest 0.1.1 (Posada 2008) and Akaike's Information Criterion (AIC) indicated that an HKY+G substitution model with unequal base frequencies, a transition/transversion bias of 28.97, and a gamma shape parameter of 0.173 was most appropriate for our locus.

For summary statistics, we used Arlequin v.3.11 (Excoffier *et al.* 2005) to calculate haplotype diversity (H_e), nucleotide diversity (π), Tajima's *D* (Tajima 1989), analysis of molecular variance (AMOVA), and pairwise F_{ST}s for the modern and ancient samples. Migrate-n v.2.3 (Beerli 2006) produced equivalent gene flow results and are not reported further in this paper.

Because mutational hotspots can confound genetic calculations, we identified nucleotides suffering from homoplasy. We did this by first identifying sites with more than two states in our dataset. Next, we concatenated our cytochrome *b* sequences ($n = 28$) with control region sequence from the same individuals and built a neighbor-joining tree in PHYLIP 3.69 (Felsenstein 2004) with F84 distances and unequal base frequencies, as suggested by Phillips et al. (2009). The cytochrome *b* nucleotides were upweighted by duplicating their sequence four times. We then mapped the control region polymorphisms onto this tree and identified sites with more than one substitution.

Substitution rates

A substitution rate was necessary for our ABC analyses, and we therefore used Bayesian methods to fossil calibrate a rate against 90 otariid sequences. We used 32 modern *C. ursinus*, 30 Steller sea lion (*Eumetopias jubatus*) and 28 California sea lion (*Zalophus californianus*) downloaded from GenBank. For this calibration, we specified an 8.2 +/- 2.1 million years ago divergence time between sea lions and *C. ursinus* (Higdon *et al.* 2007) and an HKY+G substitution model with a strict clock. Running the analysis in BEAST v.1.4.6 (Drummond & Rambaut 2007) for 20 million steps (logging every 500) produced a posterior distribution for the substitution rate with a mean of 6.7% per site per million years (My) (95% CI: 1-24%).

Because hypervariable sites and saturation within the control region can lead to under-estimates of substitution rate with phylogenetic methods, we also calibrated control region substitution rates against cytochrome *b* following the method of Alter & Palumbi (2009). In brief, cytochrome *b* haplotypes from 28 individuals were trimmed to an 85 bp segment with no missing data. Then, control region substitution rate was calculated as:

$$\mu_{CR} = \frac{x\mu_{cytb}n_{cytb}}{0.5n_{CR}}$$

where x was mean control region pairwise distance for individuals identical at cytochrome *b* haplotype (10.9±0.3 substitutions), μ_{cytb} was substitution rate for synonymous changes in cytochrome *b* (3.26% per My in pinnipeds, from Phillips et al. 2006), n_{cytb} was the number of four-fold degenerate sites in cytochrome *b* (17) plus 1/3 the number of two-fold degenerate sites

(17), and n_{CR} was the number of nucleotides in our control region fragment (157). This method suggested a substitution rate of 10.3±0.3% per My.

Both rates are similar to other control regions rates, including 5-10% per My estimated from fossil calibrations for the southern elephant seal (*Mirounga leonina*) (Slade *et al.* 1998) and 5-5.4% per My from cytochrome *b* calibration in baleen whales (Alter & Palumbi 2009). Intra-species mitochondrial substitution rates, however, are controversial (Emerson 2007; Howell *et al.* 2008), and our rates are slower than cytochrome *b*–calibrated estimates of 27% per My in the California sea lion (Phillips *et al.* 2009). Therefore, we tested the sensitivity of our ABC analyses by using both 6.7% and 30% per My mean substitution rates.

ABC analyses

For our ABC simulations, we use Bayesian Serial SimCoal (Anderson *et al.* 2005). This program uses coalescent theory to simulate genetic sequence evolution in haploid populations. Sequences from multiple time points can be generated, and the program uses Bayesian priors on demographic histories.

