VARIATION OF MITOCHONDRIAL CONTROL REGION SEQUENCES OF STELLER SEA LIONS, <u>EUMETOPIAS JUBATUS</u>: THE THREE-STOCK HYPOTHESIS

A Thesis

by

ALYSON RENEE BAKER

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 2003

Major Subject: Genetics

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ABSTRACT

Variation of Mitochondrial Control Region Sequences of Steller Sea Lions, <u>Eumetopias</u> <u>jubatus</u>: The Three-Stock Hypothesis. (December 2003) Alyson Renee Baker, B.S., Grove City College Chair of Advisory Committee: Dr. John W. Bickham

Sequence variation of a 238 bp segment of the mitochondrial control region was analyzed for 1,568 Steller sea lions (2.8% of the estimated species population) sampled from 50 rookeries representing nearly every locality at which Steller sea lions are known to breed in significant numbers. Haplotype diversity ($H = 0.9164 \pm 0.0035$) was high and nucleotide diversity ($\pi = 0.00967 \pm 0.00586$) was moderate. No evidence was observed for significant genetic bottleneck effects. Rookeries were grouped into regions and stocks to examine structure at different spatial scales. F- and Φ -statistics were computed for all pairwise comparisons of rookeries, regions and stocks. Significant (P<0.05) divergence of eastern stock (southeastern Alaska to California) animals from western stock animals was supported in analyses at all spatial scales. Likewise, rookeries and regions from Asia were found to be significantly different from all other western stock rookeries. This was most clearly demonstrated using Φ -statistics at the regional level. The Commander Islands clearly associate with Alaskan western stock rookeries, not with the Asian rookeries. Within each of the three stocks there is significant isolation by distance among rookeries. This relationship does not hold for inter-stock comparisons indicating that there are important barriers to gene flow among

stocks. Mitochondrial DNA analysis supports the recognition of three stocks for appropriate conservation of the species. The currently recognized eastern stock is unaffected, but the western stock is now partitioned west of the Commander Islands yielding a western stock which ranges from Prince William Sound west to the Commander Islands, and an Asian stock including rookeries from the Kamchatka Peninsula, Kuril Islands, and Sea of Okhtosk.

DEDICATION

This thesis is dedicated to my mother and father without whose continuous support I might not have considered tackling a higher degree, to my brother who inspires me to excel, and to my grandparents who always encouraged their children and grandchildren to further their education.

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INTRODUCTION

Distribution and Population Trends

Steller's sea lion, *Eumetopias jubatus*, was described by George Wilhelm Steller in 1742; they are the largest member of the family Otariidae (Gentry and Withrow, 1986). The Steller sea lion is endemic to the north Pacific Ocean and Bering Sea. Rookeries are distributed along an arc following the edge of the north Pacific Rim with three located in the Bering Sea. Distribution of the rookeries ranges from the west coast of the continental United States (California and Oregon), north along the Canadian and Alaskan coasts, west across the Gulf of Alaska, Aleutian Islands and Commander Islands, along the east coast of the Kamchatka Peninsula, within the Sea of Okhotsk, and southwest throughout the Kuril Islands (Fig. 1).

While Steller sea lions were believed to number between 240,000 and 300,000 in the late 1950's and early 1960's (Kenyon and Rice, 1961) and between 245,000 and 290,000 during the 1980's (Loughlin et al., 1984), their populations experienced a significant decline in the years that followed with only 116,000 present in 1989 (Loughlin et al., 1992). Likewise, the U.S. population was estimated at 192,000 in the 1960's but numbered only 52,000 in 1994 (Anonymous, 1995). Such extreme losses attracted worldwide attention and led to the Steller sea lion being listed as threatened under the U.S. Endangered Species Act in 1990.

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



Rookery locations are indicated by numbered arrows: 1 = Chernyye Brat'ya, 2 = Srednego, 3 = Raykoke, 4 = Lovushki, 5 = Antsiferova, 6 = Iony, 7 = Yamsky, 8 = Zheleznaya Bay, 9 = Kozlova Cape, 10 = Medney, 11 = Attu, 12 = Agattu, 13 = Buldir, 14, 15 = Kiska, Cape St. Stephen and Lief Cove, 16 = Amchitka, 17 = Ulak, 18 = Gramp Rock, 19 = Kasatoshi, 20 = Seguam, 21 = Yunaska, 22 = Adugak, 23 = Ogchul, 24 = Bogoslof, 25 = Walrus, 26 = Akutan, 27 = Akun, 28 = Ugamak, 29 = Amak, 30 = Clubbing Rocks, 31 = Pinnacle Rock, 32 = Chernabura, 33 = Whaleback, 34 = Atkins, 35 = Chowiet, 36 = Chirikof, 37 = Marmot, 38 = Latax Rocks, 39 = Sugarloaf, 40 = Chiswell, 41 = Fish, 42 = Seal Rocks, 43 = Cape St. Elias, 44 = White Sisters, 45 = Hazy, 46 = Forrester, 47 = North Danger Rocks, 48 = Triangle, 49 = Rogue Reef, and 50 = St. George Reef. Region designations are: BER = Bering Straight, 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.

Fig. 1. Map indicating the location of Steller sea lion rookeries sampled in this study. Regions and stocks are defined according to the results of this study.

Potential Causes of Decline

The ultimate reason for the population decline is unknown, but a number of potential factors have been tested over the years. These factors include, but are not limited to, relocation, short-term environmental stochasticity, human exploitation, pollution and disease, changed vital rates, competition with commercial fisheries and major oceanic regime shifts (Loughlin, 1998).

Upon completion of a range-wide survey in 1989, Loughlin et al. (1992) noted population declines occurring throughout the species range leading them to conclude that animals were not simply relocating from one region to another. Also, population modeling suggested that the Steller sea lion decline was due to factors more complex than natural fluctuations of the north Pacific environment (short-term environmental stochasticity; Pascual and Adkison, 1994). Furthermore, while Steller sea lions were hunted extensively for their oil, testes, whiskers and hides during the 1860's (Helling, 1984; Mate, 1976) they are no longer harvested for commercial purposes. In addition, levels of subsistence use have decreased as Steller sea lion populations have declined (Haynes and Mishler, 1994). Therefore, relocation, short-term environmental fluctuations, and human exploitation cannot explain the current decline.

Researchers have studied the impacts of pollution on pinniped populations including effects of the Exxon Valdez Oil Spill (Calkins et al., 1994; Loughlin et al., 1996), accumulation of trace metals such as copper, mercury (Sydeman and Jarman, 1998), and vanadium (Saeki et al., 1999), and biomagnification of toxic compounds such as tributyltin (TBT; Kim et al., 1996a, 1996b), organochlorines (Lee et al., 1996), and polycyclic aromatic hydrocarbons (PAHs; Albers and Loughlin, 2003). These studies do provide evidence linking pollution to the decline of Steller sea lions. The prevalence of disease has received less attention simply because disease symptoms (such as lesions, abortion, premature births, etc.) have not been observed in great numbers. Still, the impact of viruses and other pathogens is considered minimal (Loughlin, 1998).

York (1994) suggested that a 10-20% decrease in juvenile mortality could account for the degree of decline noted for Steller sea lions. While this discovery is critical, decreased juvenile mortality still represents only a proximate cause of population decline.

Competition with commercial fisheries for limited resources has long been suspected as a main contributor to marine mammal declines. Overfishing of walleye pollock (*Theragra chalcogramma*), for example, is thought to be potentially damaging to Steller sea lion populations because pollock are currently the top prey species of many marine predators (Lowry et al., 1988).

Some researchers suspect a major oceanic regime shift might have caused a change in the prey base of the Steller sea lion and indirectly contributed to the species decline (Alverson, 1998; Trites et al., 1999). However, it seems likely that the cause of the decline is multi-factorial and we may never completely understand it.

Management Issues

Following listing of the Steller sea lion as threatened in 1990, a number of studies attempted to clarify not only the cause(s) of decline but also to describe Steller

sea lion physiology, behavior, and population dynamics. Several population genetic studies contributed to our understanding of Steller sea lion genetic diversity and natural history (Bickham et al., 1996, 1998a, 1998b). In contrast to previous molecular studies that indicated little to no genetic diversity in Steller sea lion populations, or pinnipeds in general (Lidicker et al., 1981), Bickham et al. (1996) reported high variability for mitochondrial control region sequences. The mitochondrial genome is maternally inherited in mammals, undergoes no recombination, and is estimated to evolve at a rate 5-10 times faster than nuclear genes; these characteristics, combined with female philopatry, make mitochondrial DNA (mtDNA) a useful molecular marker to define population subdivision (Honeycutt, 2000).

Significant genetic divergence of control region sequences was observed between animals sampled from rookeries in the Commander and Aleutian Islands and the Gulf of Alaska and those from southeastern Alaska through Oregon (regions west and east, respectively, of Cape Suckling, Alaska; longitude 144° W). Bickham et al. (1996) suggested that the overall population be divided into two genetically distinct management units, the western and eastern stocks. Further genetic research, as well as accumulated information regarding Steller sea lion distribution, phenotypic variation, and population response, supported the decision to recognize two stocks (Loughlin, 1997; Bickham et al., 1998a, 1998b). The western stock, which is continuing to decline, was listed as endangered in 1997. The current western stock population of Alaska comprises approximately 26,000 non-pup animals (Sease and Gudmundson, 2002) and stock loses are estimated at 5% per year (Sease et al., 2001). At this rate of decline less than a thousand animals will comprise the population west of Cape Suckling, Alaska, to the westernmost tip of the Aleutian Islands in the year 2020 (Loughlin and York, 2000). In contrast, eastern stock numbers have increased it remains listed as threatened.

Management units have been assigned based on genetic and other criteria for a number of marine mammals having distributions similar to that of the Steller sea lion. For instance, harbor seals (*Phoca vitulina*) are distributed throughout the north Pacific, and the United States currently recognizes three management units within U.S. waters. Interestingly, mtDNA analysis revealed that current management stocks in Alaska were inappropriate, and researchers suggested that additional genetic data be analyzed to ensure proper conservation of the species (Westlake and O'Corry-Crowe, 2002). Sea otters (Enhydra lutris) are also distributed throughout the north Pacific. Morphological characters were used to designate three subspecies range-wide (Cronin et al., 1996). E. l. lutris occurs from Japan eastward throughout the Kuril and Commander Island chains, E. l. kenyoni is found from the westernmost tip of the Aleutian Islands east throughout the Bering Sea, Gulf of Alaska, Canada and Oregon, and E. l. nereis is distributed from California southward along the Mexican west coast. Again, mtDNA analysis resolved population substructure different from that obtained when analyzing morphological characters (Cronin et al., 1996). Analysis of the control region revealed four distinct groups, and sea otters from the Commander Islands, although morphologically like E. l. *lutris*, were most genetically similar to *E. l. kenyoni*. These studies highlight the utility of mtDNA analysis in designation of management units for marine mammal conservation.

Still further tests are needed to define population structure within the far western limits of the Steller sea lion distribution. Previous research has indicated that animals sampled from Russian rookeries (rookeries in the Sea of Okhotsk, the Kuril Islands, Kamchatka Peninsula, and the Commander Islands) were genetically distinct from other western stock sea lions (Bickham et al., 1998b; Trujillo et al., in press). However, sample sizes were generally inadequate to arrive at a confident decision regarding western stock substructure.

This study includes mtDNA sequence data for a total of 1,568 Steller sea lions taken from 50 rookeries from throughout the range of the species. Nearly every locality at which this species is known to breed was sampled, and the sample size represents 2.8% of the 53,400 extant non-pup population estimated from range-wide counts made during the years 2000 to 2002. This paper specifically focuses on a population-genetic assessment of mtDNA variability and stock structure in the western range of the Steller sea lion.

METHODS

Study Area and Sample Size

Tissue samples obtained from rear flipper punches and preserved in saturated NaCl with 20% DMSO were initially stored at room temperature (Amos and Hoelzel, 1991) and later archived at -80°C. All samples are from pups taken from their natal rookeries. The total sample size for this study was n = 1,568 and the number of animals sampled per rookery, region and stock are given in Table 1.

Molecular Methods

Total genomic DNA was extracted using established organic methods (Maniatis et al., 1982). Primers designed by LGL Inc. (Bryan, TX) were utilized for amplification of a 450 bp region of the mitochondrial control region (D-loop). These primers are LGL 283 (5'-TACACTGGTCTTCTAAACC-3') and LGL 1115 (5'-

ATGACCCTGAAGAA(A/G)GAACCAG-3'). LGL 283 is complementary to a region within the tRNA^{Thr} gene while LGL 1115 binds to a region within the D-loop. The partial D-loop sequence was amplified using the polymerase chain reaction (PCR), and PCR conditions were as follows: 0.05-0.1 μ g genomic DNA, 5 μ l 10X *Taq* salts (0.1 M Tris·HCl, pH 8.4-8.7, 0.025 M MgCl₂, 0.5 M KCl), 5 μ l dNTP mix (2 mM dATP, dCTP, dGTP, dTTP in 0.1 M Tris·HCl, pH 7.9), 1 μ l LGL 283 (10 mM stock), 1 μ l LGL 1115 (10 mM stock), 0.5 μ l *Taq* DNA polymerase and the appropriate amount of distilled water (final reaction volume = 50 μ l). PCR amplifications were performed using either the Robocycler[®] (Stratagene, La Jolla, CA) or GeneAmp[®] PCR System 2700 (Applied

STOCK	REGION	ROOKERY	SAMPLE SIZE
WESTERN STOCK	BER (n = 22)	Walrus Is.	22
	CAL (n = 203)	Amchitka Island	10
		Gramp Rocks	10
		Kasatoshi	10
		Kiska Island, Cape St. Stephen	47
		Kiska Island, Lief Cove	46
		Ogchul Island	10
		Seguam Island	31
		Ulak Island	9
		Yunaska Island	30
	COM (n = 106)	Medney Island	106
	CGA (n = 122)	Cape St. Elias	3
		Chirikof Island	31
		Chiswell Island	6
		Coweit Island	10
		Latax Rocks	1
		Marmot Island	50
		Sugarloaf Island	21
	EAL $(n = 227)$	Adugak Island	10
		Akun Island	13
		Akutan Island	85
		Amak Island	9
		Bogoslof Island	11
		Ugumak Island	99
	PWS $(n = 124)$	Fish Island	47
		Seal Rocks	77
	WAL $(n = 55)$	Agatu Island	25
		Attu Island	10
		Buldir	20
	WGA (n = 99)	Atkins Island	36
		Chernabura Island	5
		Clubbing Rocks	26
		Pinnacle Island	30
		Whaleback Island	2
	Western Stock Total		958
ASIAN STOCK	KUR (n = 207)	Antsiferova Island	45
		Chernyye Brat'ya	31
		Lovushki Island	39
		Raikoke Island	51
		Srednego Island	41
	OKH (n = 148)	Iony Island	100
		Yamsky Island	48
	KAM (n = 71)	Kozlova Cape	59
		Zheleznaya Bay	12
	Asian Stock Total		426
EASTERN STOCK	BRC (n = 23)	North Danger Rocks	10
		Triangle Island	13
	NCA (n = 10)	St. George Reef	10
	ORE (n = 83)	Rogue Reef	83
	SEA (n = 68)	Forester Island	11
		Hazy Islands	37
		White Sisters Is.	20
	Eastern Stock Total		184
ENTIRE RANGE	Total Sample Size		1568

Table 1. Number of Steller sea lions sampled from throughout the range of the species.

