A COMPARISON OF DIVERSITY IN THE *ZFY* GENE IN TWO SPECIES OF PINNIPEDS WITH DIFFERENT BREEDING STRATEGIES

A Thesis

by

JASON MICHAEL SWENY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2005

Major Subject: Genetics

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Approved by:

Chair of Committee,	John W. Bickham
Committee Members,	Rodney L. Honeycutt
	J. Spencer Johnston
Chair of Genetics Faculty,	James Wild

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ABSTRACT

A Comparison of Diversity in the *Zfy* Gene in Two Species of Pinnipeds with Different Breeding Strategies. (December 2005)

Jason Michael Sweny, B.S., Texas A&M University

Chair of Advisory Committee: Dr. John W. Bickham

Sequence variation was examined for the Zinc-finger Y (*zfy*) gene and the mitochondrial control region for two species of pinnipeds, the Steller sea lion (*Eumetopias jubatus*) and harbor seal (*Phoca vitulina*). The two species differ in aspects of their breeding strategies, dispersal, and life histories. Comparable stock sample sizes of males from each species were taken from localities that span at least one well-recognized phylogeographic stock as defined by mtDNA markers. Variation in *zfy*, a strictly paternally inherited marker located on the Y chromosome, was low in both species. An interesting pattern of subdivision was found for *zfy* in harbor seals that was concordant with population subdivision for mtDNA. In Steller sea lions, no such concordant pattern was evident with only a single rare *zfy* variant being observed. One explanation for the different patterns observed is that dispersal is less in male harbor seals than in male Steller sea lions.

DEDICATION

To my family.

ACKNOWLEDGMENTS

I wish to thank Dr. Bickham for helping me to learn and understand while under his tutelage, and for his patience with my many revisions. I also want to thank the members of my committee, Dr. Honeycutt and Dr. Johnston, for their advice and guidance through the exam process. Also, thank you to Cole Matson for his assistance with data analysis.

I wish to thank the many people involved in collecting the tissues used in this study, especially Thomas Gelatt, Harriet Huber, and Thomas Loughlin. Funding for the laboratory analyses was provided by National Marine Fisheries Service (NMFS) and Alaska Department of Fish and Game (ADF&G). Funding for field work was provided by NMFS, ADF&G, and the Alaska Sea Life Center.

I wish a very special and heartfelt thank you to Dr. John C. Patton, whose years of experience he shared with me. In hours upon hours of conversations, he helped me to wrap my mind around the fundamental theories of population genetics. He was always there when I needed technical help as well. Without his help, this would not have been possible.

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INTRODUCTION

The Y chromosome of eutherian mammals is usually comprised of two pseudo-autosomal regions (PAR) at either end of the chromosome that are required for proper disjunction in meiosis. The PARs are homologous with the ends of the X chromosome and undergo recombination as do the autosomes. The NRY, which comprises the intervening 95% of the length of the Y chromosome, is not homologous with the X and does not undergo crossing over. Recently 20 genes have been identified on the Y chromosome (Lahn and Page 1997), of which 55% are involved in the development of the testes and sperm production. The *zfy* gene codes for a zinc-finger protein originally thought to be the testes determining factor. It "is actively transcribed in males and appears to be involved in sperm or testes maturation" (Dorit et al. 1996). The *zfy* gene is highly conserved in many species of mammals, and has been used as a marker for the Y chromosome in population studies of rodents and humans (Tucker and Lundrigan 1993; Dorit et al. 1996; Jobling and Tyler-Smith 2003) and as a sex-specific marker in wildlife studies (Shaw et al. 2003; Aasen and Medrano 1990). It has also been used in phylogenetic studies of primates, carnivores, cervids, and rodents (Dorit et al. 1996; Slattery and O'Brien 1998; Cathey et al. 1998).

Y-chromosome markers have potentially high value for the reconstruction of the male's genetic and phylogeographic history. Many of the advantageous features of mitochondrial DNA (mtDNA) for the study of female population genetics are shared with the Y chromosome. Specifically, both are haploid, do not undergo recombination, are

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This thesis follows the style and format of Journal of Mammalogy.

clonally inherited, and evolve relatively rapidly compared to biparentally inherited nuclear loci (Shimmin et al. 1993a, Shimmin et al. 1993b, Chang et al. 1996, Huang et al. 1997, Li 1997). The *zfy* gene, which is located in the non-recombining region (NRY) of the Y chromosome in eutherian mammals, is a good candidate for the comparison of paternally and maternally inherited molecular markers.

Y-chromosomal loci exhibit an accelerated evolutionary rate compared to orthologous sequences on the X chromosome (Shimmin et al. 1993a, Shimmin et al. 1993b, Chang et al. 1996, Huang et al. 1997, Li 1997). Moreover, neutral mutations on the Y evolve at a higher rate than on autosomal loci. This phenomenon presumably relates to the higher number of divisions required in spermatogenesis versus oogenesis and the fact that Y chromosomes only pass through spermatogenesis. Interestingly, areas of the genome with little or no recombination sometimes show reduced variability due to gene hitch-hiking (selective sweeps) or background selection. Gene hitch-hiking is the result of strong positive selective forces acting on a gene in the area of reduced recombination. This causes alleles at linked loci to be selected by association, causing a reduction in variability. Similarly in background selection, a mutation appears inferring strong negative selection will result in all alleles associated with the novel mutation being removed from the population. Such sweeps are particularly effective for male-specific markers. Such markers have small effective population sizes that result from two aspects of male biology: males comprise half or (more typically) less of the total population, and they generally have higher variance in reproductive success than females.

The full cDNA sequence of human and mouse is available and primers for PCR amplification and sequencing have been developed in primates, rodents, carnivores, cervids, and chiropterans. Presently, primers have been developed along approximately 3,000 base-pairs of its length between exon 3 and exon 7 in pinnipeds. The gene includes both relatively rapidly evolving introns and highly conserved exons.