In our ABC-Bottleneck analysis, we simulated a population that declined exponentially from 13 to 7 generations ago, then recovered exponentially from 7 to 3 generations ago. This model was appropriate for northern fur seals given their rapid decline and recovery between the late 1700s and mid 1900s. We used an average generation time of 15 years because females breed from age 7 to 23 (Lander 1981). Priors on ancient effective female population size (1-10,000,000) and bottleneck size (1-10,000,000) were uniform on a log10 scale. The prior for substitution rate was lognormal to match the mean and confidence limits of our estimated rates (6.7% or 30%).

For summary statistics, we used 1) nucleotide diversity, 2) segregating sites, 3) Tajima's D, and 4) number of private alleles. Each statistic was calculated for both the ancient (n = 40) and modern (n = 365) samples. We only retained simulations where bottleneck size was smaller than ancient size, which produced skewed priors. We therefore divided our posterior densities by the prior densities to calculate an unskewed posterior.

We also developed an ABC-Dispersal analysis to estimate modern and ancient dispersal rates. By separating initial colonization from ongoing migration into the modern California population, we were able to differentiate between these two processes and determine whether the observed genetic distance between modern Alaska and California populations was a result of recent separation or ongoing gene flow. Without similar information on colonization of the ancient California population, we did not separate the two processes for our ancient samples. We simulated two populations, representing the Alaska and San Miguel colonies for which we had both modern and ancient samples. We specified that the California population was extirpated and then recolonized two generations before the present by 10-100 females and that gene flow between the two populations continued. This choice of parameters matches what we know about colonization of the San Miguel colony in the 1960s (Peterson *et al.* 1968). We used uniform priors for the Alaska female effective population size (10-10,000,000), California ancient size (10-10,000,000), California 1960s founding size (10-100), California modern size (100-1,500), ancient dispersal between the two populations (0-100% per generation), and modern dispersal (0-100% per generation). The Alaska and ancient California priors were on a log10 scale. The California modern effective size prior was based on calculations from census data (National Marine Fisheries Service 2003). Our summary statistics were 1) nucleotide diversity, 2)

segregating sites, and 3) F_{ST} between each pair of populations. Each statistic was calculated for the ancient Alaska, ancient California, modern Alaska, and modern California samples.

For each ABC analysis, we calculated the posterior mode, 95% Credible Intervals (CIs), and posterior parameter densities using a rejection-sampling method that has been described previously. In brief, from 3 million simulations, we accepted the 1000 that had the smallest normalized Euclidean error when compared to observed summary statistics. We then used the locfit() functions in R v.2.8.1 to estimate posterior densities with smooth weighting (Beaumont *et al.* 2002; Chan *et al.* 2006). Population sizes were log transformed before fitting.

Results

Sequencing

We successfully obtained mtDNA control region sequence from 42 ancient samples out of 49 from which we attempted extractions. Two Chaluka samples were identified as *Phoca vitulina* based on BLAST searches. Therefore, our study analyzed 40 ancient *C. ursinus* sequences (Table 1). Two sequences at Umpqua/Eden were identical, though they lay in different excavation quadrats. In addition, we obtained sequences from 365 modern seals.

We identified six nucleotides with more than two states. In addition, the cytochrome *b* tree had two clades. Mapping the control region substitutions onto this tree identified an additional eight nucleotides that likely had more than one substitution. These fourteen sites might

suffer from homoplasy. We removed them as part of our sensitivity analyses, leaving 46 polymorphic sites.

Changes in genetic diversity and population size

The 40 ancient samples contained 37 unique haplotypes, while the 365 modern samples contained 186 unique haplotypes. Estimates of haplotype diversity were high in both modern (0.989 ± 0.002) and ancient samples (0.996 ± 0.007) (Table 2). Nucleotide diversity was similarly high (modern: 0.048 ± 0.025; ancient: 0.048 ± 0.026) (Table 2). Only twelve haplotypes were shared between modern and ancient samples, which meant that two-thirds of the ancient haplotypes where only found in ancient samples. Our ABC-Bottleneck analysis (below) explored the implications of this information for this size of the population bottleneck. Tajima's D statistic was negative in both modern and ancient samples (indicative of population growth), but was not significantly different from zero (Table 2). Removing the potentially duplicate individual from Umpqua/Eden suggested only slightly higher diversity (Table S2).