Note- Region designations are: BER = Bering Straight, 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. The total number of animals sampled per region is indicated in parentheses. Regions and stocks are defined according to the results of this study.

Biosystems, Foster City, CA). When amplifying with the Robocycler[®], the following PCR parameters were utilized: initial cycle (denature at 95 °C for 3 min, anneal at 50 °C for 1 min 25 s, extend at 70 °C for 2 min 50 s) followed by 32 cycles (denature at 95 °C for 1 min 10 s, anneal at 50° C for 1 min 25 s, extend at 70 °C for 2 min 50 s), and hold at 4 °C. When amplifying with the GeneAmp[®] 2700, the PCR parameters were as follows: 1 cycle (94 °C for 5 min), 32 cycles (denature at 94 °C for 45 s, anneal at 50 °C for 7 min, hold at 4 °C).

Amplified products were visualized using agarose gel electrophoresis (1% agarose). The QIAquick[®] PCR purification kit (Qiagen, Valencia, CA) was used to purify PCR products in preparation for sequencing. Sequencing reactions utilized fluorescent dye-terminator technology and were run on either the Robocycler[®] or GeneAmp[®] 2700. PCR products were sequenced in only one direction with LGL 1115. The sequencing reaction conditions were as follows: 0.04-0.05 μ g purified PCR product, 2 μ l BigDye[®] terminator (Applied Biosystems, Foster City, CA), 1.8 μ l 5X sequencing buffer (400 mM Tris·HCl pH 9.0, 10 mM MgCl₂), 2 μ l LGL 1115 (10 mM stock) and the appropriate volume of distilled water (final reaction volume = 10 μ l). The following PCR parameters were applied for all sequencing reactions run on the Robocycler[®]: initial cycle (denature at 96 °C for 3 min, anneal at 50 °C for 1 min, extend at 60 °C for 4 min), 25 cycles (denature at 96 °C for 1 min, anneal at 50 °C for 1 min, extend at 60 °C for 4 min). When using the GeneAmp[®] 2700, the following parameters were applied:

1 cycle (96 °C for 5 min), 25 cycles (denature at 96 °C for 30 s, anneal at 50 °C for 15 s, extend at 60 °C for 4 min), ending with 2 cycles (extend at 60 °C for 4 min, hold at 4 °C).

Sequencing reactions were purified using sephadex columns. The purified products were then pelleted and later prepared for loading on an ABI Prism[®] 377 automated DNA sequencer (Applied Biosystems, Foster City, CA). ABI Prism[®] software was used to collect the raw sequence data which was later analyzed using Sequencher[™] 4.1.2 (Gene Codes, Ann Arbor, MI). Haplotypes were assigned to individuals based on nucleotide differences within the 238 bp region of the mitochondrial control region.

Statistical Methods

The proportion of nucleotide sites that differ (p_n) within the 238 bp sequence was calculated by dividing the number of variable sites by the total number of nucleotides (Hedrick, 2000). Haplotype diversity (*H*; Nei and Tajima, 1981) and nucleotide diversity (π ; Nei, 1987) were determined for rookery and region population levels using ARLEQUIN (Schneider et al., 2000).

Exact tests for significant population differentiation for all pairwise comparisons using rookeries with N \geq 10, regions and stocks were conducted in ARLEQUIN. This test is analogous to Fisher's exact test on a 2x2 contingency table but extended to an *r* x *k* contingency table (Raymond and Rousset, 1995). Two separate measures of the degree of genetic divergence occurring between subdivisions of a population, conventional F-(Wright, 1951) and Φ -statistics (Excoffier, 1992), were estimated using ARLEQUIN. Conventional F_{st} parameter estimates infer population structure using only haplotype frequencies, while Φ_{st} (F-statistic analogues) parameter estimates incorporate both haplotype frequencies and the number of mutations observed between haplotypes. The F- and Φ -statistics are therefore referred to as frequency- and genetic-based parameters, respectively (Westlake and O'Corry-Crowe, 2002). The Tamura and Nei (1993) measure of evolutionary distance between nucleotide sequences was used to calculate the approximate number of mutations differing between haplotypes prior to running Φ_{st} analyses. 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 both F_{st} and Φ_{st} estimates to linearize population divergence time and distance (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 at the rookery, region and stock levels (for both the F_{st} and Φ_{st} methods) using PAUP* 4.0 (Swofford, 1998). All trees were constructed using midpoint rooting.

Regressions of genetic distance (F_{st} and Φ_{st}) on geographic distance and correlations between genetic and geographic distances among rookeries were computed using the R Package, version 4.0 (Casgrain and Legendre, 2001). Matrices of geographic distances were constructed using surface distances for all possible pairwise comparisons among the 43 rookeries represented by a sample size of N \geq 10. The R Package was then used to test the null hypothesis of independence between genetic and geographic distances by estimating departures from randomness using a variation of the Z-statistic (Mantel, 1967). Significance of the test statistic was then estimated using 99,999 permutations of the data.

Lastly, a maximum-likelihood approach was applied at the stock level to estimate the number of effective migrants per generation, N_fm , where N_f represents the number of effectively breeding females and *m* is the migration rate (Hartl and Clark, 1997). Original estimates of N_fm were obtained by running two replicates using MIGRATE (Beerli, 1997-2002) default settings which calculate initial parameter estimates from F_{st} values. The average of the two estimates was then calculated for each parameter, and these values replaced F_{st} estimates in following runs. The program was then run until equivalent estimates were obtained between replicates. The length of runs (number of short and long chains and length of chains) was generally increased to ensure a more accurate estimation of population parameters.

Rookery	Haplotype Diversity (H)	Nucleotide Diversity (π)
Adugak Is.	0.867 ± 0.0714	0.00871 ± 0.00601
Agatu Is.	0.873 ± 0.039	0.00848 ± 0.0055
Akun Is.	0.859 ± 0.0633	0.00921 ± 0.00611
Akutan Is.	0.879 ± 0.0187	0.00928 ± 0.00574
Amchitka Is.	0.844 ± 0.103	0.00662 ± 0.00485
Antsiferova Is.	0.929 ± 0.0241	0.00924 ± 0.00578
Atkins Is.	0.89 ± 0.0245	0.00881 ± 0.0056
Attu Is.	0.889 ± 0.0754	0.00817 ± 0.00571
Bogoslof Is.	0.873 ± 0.0891	0.0101 ± 0.0067
Buldir Is.	0.916 ± 0.0413	0.00887 ± 0.00576
Chernyye Brat'ya	0.873 ± 0.0358	0.0079 ± 0.00516
Chirikof Is.	0.837 ± 0.0432	0.00879 ± 0.00561
Chowiet Is.	0.644 ± 0.152	0.00605 ± 0.00454
Clubbing Rocks	0.831 ± 0.0485	0.00629 ± 0.00436
Fish Is.	0.878 ± 0.0232	0.00924 ± 0.00577
Forester Is.	0.982 ± 0.0463	0.0123 ± 0.00787
Gramp Rocks	0.911 ± 0.0773	$0.00737 \pm \ 0.00527$
Hazy Is.	0.89 ± 0.033	0.0104 ± 0.00639
Iony Is.	0.782 ± 0.0385	0.0066 ± 0.0044
Kasatoshi Is.	0.689 ± 0.104	0.00585 ± 0.00442
Kiska, Cape St. Stephen	0.881 ± 0.0225	0.00877 ± 0.00554
Kiska, Lief Cove	0.838 ± 0.0344	0.0084 ± 0.00536
Kozlova Is.	0.863 ± 0.033	0.00786 ± 0.00506
Lovushki Is.	0.888 ± 0.0294	0.00794 ± 0.00514
Marmot Is.	0.8045 ± 0.0454	0.00733 ± 0.00481
Medney Is.	0.9 ± 0.0141	0.00989 ± 0.00602
North Danger Rocks	0.8 ± 0.1	0.00875 ± 0.00603
Ogchul	0.933 ± 0.062	0.012 ± 0.00782
Pinnacle Rocks	0.86 ± 0.0472	0.00861 ± 0.00553
Raykoke Is.	0.882 ± 0.0265	0.00697 ± 0.00463
Rogue Reef	0.909 ± 0.0167	0.0111 ± 0.00666
Seal Rocks	0.876 ± 0.0253	0.00905 ± 0.00563
Seguam Is.	0.89 ± 0.033	0.00942 ± 0.00593
Sredgego Is.	0.867 ± 0.0332	0.00683 ± 0.00458
St. George Reef	0.867±0.107	0.00902 ± 0.00617
Sugarloaf Is.	0.9 0.039	0.0101 ± 0.00643
Triangle Is.	0.961 ± 0.0412	$0.0114 \pm 0.00/2/$
Ugamak Is. Walma Ia	0.869 ± 0.0235	0.00904 ± 0.00561
Walfus Is. White Sistema Is	0.866 ± 0.0519	0.00918 ± 0.00389
Vomelar Ic	0.903 ± 0.0233	0.0101 ± 0.00943
Tallisky IS. Vunaska Is	0.871 ± 0.0303	0.0071 ± 0.0047
Tullaska 15. Zheleznava Bay	0.732 ± 0.0711	0.00794 ± 0.00319
Region	Hanlotyne Diversity (H)	Nucleotide Diversity (π)
Region See of Okhotek		
Sea of Oknoisk	0.813 ± 0.0271	$0.006/3 \pm 0.00443$
Kuffi Islanus Kamahatka Daningula	0.894 ± 0.0127	0.00782 ± 0.00498
Commondor Islanda	0.807 ± 0.0308	0.00762 ± 0.00493
Western Aleution Islands	0.9 ± 0.0141	0.00989 ± 0.00602
Central Aleutian Islanda	0.075 ± 0.0204 0.858 ± 0.0145	0.00007 ± 0.00047 0.00882 + 0.00547
Fastern Aleutian Islands	0.030 ± 0.0143 0.871 + 0.01/1	$\frac{0.0032 \pm 0.00347}{0.00918 \pm 0.00564}$
Western Gulf of Alaska	0.856 ± 0.0141	0.00918 ± 0.00504 0.00808 ± 0.00513
Central Gulf of Alaska	0.818 ± 0.0174	0.00812 ± 0.00514
Bering Sea	0.866 + 0.0519	0.00918 ± 0.00514
Prince William Sound	0.879 ± 0.00171	0.00923 ± 0.00569
Southeastern Alaska	0.931 + 0.0143	0.0122 ± 0.00719
British Columbia	0.901 ± 0.0414	0.0101 ± 0.00637
Oregon	0.909 ± 0.0167	0.0111 ± 0.00666
Northern California	0.867 ± 0.107	0.00902 ± 0.00617

Table 2. Haplotype (H) and nucleotide (π) diversities for rookeries and regions. Standard deviations for all estimates are also provided.

RESULTS

General Diversity Measures

A 238 base pair region of the mitochondrial control region (D-loop) was analyzed for sequence variation. The number of polymorphic sites equaled 46, all of which were substitutions (40 transitions, 6 transversions). The proportion of polymorphic sites (p_n) equaled 46/238, or 0.193. Haplotype diversity was high (H = 0.9164 ± 0.0035) as expected due to rapid evolution and divergence of the D-loop. Nucleotide diversity was low ($\pi = 0.00967 \pm 0.00586$) because nearly all haplotypes differed by a single substitution event. Haplotype and nucleotide diversities for rookeries and regions are provided in Table 2.

A total of 121 haplotypes was observed (all individuals sampled, sample information, and assigned D-loop haplotypes for the additional 359 sea lions sampled from Asia are listed in Appendix I) including 46 new haplotypes (AAAA-NNNN, PPPP-ZZZZ, AAAAA, QQQQ-ZZZZZ, AAAAAA-JJJJJJJ; J. W. Bickham, pers. comm.). S and BB were by far the most common haplotypes detected, representing 18.2% and 15.9% of the sample, respectively (Table 3). Frequencies of all other haplotypes were less than 10%. Thus, an L-shaped distribution was obtained when haplotype number was plotted against haplotype frequency class (Fig. 2). Many haplotypes were restricted to certain regions. For instance, LLL was found only in Asia, DD was restricted to the Aleutian Islands and Gulf of Alaska, H was only found in eastern stock rookeries, and A was distributed range-wide (Fig. 3).

Table 3. Control region haplotype designations, the number of haplotypes found, and the proportion of the total sample for 1,568 Steller sea lions sampled from rookeries throughout the range of the species.