The purpose of this study was to compare levels and patterns of Y-chromosome variation in two species of pinnipeds, *Eumetopias jubatus* (Steller's sea lion) and *Phoca vitulina* (harbor seal) that differ in aspects of their breeding strategies, dispersal, and life histories. We analyzed comparable sample sizes of males from each species taken from localities that span at least one well-recognized phylogeographic stock as defined by mtDNA markers.

METHODS

Study Area and Sample Size

Zfy of Steller Sea Lions.--Male Steller sea lions were sampled throughout their range (Fig. 1). Samples included skin biopsies taken from the distal portion of the hind flippers of pups preserved in 20% DMSO in saturated NaCl solution and stored at room temperature (Amos and Hoelzel 1991). Sea lion pups (n = 24) were sampled from the following rookeries: Iony Island (Sea of Okhotsk) n=2, Chernyye Brat'ya Island (Kuril Islands) n=4, Kiska Island (Central Allutian Islands) n=3, Akutan Island (Eastern Aleutian Islands) N=2, Marmot Island (Gulf of Alaska) n=5, White Sisters Island (Southeastern Alaska) n=4, and Rogue Reef (Oregon) n=4. The samples were pooled into previously established stocks to increase sample sizes for comparisons (Baker et al. in press). The stocks include the Asian stock (Iony Island and Chernyye Brat'ya), the western stock (Kiska Island, Akutan Island and Marmot Island), and the eastern stock (White Sisters Island and Rogue Reef) (Baker et al. in press).

Zfy of Harbor Seals.--Male harbor seals (n = 20) were sampled from a portion of the range of *Phoca vitulina richardsi* from Washington and California (Fig. 2). Samples were collected at the seven following sites: Gertrude Island, Washington n=6; Hood Canal, Washington n=3; Protection Island, Washington n=2; Neah Bay, Washington n=1; Whitcomb Flats, Washington n=3; Umpqua River, Oregon n=2; and Central California n=3. The samples were pooled into three groups California, Outer Coast (Umpqua River and Whitcomb Flats), and Inner Coast (Neah Bay, Protection Island, Hood Canal and Gertrude Island).

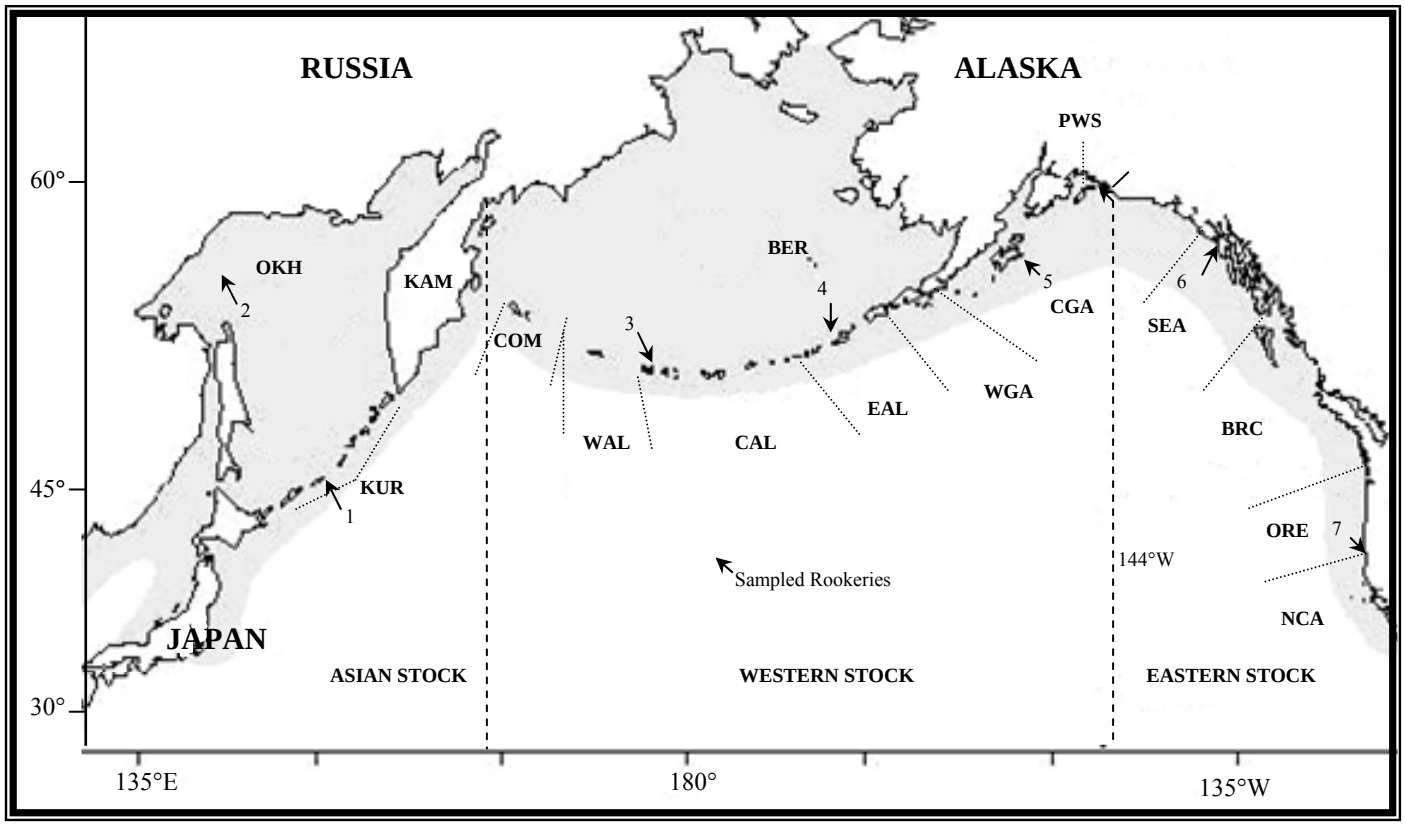

Figure 1.— Map indicating the overall distribution of Steller sea lions (shaded area) and rookeries sampled (arrows), dashed lines denote boundaries of three stocks.