To find the largest bottleneck consistent with our observed data, our ABC-Bottleneck analysis simulated the northern fur seal decline and recovery between the late 1700s and mid 1900s. This analysis provided a posterior density with highest support for an ancient female effective size of 601,000 (95% CI: 131,000-3,920,000) (Figure 2a). The posterior density also suggested the highest support for a bottleneck size of 228,000 (95% CI: 17,000-2,400,000) (Figure 2b), or 63% (95% CI: 2-100%) of pre-bottleneck abundance.

Running our analysis with a much higher substitution rate (30% per My) suggested lower effective sizes (ancient size: 157,000, 95% CI: 18,000-497,000; bottleneck size: 26,000, 95% CI:

312 3,500-289,000), but the ratio of bottleneck to pre-bottleneck abundance was similar (50%, 95%
313 CI: 12-100%). Re-doing the analysis with summary statistics after removing the sites with
314 homoplasy (Table S3) suggested a similar ratio of bottleneck to pre-bottleneck abundance (59%,
315 95% CI: 2-100%).

316 These results suggest that, globally, the northern fur seal declined but did not reach
317 extremely low abundance, even during the height of the presumed bottleneck.

318 *Changes in dispersal rates*

319 The AMOVA indicated that, in the ancient samples, the vast majority of genetic variation
320 was contained within colonies (99.2%), with only 0.8% distributed among colonies. This was not
321 significantly different from panmixia (F_{ST} = 0.0078, p = 0.36). Among modern samples, the
322 hypothesis of panmixia also could not be rejected (F_{ST} = 0.0027, p=0.17), with 99.7% of genetic
323 variation contained within colonies. Removing the nucleotides with homoplasy did not change
324 the overall conclusions (ancient: 0% among, p = 0.54; modern: 0.3% among, p = 0.17), nor did
325 removing the possible duplicate sample (ancient: 0% among, p = 0.49). Results were similar
326 when colonies were combined into regions (California, Pacific Northwest, and Alaska), and a
327 neighbor-joining tree confirmed that ancient samples did not cluster by region (Figures S1 and
328 S2). These results suggest high gene flow in both modern and ancient periods.

329 Including knowledge about the extinction/recolonization history of the recent San Miguel
330 colony allowed for greatly improved precision when estimating modern dispersal rates in our
331 ABC-Dispersal analysis. This analysis showed that the dispersal rate between Alaska and San
332 Miguel has likely been extremely high in recent years (Figure 2), even after accounting for the

recent colonization of San Miguel from Alaska. The modal estimate of dispersal rate was 86% per generation (95% CI: 27-100%) or 816 effective immigrants per generation into San Miguel (95% CI: 96-1,390). In contrast, the ABC-Dispersal analysis showed that our samples were not as strongly informative about the ancient dispersal rate, though this rate was also likely to be high (85% per generation, 95% CI: 9-97%) (Figure 2). This rate was equivalent to a large absolute number of immigrants into the ancient California population each generation (7,950, 95% CI: 504-3,320,000) because the California population was inferred to be larger in the past than it is now.

Running the analysis with a higher substitution rate suggested similarly high modern (84%, 95% CI: 24-100%) and ancient dispersal rates (83%, 95% CI: 6-96%), similar numbers of modern immigrants into California (747, 95% CI: 102-1,377), and fewer but still large numbers of ancient immigrants (1,690, 95% CI: 74-1,900,000).

Discussion

Widespread availability of northern fur seal fossils in the eastern Pacific allowed us to study temporal changes in genetic population structure while the northern fur seal was extirpated from much of its range over the past few hundred years. Our evidence from a Bayesian analysis of the rapidly evolving mitochondrial control region suggests that the species maintained a large abundance during this event and that dispersal rates between breeding colonies were high enough to prevent any colony from containing unique genetic lineages. Extensive loss of breeding range did not, therefore, result in loss of genetic diversity in this species. Low population structure in

354 modern seals was confirmed by aDNA samples to be typical for the species rather than an artifact
355 of recent colonization events. It appears that a high dispersal rate combined with the maintenance
356 of a large refuge during the extreme disturbance experienced by this species provided genetic
357 resilience and continues to assist in the recovery of the northern fur seal breeding range.