Haplotype	Number	Proportion (%)	Haploty	pe Number	Proportion (%)
А	121	7.72	MMMM	1	0.06
AA	2	0.13	Ν	15	0.96
AAA	38	2.42	NN	1	0.06
AAAA	14	0.89	NNN	1	0.06
AAAAA	1	0.06	NNNN	1	0.06
AAAAAA	2	0.13	0	1	0.06
В	1	0.06	00	1	0.06
BB	249	15.88	000	2	0.13
BBB	1	0.06	Р	4	0.26
BBBB	1	0.06	PP	1	0.06
BBBBBB	1	0.06	PPP	1	0.06
С	2	0.13	PPPP	1	0.06
CC	115	7.33	Q	9	0.57
CCC	1	0.06	QQ	1	0.06
CCCC	1	0.06	QQQ	1	0.06
CCCCCC	1	0.06	QQQQ	1	0.06
D	1	0.06	QQQQQ	1	0.06
DD	40	2.55	R	9	0.57
DDD	6	0.38	RR	2	0.13
DDDD	1	0.06	RRR	1	0.06
DDDDDD	1	0.06	RRRR	2	0.13
E	59	3.76	RRRRR	1	0.06
EE	9	0.57	S	286	18.24
EEE	4	0.26	SS	2	0.13
EEEE	4	0.26	SSS	1	0.06
EEEEEE	1	0.06	SSSS	1	0.06
F	4	0.26	SSSSS	4	0.26
FF	50	3.19	Т	7	0.45
FFF	5	0.32	TT	1	0.06
FFFF	17	1.08	TTT	2	0.13
FFFFFF	1	0.06	TTTT	1	0.06
G	24	1.53		1	0.06
66	1	0.06	U	13	0.83
GGG	1	0.06	00	1	0.06
GGGG	3	0.19	000	13	0.83
000000	22	0.06		5	0.19
Н	32	2.04	V	1	0.06
нн	20	1.00	V	1	0.06
ннн	1	0.06	VV	1	0.00
пппп	2	0.00			0.13
пппппп т	2	0.13		4 7 1	0.20
1	3	0.19	W	28	1.70
	7	0.00	W	28	0.26
	2	0.43	WWW	4	0.20
	1	0.15	WWWW	 Л	0.19
T	2	0.13	W/W/W/W	/W/ 2	0.20
5 11	6	0.15	X	<u>4 vv 2</u>	0.15
111	6	0.38	XXX	2	0.13
1111	1	0.06	XXXX	1	0.06
	1	0.00	XXXXX	1	0.06
K	12	0.77	Y	. 1	0.06
ккк	9	0.57	ŶŶ	6	0.38
КККК	2	0.13	YYYY	1	0.06
L	4	0.26	YYYYY	4	0.26
LL	2	0.13	Z	143	9.12
	23	1.47	77	4	0.26
	2	0.13	7.7.7	5	0.32
M	4	0.26	7777	3	0.19
MM	1	0.06	77777	1	0.06
MMM	12	0.77	Total	1568	100%
141141141	14	0.77	1 Julai	1300	. 100/0



Fig. 2. Distribution of haplotype frequencies observed in 1,568 Steller sea lions rangewide. Note that the distribution is L-shaped.

Measures of Genetic Distance

Haplotype data were used to perform range-wide analyses of population structure. Exact tests of population subdivision, Slatkin's linearized F-statistics, and Φ statistics were calculated for all pairwise comparisons at rookery, region and stock population levels. The resulting matrix for the F- and Φ -statistics for the rookery comparisons is provided in Appendix II.

Exact tests of population differentiation yielded largely significant values at all levels of comparisons. The numbers of significant pairwise comparisons ($P \le 0.05$)



Note- Rookeries are listed according to longitude with the most westward rookery (Iony Island) listed to the left and the most eastward rookery (St. George Reef) placed at the far right. Only rookeries having a sample size of 10 or more were included in the figure. Rookery designations are as follows: 1 = Iony, 2 = Chernyye Brat'ya, 3 = Srednego, 4 = Raykoke, 5 = Lovushki, 6 = Antsiferova, 7 = Yamsky, 8 = Zheleznaya Bay, 9 = Kozlova Cape, 10 = Medney, 11 = Attu, 12 = Agattu, 13 = Buldir, 14 = Cape St. Stephen, 15 = Lief Cove, 16 = Amchitka, 17 = Gramp Rock, 18 = Kasatoshi, 19 = Seguam, 20 = Yunaska, 21 = Adugak, 22 = Ogchul, 23 = Bogoslof, 24 = Walrus, 25 = Akutan, 26 = Akun, 27 = Ugamak, 28 = Clubbing Rocks, 29 = Pinnacle Rock, 30 = Atkins, 31 = Chowiet, 32 = Chirikof, 33 = Marmot, 34 = Sugarloaf, 35 = Fish, 36 = Seal Rocks, 37 = White Sisters, 38 = Hazy, 39 = Forrester, 40 = North Danger Rocks, 41 = Triangle, 42 = Rogue Reef, 43 = St. George Reef.

Fig. 3. Distribution of four common D-loop haplotypes, A, DD, H, and LLL at the rookery level.

were 537 of 903 comparisons of rookeries (59%), 87 of 105 comparisons of regions (83%), and 3 of 3 comparisons of stocks (100%).

F- and Φ -statistics were calculated for all pairwise comparisons (Appendix II). Among the 43 rookeries with N \geq 10, the numbers of significant pairwise comparisons ($P \leq 0.05$) for F_{st} were 468 of 903 comparisons (51.8%), and for Φ_{st} they were 549 of 903 comparisons (61.0%). A neighbor-joining (NJ) tree was next constructed from the distance matrix (Fig. 4) using only the 43 rookeries with N \geq 10 (i.e., excluding Amak Island, Cape St. Elias, Chernabura Island, Chiswell Island, Latax Rocks, Ulak Island and Whaleback Island). The resultant tree exhibited some of the expected groupings. For instance, the eastern stock rookeries located along the coasts of British Columbia (BRC), Oregon (ORE), and northern California (NCA) formed a lineage distinct from all western stock rookeries. Rookeries from southeastern Alaska (SEA; White Sisters Islands, Hazy Islands, and Forrester Islands), however, are also expected to cluster with the eastern stock. Instead, SEA rookeries grouped closely with Asian rookeries from the Sea of Okhotsk (OKH), Kuril Islands (KUR), and Kamchatka Peninsula (KAM) at or near the base of the branch leading to all western stock rookeries.

The majority of Asian rookeries comprise a cluster with Hazy Islands (SEA) located near the base of the branch leading to the western stock rookeries. This branch does not include Antsiferova Island (KUR) and Kozlova Cape (KAM) which form a branch placed sister to rookeries belonging to the remaining western stock rookeries. Medney Island, the only rookery from the Commander Islands (COM), was placed



Note- Region designations are: BER = Bering Straight, 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. Forrester Island, Hazy Islands, and White Sisters Islands (italics) are also part of the Eastern Stock.

Fig. 4. Neighbor joining tree based on Slatkin's linearized F_{st} (conventional) values at the rookery level. Note the presence of three eastern stock rookeries (italicized) on the western stock branch.



Note- Region designations are: BER = Bering Straight, 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.

Fig. 5. Neighbor joining tree based on Slatkin's linearized F_{st} analogues (Φ_{st}) at the rookery level.

among Alaskan western stock rookeries. All Alaskan western stock rookeries, plus Medney Island, comprise a single branch beginning with Gramp Rocks (Fig. 4).

The NJ tree constructed from the pairwise distance matrix of Φ_{st} values (Fig. 5) indicated strong divergence of eastern stock rookeries. Rookeries belonging to the western stock formed a single branch, with Asian rookeries occupying the most basal positions. Again, Medney Island (COM) was located well within the lineage among Alaskan western stock rookeries. Kozlova Cape also was nested among Alaskan western stock rookeries but was separated from the other Asian rookeries only by Gramp Rocks and Ogchul Island (both CAL), both of which are represented by small sample sizes (N = 10).

Next, both F- and Φ -statistics were calculated for all pairwise comparisons of the 15 sampled regions (Table 4). Using conventional F-statistics, 79.1% of regional comparisons were significant (P<0.05) and 44.8% of those were highly significant (P<0.001). A total of 72.4% of the Φ_{st} values were significant (P<0.05) among regional comparisons. This included 64.8% that were highly significant (P<0.001). For both F and Φ -statistics, SEA, BRC, ORE and NCA were shown to be genetically divergent from all other non-eastern stock regions. KUR, OHK and KAM were also significantly different from nearly all other regions, while COM individuals were not significantly different from the nearby western and central Aleutian Islands.

As with the rookeries, NJ trees (Fig. 6) were constructed from the pairwise distance matrices generated in ARLEQUIN. The tree constructed from a matrix of conventional F-statistics indicated strong differentiation of regions from the eastern

Table 4. Slatikin's linearized F-statistics (conventional F_{st} above diagonal; F_{st} analogues (Φ_{st}) below diagonal) for all pairwise region comparisons based on mtDNA data. Significant values (P<0.05) are in bold.

	ОКН	KUR	RUS	COM	WAL	CAL	EAL	WGA	CGA	BER	PWS	SEA	BRC	ORE	NCA
OKH		0.02	0.02	0.11	0.10	0.15	0.13	0.13	0.18	0.17	0.13	0.06	0.11	0.07	0.14
KUR	0.03		0.02	0.06	0.05	0.08	0.07	0.07	0.11	0.09	0.07	0.02	0.07	0.05	0.09
RUS	0.04	0.05		0.04	0.02	0.07	0.06	0.06	0.10	0.08	0.06	0.04	0.08	0.06	0.11
COM	0.13	0.11	0.03		0.00	0.00	0.02	0.02	0.03	0.02	0.02	0.05	0.09	0.08	0.11
WAL	0.12	0.10	0.01	0.00		0.00	0.01	0.01	0.02	0.01	0.01	0.05	0.09	0.08	0.11
CAL	0.12	0.10	0.03	0.00	0.00		0.01	0.01	0.01	0.01	0.01	0.08	0.13	0.11	0.15
EAL	0.12	0.09	0.04	0.01	0.00	0.01		0.00	0.00	0.00	0.00	0.07	0.11	0.10	0.13
WGA	0.13	0.08	0.04	0.03	0.01	0.02	0.00		0.01	0.00	0.00	0.06	0.12	0.11	0.14
CGA	0.16	0.12	0.05	0.01	0.01	0.01	0.00	0.01		0.00	0.00	0.10	0.16	0.14	0.18
BER	0.14	0.10	0.02	0.01	0.00	0.00	0.00	0.00	0.00		0.00	0.08	0.12	0.11	0.14
PWS	0.14	0.09	0.04	0.02	0.01	0.01	0.01	0.01	0.01	0.00		0.06	0.11	0.10	0.13
SEA	0.26	0.19	0.25	0.30	0.27	0.32	0.29	0.27	0.34	0.24	0.25		0.02	0.01	0.01
BRC	0.48	0.35	0.48	0.48	0.50	0.51	0.48	0.50	0.59	0.46	0.44	0.01		0.02	0.02
ORE	0.26	0.20	0.25	0.31	0.29	0.32	0.30	0.29	0.35	0.26	0.27	0.00	0.01		0.00
NCA	0.39	0.26	0.36	0.37	0.38	0.39	0.35	0.38	0.45	0.35	0.31	0.00	0.00	0.00	

Note- Regional designations are as follows: OKH = Sea of Okhotsk; KUR = Kuril Islands; KAM = Kamkatcha Peninsula; COM = Commander Islands; WAL = Western Aleutian Islands; CAL = Central Aleutian Islands; EAL = Eastern Aleutian Islands; WGA = Western Gulf of Alaska; CGA = Central Gulf of Alaska; BER = Bering Sea; PWS = Prince William Sound; SEA = Southeastern Alaska; BRC = British Columbia; ORE = Oregon; NCA = Northern California.

stock. The Asian regions, KAM, KUR and OKH, formed a branch which was placed sister to a clustering of Alaskan regions (the Aleutian Islands, Gulf of Alaska and PWS). Once again, COM was clustered among Alaskan western stock regions rather than among Asian regions. The NJ tree constructed from Φ -statistics for the region level also indicated strong genetic differentiation of regions from the eastern stock. The Asian regions, KUR, OKH, and KAM, were shown to be closely related, although they did not form a separate branch. The Alaskan western stock regions formed a branch that included COM and which was placed sister to KAM.

Next, F- and Φ -statistics were generated at the stock level. KAM, KUR, and OKH were placed in the Asian stock. COM, WAL, CAL, the eastern Aleutian Islands



(A) Conventional F_{st} Values

(B) F_{st} Analogues (Φ_{st})

Note- Region designations are: BER = Bering Straight, 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.

Fig. 6. Neighbor joining trees based on Slatkin's linearized F-statistics at the region level.



Fig. 7. Neighbor joining trees based on Slatkin's linearized F-statistics at the stock level. Note that the relationship between stocks differs depending on which analysis is applied.

(EAL), Bering Sea (BER), western Gulf of Alaska (WGA), central Gulf of Alaska (CGA) and PWS were placed in the western stock. SEA, BRC, ORE and NCA comprised the eastern stock. All pairwise comparisons yielded highly significant (P <<0.001) F_{st} values of 0.0838 (Asian-western), 0.0887 (western-eastern), and 0.0463 (Asian-eastern). The NJ tree constructed from these values (Fig. 7), suggested that the Asian stock was more closely related to the eastern stock than to the geographically adjacent western stock. All three Φ_{st} values were significant (P<<0.001; Asian-western = 0.0809, Asian-eastern = 0.241, western-eastern = 0.339), and the NJ tree suggested that the Asian and western stocks were more closely related to one another than to the eastern stock.