Note- Sampled rookery locations are indicated by numbered arrows: 1 = Chernyye Brat'ya, 2 = Iony, 3 = Kiska, 4 = Akutan, 5 = Marmot, 6 = White Sisters, 7 = Rogue Reef. Region designations are: BER = Bering Sea, CAL = Central Aleutian Islands, CGA = Central Gulf of Alaska, EAL = Eastern Aleutian Islands, WAL = Western Aleutian Islands, WGA = Western Gulf of Alaska, COM = Commander Islands, KUR = Kuril Islands, OKH = Sea of Okhotsk, KAM = Kamchatka Peninsula, BRC = British Columbia, NCA = Northern California, ORE = Oregon, PWS = Prince William Sound, SEA = Southeastern Alaska.

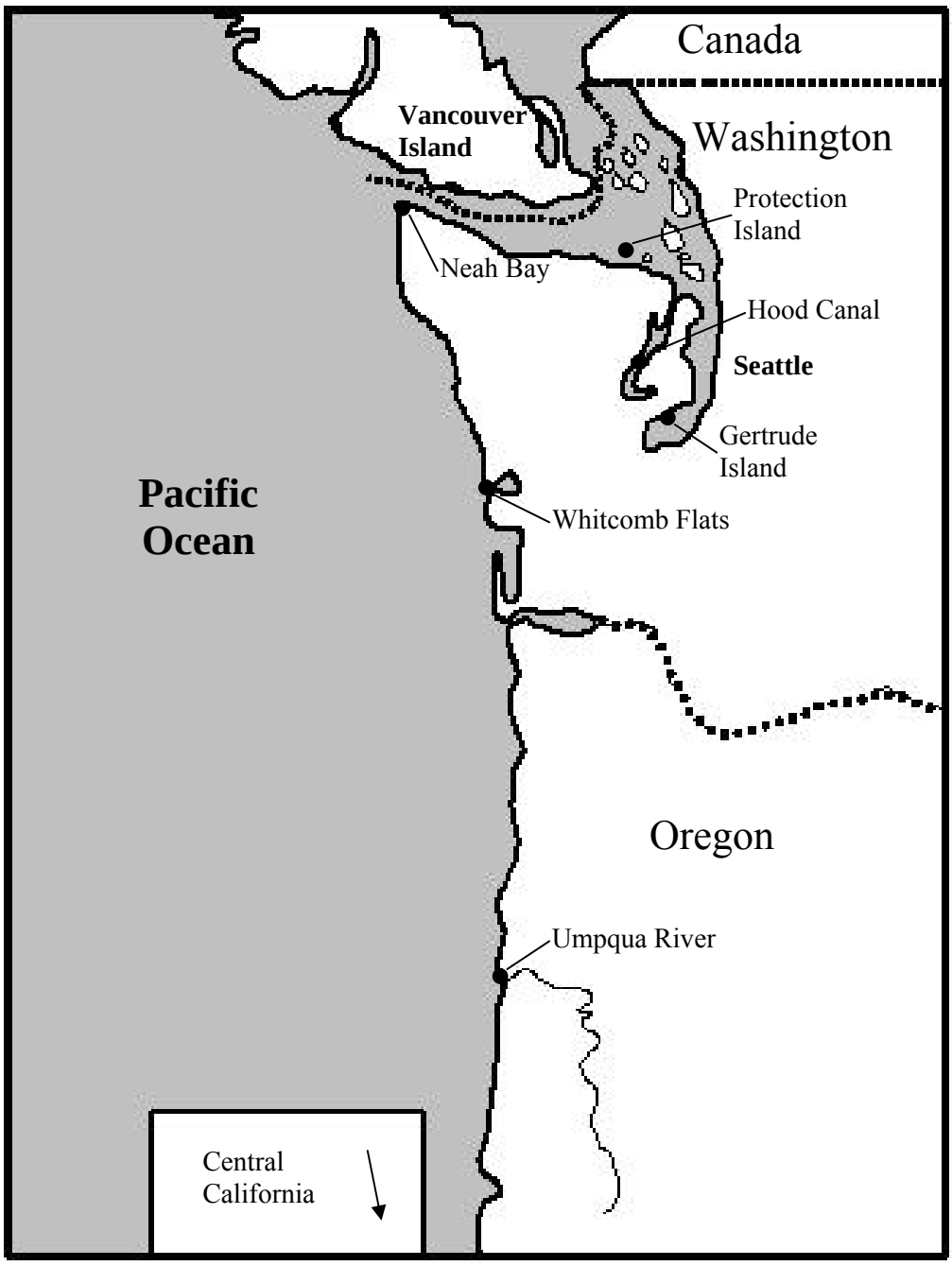

Figure 2. – Map indicating sampling locations for harbor seal.

MtDNA of Harbor Seals.-- Harbor seals (n=45) were studied from seven populations that included: Central California (N = 5,); Umpqua River, Oregon (N = 5,); Whitcomb Flats, Washington (N = 8,); Neah Bay, Washington (N = 4,); Protection Island, Washington (N = 5,); Hood Canal, Washington (N = 8,); Gertrude Island, Washington (N = 10,). These samples included the males listed for the *zfy* analysis. Genomic DNA was used for polymerase chain reaction (PCR) amplification using primer pairs LGL 283 to LGL 1115 to amplify an approximately 500 bp segment of the control region. Products of PCR amplification were subjected to analysis by automated DNA sequencing using dye-labeled terminators (Bickham et al., 1996). The PCR products were sequenced from the LGL 1115 primer end with an ABI 373A automated DNA sequencer. A segment of the control region of 330 bp in length was sequenced for each sample. This region is the same as that reported for Steller sea lions. (Bickham et al. 1996).