358 Stable isotope, ecological, and genetic data for the northern fur seal provide different and
359 therefore informative views of this species' response to disturbance. Archaeological studies
360 indicate a collapse of the species' breeding range (Newsome *et al.* 2007), and hunting records
361 show a precipitous decline in abundance (Busch 1985). Isotope differences suggest a distinct
362 temperate population with a unique life history strategy (longer weaning period) that was
363 extirpated (Newsome *et al.* 2007), consistent with tagging studies suggesting that female northern
364 fur seals in particular show strong natal site fidelity (Baker *et al.* 1995).

365 In contrast, the genetic evidence showed that diversity did not decline through time and
366 that colonies are not differentiated at the mitochondrial locus. The simulations in our ABC-
367 Bottleneck analysis showed that declines to extremely low abundance were unlikely given what
368 we know about the bottleneck's timing and duration. We note that absolute estimates of effective
369 population size require accurate control region substitution rates because estimates of population
370 size are inversely related to substitution rate. Both our phylogenetic and cytochrome *b*-calibrated
371 substitution rates suggested 7-10% per My, giving us reasonable confidence that this is
372 appropriate for *C. ursinus*. However, it is possible that these are underestimates of true
373 substitution rates because saturated hypervariable sites can bias phylogenetic methods (Alter &
374 Palumbi 2009), and the section of cytochrome *b* that we used was relatively short. Even using a
375 much higher substitution rate (30%) in our ABC-Bottleneck analysis still suggested that tens of

thousands of seals persisted during the bottleneck, representing approximately 50% of ancient abundance. The relatively low sensitivity of our core results to differences in substitution rate increases our confidence in these conclusions. Combined with previous knowledge on range contraction and surviving colonies in this species, we presume that most of the surviving seals were in the Bering Sea on the Pribilof Islands, though historical reports suggest that smaller breeding colonies also survived on the Commander Islands and Robben Island in the western Pacific (Busch 1985).

In addition, our aDNA and ABC analyses provided two lines of evidence to suggest that dispersal rates were and continue to be relatively high among colonies. First, our ABC-Dispersal analysis showed that levels of genetic diversity and divergence are most consistent with a high modern dispersal rate across the latitudinal range of the species (Alaska to California). Without this analysis, a low genetic divergence between two populations at neutral loci could suggest either recent time of divergence or high rates of ongoing gene flow (Won, Hey, 2005). From historical records, we knew that two of the four colonies from which we had modern samples (Bogoslof and San Miguel) have been colonized from the Pribilof Islands only in the past few generations (Peterson *et al.*, 1968). This short divergence time could be invoked as the explanation for low levels of modern genetic population structure, even if dispersal rates were low. However, by modeling initial colonization of the California population and ongoing gene flow as separate processes, our analysis showed that the genetic diversity present in California couldn't be explained simply by colonization with 10-100 females. Instead, high rates of gene flow after colonization were also required. An alternative possibility is that the California colonizing population was dramatically larger than 100 effective females, which would also

398 explain the high diversity in that population. However, this would be inconsistent with historical
399 reports that the initial colonizing group was small (Peterson *et al.* 1968).

400 Because the Pribolofs population (Alaska) is about 75 times bigger than that on San
401 Miguel Island (National Marine Fisheries Service 2007), our dispersal rate is most plausibly
402 interpreted as an immigration rate into San Miguel. For example, an 85% immigration rate into
403 San Miguel implies a 1% emigration rate out of Alaska and towards California. This latter rate is
404 well within the 0-24% straying rates for breeding-age females estimated from ecological surveys
405 (Baker *et al.* 1995), and is consistent with substantial natal site fidelity.

406 Complementing this conclusion of high modern mobility are the aDNA data, which give
407 us a view into the past. The low F_{ST} among the ancient colonies suggests that lack of genetic
408 structure may be typical for the northern fur seal, regardless of time since colonization, and
409 therefore that high dispersal rates rather than short time since colonization is a better explanation
410 for the low levels of genetic divergence among colonies. Our ABC-Dispersal analysis suggested
411 that large numbers of migrants likely moved between colonies, but provided only broad
412 credibility intervals. Our low ancient sample size likely caused this lack of precision. However,
413 without colonization information for the ancient California population (as we had for the modern
414 population), we cannot exclude the possibility that low ancient divergence results from shared
415 ancestry rather than gene flow.