The test for isolation by distance revealed no significant linear correlation between geographic distances and genetic distances (F_{st} and Φ_{st} values) at the rookery level. In fact, the null hypothesis (random distribution of data points with no linear correlation between genetic and geographic distances) was supported by the data ($P \le 0.0001$). However, when comparisons were restricted to rookeries of the same stock, all tests revealed significant linear correlation except one. The Asian stock rookeries showed no significant correlation between F_{st} and geographic distance (support for H_0 , $P \le 0.05$). However, there was a significant correlation between Φ_{st} and geographic distance (support for H_0 , P ≤ 0.05). However, there was a significant correlation between Φ_{st} and geographic distance from the same driving this effect, the analysis was performed on the combined western stock and Asian stock rookeries. No significant correlation between geographic distance and genetic distance was observed for either F_{st} or Φ_{st} .

Maximum likelihood estimates of N*m* were next obtained using the program MIGRATE. Given the F_{st} and Φ_{st} results provided above, three stocks (or populations) were assumed including the Asian stock (OKH, KUR, and KAM), the western stock (COM, WAL, CAL, EAL, BER, WGA, CGA, PWS), and the eastern stock (SEA, BRC, ORE, NCA). Migration rates between stocks (number of effective migrants per generation, N*m*) were as follows: western to Asian 95% confidence interval of 11.5 to 18.9 with a best estimate of 14.8, Asian to western 95% confidence interval of 11.7 to 18.0 with a best estimate of 14.6, eastern to Asian 95% confidence interval of 0.133 to 0.854 with a best estimate of 0.177, Asian to eastern 95% confidence interval of 1.01 to 4.36 with a best estimate of 2.72, eastern to western 95% confidence interval of 0.756 to 2.73 with a best estimate of 1.54, and western to eastern 95% confidence interval of 1.66 to 5.32 with a best estimate of 3.19. Thus, there was an average migrant exchange of

14.7 females per generation between the Asian and western stocks, 1.45 females per generation between the eastern and Asian stocks, and 2.37 females per generation between the western and eastern stocks.

Migration rates between stocks were also calculated from F- and Φ -statistics. The number of female migrants per generation estimated from F-statistics was 5.97 between the Asian and western stocks, 10.8 between the Asian and eastern stocks, and 5.64 between the eastern and western stocks. Likewise, the number of female migrants estimated from Φ -statistics was 6.18 between the Asian and western stocks, 2.07 between the Asian and eastern stocks, and 1.48 between the eastern and western stocks.

DISCUSSION

Mitochondrial Control Region Diversity

To date, 145 haplotypes have been reported for a 238 bp segment of the Steller sea lion mitochondrial control region (J. W. Bickham, pers. comm.). Of these, 121 were found in pups sampled at their natal rookery (Table 3) and the rest have only been observed in scats, or in juveniles or adults for which the rookery of origin is unknown. It is reasonable to assume that more haplotypes will be identified as sample sizes increase. Thus, the high haplotypic diversity observed range-wide (H = 0.9164 ± 0.0035) was expected, and a similar degree of diversity has been reported for the mitochondrial control region of other marine mammals, including harbor seals, *Phoca vitulina*, (H = 0.975; Westlake & O'Corry-Crowe, 2002) and Dall's porpoise, *Phocoenoides dalli*, (H = 0.96; Escorza-Trevino & Dizon, 2000). Previous reports for haplotype (nucleon) diversity for various rookeries and regions in Steller sea lions were similar to those found here (Bickham, 1996; Bickham et al., 1998a, 1998b). Furthermore, the moderately low nucleotide diversity observed ($\pi = 0.00967 \pm 0.00596$) is consistent with the vast majority of haplotypes differing by a single substitution event from one or more haplotypes (J. W. Bickham, pers. comm.). Despite the recent decline in numbers of Steller sea lions, mtDNA haplotype diversity does not seem to have been appreciably reduced. The L-shaped distribution of haplotype frequencies (Fig. 2) provides strong evidence for an absence of bottleneck effects on haplotype diversity (Luikart et al., 1998). Likewise, the high range-wide haplotype diversity estimate is comparable to other marine mammals (cetaceans) which have not experienced a bottleneck (Rooney et

al., 2001). Nucleotide diversity in Steller sea lions is intermediate between whale populations that have bottlenecked and those that have not (Rooney et al., 2001).

Phylogeography

Although most haplotypes occurred at a frequency of less than 10% (Table 3), several were quite common. The most common haplotypes were S (18.2%) and BB (15.9%). Two haplotypes (A and BB) were distributed throughout the entire species range whereas most were restricted to certain regions. For example, haplotypes LLL, DD and H were restricted to the Asian, western and eastern stocks, respectively (Fig. 3). The geographic partitioning of various haplotypes resulted in definite patterns of population subdivision at both the rookery and region levels. Despite the generally high sample size in this study, resolution of population substructure increased when rookeries were grouped into their respective regions. One possible reason for this is a sample-size effect. Eastern stock rookeries, or those rookeries belonging to SEA, BRC, ORE, and NCA, were clearly differentiated from all other rookeries when using Φ -statistics (Fig. 4). Differentiation of eastern stock rookeries was less clear when conventional Fstatistics were applied (Fig. 5). The NJ tree constructed at the regional level using conventional F-statistics resolved three distinct lineages, whereas, the tree constructed from Φ -statistics resolved only two separate lineages, although Asian regions clearly occupied the most basal positions and were genetically differentiated from all other groups (Fig. 6).

All analyses placed Medney Island, the only rookery of the Commander Islands (COM), with Alaskan western stock rookeries rather than with Asian rookeries. This result is opposite of that predicted by Trujillo et al. (in press) and parallels a similar relationship reported along the Commander-Aleutian Island chain for sea otters (Cronin et al., 1996) and harbor seals (Westlake and O'Corry-Crowe, 2002). F_{st} estimates do a good job at isolating the Alaskan western stock from the eastern stock and from the Asian rookeries (Fig. 4). This analysis shows Medney Island to be part of the Alaskan western stock. Since this rookery is of recent origin, beginning in 1972 (Mamaev and Burkanov, 1996), it is clear that it must have been founded by immigrants from Alaska, not from Asia. This arrangement is supported in all assessments of rookeries and regions (Figs. 4-6). The present study includes a larger sample size from Medney Island (N = 106) than was available to Trujillo et al. (in press; N = 10).

Given the F_{st} and Φ_{st} results obtained at the rookery and region levels, three populations were assumed for analyses of stock structure, the Asian, western, and eastern stocks. COM fell within the western stock for all analyses at the stock level. All F_{st} and Φ_{st} values were significant supporting the recognition of three stocks, although the relationships between stocks differed between analyses (Fig. 7). The currently recognized eastern stock would be unaltered, but the western stock should be partitioned west of the Commander Islands yielding a western stock which ranges from Prince William Sound west to the Commander Islands, and an Asian stock including rookeries from the Kamchatka Peninsula, Kuril Islands, and Sea of Okhtosk (Fig. 1). Analyses of isolation by distance indicated significant linear correlations between measures of genetic distance and geographic distance among rookeries (with one exception), but only when rookeries within stocks are considered. These results support the partitioning of the range of Steller sea lions into three genetically differentiated stocks, each of which contain a number of populations (rookeries) that follow an isolation by distance model of population subdivision. The zones of contact between the Asian and western stocks and between the eastern and western stocks likely do not represent barriers to gene flow. Rather they are the historical points of contact of three expanding populations that have adjusted their ranges in response to increased habitat availability since the last glaciation.

Inter- and Intra-Stock Patterns of Migration and Stock Structure

Maximum likelihood estimation of N_fm revealed a level of migrant exchange between the western and Asian stocks that was roughly 10 times the rate of exchange between the Asian and eastern stocks and approximately 6 fold greater than the exchange between the western and eastern stocks. Such low levels of mitochondrial gene flow occurring between Asian and eastern and especially between western and eastern stocks explain the distinct differentiation of eastern stock rookeries and regions observed when running F_{st} and Φ_{st} analyses. In fact, all inter-stock migration rates were generally low, which is consistent with the relatively high degree of natal site fidelity thought to characterize this species. It is likely that female interchange among rookeries within stocks is relatively high, at least over evolutionary time scales. This can be inferred from the fact that the NJ trees of rookeries show relatively little concordance with geographic distribution (Figs. 4 and 5). However, NJ trees based on regions tend to more precisely reflect geographic distributions, especially using conventional F_{st} estimates (Fig. 6a). In Fig. 6a the arrangements of the regions precisely reflect their geographic relationships within both the Asian and eastern stocks. Among the western stock regions the relationship is not quite perfect but the most western regions (WAL, COM, and CAL) are the most basal and the eastern-most regions form a tight cluster at the tip. It is also apparent that western stock regions generally show shorter branch lengths than do the eastern stock and Asian stock regions (Fig. 6a). This is especially true for the Φ_{st} estimates (Fig. 6b). This likely reflects high exchange of migrants among the rookeries of the eastern-most western stock regions (from Prince William Sound to the eastern Aleutian Islands and the Bering Sea).

Estimates of migrant exchange obtained from F_{st} and Φ_{st} analyses in some cases differed significantly from maximum-likelihood estimates (MLE). For instance, the average of the MLE of female migrants exchanged between the Asian stock and the western stock was at least twice as high as the rates obtained from both F_{st} and Φ_{st} estimates. The values estimated from Φ -statistics for the Asian-eastern and westerneastern migrant exchange, however, were similar to MLE whereas the rates of exchange estimated from F-statistics were unlike those obtained using either the maximumlikelihood approach or those estimated from Φ -statistics. Obviously, more modeling is needed to determine which approach is best for estimation of migration rates. Still, MLE appear to be the most logical, indicating the highest level of gene flow occurring

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between the Asian and western stocks and low levels of exchange occurring between the eastern stock and both the western and Asian stocks.

Patterns of population subdivision (stock structure) result from historical processes, mutation, genetic drift, and current patterns of migration (Avise, 1994). The high degree of differentiation of the eastern stock likely reflects some or all of these processes. The eastern stock haplotypes form a well differentiated network in the phylogenetic analyses (J. W. Bickham, pers. comm.) which might explain why the NJ tree based on estimates of Φ_{st} shows longer branch lengths leading to the eastern stock regions (Fig. 6b). The eastern stock is also well differentiated by haplotype frequencies alone (Fig. 6a). It was suggested that the eastern stock likely differentiated from the western stock as a result of isolation in different Pleistocene glacial refugia (Bickham et al., 1996). The fact that two other species of marine mammals, harbor seals (Westlake and O'Corry-Crowe, 2002) and sea otters (Cronin et al., 1996) show a major break between populations east and west of 144° W supports this conclusion. Such genealogical concordance involving shared phylogeographic patterns among unrelated species with similar distributions is presumably the result of similar historic influences on the intraspecific genetic architecture (Avise, 1994). Likewise, sockeye salmon (Onchorhynchus nerka), which have a similar distribution to Steller sea lions, were hypothesized to have been isolated in Pleistocene glacial refugia in Beringia and the Pacific Northwest (Columbia River; Lindsey and McPhail, 1986; McPhail and Lindsey, 1970, 1986). The differentiation of the southernmost populations, presumably descended from the Pacific Northwest refugium, and the northern populations,

presumably from the Beringian refugium, was well supported by allozyme and mtDNA data (Bickham et al., 1995).

CONCLUSIONS

Mitochondrial DNA analysis supports the recognition of three stocks, the Asian, western and eastern stocks, in Steller sea lions. Medney Island, the only rookery of the Commander Island chain (COM), is placed within the western, rather than within the Asian stock. Generally, low rates of migration were estimated among stocks. Higher rates of migrant exchange were estimated between the Asian and western stocks, than between the eastern and western stocks. This is consistent with the conclusion that the major phylogeographic break within the species is between the eastern and western stocks. Estimates of population subdivision based on F_{st} and Φ_{st} at the rookery and region levels support this conclusion, as do patterns of among-stock migration and isolation by distance.