Laboratory Methods

Total Genomic DNA was extracted using established protocols (Sambrook and Russell 2001). An approximately 2,700 bp region of the *zfy* gene between exon 3 and exon 7 was amplified by Polymerase Chain Reaction (PCR) in two sections using primer pairs 333/Pin33X5YR and 33X5F/Pin 331YR. PCR reaction mix contained 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 2.5 mM $MgCl_2$, 200 μM each dNTP, 0.5 μM each primer, 500 ng template, and 1.25 units AmpliTaq polymerase in a 50 μL total reaction. PCR cycle was one cycle 94ºC for 5 minutes; 32 cycles of 94ºC for 45 seconds, 50ºC for 40 seconds, 72ºC for 1 minute; one cycle 72ºC for 7 minutes and 4ºC hold.

The fragments were then cleaned up using a QIAquick® PCR purification kit (Qiagen, Chatsworth, CA). The cleaned products were then sequenced using either internal or external primers. Primers annealing to exon 4, V33X4F and V33X4R, and exon 5, 33X5R, were the internal primers used to sequence the fragment 333-33X5YR. The fragment 33X5F-Pin 331YR was sequenced with the primers 332 and 335 (Cathey et al.1998) located in the exon 6 and PIN33X5YDF near exon 5 (Fig.3 and Table 1).

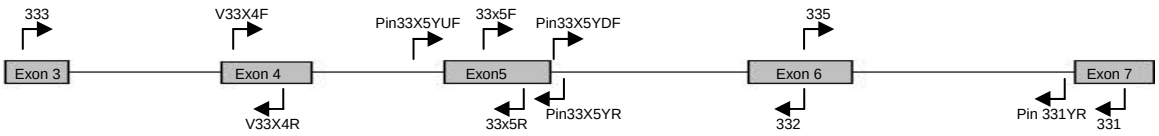

Figure 3. –Diagram of the *Zfy* gene showing the locations of the primers used in this study.

Table 1. Sequences of all primers used for amplification and sequencing.

Primer	Sequence (5'-3')
333 ……	GGATGATGCTGGTAAAATAG
V33X4R……...……......	GTCATATAAACCATCTTTTCCCTT
V33X4F……...……	CCGTAGACATTGTGGAGAGTGAGC
33X5R……...…….....	ACGCTATTGGCATGAAGGTTT
33X5F……...……..…	ATCGTAGGAGAGGAGGATGC
PIN33X5YR ……...……..……..	ATCCTTTGAGGCACTATGC
PIN33X5YUF……...……	TGAGAGCCAAGAAGGTAATGGT
PIN33X5YDF……...……...	GCTTATGGTAAGTCACATGC
335……..……	AGACCTGATTCCAGACAGTACCA
332……..……..	GGTACTGTCTGGAATCAGGTC
PIN331YR……..……	CAGACAAGTACTCCCAAGWGTTAA
331……..……	CAAATCATGCAAGGATAGAC

For mtDNA analyses, I used primer pairs LGL 283 and LGL 1115 to amplify an approximately 500 bp segment which included the upstream side of the control region using previously described methods (Bickham et al., 1996; Baker et al., in press).

DNA sequence reactions were done using previously described methods (Bickham et al., 1996). Reactions were analyzed using an ABI PRISM® 377 DNA Sequencer (Applied Biosystems, Foster City, CA). Peaks were assigned bases using ABI Sequencing Analysis. Sequence alignment was done using Sequencher ver. 4.1 software (Gene Codes Corp., Ann Arbor, MI) and verified by eye.

Analytical Methods

Exact tests for significant population differentiation for all pairwise comparisons were conducted in ARLEQUIN. Modified F-statistics (Wright, 1951) were estimated using ARLEQUIN. Conventional F_{st} parameter estimates infer population structure using only haplotype frequencies, whereas Φ_{st} estimates take into account haplotype sequence divergence as well. The Tamura and Nei (1993) mutation model was used to estimate sequence divergence between haplotypes. Probabilities for all measures of genetic distance were estimated using 10,000 randomizations of the original data set; this represents a 10-fold increase over the minimum number of permutations required to obtain an accurate probability estimate (Schneider et al., 2000). In addition, a transformation (Slatkin, 1995) was applied when calculating Φ_{st} estimates to linearize population distances (Schneider et al., 2000). The results are matrices of genetic distances consisting of positive values only. Neighbor-joining (NJ) trees were generated using the matrices of

genetic distances calculated for all pairwise comparisons using PAUP* 4.0 (Swofford, 1998). All trees were constructed using midpoint rooting.

RESULTS

Eumetopias jubatus

In Steller sea lions, I analyzed 2,635 bases in 15 individuals and 2231 bases in 9 individuals, for a total of 24 animals. A single variable site was observed in one individual. The proportion of polymorphic sites was 1/2635 (pn = 0.0003795). Nucleotide diversity was < 0.00001, due to the low level of polymorphic sites. The singleton (EJ2) was found in the Rogue Reef population. The common haplotype (EJ1) has a thymidine at base number 1459 (86 bases down stream of exon 5), and EJ2 has an adenosine (Fig. 4). The low level of polymorphism found in this study did not allow for a significant population analysis.

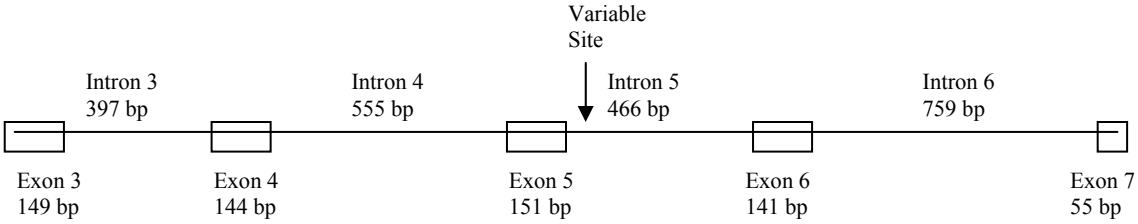

Figure 4. – Diagram of the *Zfy* gene in *Eumetopias jubatus*, showing the sizes of the introns and exons and indicating the position of the single variable site.