416 It has been suggested that homoplasy at hypervariable sites in the control region may
417 produce false evidence of dispersal (Phillips *et al.* 2009). In our dataset, we found evidence of
418 mutational hotspots both from nucleotides with more than two states and by mapping control

region substitutions onto a cytochrome *b* tree. However, removing these hotspots had little impact on our estimates of AMOVA or F_{ST}. This increases our confidence that homoplasy did not greatly bias our estimates of gene flow in *C. ursinus*. Investigations into *C. ursinus* control region substitutional patterns with longer cytochrome *b* haplotypes would be a productive method for further identifying hotspots and site-specific mutation rates.

Non-random sampling from populations could also confound our estimates of both bottleneck size and gene flow. For example, if our ancient samples are from non-breeding season haul-outs, individuals at a single site may come from many breeding colonies, leading us to over-estimate population diversity and under-estimate population divergence. However, it appears unlikely that individuals at the same site are from multiple colonies because *C. ursinus* males and females are pelagic during non-breeding seasons (Ream *et al.* 2005), and indigenous harvest of pelagic seals was likely rare (Newsome *et al.* 2007). In contrast, during the breeding season, seals haul out near rookeries. In addition, presence of pre-weaning pups at many of the archaeological sites suggest that individuals were harvested at breeding colonies (Newsome *et al.* 2007).

An alternative possibility is that our ancient samples are from close relatives within breeding colonies, which would lead us to under-estimate population diversity and over-estimate population divergence. This scenario could occur if hunters primarily took seals from one part of the colony (perhaps the most accessible). Site fidelity in female fur seals, sometimes to subsections of a colony (Baker *et al.* 1995), make this scenario plausible. However, ancient haplotypes do not cluster by site (Figure S1) and removing the only pair of identical samples within the same site had little impact on our results. Therefore, any potential bias from sampling close relatives seems minimal.

Insights into traits that confer resilience

Our evidence for high gene flow and stable genetic diversity in the northern fur seal provides new insight into how species respond genetically to disturbance events over timescales of decades to millennia. Conventional approaches to understanding genetic impacts of declines in abundance and range focus on reduced effective population size and an erosion of genetic diversity (Chan *et al.* 2006; Spielman *et al.* 2004). Genetic samples for the northern fur seal across time and space, however, allowed us to understand the simultaneous importance of gene flow and population size. It appears that the northern fur seal avoided a loss of genetic diversity because of two critical traits: 1) a refuge that maintained a high abundance, and 2) high dispersal rates among colonies.

When dispersal rates between populations are low, each population will tend to contain unique genetic diversity (Wright 1931), and loss of populations will lead to reduced species-level diversity. On the other hand, it appears that *C. ursinus* populations connected by high gene flow were in effect genetic replicates of each other and loss of some populations had little impact on species-level diversity. When the species' breeding range contracted, a refuge (or refugia) safeguarded species-level diversity even as populations went extinct. The large size of the refuge allowed the northern fur seal to maintain genetic diversity rather than lose it through genetic drift. This refuge then provided the source for rapid recolonization of the seal's original breeding range that continues to the present day.

While it appears that Pribilof Islands provided this critical refuge, their value as a refuge may be diminishing. Pup production has declined more than 50% since 1975, and this reduction

462 cannot be explained by emigration to other colonies (Towell *et al.* 2006). Possible explanations
463 for this decline include competition with industrial fisheries for food (Trites 1992), changes in
464 climate (York 1995), and prey-switching by top predators (Springer *et al.* 2003). Loss of the
465 Pribilofs as a refuge would significantly reduce the long-term resilience of the northern fur seal.

466 Our work also highlights the importance of high mobility in providing genetic resilience
467 to disturbance, and this conclusion mirrors similar findings on demographic resilience. For
468 example, metapopulation models show that high dispersal species are more likely to survive
469 disturbances (Frank & Wissel 1998). In British butterflies threatened by habitat loss and climate
470 change, mobile species increased their distribution over the past 30 years, while non-mobile
471 species have declined (Warren *et al.* 2001). Similarly, animal-dispersed trees appear less
472 vulnerable to decreased forest cover than other species (Montoya *et al.* 2008).