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APPENDIX I

Steller Sea Lion mtDNA Haplotypes and Sample Information

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Asian	Kamchatka	Kozlov C.	K219	5-Jul-02	31.0	F	A
Asian	Kamchatka	Kozlov C.	K236	5-Jul-02	23.0	F	А
Asian	Kuril Islands	Antsiferov Island	Y483	26-Jun-01	-	-	А
Asian	Kuril Islands	Chernyye Brat'ya	Br610	7-Jul-01	-	-	А
Asian	Kuril Islands	Chernyye Brat'ya	Br612	7-Jul-01	-	-	А
Asian	Kuril Islands	Chernyye Brat'ya	Br617	7-Jul-01	-	-	А
Asian	Kuril Islands	Lovushki Island	Lr415	1-Jul-01	-	-	А
Asian	Kuril Islands	Lovushki Island	Lr424	1-Jul-01	-	-	А
Asian	Kuril Islands	Lovushki Island	Lr429	1-Jul-01	-	-	А
Asian	Kuril Islands	Lovushki Island	Lr437	1-Jul-01	-	-	А
Asian	Kuril Islands	Lovushki Island	Lr442	1-Jul-01	-	-	А
Asian	Kuril Islands	Raikoke Island	P608	2-Jul-01	-	-	А
Asian	Kuril Islands	Raikoke Island	P623	2-Jul-01	-	-	А
Asian	Kuril Islands	Raikoke Island	P627	2-Jul-01	-	-	А
Asian	Kuril Islands	Raikoke Island	P629	2-Jul-01	-	-	А
Asian	Kuril Islands	Srednego Island	C503	4-Jul-01	-	-	А
Asian	Sea of Okhotsk	Iony Island	N258	16-Jul-01	-	-	А
Asian	Sea of Okhotsk	Iony Island	N260	16-Jul-01	-	-	А
Asian	Sea of Okhotsk	Iony Island	N406	29-Jun-02	27.0	М	А
Asian	Sea of Okhotsk	Iony Island	N408	29-Jun-02	17.5	М	А
Asian	Sea of Okhotsk	Iony Island	N436	29-Jun-02	23.0	М	А
Asian	Sea of Okhotsk	Iony Island	N438	29-Jun-02	15.5	F	А
Asian	Sea of Okhotsk	Yamsky Island	R245	7-Mar-02	31.0	F	А
Asian	Sea of Okhotsk	Yamsky Island	R269	7-Mar-02	20.5	М	А
Asian	Sea of Okhotsk	Yamsky Island	R290	7-Mar-02	30.0	М	А
Central	Commander Islands	Medney Island	M423	2-Jul-02	23.0	F	А
Central	Commander Islands	Medney Island	M446	2-Jul-02	33.0	F	А
Central	Commander Islands	Medney Island	M469	2-Jul-02	33.5	М	А
Central	Commander Islands	Medney Island	M473	2-Jul-02	41.5	М	А
Asian	Kamchatka	Kozlov C.	K226	5-Jul-02	29.5	F	AAA
Asian	Kuril Islands	Antsiferov Island	Y468	26-Jun-01	-	-	AAA
Asian	Kuril Islands	Chernyye Brat'ya	Br603	7-Jul-01	-	-	AAA
Asian	Kuril Islands	Chernyye Brat'ya	Br623	7-Jul-01	-	-	AAA
Asian	Kuril Islands	Lovushki Island	Lr406	1-Jul-01	-	-	AAA
Asian	Kuril Islands	Lovushki Island	Lr432	1-Jul-01	-	-	AAA
Asian	Kuril Islands	Lovushki Island	Lr444	1-Jul-01	-	-	AAA
Asian	Kuril Islands	Raikoke Island	P611	2-Jul-01	-	-	AAA
Asian	Kuril Islands	Raikoke Island	P620	2-Jul-01	-	-	AAA
Asian	Kuril Islands	Srednego Island	C481	4-Jul-01	-	-	AAA
Asian	Kuril Islands	Srednego Island	C496	4-Jul-01	-	-	AAA
Asian	Sea of Okhotsk	Iony Island	N267	16-Jul-01	-	-	AAA
Asian	Sea of Okhotsk	Iony Island	N284	16-Jul-01	-	-	AAA
Asian	Sea of Okhotsk	Yamsky Island	R234	7-Mar-02	29.0	F	AAA

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Asian	Sea of Okhotsk	Yamsky Island	R263	7-Mar-02	38.5	М	AAA
Central	Commander Islands	Medney Island	M435	2-Jul-02	31.0	F	AAA
Central	Commander Islands	Medney Island	M437	2-Jul-02	37.5	М	AAA
Central	Commander Islands	Medney Island	M440	2-Jul-02	25.5	F	AAA
Asian	Kuril Islands	Raikoke Island	P603	2-Jul-01	-	-	AAAA
Asian	Sea of Okhotsk	Iony Island	N262	16-Jul-01	-	-	AAAA
Asian	Sea of Okhotsk	Iony Island	N275	16-Jul-01	-	-	AAAA
Asian	Sea of Okhotsk	Iony Island	N276	16-Jul-01	-	-	AAAA
Asian	Sea of Okhotsk	Iony Island	N401	29-Jun-02	26.0	М	AAAA
Asian	Sea of Okhotsk	Iony Island	N412	29-Jun-02	29.5	М	AAAA
Asian	Sea of Okhotsk	Yamsky Island	R200	7-Mar-02	24.0	F	AAAA
Asian	Sea of Okhotsk	Yamsky Island	R208	7-Mar-02	14.0	F	AAAA
Asian	Sea of Okhotsk	Yamsky Island	R211	7-Mar-02	34.0	М	AAAA
Asian	Sea of Okhotsk	Yamsky Island	R286	7-Mar-02	24.0	F	AAAA
Asian	Sea of Okhotsk	Yamsky Island	R288	7-Mar-02	39.0	М	AAAA
Asian	Sea of Okhotsk	Yamsky Island	R292	7-Mar-02	26.5	F	AAAA
Asian	Kamchatka	Kozlov C.	K201	5-Jul-02	32.0	F	BB
Asian	Kamchatka	Kozlov C.	K205	5-Jul-02	36.0	F	BB
Asian	Kamchatka	Kozlov C.	K206	5-Jul-02	40.0	М	BB
Asian	Kamchatka	Kozlov C.	K207	5-Jul-02	28.5	F	BB
Asian	Kamchatka	Kozlov C.	K211	5-Jul-02	38.0	М	BB
Asian	Kamchatka	Kozlov C.	K216	5-Jul-02	31.0	Μ	BB
Asian	Kamchatka	Kozlov C.	K221	5-Jul-02	30.5	F	BB
Asian	Kamchatka	Kozlov C.	K222	5-Jul-02	28.5	F	BB
Asian	Kamchatka	Kozlov C.	K225	5-Jul-02	28.5	Μ	BB
Asian	Kamchatka	Kozlov C.	K232	5-Jul-02	34.0	F	BB
Asian	Kamchatka	Kozlov C.	K235	5-Jul-02	35.0	Μ	BB
Asian	Kamchatka	Kozlov C.	K237	5-Jul-02	23.5	F	BB
Asian	Kamchatka	Kozlov C.	K242	5-Jul-02	30.0	Μ	BB
Asian	Kamchatka	Kozlov C.	K249	5-Jul-02	36.0	F	BB
Asian	Kuril Islands	Antsiferov Island	Y457	26-Jun-01	-	-	BB
Asian	Kuril Islands	Antsiferov Island	Y472	26-Jun-01	-	-	BB
Asian	Kuril Islands	Antsiferov Island	Y486	26-Jun-01	-	-	BB
Asian	Kuril Islands	Antsiferov Island	Y489	26-Jun-01	-	-	BB
Asian	Kuril Islands	Antsiferov Island	Y492	26-Jun-01	-	-	BB
Asian	Kuril Islands	Chernyye Brat'ya	Br601	7-Jul-01	-	-	BB
Asian	Kuril Islands	Chernyye Brat'ya	Br607	7-Jul-01	-	-	BB
Asian	Kuril Islands	Chernyye Brat'ya	Br613	7-Jul-01	-	-	BB
Asian	Kuril Islands	Chernyye Brat'ya	Br618	7-Jul-01	-	-	BB
Asian	Kuril Islands	Chernyye Brat'ya	Br634	7-Jul-01	-	-	BB
Asian	Kuril Islands	Chernyye Brat'ya	Br637	7-Jul-01	-	-	BB
Asian	Kuril Islands	Lovushki Island	Lr404	1-Jul-01	-	-	BB
Asian	Kuril Islands	Lovushki Island	Lr412	1-Jul-01	-	-	BB
Asian	Kuril Islands	Lovushki Island	Lr435	1-Jul-01	-	-	BB
Asian	Kuril Islands	Raikoke Island	P605	2-Jul-01	-	-	BB
Asian	Kuril Islands	Raikoke Island	P606	2-Jul-01	I _	_	BB

Appendix I Continued

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Asian	Kuril Islands	Raikoke Island	P622	2-Jul-01	-	-	BB
Asian	Kuril Islands	Raikoke Island	P625	2-Jul-01	-	-	BB
Asian	Kuril Islands	Srednego Island	C492	4-Jul-01	-	-	BB
Asian	Kuril Islands	Srednego Island	C494	4-Jul-01	-	-	BB
Asian	Kuril Islands	Srednego Island	C497	4-Jul-01	-	-	BB
Asian	Kuril Islands	Srednego Island	C507	4-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N253	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N255	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N261	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N266	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N268	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N269	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N271	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N274	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N278	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N279	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N280	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N282	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N283	16-Jul-01	-	-	BB
Asian	Sea of Okhotsk	Iony Island	N403	29-Jun-02	30.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N405	29-Jun-02	22.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N407	29-Jun-02	23.5	F	BB
Asian	Sea of Okhotsk	Iony Island	N413	29-Jun-02	26.5	М	BB
Asian	Sea of Okhotsk	Iony Island	N414	29-Jun-02	23.5	F	BB
Asian	Sea of Okhotsk	Iony Island	N415	29-Jun-02	25.5	М	BB
Asian	Sea of Okhotsk	Iony Island	N418	29-Jun-02	28.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N420	29-Jun-02	26.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N424	29-Jun-02	18.5	F	BB
Asian	Sea of Okhotsk	Iony Island	N426	29-Jun-02	17.0	F	BB
Asian	Sea of Okhotsk	Iony Island	N428	29-Jun-02	21.0	F	BB
Asian	Sea of Okhotsk	Iony Island	N429	29-Jun-02	22.5	F	BB
Asian	Sea of Okhotsk	Iony Island	N431	29-Jun-02	25.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N433	29-Jun-02	21.5	F	BB
Asian	Sea of Okhotsk	Iony Island	N434	29-Jun-02	28.5	М	BB
Asian	Sea of Okhotsk	Iony Island	N439	29-Jun-02	19.0	F	BB
Asian	Sea of Okhotsk	Iony Island	N440	29-Jun-02	17.5	F	BB
Asian	Sea of Okhotsk	Iony Island	N441	29-Jun-02	24.5	М	BB
Asian	Sea of Okhotsk	Iony Island	N442	29-Jun-02	26.5	М	BB
Asian	Sea of Okhotsk	Iony Island	N444	29-Jun-02	29.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N445	29-Jun-02	16.0	F	BB
Asian	Sea of Okhotsk	Iony Island	N449	29-Jun-02	21.0	М	BB
Asian	Sea of Okhotsk	Iony Island	N451	29-Jun-02	29.5	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R203	7-Mar-02	22.5	F	BB
Asian	Sea of Okhotsk	Yamsky Island	R228	7-Mar-02	23.5	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R230	7-Mar-02	38.0	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R235	7-Mar-02	24.5	F	BB

Appendix I Continued

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Asian	Sea of Okhotsk	Yamsky Island	R250	7-Mar-02	29.5	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R252	7-Mar-02	29.0	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R255	7-Mar-02	24.0	F	BB
Asian	Sea of Okhotsk	Yamsky Island	R261	7-Mar-02	33.0	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R265	7-Mar-02	28.0	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R274	7-Mar-02	30.0	F	BB
Asian	Sea of Okhotsk	Yamsky Island	R276	7-Mar-02	36.5	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R294	7-Mar-02	23.5	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R297	7-Mar-02	38.5	М	BB
Asian	Sea of Okhotsk	Yamsky Island	R300	7-Mar-02	17.5	М	BB
Central	Commander Islands	Medney Island	M408	2-Jul-02	31.0	F	BB
Central	Commander Islands	Medney Island	M414	2-Jul-02	39.0	М	BB
Central	Commander Islands	Medney Island	M432	2-Jul-02	32.0	F	BB
Central	Commander Islands	Medney Island	M434	2-Jul-02	32.5	М	BB
Central	Commander Islands	Medney Island	M443	2-Jul-02	28.5	F	BB
Central	Commander Islands	Medney Island	M463	2-Jul-02	32.5	F	BB
Central	Commander Islands	Medney Island	M466	2-Jul-02	36.0	М	BB
Asian	Kamchatka	Kozlov C.	K200	5-Jul-02	29.5	М	CC
Asian	Kamchatka	Kozlov C.	K210	5-Jul-02	40.0	М	CC
Asian	Kamchatka	Kozlov C.	K227	5-Jul-02	36.5	М	CC
Asian	Kamchatka	Kozlov C.	K231	5-Jul-02	30.5	F	CC
Asian	Kamchatka	Kozlov C.	K238	5-Jul-02	40.0	Μ	CC
Asian	Kamchatka	Kozlov C.	K246	5-Jul-02	40.0	М	CC
Asian	Kamchatka	Kozlov C.	K247	5-Jul-02	34.0	Μ	CC
Asian	Kuril Islands	Antsiferov Island	Y453	26-Jun-01	-	-	CC
Central	Commander Islands	Medney Island	M403	2-Jul-02	32.5	М	CC
Central	Commander Islands	Medney Island	M406	2-Jul-02	26.5	F	CC
Central	Commander Islands	Medney Island	M410	2-Jul-02	37.5	М	CC
Central	Commander Islands	Medney Island	M416	2-Jul-02	29.0	F	CC
Central	Commander Islands	Medney Island	M417	2-Jul-02	39.0	М	CC
Central	Commander Islands	Medney Island	M418	2-Jul-02	22.5	F	CC
Central	Commander Islands	Medney Island	M427	2-Jul-02	24.0	М	CC
Central	Commander Islands	Medney Island	M431	2-Jul-02	32.5	М	CC
Central	Commander Islands	Medney Island	M433	2-Jul-02	36.0	М	CC
Central	Commander Islands	Medney Island	M441	2-Jul-02	32.5	F	CC
Central	Commander Islands	Medney Island	M447	2-Jul-02	31.5	F	CC
Central	Commander Islands	Medney Island	M455	2-Jul-02	35.5	М	CC
Central	Commander Islands	Medney Island	M458	2-Jul-02	34.0	F	CC
Central	Commander Islands	Medney Island	M462	2-Jul-02	28.0	F	CC
Central	Commander Islands	Medney Island	M465	2-Jul-02	32.0	F	CC
Central	Commander Islands	Medney Island	M467	2-Jul-02	33.5	F	CC
Central	Commander Islands	Medney Island	M471	2-Jul-02	31.0	F	CC
Central	Commander Islands	Medney Island	M477	2-Jul-02	35.0	F	CC
Central	Commander Islands	Medney Island	M444	2-Jul-02	26.0	F	DD
Central	Commander Islands	Medney Island	M448	2-Jul-02	36.0	F	DD
Central	Commander Islands	Medney Island	M472	2-Jul-02	33.0	F	DD