Phoca vitulina

For *zfy* in harbor seals, we analyzed 2650 bases in 3 individuals, and 1377 bases in 17 individuals, for a total of 20 animals. We found one variable site which defines two haplotypes (haplotype PV1 and PV2). The proportion of polymorphic sites was 1/2650 (pn = 0.0003774). Nucleotide diversity was < 0.00001, also due to the low level of polymorphic sites. The PV1 haplotype has an adenosine at base number 26, and haplotype

PV2 has a guanine (Fig. 5). Within the entire dataset their respective frequencies are 0.3 and 0.7. The frequencies of alleles for the three populations are California PV1=1.0, Outer Coast PV2=1.0, and Inner Coast PV1=0.25 and PV2=0.75. Φ_{st} estimations show a significant division between the California population and the Outer (p=0.02) and Inner Coast (p=0.04) populations.

Nucleotide sequence analysis of the mtDNA control region of 45 harbor seals revealed a total of 33 haplotypes defined by variable nucleotides at 39 positions. No more than two alternative nucleotides were found at any position. The mutations included: 15 T/C transitions; 23 A/G transitions; 1 C/G transversion; 1 A/T transversion; 1 T/G transversion; and 2 deletions. Therefore the ratio of transitions to transversions was 38:3 which is similar to transition biases previously reported for the control region (Bickham et al., 1996; Greenberg et al., 1983).

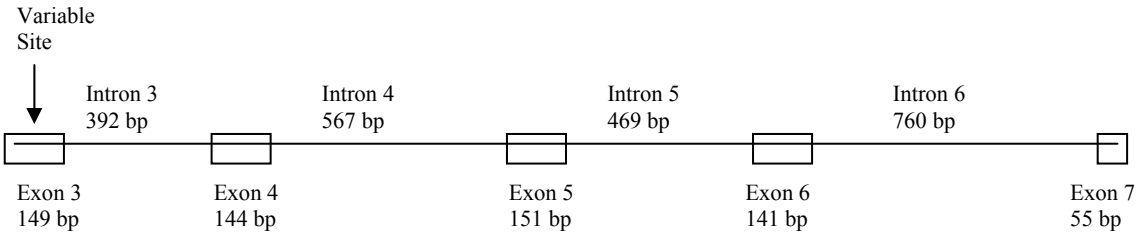

Figure 5. – Diagram of the *Zfy* gene in *Phoca vitulina*, showing the sizes of the introns and exons and indicating the position of the single variable site.

Genotypic diversity.--Harbor seals are extremely variable in control region sequences. Of the 33 haplotypes found, 28 were observed in only a single individual, 2 were found in only two individuals, 1 was found in 3 individuals, 1 was found in 4 individuals, and 1 was found in 6 individuals (Table 2).

Genotypic diversity was estimated using the nucleotide (nucleon) diversity index as calculated according to the method of Nei and Tajima (1981, equation 7). Haplotype diversity (h) ranges from h = 1, in which all individuals of a population have different haplotypes, to h = 0 where all individuals have identical haplotypes. The harbor seal populations invariably had high values for h: Gertrude Island, h = 1; Hood Canal, h = 0.855; Protection Island, h = 1; Neah Bay, h = 1; Whitcomb Flats, h = 0.641; Umpqua River, h = 0.9; Central California, h = 1. The nucleotide diversity estimate for the total population (N = 45) was h = 0.923. This is nearly the same as the value (h = 0.916) reported for 1,685 Steller sea lions (Baker et al., in press).

Geographic variation.--Pairwise Φ_{st} comparisons between populations were made using Tamura-Nei distances. The comparisons show a significant difference between the Inner Coast population and the Outer Coast population (Φ_{st} = 0.17224, p=0.00079), a significant difference also exists between the Outer Coast population and the California Coast Population (Φ_{st} = 0.56252, p=0.00099). No significant difference is found in the comparison between the Inner Coast and California (Φ_{st} = 0, p=0.43996), which may be due to the small sample size of the California population. The NJ tree using Tamura-Nei distances shows fifteen of the nineteen Inner Coast haplotypes in three distinct clades within the tree (Fig. 6). All of the haplotypes shared by more than one individual fall within a single population, except one that is shared between three individuals from the Outer Coast and one from the Inner Coast. The individual from the Inner Coast is from Neah Bay at the mouth of Peuget Sound and the border between the Inner Coast and Outer Coast.

Table 2.—Substitutions and deletions (indicated by *) observed in 330 bp of the control region in *Phoca vitulina*. On the right the number of individuals per haplotype per population are indicated (CA= California, IC= Inner Coast, OC= Outer Coast)