473 The demographic and genetic histories of northern elephant seals (*Mirounga*
474 *angustirostris*) and sea otters (*Enydra lutris)* serve to underscore our conclusions about refugia
475 and dispersal. The northern elephant seal is highly mobile, but lacked a refuge of moderate size,
476 instead surviving on only one island of less than a hundred individuals (Weber *et al.* 2000). The
477 sea otter maintained multiple refuges throughout its range, but is not highly mobile (Gorbics &
478 Bodkin 2001). In contrast to the northern fur seal, both species lost genetic diversity as a result of
479 overexploitation during the 18th and 19th centuries (Larson *et al.* 2002; Weber *et al.* 2000).

480 In addition to high dispersal rates and large refugia, our research suggests that behavioral
481 plasticity provides the northern fur seal with resilience by allowing the species to use a wide
482 geographic range without requiring local adaptation. Previous evidence suggested divergent

483 weaning strategies in ancient high latitude (weaning at ~ 4 months of age) and temperate (~ 12
484 months) populations (Newsome *et al.* 2007). The high rate of gene flow suggested by our study
485 make local adaptation unlikely (Lenormand 2002), leaving plasticity as the more likely
486 explanation for divergent weaning strategies. Short weaning periods are likely beneficial in the
487 short but highly productive Arctic summer, while long weaning periods may buffer the species
488 against interannual variability and lower productivity typical at temperate latitudes (e.g., El Niño
489 Southern Oscillation) (Newsome *et al.* 2007). Plasticity in weaning strategy could allow the
490 species to exploit a wide range of climatic conditions, from the arctic Pribilof Islands to the
491 mediterranean Channel Islands. The long-distance feeding migrations of females – from the
492 northern to the southern edge of the species range – put them close to distant breeding sites and
493 allow individuals of this species tp experience the entire range of climate conditions to which the
494 species is adapted (Ream *et al.* 2005). Additional research will be needed to determine whether
495 the San Miguel colony used this longer weaning strategy in the past and whether it will develop
496 this strategy in the future.

497 By combining ancient and modern population genetics in a flexible ABC framework, our
498 data suggest that maintenance of refugia combined with high dispersal and behavioral plasticity
499 helped to maintain genetic diversity in *C. ursinus* despite large reductions in abundance and
500 range size.

501 *Implications for other species*

502 In the future, anthropogenic and climate-related stressors are only expected to become
503 more common and larger in magnitude for most species. We posit that convincing evidence of

low or even lack of population structure, a secure refuge, and a distribution that encompasses a wide geographic range can be identifying traits for species that possess higher resilience to these stressors. Our study suggests that the northern fur seal may fit these criteria if the Pribilof colonies are secure. Other panmictic or nearly panmictic species with wide ranges appear to include the monarch butterfly (Brower & Jeansonne 2004), certain bees (Beveridge & Simmons 2006), North Sea plaice (Hoarau *et al.* 2002), and tuna (Appleyard *et al.* 2002).

In cases of panmixia or near panmixia extending across an entire species, it is interesting to note that the species and the population are effectively indistinguishable. This may be powerful information for resource managers, as long as appropriate methods have been used to ensure that panmixia is not mistakenly concluded for lack of power (Brosi & Biber 2009). For example, we would expect that relocation of organisms for assisted migration (Hoegh-Guldberg *et al.* 2008) would be more successful in panmictic species than in species that are locally adapted. Temporal sampling may be critical to show that panmixia is a typical, rather than a recent, state for a species (Ibrahim *et al.* 1996).

Our data demonstrate the value of using temporal genetic data in a Bayesian framework to understand the importance of dispersal to population responses to disturbance and potentially in defining which species might be candidates for management manipulations in the future. However, we caution that no species is immune from extinction, particularly if threatened with stressors across its entire range, and we emphasize that the timing for rescue of such populations is critical to maintain high levels of genetic diversity.