Appendix I Continued

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Central	Commander Islands	Medney Island	M401	2-Jul-02	28.0	F	DDD
Central	Commander Islands	Medney Island	M404	2-Jul-02	36.0	М	DDD
Central	Commander Islands	Medney Island	M411	2-Jul-02	34.0	М	DDD
Central	Commander Islands	Medney Island	M454	2-Jul-02	21.5	F	Е
Asian	Kuril Islands	Lovushki Island	Lr423	1-Jul-01	-	-	EE
Asian	Kamchatka	Kozlov C.	K229	5-Jul-02	30.0	F	EEE
Asian	Kamchatka	Kozlov C.	K215	5-Jul-02	39.5	М	EEEE
Asian	Kuril Islands	Antsiferov Island	Y487	26-Jun-01	-	-	EEEE
Asian	Kuril Islands	Raikoke Island	P601	2-Jul-01	-	-	EEEE
Asian	Kamchatka	Kozlov C.	K220	5-Jul-02	34.5	М	FF
Asian	Kuril Islands	Chernyye Brat'ya	Br627	7-Jul-01	-	-	FF
Asian	Kuril Islands	Lovushki Island	Lr427	1-Jul-01	-	-	FF
Asian	Kuril Islands	Srednego Island	C484	4-Jul-01	-	-	FF
Asian	Kuril Islands	Srednego Island	C486	4-Jul-01	-	-	FF
Asian	Kuril Islands	Srednego Island	C488	4-Jul-01	-	-	FF
Asian	Kuril Islands	Srednego Island	C499	4-Jul-01	-	-	FF
Asian	Sea of Okhotsk	Iony Island	N251	16-Jul-01	-	I	FF
Asian	Sea of Okhotsk	Iony Island	N256	16-Jul-01	-	I	FF
Asian	Sea of Okhotsk	Iony Island	N411	29-Jun-02	21.5	М	FF
Asian	Sea of Okhotsk	Iony Island	N421	29-Jun-02	20.0	М	FF
Asian	Sea of Okhotsk	Iony Island	N427	29-Jun-02	25.0	М	FF
Asian	Sea of Okhotsk	Iony Island	N430	29-Jun-02	21.5	М	FF
Asian	Sea of Okhotsk	Iony Island	N446	29-Jun-02	17.0	М	FF
Asian	Sea of Okhotsk	Iony Island	N447	29-Jun-02	02 25.0		FF
Asian	Sea of Okhotsk	Yamsky Island	R214	7-Mar-02	29.0	М	FF
Asian	Sea of Okhotsk	Yamsky Island	R226	7-Mar-02	35.0	М	FF
Asian	Sea of Okhotsk	Yamsky Island	R237	7-Mar-02	27.5	F	FF
Asian	Sea of Okhotsk	Yamsky Island	R272	7-Mar-02	26.0	Μ	FF
Asian	Sea of Okhotsk	Yamsky Island	R280	7-Mar-02	34.0	М	FF
Asian	Sea of Okhotsk	Yamsky Island	R282	7-Mar-02	25.5	М	FF
Asian	Sea of Okhotsk	Yamsky Island	R295	7-Mar-02	36.0	F	FF
Central	Commander Islands	Medney Island	M409	2-Jul-02	35.0	Μ	FF
Asian	Kamchatka	Kozlov C.	K243	5-Jul-02	31.0	М	FFFF
Asian	Kuril Islands	Antsiferov Island	Y475	26-Jun-01	-	-	FFFF
Asian	Kuril Islands	Chernyye Brat'ya	Br632	7-Jul-01	-	-	FFFF
Asian	Kuril Islands	Lovushki Island	Lr434	1-Jul-01	-	-	FFFF
Asian	Kuril Islands	Lovushki Island	Lr440	1-Jul-01	-	-	FFFF
Asian	Kuril Islands	Raikoke Island	P610	2-Jul-01	-	-	FFFF
Asian	Sea of Okhotsk	Iony Island	N252	16-Jul-01	-	-	FFFF
Asian	Sea of Okhotsk	Iony Island	N425	29-Jun-02	23.0	М	FFFF
Asian	Sea of Okhotsk	Yamsky Island	R217	7-Mar-02	20.5	F	FFFF
Asian	Sea of Okhotsk	Yamsky Island	R281	7-Mar-02	25.5	Μ	FFFF
Asian	Kuril Islands	Antsiferov Island	Y479	26-Jun-01	-	-	G
Asian	Kuril Islands	Antsiferov Island	Y481	26-Jun-01	-	-	G
Central	Commander Islands	Medney Island	M468	2-Jul-02	30.0	М	G
Asian	Kamchatka	Kozlov C	K224	5-Jul-02	35.5	м	GGGGGG

Appendix I Continued

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Central	Commander Islands	Medney Island	M402	2-Jul-02	37.0	М	HH
Central	Commander Islands	Medney Island	M412	2-Jul-02	30.0	М	HH
Central	Commander Islands	Medney Island	M420	2-Jul-02	33.0	М	HH
Central	Commander Islands	Medney Island	M429	2-Jul-02	33.5	М	HH
Central	Commander Islands	Medney Island	M450	2-Jul-02	26.5	F	HH
Central	Commander Islands	Medney Island	M452	2-Jul-02	32.0	F	HH
Central	Commander Islands	Medney Island	M460	2-Jul-02	25.0	F	HH
Central	Commander Islands	Medney Island	M464	2-Jul-02	43.0	М	HH
Central	Commander Islands	Medney Island	M479	2-Jul-02	42.0	М	HH
Asian	Kamchatka	Kozlov C.	K204	5-Jul-02	33.5	М	НННННН
Asian	Kamchatka	Kozlov C.	K241	5-Jul-02	42.5	М	HHHHHH
Asian	Kuril Islands	Chernyye Brat'ya	Br625	7-Jul-01	-	I	III
Asian	Sea of Okhotsk	Iony Island	N402	29-Jun-02	23.0	F	IIIIII
Central	Commander Islands	Medney Island	M424	2-Jul-02	27.5	F	JJJ
Central	Commander Islands	Medney Island	M470	2-Jul-02	43.5	М	JJJ
Asian	Sea of Okhotsk	Iony Island	N423	29-Jun-02	31.5	М	JJJJJJ
Asian	Kamchatka	Kozlov C.	K228	5-Jul-02	25.5	F	KKK
Asian	Kamchatka	Kozlov C.	K234	5-Jul-02	34.0	М	KKK
Asian	Kamchatka	Kozlov C.	K244	5-Jul-02	30.5	М	KKK
Asian	Sea of Okhotsk	Yamsky Island	R232	7-Mar-02	26.5	F	KKK
Asian	Sea of Okhotsk	Yamsky Island	R242	7-Mar-02	32.0	М	KKK
Asian	Sea of Okhotsk	Yamsky Island	R254	7-Mar-02	23.5	F	KKK
Central	Commander Islands	Medney Island	M483	2-Jul-02	31.5	F	KKK
Asian	Kamchatka	Kozlov C.	K245	5-Jul-02	27.5	F	LLL
Asian	Kamchatka	Kozlov C.	K248	5-Jul-02	39.0	F	LLL
Asian	Kuril Islands	Antsiferov Island	Y477	26-Jun-01	-	-	LLL
Asian	Kuril Islands	Chernyye Brat'ya	Br604	7-Jul-01	-	-	LLL
Asian	Kuril Islands	Chernyye Brat'ya	Br616	7-Jul-01	-	-	LLL
Asian	Kuril Islands	Chernyye Brat'ya	Br630	7-Jul-01	-	-	LLL
Asian	Kuril Islands	Raikoke Island	P607	2-Jul-01	-	-	LLL
Asian	Kuril Islands	Srednego Island	C491	4-Jul-01	-	-	LLL
Asian	Kuril Islands	Srednego Island	C500	4-Jul-01	-	-	LLL
Asian	Kuril Islands	Srednego Island	C504	4-Jul-01	-	-	LLL
Asian	Sea of Okhotsk	Iony Island	N443	29-Jun-02	30.5	M	LLL
Asian	Sea of Okhotsk	Yamsky Island	R206	7-Mar-02	27.5	M	LLL
Asian	Sea of Okhotsk	Yamsky Island	R222	7-Mar-02	32.0	M	LLL
Asian	Sea of Okhotsk	Yamsky Island	R224	7-Mar-02	32.5	M	LLL
Asian	Sea of Okhotsk	Yamsky Island	K299	/-Mar-02	28.0	M	
Asian	Kamchatka	Kozlov C.	K202	5-Jul-02	22.5	М	MMM
Asian	Sea of Okhotsk	Iony Island	N254	16-Jul-01	-	-	MMM
Asian	Sea of Okhotsk	Iony Island	N264	16-Jul-01	-	-	MMM
Asian	Sea of Okhotsk	Iony Island	N2/5	10-Jul-01	-	- E	MMM
Asian	Sea of Oknotsk	Iony Island	IN41/	29-Jun-02	27.0	Г	
Asian	Sea of Oknotsk	Iony Island	IN43/	29-Jun-02	23.0	M	MNAM
Asian	Sea of Oknoisk	Vomsky Island	D240	29-Jun-02	24.0	IVI M	
Aslan	Sea of Oknotsk	i anisky Island	K249	/-1v1ar-02	57.0	IVI	IVIIVIIVI

Appendix I Continued

Stock	Region	Rookery	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Asian	Kuril Islands	Lovushki Island	Lr417	1-Jul-01	-	-	QQQQ
Asian	Kuril Islands	Chernyye Brat'ya	Br639	7-Jul-01	-	-	RR
Asian	Kamchatka	Kozlov C.	K214	5-Jul-02	31.5	F	S
Asian	Kamchatka	Kozlov C.	K239	5-Jul-02	35.0	F	S
Asian	Kamchatka	Kozlov C.	K240	5-Jul-02	31.0	М	S
Asian	Kuril Islands	Antsiferov Island	Y462	26-Jun-01	-	-	S
Asian	Kuril Islands	Antsiferov Island	Y470	26-Jun-01	-	-	S
Asian	Kuril Islands	Antsiferov Island	Y491	26-Jun-01	-	I	S
Asian	Kuril Islands	Lovushki Island	Lr402	1-Jul-01	-	1	S
Asian	Kuril Islands	Lovushki Island	Lr409	1-Jul-01	-	1	S
Asian	Kuril Islands	Raikoke Island	P615	2-Jul-01	-	1	S
Asian	Kuril Islands	Raikoke Island	P621	2-Jul-01	-	1	S
Asian	Sea of Okhotsk	Iony Island	N277	16-Jul-01	-	I	S
Central	Commander Islands	Medney Island	M400	2-Jul-02	31.5	F	S
Central	Commander Islands	Medney Island	M407	2-Jul-02	27.5	М	S
Central	Commander Islands	Medney Island	M413	2-Jul-02	21.0	F	S
Central	Commander Islands	Medney Island	M415	2-Jul-02	29.0	F	S
Central	Commander Islands	Medney Island	M421	2-Jul-02	22.5	F	S
Central	Commander Islands	Medney Island	M436	2-Jul-02	26.5	F	S
Central	Commander Islands	Medney Island	M438	2-Jul-02	36.5	F	S
Central	Commander Islands	Medney Island	M445	2-Jul-02	36.5	М	S
Central	Commander Islands	Medney Island	M449	2-Jul-02	40.5	М	S
Central	Commander Islands	Medney Island	M453	2-Jul-02	24.0	F	S
Central	Commander Islands	Medney Island	M457	57 2-Jul-02 42.0		М	S
Central	Commander Islands	Medney Island	M459	2-Jul-02	40.0	М	S
Central	Commander Islands	Medney Island	M461	2-Jul-02 35.0		М	S
Central	Commander Islands	Medney Island	M475	2-Jul-02	40.5	М	S
Central	Commander Islands	Medney Island	M476	2-Jul-02	31.5	F	S
Central	Commander Islands	Medney Island	M478	2-Jul-02	44.0	Μ	S
Central	Commander Islands	Medney Island	M480	2-Jul-02	25.0	F	S
Central	Commander Islands	Medney Island	M482	2-Jul-02	31.5	F	S
Central	Commander Islands	Medney Island	M484	5-Jul-02	39.5	М	S
Asian	Kuril Islands	Chernyye Brat'ya	Br621	7-Jul-01	-	-	SSSSS
Asian	Kuril Islands	Chernyye Brat'ya	Br633	7-Jul-01	-	-	SSSSS
Asian	Sea of Okhotsk	Iony Island	N416	29-Jun-02	24.0	F	SSSSS
Asian	Sea of Okhotsk	Iony Island	N432	29-Jun-02	32.0	М	SSSSS
Central	Commander Islands	Medney Island	M442	2-Jul-02	35.5	М	Т
Asian	Kuril Islands	Raikoke Island	P618	2-Jul-01	-	-	TTT
Asian	Kuril Islands	Srednego Island	C482	4-Jul-01	-	-	TTTTT
Asian	Kuril Islands	Raikoke Island	P614	2-Jul-01	-	-	U
Asian	Kuril Islands	Srednego Island	C490	4-Jul-01	-	-	U
Asian	Kuril Islands	Antsiferov Island	Y465	26-Jun-01	-	-	UUU
Asian	Kuril Islands	Srednego Island	C508	4-Jul-01	-	-	UUU
Asian	Sea of Okhotsk	Iony Island	N263	16-Jul-01	-	-	UUU
Asian	Sea of Okhotsk	Iony Island	N272	16-Jul-01	-	-	UUU
Asian	Sea of Okhotsk	Iony Island	N409	29-Jun-02	18.5	F	UUU