	0 2 8	0 3 9	0 5 9	0 6 1	0 6 5	0 7 9	0 8 0	0 8 2	0 9 9	0 9 0	0 9 5	0 9 6	0 9 8	1 0 2	1 1 0	1 1 3	1 3 7	1 4 0	1 7 1	1 7 8	1 8 7	1 8 8	1 8 9	1 9 7	1 9 8	1 9 9	2 0 7	2 1 3	2 3 6	2 3 2	2 3 4	2 5 8	2 6 1	2 8 5	3 0 9	3 3 3	3 3 0	3 4 7	C A	I C	O C
Hap. 13	A	A	A	G	A	T	T	G	G	C	*	C	C	C	G	C	T	T	G	A	A	T	A	C	G	G	A	T	T	G	T	A	T	G	G	A	A	G	G		1	
Hap. 1	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			2
Hap. 2	.	.	.	.	.	C	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.		1	
Hap. 3	.	.	.	.	*	.	.	.	.	.	.	T	.	.	T	.	.	.	.	.	C	.	.	A	.	G	.	C	.	C	.	.	.	.	.	.	.	.	.	.		1	
Hap. 4	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.		1	
Hap. 5	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	A	.	.		1	
Hap. 6	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	
Hap. 7	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A		2	
Hap. 8	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	
Hap. 9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	C	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.		1	
Hap. 10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1		
Hap. 11	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	A	.	.	.	.	.			1
Hap. 12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A		1	
Hap. 14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			1
Hap. 15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			6
Hap. 16	.	.	G	.	*	.	.	.	.	.	C	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	1		
Hap. 17	.	.	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			1
Hap. 18	.	.	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	A	.	.	.	.	.	.	G	.	.	.	.	A	.	.	.		1	
Hap. 19	.	.	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	A	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.		3	
Hap. 20	.	.	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	C	G	.	A	.	.	.	.	.	.	.	.		1	
Hap. 21	.	.	G	.	*	.	.	.	.	T	C	.	.	.	.	.	.	.	.	G	.	.	.	.	A	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.		1	3
Hap. 22	.	G	.	.	*	.	.	.	.	T	.	.	.	.	T	.	C	.	.	G	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	G	.	.	.	.		1	
Hap. 23	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.			1
Hap. 24	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	
Hap. 25	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			1
Hap. 26	.	G	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	G	.	.	G	.	.	.	A	.	.	.	.	.	C	G	.	.	.	.	.	A		1	
Hap. 27	.	G	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	1		
Hap. 28	.	G	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1		
Hap. 29	G	.	.	.	*	.	.	A	.	T	.	T	T	.	.	.	.	.	.	.	C	.	.	A	.	G	C	.	A	G	.	G	.	A	.	.	C	.		1	
Hap. 30	G	.	.	.	*	.	.	A	.	T	.	T	T	.	.	.	.	.	.	.	C	.	.	A	.	G	C	.	A	G	.	G	.	A	.	.	.	.		1	
Hap. 31	G	.	.	.	*	.	.	A	.	T	.	T	T	.	.	.	.	.	.	.	C	.	.	A	.	G	C	.	A	G	.	G	.	.	.	.	.	.		1	
Hap. 32	.	.	G	.	*	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	1		
Hap. 33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	A	.	.	.			1

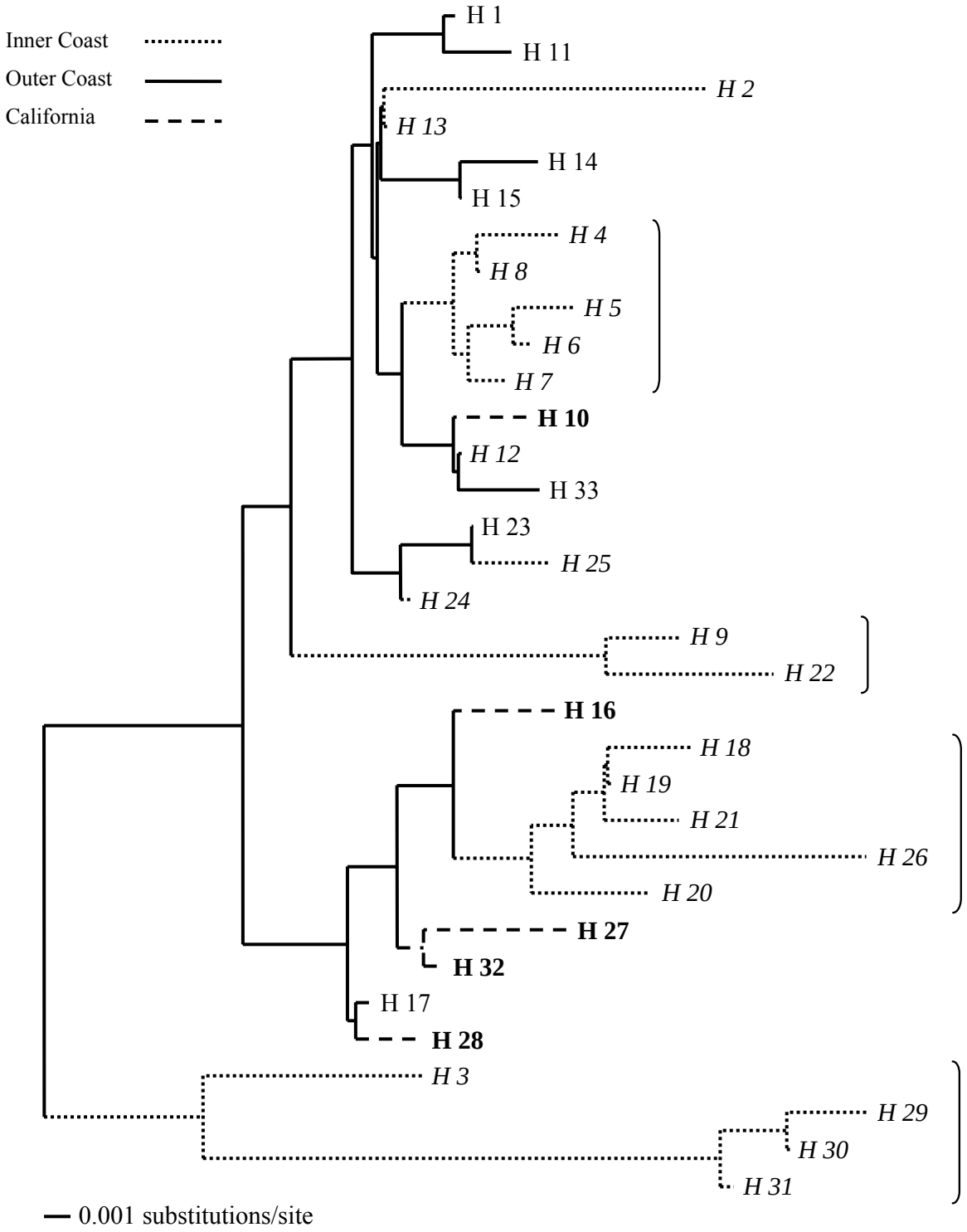

Figure 6. --Harbor seal mtDNA control region NJ midpoint-rooted Phylogram.