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682

Acknowledgements

We thank the following individuals and institutions for access to samples: R. Knecht (Museum of the Aleutians); E. Pillaert (University of Wisconsin Zoological Museum, Madison, WI); J. Bowchop (Makah Cultural and Research Center, Neah Bay, WA); D. Brauner (Oregon State University, Corvallis, OR); and T. Wake (University of California, Los Angeles, CA). C. Anderson provided insightful advice regarding ABC analyses. This work was funded in part by National Science Foundation grant OCE-0550827. Support for MLP came from a NDSEG Fellowship and a NSF Graduate Research Fellowship.

692 **Figure Legends**

693 **Figure 1.** The northeastern Pacific coastline showing locations from which ancient and modern
694 *C. ursinus* samples were collected. Ancient samples came from Chaluka (AK), Ozette (WA), Seal
695 Rock (OR), Umpqua (OR), Duncan's Point Cave (CA), and San Miguel Island (CA). Modern
696 samples came from the major eastern Pacific colonies: St. George and St. Paul Islands in the
697 Pribilofs (AK), Bogoslof Island (AK), and San Miguel Island (CA).

698

699 **Figure 2.** Posterior densities (black line) for population sizes and dispersal rates of the northern
700 fur seal over the past 2000 years. a) ancient effective female population size from ABC-
701 Bottleneck analysis, b) bottleneck effective size from ABC-Bottleneck, c) dispersal rate among
702 modern populations from ABC-Dispersal analysis, and d) dispersal rate among ancient
703 populations from ABC-Dispersal. Prior densities are shown as grey shading.

704

705 **Tables**

706 **Table 1.** Archaeological sites where northern fur seal bones and teeth were obtained. Dates are
707 calibrated radiocarbon measurements on fur seal bones or associated materials (see Table S1).
708 The right-most column lists the number of specimens from which we obtained useable *C. ursinus*
709 DNA sequence.

Site ID	Name	2σ Calibrated Age Range (years before present)	Sample size
	Chaluka, Umnak Is., AK	314 - 1031	11
35-LNC-14	Seal Rock, OR	432 - 616	6
35-DO-83	Umpqua/Eden, OR	481 - 2425	7
WA-CA-24	Ozette, WA	0 - 539	6
CA-SON-348H L10-30	Duncan's Point, Sonoma, CA	939 - 1135	1
CA-SMI-525	Point Bennett, San Miguel Is., CA	1914 - 2336	2
CA-SMI-528	Point Bennett, San	801 - 1460	4

Stratum I	Miguel Is., CA		
CA-SMI-602	Point Bennett, San Miguel Is., CA	0 - 458	3
		Total	40

710 **Table 2.** Comparison of ancient and modern mtDNA control region diversity in *C. ursinus*.

	n	S	H_e	π	D	P	F_{ST}
Ancient (A)	40	35 (157)	0.996 ±0.007	0.0484 ±0.0256	-0.263 (>0.1)	25 (M)	0.0087 (M)
Ancient Alaska (AA)	11	23 (157)	1.00 ±0.039	0.0433 ±0.0249	-0.613 (>0.1)	11 (AC)	-0.0234 (AC) 0.0245 (MA)
Ancient California (AC)	9	20 (157)	1.00 ±0.052	0.0556 ±0.0322	0.911 (>0.1)	9 (AA)	-0.0020 (MA) -0.0183 (MC)
Modern (M)	365	55 (157)	0.989 ±0.002	0.0477 ±0.0247	-0.339 (>0.1)	174 (A)	
Modern Alaska (MA)	279	52 (157)	0.988 ±0.002	0.0473 ±0.0245	-0.332 (>0.1)	122 (MC)	0.0036 (MC)
Modern California (MC)	86	40 (157)	0.990 ±0.004	0.0488 ±0.0254	-0.120 (>0.1)	39 (MA)	0.0047 (AA)

711 n: Number of samples

712 S: Segregating sites (total sites sequenced)

713 H_e: Haplotype diversity ± standard deviation

714 π: Nucleotide diversity, per site ± standard deviation

715 D: Tajima's D (p-value)

716 P: Private haplotypes as compared to population in parentheses

717 F_{ST}: Pairwise comparisons against population in parentheses