Appendix I Continued

Stock	Region	Rookerv	Sample	Date Collected	Weight (kg)	Sex	Haplotype
Asian	Sea of Okhotsk	Iony Island	N410	29-Jun-02	21.0	F	UUU
Asian	Sea of Okhotsk	Iony Island	N419	29-Jun-02	24.5	М	UUU
Asian	Sea of Okhotsk	Yamsky Island	R219	7-Mar-02	31.0	М	UUU
Asian	Sea of Okhotsk	Yamsky Island	R259	7-Mar-02	32.0	М	UUU
Asian	Sea of Okhotsk	Yamsky Island	R284	7-Mar-02	23.0	F	UUU
Asian	Sea of Okhotsk	Iony Island	N250	16-Jul-01	-	-	UUUU
Asian	Kuril Islands	Srednego Island	C489	4-Jul-01	-	-	UUUUU
Asian	Kuril Islands	Srednego Island	C502	4-Jul-01	-	-	VVVVV
Central	Commander Islands	Medney Island	M426	2-Jul-02	35.0	М	W
Central	Commander Islands	Medney Island	M456	2-Jul-02	36.0	F	W
Asian	Kuril Islands	Lovushki Island	Lr439	1-Jul-01	-	-	WWW
Asian	Sea of Okhotsk	Iony Island	N422	29-Jun-02	26.5	F	WWW
Asian	Kuril Islands	Raikoke Island	P612	2-Jul-01	-	-	WWWWW
Asian	Sea of Okhotsk	Iony Island	N404	29-Jun-02	26.0	М	WWWWW
Asian	Kamchatka	Kozlov C.	K217	5-Jul-02	33.5	М	Х
Asian	Kuril Islands	Raikoke Island	P616	2-Jul-01	-	-	XXXXX
Asian	Kuril Islands	Antsiferov Island	Y452	26-Jun-01	-	-	YYYYY
Asian	Sea of Okhotsk	Iony Island	N435	29-Jun-02	28.5	М	YYYYY
Asian	Sea of Okhotsk	Yamsky Island	R239	7-Mar-02	30.0	F	YYYYY
Asian	Sea of Okhotsk	Yamsky Island	R247	7-Mar-02	29.5	F	YYYYY
Asian	Kamchatka	Kozlov C.	K208	5-Jul-02	24.5	F	Z
Asian	Kamchatka	Kozlov C.	K209	5-Jul-02	35.0	М	Z
Asian	Kamchatka	Kozlov C.	K212	5-Jul-02	37.5	М	Z
Asian	Kamchatka	Kozlov C.	K213	5-Jul-02	36.0	F	Z
Asian	Kamchatka	Kozlov C.	K230	5-Jul-02	36.5	М	Z
Asian	Kamchatka	Kozlov C.	K233	5-Jul-02	29.0	F	Z
Asian	Kuril Islands	Antsiferov Island	Y455	26-Jun-01	-	I	Z
Central	Commander Islands	Medney Island	M419	2-Jul-02	28.0	F	Z
Central	Commander Islands	Medney Island	M422	2-Jul-02	27.0	F	Z
Central	Commander Islands	Medney Island	M428	2-Jul-02	38.5	М	Z
Central	Commander Islands	Medney Island	M430	2-Jul-02	30.5	F	Z
Central	Commander Islands	Medney Island	M451	2-Jul-02	38.5	М	Z
Central	Commander Islands	Medney Island	M474	2-Jul-02	37.0	М	Z
Central	Commander Islands	Medney Island	M481	2-Jul-02	31.5	F	Z
Asian	Kamchatka	Kozlov C.	K218	5-Jul-02	36.0	М	ZZZ
Asian	Kamchatka	Kozlov C.	K223	5-Jul-02	32.5	М	ZZZ
Central	Commander Islands	Medney Island	M439	2-Jul-02	37.5	F	ZZZ
Asian	Sea of Okhotsk	Yamsky Island	R216	7-Mar-02	27.5	F	ZZZZ
Central	Commander Islands	Medney Island	M405	2-Jul-02	25.5	F	ZZZZ
Asian	Kuril Islands	Antsiferov Island	Y460	26-Jun-01	_	-	ZZZZZ

Appendix I Continued

Appendix II

<u>Slatikin's Linearized F-Statistics (Conventional F_{st} above Diagonal; F_{st} Analogues (Φ_{st}) below Diagonal)</u>

	ADU	AGA	AKN	AKT	AMA	AMC	ANT	ATK	ATT	BOG	BUL	CAP	CHE
ADU		0.016	0.016	0.009	0.006	0.000	0.024	0.014	0.000	0.066	0.003	0.362	0.157
AGA	0.054		0.048	0.027	0.000	0.000	0.030	0.020	0.000	0.033	0.024	0.236	0.150
AKN	0.056	0.041		0.000	0.000	0.000	0.028	0.003	0.000	0.026	0.009	0.197	0.125
AKT	0.062	0.000	0.004		0.000	0.000	0.033	0.000	0.000	0.021	0.002	0.212	0.074
AMA	0.017	0.000	0.000	0.000		0.000	0.025	0.000	0.000	0.000	0.026	0.056	0.147
AMC	0.000	0.000	0.000	0.000	0.000		0.013	0.000	0.000	0.000	0.015	0.102	0.150
ANT	0.157	0.057	0.022	0.043	0.029	0.057		0.027	0.000	0.062	0.027	0.311	0.147
ATK	0.103	0.015	0.000	0.000	0.004	0.010	0.020		0.000	0.042	0.000	0.262	0.088
ATT	0.000	0.009	0.022	0.015	0.000	0.000	0.102	0.037		0.012	0.000	0.196	0.115
BOG	0.079	0.053	0.052	0.055	0.000	0.000	0.111	0.076	0.002		0.066	0.117	0.026
BUL	0.103	0.011	0.013	0.000	0.039	0.032	0.042	0.000	0.047	0.117		0.370	0.086
CAP	0.066	0.142	0.089	0.117	0.000	0.018	0.212	0.171	0.000	0.000	0.266		0.848
CHE	0.346	0.180	0.110	0.085	0.279	0.289	0.142	0.085	0.296	0.154	0.087	0.788	
CHB	0.350	0.146	0.119	0.108	0.192	0.215	0.019	0.076	0.282	0.252	0.092	0.530	0.160
CHF	0.084	0.014	0.000	0.000	0.000	0.000	0.028	0.000	0.018	0.038	0.000	0.101	0.085
CHW	0.103	0.029	0.000	0.001	0.000	0.003	0.045	0.012	0.042	0.000	0.049	0.101	0.000
СНО	0.038	0.073	0.070	0.061	0.000	0.000	0.176	0.098	0.000	0.006	0.137	0.000	0.479
CLU	0.073	0.003	0.006	0.000	0.000	0.000	0.051	0.000	0.000	0.031	0.016	0.109	0.231
FIS	0.106	0.000	0.053	0.005	0.026	0.019	0.074	0.025	0.050	0.076	0.016	0.173	0.137
FOR	0.420	0.292	0.228	0.265	0.314	0.333	0.204	0.234	0.375	0.316	0.226	0.495	0.188
GRA	0.071	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.220	0.191
HAZ	0.461	0.286	0.250	0.258	0.339	0.343	0.193	0.222	0.407	0.372	0.216	0.576	0.205
ION	0.314	0.125	0.189	0.108	0.159	0.176	0.034	0.088	0.228	0.277	0.102	0.535	0.312
KAS	0.029	0.000	0.074	0.017	0.000	0.000	0.127	0.044	0.000	0.035	0.051	0.119	0.425
CSS	0.045	0.000	0.012	0.000	0.000	0.000	0.049	0.000	0.006	0.077	0.000	0.152	0.134
LIE	0.065	0.000	0.064	0.012	0.000	0.000	0.077	0.028	0.017	0.072	0.019	0.151	0.221
KOZ	0.132	0.004	0.082	0.019	0.048	0.039	0.041	0.014	0.063	0.138	0.006	0.295	0.195
LAT	0.179	0.000	0.000	0.000	0.137	0.162	0.000	0.000	0.155	0.000	0.000	00	0.000
LOV	0.291	0.100	0.106	0.083	0.131	0.157	0.014	0.057	0.222	0.190	0.068	0.425	0.162
MAR	0.069	0.000	0.032	0.006	0.000	0.000	0.070	0.024	0.000	0.025	0.044	0.062	0.232
MED	0.013	0.000	0.029	0.008	0.000	0.000	0.062	0.024	0.000	0.045	0.019	0.068	0.165
NOR	0.86/	0.620	0.544	0.530	0.746	0.804	0.434	0.517	0.827	0.66/	0.51/	1.265	0.498
OGC	0.128	0.03/	0.052	0.021	0.012	0.051	0.020	0.019	0.075	0.029	0.025	0.141	0.032
PIN	0.074	0.016	0.000	0.000	0.000	0.000	0.039	0.000	0.010	0.003	0.022	0.041	0.081
RAY	0.275	0.092	0.091	0.007	0.118	0.132	0.012	0.044	0.199	0.190	0.001	0.424	0.184
RUG	0.428	0.277	0.254	0.261	0.315	0.318	0.205	0.226	0.377	0.360	0.218	0.514	0.217
SEA	0.092	0.011	0.000	0.000	0.000	0.000	0.043	0.009	0.042	0.037	0.022	0.080	0.085
SEG	0.000	0.000	0.008	0.000	0.000	0.000	0.075	0.019	0.000	0.038	0.014	0.047	0.178
SKE	0.545	0.155	0.178	0.109	0.194	0.207	0.055	0.087	0.204	0.274	0.097	0.389	0.231
SUC	0.390	0.382	0.323	0.322	0.499	0.010	0.200	0.303	0.040	0.401	0.300	0.914	0.200
TDI	0.571	0.000	0.025	0.000	0.000	0.000	0.000	0.007	0.527	0.057	0.000	0.110	0.151
	0.371	0.410	0.040	0.375	0.455	0.465	0.290	0.343	0.012	0.430	0.528	0.709	0.282
	0.074	0.009	0.009	0.000	0.000	0.000	0.040	0.000	0.015	0.023	0.009	0.071	0.087
WAI	0.105	0.070	0.087	0.085	0.007	0.007	0.043	0.005	0.001	0.079	0.008	0.107	0.117
WHAL	0.037	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.001	0.003	0.000	0.145	0.090
WHI	0 3 3 0	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.101
VAM	0.339	0.202	0.101	0.204	0.245	0.239	0.201	0.210	0.290	0.207	0.165	0.528	0.121
VIIN	0.0290	0.014	0.025	0.036	0.000	0.000	0.020	0.062	0.215	0.240	0.090	0.000	0.260
745	0.020	0.014	0.025	0.037	0.132	0.134	0.004	0.005	0.157	0.125	0.03/	0.638	0.141
LUL	0.231	0.000	0.070	0.057	0.132	0.134	0.004	0.021	0.157	0.125	0.034	0.050	0.141

for a	<u>ıll P</u>	airwise	Rookery	Com	oarisons	Based	on	mtDNA Data	
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Note- Rookery designations are as follows: ADU = Adugak Island, AGA = Agattu Island, AKN = Akun Island, AKT = Akutan Island, AMA = Amak Island, AMC = Amchitka Island, ANT = Antsiferova Island, ATK = Atkins Island, ATT = Attu Island, BOG = Bogoslof Island, BUL = Buldir Island, CAP = Cape St. Elias, CHE = Chernabura Island, CHB = Chernyye Brat'ya, CHF = Chirikof Island, CHW = Chiswell Island, CHO = Chowiet Island, CLU = Clubbing Rocks, FIS = Fish Island, FOR = Forrester Island, designations continued on following page.