DISCUSSION

Eumetopias jubatus

Steller sea lions inhabit the north Pacific Rim from central California, United States, in the east to the Kuril Islands and Sea of Okhotsk, Russia, in the west (Loughlin 1997). Census data on Steller sea lions from the last ninety years shows a marked decline beginning in the 1960s when estimates put the Steller sea lion population at 240,000 – 300,000 individuals (Kenyon and Rice 1961). In 1989 the total population of Steller sea lions fell to an estimated 116,000 individuals (Loughlin et al. 1992). Subsequently, the Steller sea lion was listed as threatened under the United States Endangered Species Act in 1991. The species was later subdivided into two separate breeding stocks based on mtDNA studies by Bickham et al. (1996, 1998a, 1998b). The dividing line between the stocks is 144º W longitude. The western stock is still declining and in 1997 was listed as endangered, while eastern stock populations are either stable or increasing slightly. Studies of mtDNA show strong indications of population subdivision with three recognized stocks (Fig. 1): an eastern stock ranges from California to southeastern Alsaka, the western stock ranges from Prince William Sound to the Commander Islands, and the Asian stock includes rookeries from the Kamchatka Peninsula, Kuril Islands, and Sea of Okhotsk in Russia (Baker et al. in press; Bickham et al. 1996, 1998). This distinctive pattern is not apparent with binuclear inherited microsatellite loci which led to the conclusion that gene dispersal is male driven in Steller sea lions (Trujillo et al., 2004). Juveniles and young adults up to breeding age are known to cover great distances. For example, tag data have shown animals from the Kuril Islands sighted near Yokohama, Japan and in the Yellow

Sea, and pups marked near Kodiak, Alaska, were sighted near Vancouver, British Columbia (Loughlin 1998). Nonetheless, Steller sea lions are thought typically to be philopatric, returning to their natal rookery to breed.

Both males and females reach sexual maturity between three to six years of age. At this age, females begin to breed whereas young males are not yet large enough to hold breeding territory until 9-11 years of age (Pitcher and Calkins 1981, Loughlin 1998). Males defend territory on the rookeries where females come to give birth. Pupping occurs throughout the range from mid-May to mid-July with a peak in June (Pitcher and Calkins 1981). Three days after a female has her pup she mates with a male at her rookery. Implantation is delayed until September or October (Pitcher and Calkins 1981). Females may continue to give birth into their twenties, while males are too old and battered to establish and maintain territories by the time they are 13-14 (Loughlin 1998).

The data presented here fails to reveal any pattern of subdivision in the males throughout the range of Steller's sea lion. These results have one of two possible causes. Either our study was not sufficiently large to capture what variation there may be, or due to the dominant male breeding strategy employed by the sea lions Y chromosome sweeps move quickly throughout the population. In a polygynous mating system, such as that of Steller's sea lion, a few males are responsible for most of the offspring, hastening Y chromosome sweeps. As an example, in elephant seals 3% of males were responsible for 92% of matings (Le Boeuf and Reiter, 1988).

Phoca vitulina

The harbor seal or common seal (*Phoca vitulina*) inhabits the northern temperate and sub-arctic regions in both the Pacific Ocean and the Atlantic Ocean. Their range extends from the Baltic Sea in the east to Japan in the west. The species is divided into four sub-species historically based on geographic separation and morphological studies of the populations (Baird 2001). Stanley et al. (1996) confirmed this subdivision with mtDNA analysis, although, Westlake and O'Corry–Crowe (2002) argue that there is not enough evidence for the sub-species level distinctions between the east and west sides of the Pacific Ocean. They suggest that the subspecies differences are a result of a cline caused by the wide range of *Phoca vitulina* relative to the distance traveled by individuals. Harbor seals have been shown to be highly philopatric (Stanley et al. 1996, Schaeff et al. 1999, Thompson et al. 1994). Although tag data suggest that some seals travel many hundreds of kilometers, seals usually return to their natal rookery to reproduce.

I found significant levels of population subdivision using *zfy* and using mtDNA, in a relatively small portion of the range of the harbor seal in the eastern Pacific Ocean. This indicates that both males and females are highly philopatric, since *zfy* shows only male population history and mtDNA shows only female population history.

Unlike the Otariids, most Phocids breed in the water, including harbor seals. Harbor seals are believed to be polygynous because of sexual dimorphism in size. Fisher (1954) showed that *Phoca vitulina* ovulates within days of weaning. Subsequent studies show implantation is delayed from 1.5 to 3 months (Thompson 1988). Timing of mating in harbor seals varies with latitude although it is not linear (Thompson 1988). Pupping has

been recorded in California from April to May, on the outer coast of Washington and Oregon from April through June, in Puget Sound, Washington from late July to September, and in the western Gulf of Alaska from May to June (Thompson 1988, King 1983). Lamont et al.(1996) suggested that it is controlled genetically based on population subdivision in mtDNA that corresponds to the differences seen in pupping times.

Similar levels of variability in mtDNA were observed in the two species, from which I conclude that the rate of mutation is equivalent in both species. But, the level of polygyny observed in *Phoca* is less than levels observed in *Eumetopias*. Aquatic mating of the harbor seals reduces polygyny because it is harder for males to defend a three dimensional territory (Bartholomew 1970). The fact that less variability was observed for *zfy* in *Eumetopias* over a wider range than the area studied in *Phoca* could mean that Y-chromosome sweeps move more quickly through the Steller sea lion population. The sweeps move faster through the *Eumetopias* populations because the breeding strategy allows for more control of the mating by the dominant male than is seen in *Phoca*.

While the harbor seals are not listed as threatened or endangered, the population size has decreased significantly in some parts of the range since the 1970's (Pitcher 1990). Even as areas in Alaska show a population decline, populations on the west coast of Canada have increased steadily since the culling programs in the United States and Canada were halted in the late 1960's and early 1970's (Baird 2001). In fact, the populations in the coastal waters of Washington State are reported to be above the maximum net productivity level and near the current carrying capacity of the environment (Jefferies et al. 2003).

CONCLUSIONS

This study represents a preliminary investigation as to the utility of the *zfy* gene as a marker for population genetic studies among males of two species of pinnipeds. An interesting pattern of subdivision was found for *zfy* in harbor seals that was concordant with subdivision for mtDNA. In Steller sea lions, no such concordant pattern was observed with only a single rare *zfy* variant being observed. There are several possible explanations for these differences. First, there could be variability in *Eumetopias* which we did not sample. Perhaps other Y-chromosome genes or longer segments of the *zfy* gene would give adequate variability and uncover a phylogeographic pattern concordant with that seen in mtDNA. Second, there is not a real population division in *Phoca* and we happened to catch a selective sweep before it had run its course. This is unlikely since a similar pattern was observed with mtDNA. Third, there is a true population subdivision for *zfy* in *Phoca* and not in *Eumetopias*. If this is true, the reason for the difference could lie in the nature of their breeding habits. *Eumetopias* is more polygynous and less philopatric than *Phoca*, which allows for selective sweeps to move throughout the range of *Eumetopias.* What is clear is that the molecular approach used here has great potential to reveal the contribution of males to population genetic patterns in mammals.

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APPENDIX

SEQUENCE DATA FOR THIS STUDY

Phoca vitulina- mtDNA

Haplotype 1
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TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
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CAATGCACGA AGTACATAGG CCAGTGTGTG TGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 2
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TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
CATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
CAATGCACGG GGTACATAGG CCAGTGTGCG TGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 3
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TTCATGACAG GTAGTTATGC TTTAGAACTT GGCGTTACAA CTGTATGCCA
TGTATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGATCC GAGGATGGGG GAGG*ACATG
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TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 4
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TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 5
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Haplotype 6
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TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
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TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 7
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Haplotype 8
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TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
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TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 9
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Haplotype 10
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Haplotype 11
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Haplotype 12
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CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
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TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 13
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Haplotype 14
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Haplotype 15
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Haplotype 16
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Haplotype 17
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CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
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TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 18
ACATGTTATG GGCCCGGAGT GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA TCGTATGCCA
TACATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 19
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA TCGTATGCCA
TACATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 20
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
TTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TCCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TACATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 21
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA TCGTATGCCA
TACATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGGGACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 22
ACATGTTATG GGCCCGGAGC GAGATCCAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTAG GTGAAATGCG
TTCATAATAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ACCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCGTTAATGC ACGATATACA TAGGGGGTCT GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG TGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 23
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
TTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTAG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
CAATGCACGA AGTACATAGG CCAGTGTGCG TGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 24
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTAG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
CAATGCACGA AGTACATAGG CCAGTGTGCG TGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 25
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TTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTAG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCATATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
CAATGCACGA AGTACATAGG CCAGTGTGCG TGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 26
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CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TCCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA TCGTATGCCA
TACATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAC
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 27
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCATT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 28
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTAG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
CAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 29
ACATGTTATG GGCCCGGAGG GAGATCTAGG TACACGTTTC ACAAGGGTTG
TTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATGATAG GTAATTATGC TTTAGAGCTT GGCGTTACAA CTGTATGCCA
TGTATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GAGA*ACATA
CAATGCATGA AGTACATAGG CCAG*GTGCG TGAATACTGT GATAGCACAG
TAAGGTGATA TCATTATATG AATTGAGGAG

Haplotype 30
ACATGTTATG GGCCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
TTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATGATAG GTAATTATGC TTTAGAGCTT GGCGTTACAA CTGTATGCCA
TGTATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GAGA*ACATA
CAATGCATGA AGTACATAGG CCAG*GTGCG TGAATACTGT GATAGCACAG
TAAGGTGATA TCATTATATG AATTGAGGAG

Haplotype 31
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CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATGATAG GTAATTATGC TTTAGAGCTT GGCGTTACAA CTGTATGCCA
TGTATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GAGA*ACATA
CAATGCATGA AGTACATAGG CCAG*GTGCG TGAATACTGT GATAGCACAG
TAAGGTGATA TCATTATATG AATTGAGGAG

Haplotype 32
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CTGATTTCCC GAGGCATGGT GATTAAGGCT CGTGGACTGG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATA
CAATGCACGA AGTACATAGG CCAG*GTGCG CGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Haplotype 33
ACATGTTATG GGTCCGGAGC GAGATCTAGG TACACGTTTC ACAAGGGTTG
CTGATTTCCC GAGGTATGGT GATTAAGGCT CGTGGACTAG GTGAAATGCG
TTCATAACAG GTAATTATGC TTTAGAACTT GGTGTTACAA CCGTATGCCA
TATATGTAAA ATCAACCACT CTATGTACAT GCTTATATGC ATGGGGCAAA
CCATTAATGC ACGATATACA TAGGGGGTCC GAGGATGGGG GGGG*ACATG
CAATGCACGA AGTACATAGG CCAGTGTGCG TGAATACTGT GATAGCACAG
TAAGGTGATA TTATTATATG AATTGAGGAG

Phoca vitulina- Zfy

Haplotype PV1
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Haplotype PV2
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GTGGTTTAGATTGAGAACATTTGAAATATTTTCTGAAAATAACTTTTTTTTTAA
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Eumetopias jubatus- Zfy

Haplotype EJ1
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Haplotype EJ2
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AAATGGAACTTGGTTTGATCACTCATGCTCCTTTCTTTTCCTTTTGTAGCAATAA
TTATTGGCCCTGATGGACATCCCTTGACAGTCTATCCTTG

VITA

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M.S., Genetics, Texas A&M University, College Station, TX, 2005