Appendix II Continued

	CHB	CHF	CHW	CHO	CLU	FIS	FOR	GRA	HAZ	ION	KAS	CSS	LIE
ADU	0.090	0.028	0.038	0.112	0.017	0.026	0.042	0.000	0.075	0 1 1 4	0.067	0.003	0.022
AGA	0.074	0.052	0.011	0.106	0.009	0.018	0.035	0.000	0.070	0 117	0.026	0.010	0.000
AKN	0.131	0.000	0.026	0.019	0.002	0.011	0.050	0.000	0.118	0.184	0.031	0.019	0.048
AKT	0.087	0.001	0.005	0.045	0.000	0.000	0.040	0.000	0.081	0.132	0.042	0.004	0.037
AMA	0.135	0.000	0.000	0.000	0.000	0.001	0.044	0.000	0.120	0 181	0.000	0.004	0.003
AMC	0.076	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.069	0.114	0.000	0.000	0.001
ANT	0.026	0.049	0.025	0.143	0.039	0.034	0.015	0.004	0.027	0.037	0.124	0.049	0.065
ATK	0.059	0.008	0.020	0.081	0.000	0.012	0.026	0.000	0.059	0.124	0.049	0.000	0.033
ATT	0.077	0.000	0.000	0.004	0.000	0.000	0.020	0.000	0.063	0.099	0.000	0.000	0.000
BOG	0.146	0.007	0.000	0.017	0.015	0.012	0.043	0.000	0.133	0.219	0.046	0.041	0.068
BUL	0.074	0.023	0.043	0.124	0.020	0.020	0.032	0.000	0.069	0.129	0.056	0.000	0.014
CAP	0.523	0.165	0.244	0.000	0.145	0.222	0.354	0.172	0.492	0.616	0.120	0.245	0.260
CHE	0.233	0.064	0.000	0.258	0.124	0.097	0.138	0.122	0.216	0.320	0.240	0.100	0.175
CHB	0.200	0.150	0.099	0.284	0.086	0.088	0.035	0.058	0.012	0.042	0.256	0.085	0.137
CHE	0 116	0.100	0.000	0.014	0.003	0.015	0.069	0.000	0.137	0.201	0.020	0.020	0.049
CHW	0.143	0.000	0.000	0.072	0.000	0.007	0.027	0.000	0.084	0.135	0.082	0.038	0.071
СНО	0.410	0.053	0.089		0.023	0.053	0 1 5 9	0.029	0.266	0 357	0.000	0.071	0.099
CLU	0.171	0.000	0.007	0.025		0.009	0.044	0.000	0.084	0.140	0.011	0.000	0.031
FIS	0.135	0.021	0.041	0.092	0.025		0.039	0.000	0.080	0.132	0.056	0.017	0.041
FOR	0.155	0.272	0.205	0.508	0.359	0.269		0.008	0.000	0.098	0.140	0.040	0.076
GRA	0.078	0.000	0.022	0.079	0.000	0.000	0.213		0.060	0 117	0.000	0.000	0.000
HAZ	0.117	0.271	0.243	0.522	0.326	0.260	0.000	0.216		0.037	0.239	0.088	0.133
ION	0.062	0.135	0.201	0.369	0.140	0.140	0.322	0.037	0.258		0.330	0.164	0.193
KAS	0.326	0.022	0.104	0.000	0.000	0.022	0.446	0.000	0.444	0.254		0.021	0.000
CSS	0.126	0.000	0.035	0.073	0.000	0.013	0.285	0.000	0.275	0.110	0.009		0.008
LIE	0.173	0.028	0.066	0.076	0.016	0.006	0.341	0.000	0.329	0.138	0.000	0.000	
KOZ	0.097	0.036	0.090	0.163	0.035	0.023	0.309	0.000	0.270	0.054	0.052	0.013	0.018
LAT	0.000	0.000	0.000	0.555	0.068	0.000	0.000	0.000	0.000	0.000	0.457	0.000	0.000
LOV	0.000	0.092	0.109	0.330	0.119	0.109	0.176	0.018	0.146	0.039	0.246	0.086	0.118
MAR	0.195	0.002	0.014	0.017	0.000	0.013	0.398	0.000	0.375	0.163	0.000	0.013	0.008
MED	0.146	0.019	0.030	0.043	0.005	0.018	0.304	0.000	0.308	0.122	0.000	0.000	0.000
NOR	0.382	0.575	0.580	1.084	0.788	0.538	0.011	0.548	0.057	0.607	0.993	0.569	0.653
OGC	0.057	0.029	0.000	0.132	0.047	0.049	0.155	0.000	0.185	0.070	0.096	0.026	0.049
PIN	0.129	0.000	0.000	0.038	0.000	0.033	0.275	0.000	0.278	0.158	0.028	0.011	0.037
RAY	0.011	0.080	0.093	0.311	0.092	0.103	0.211	0.013	0.171	0.031	0.237	0.070	0.112
ROG	0.139	0.268	0.245	0.466	0.298	0.256	0.000	0.207	0.000	0.251	0.399	0.269	0.313
SEA	0.110	0.000	0.000	0.071	0.003	0.025	0.261	0.000	0.261	0.149	0.042	0.015	0.031
SEG	0.185	0.009	0.024	0.018	0.000	0.019	0.318	0.000	0.330	0.168	0.000	0.000	0.000
SRE	0.011	0.139	0.186	0.416	0.159	0.141	0.236	0.048	0.181	0.018	0.307	0.111	0.151
SGR	0.211	0.352	0.342	0.761	0.495	0.324	0.000	0.344	0.000	0.394	0.667	0.356	0.426
SUG	0.143	0.002	0.041	0.055	0.008	0.000	0.258	0.000	0.272	0.150	0.000	0.000	0.000
TRI	0.226	0.390	0.333	0.689	0.506	0.378	0.000	0.312	0.000	0.408	0.609	0.393	0.458
UGA	0.120	0.000	0.000	0.045	0.000	0.026	0.286	0.000	0.284	0.115	0.015	0.001	0.021
ULA	0.065	0.090	0.047	0.198	0.110	0.095	0.018	0.000	0.057	0.091	0.141	0.082	0.093
WAL	0.141	0.000	0.016	0.054	0.000	0.009	0.265	0.000	0.270	0.142	0.003	0.000	0.010
WHA	0.166	0.000	0.000	0.000	0.000	0.000	0.166	0.000	0.252	0.135	0.000	0.000	0.000
WHI	0.144	0.239	0.148	0.378	0.291	0.260	0.000	0.168	0.000	0.327	0.332	0.263	0.319
YAM	0.043	0.127	0.182	0.349	0.137	0.132	0.282	0.029	0.229	0.000	0.243	0.102	0.129
YUN	0.255	0.034	0.012	0.003	0.010	0.057	0.391	0.011	0.399	0.260	0.000	0.038	0.027
ZHE	0.014	0.058	0.074	0.351	0.085	0.064	0.176	0.005	0.143	0.006	0.250	0.045	0.083

Note- Region designations continued: GRA = Gramp Rocks, HAZ = Hazy Islands, ION = Iony Island, KAS = Kasatoshi Island, CSS = Kiska Island, Cape St. Stephen, LIE = Kiska Island, Lief Cove, KOZ = Kozlova Cape, LAT = Latax Rocks, LOV = Lovushki Island, MAR = Marmot Island, MED = Medney Island, NOR = North Danger Rocks, OGC = Ogchul Island, PIN = Pinnacle Rocks, RAY = Raykoke Island, ROG = Rogue Reef, SEA = Seal Rocks, SEG = Seguam Island, SRE = Srednego Island, SGR = St. George Reef, SUG = Sugarloaf Island, TRI = Triangle Island, UGA = Ugamak Island, ULA = Ulak Island, WAL = Walrus Island, WHA = Whaleback Island, WHI = White Sisters Islands, YAM = Yamsky Island, YUN = Yunaska Island, and ZHE = Zheleznaya Bay.

Appendix II Continued

					1000	NOR	0.00	D.D.Y		BAG	0.5.1	ana	ODE
	KOZ	LAT	LOV	MAR	MED	NOR	OGC	PIN	RAY	ROG	SEA	SEG	SRE
ADU	0.023	0.154	0.071	0.038	0.000	0.176	0.067	0.024	0.067	0.085	0.031	0.000	0.086
AGA	0.031	0.053	0.049	0.013	0.000	0.170	0.048	0.020	0.049	0.087	0.010	0.000	0.079
AKN	0.077	0.164	0.105	0.002	0.030	0.194	0.049	0.000	0.094	0.112	0.000	0.000	0.132
AKT	0.047	0.057	0.073	0.014	0.018	0.167	0.036	0.000	0.061	0.093	0.004	0.000	0.092
AMA	0.066	0.200	0.098	0.000	0.001	0.211	0.031	0.000	0.083	0.118	0.000	0.000	0.131
AMC	0.027	0.066	0.054	0.000	0.000	0.192	0.035	0.000	0.038	0.092	0.000	0.000	0.081
ANT	0.013	0.052	0.019	0.056	0.033	0.119	0.036	0.038	0.020	0.043	0.036	0.028	0.017
ATK	0.036	0.000	0.053	0.026	0.012	0.161	0.038	0.000	0.037	0.083	0.006	0.000	0.073
ATT	0.004	0.125	0.053	0.000	0.000	0.161	0.032	0.000	0.046	0.073	0.000	0.000	0.074
BOG	0.125	0.146	0.114	0.000	0.035	0.195	0.000	0.000	0.103	0.119	0.000	0.017	0.148
BUL	0.019	0.037	0.063	0.049	0.009	0.147	0.044	0.022	0.060	0.076	0.022	0.000	0.081
CAP	0.434	00	0.432	0.089	0.232	0.761	0.281	0.129	0.401	0.448	0.142	0.190	0.520
CHE	0.195	0.429	0.206	0.128	0.126	0.318	0.013	0.039	0.199	0.195	0.073	0.098	0.236
CHB	0.035	0.000	0.000	0.151	0.080	0.158	0.104	0.107	0.000	0.061	0.098	0.096	0.000
CHF	0.089	0.195	0.122	0.000	0.036	0.210	0.040	0.000	0.109	0.130	0.002	0.003	0.150
CHW	0.069	0.154	0.074	0.000	0.029	0.185	0.000	0.000	0.064	0.089	0.000	0.008	0.097
СНО	0.207	0.552	0.230	0.004	0.087	0.385	0.115	0.017	0.209	0.240	0.033	0.040	0.285
CLU	0.051	0.019	0.071	0.000	0.014	0.205	0.052	0.000	0.049	0.110	0.000	0.000	0.097
FIS	0.053	0.066	0.073	0.013	0.018	0.163	0.042	0.007	0.063	0.092	0.005	0.002	0.093
FOR	0.048	0.000	0.032	0.077	0.033	0.040	0.025	0.042	0.027	0.000	0.038	0.034	0.044
GRA	0.017	0.000	0.019	0.000	0.000	0.157	0.000	0.000	0.019	0.070	0.000	0.000	0.056
HAZ	0.032	0.000	0.025	0.139	0.076	0.093	0.094	0.099	0.016	0.016	0.095	0.087	0.017
ION	0.034	0.000	0.020	0.139	0.128	0.020	0.160	0.055	0.045	0.010	0.155	0.007	0.021
L'AS	0.034	0.152	0.000	0.100	0.120	0.212	0.100	0.100	0.040	0.000	0.133	0.142	0.021
CSS	0.171	0.452	0.201	0.000	0.027	0.575	0.110	0.020	0.152	0.210	0.022	0.004	0.230
	0.050	0.000	0.000	0.020	0.000	0.175	0.042	0.010	0.050	0.101	0.011	0.000	0.033
LIL VO7	0.001	0.100	0.027	0.029	0.002	0.200	0.077	0.042	0.105	0.120	0.051	0.000	0.139
KUZ LAT	0.000	0.100	0.035	0.005	0.040	0.157	0.101	0.070	0.052	0.004	0.000	0.042	0.027
	0.000	0.000	0.000	0.218	0.057	0.230	0.070	0.080	0.000	0.000	0.033	0.087	0.000
	0.078	0.000	0.140	0.116	0.038	0.149	0.079	0.065	0.000	0.038	0.078	0.075	0.004
MAK	0.042	0.040	0.148	0.007	0.024	0.251	0.055	0.000	0.107	0.140	0.000	0.001	0.151
MED	0.027	0.000	0.104	0.007	0.550	0.152	0.057	0.020	0.057	0.084	0.015	0.000	0.085
NOR	0.629	0.000	0.580	0.782	0.558	0.250	0.154	0.18/	0.152	0.053	0.1/4	0.105	0.15/
OGC	0.056	0.000	0.014	0.064	0.032	0.358	0.000	0.014	0.080	0.077	0.025	0.028	0.089
PIN	0.057	0.000	0.100	0.000	0.019	0.593	0.022	0.002	0.072	0.107	0.000	0.000	0.115
RAY	0.067	0.000	0.000	0.127	0.090	0.462	0.021	0.083	<u>^ 177</u>	0.060	0.068	0.067	0.004
ROG	0.264	0.000	0.160	0.347	0.309	0.035	0.188	0.276	0.177		0.103	0.090	0.056
SEA	0.059	0.000	0.082	0.012	0.023	0.527	0.035	0.000	0.070	0.269		0.000	0.108
SEG	0.039	0.000	0.136	0.000	0.000	0.625	0.042	0.008	0.119	0.319	0.015		0.096
SRE	0.074	0.000	0.003	0.188	0.129	0.490	0.051	0.155	0.005	0.185	0.136	0.173	
SGR	0.378	0.000	0.238	0.504	0.369	0.001	0.259	0.368	0.280	0.000	0.322	0.409	0.307
SUG	0.015	0.000	0.106	0.000	0.000	0.543	0.031	0.019	0.107	0.272	0.009	0.000	0.151
TRI	0.425	0.000	0.238	0.547	0.412	0.000	0.225	0.403	0.291	0.000	0.378	0.438	0.298
UGA	0.037	0.000	0.083	0.004	0.014	0.553	0.003	0.000	0.066	0.285	0.005	0.006	0.114
ULA	0.090	0.000	0.030	0.134	0.084	0.192	0.000	0.089	0.047	0.069	0.094	0.095	0.067
WAL	0.019	0.000	0.109	0.011	0.005	0.572	0.021	0.000	0.093	0.262	0.011	0.000	0.140
WHA	0.000	0.005	0.111	0.000	0.000	0.673	0.000	0.000	0.094	0.222	0.000	0.000	0.170
WHI	0.298	0.000	0.164	0.365	0.313	0.000	0.136	0.243	0.194	0.000	0.258	0.289	0.212
YAM	0.055	0.000	0.028	0.158	0.112	0.554	0.045	0.145	0.024	0.224	0.139	0.152	0.005
YUN	0.107	0.057	0.193	0.005	0.013	0.773	0.088	0.008	0.177	0.374	0.017	0.000	0.265
ZHE	0.022	0.000	0.000	0.105	0.060	0.491	0.002	0.059	0.000	0.149	0.057	0.091	0.000

Appendix II Continued

	SGR	SUG	TRI	UGA	ULA	WAL	WHA	WHI	YAM	YUN	ZHE
ADU	0 1 3 1	0.023	0.059	0.025	0.051	0.013	0.000	0.056	0.083	0.066	0.089
	0.121	0.000	0.059	0.024	0.021	0.037	0.000	0.051	0.085	0.021	0.071
AGA	0.121	0.000	0.039	0.024	0.035	0.037	0.000	0.031	0.085	0.021	0.071
AKN	0.150	0.007	0.086	0.000	0.116	0.000	0.000	0.049	0.129	0.032	0.141
AKT	0.123	0.001	0.066	0.000	0.072	0.000	0.000	0.041	0.096	0.049	0.082
AMA	0.163	0.000	0.091	0.000	0.104	0.000	0.000	0.052	0.131	0.000	0.134
AMC	0.134	0.000	0.063	0.000	0.052	0.000	0.000	0.036	0.088	0.000	0.073
ANT	0.082	0.049	0.021	0.043	0.011	0.051	0.000	0.040	0.010	0.104	0.026
АТК	0.105	0.000	0.050	0.009	0.044	0.000	0.000	0.022	0.087	0.064	0.052
ATT	0.116	0.000	0.046	0.000	0.038	0.000	0.000	0.034	0.071	0.006	0.075
BOC	0.110	0.000	0.040	0.000	0.036	0.000	0.000	0.034	0.071	0.000	0.075
BUG	0.130	0.020	0.089	0.000	0.130	0.013	0.000	0.047	0.147	0.020	0.130
BUL	0.103	0.000	0.046	0.022	0.045	0.000	0.000	0.032	0.079	0.081	0.075
САР	0.644	0.217	0.470	0.141	0.628	0.208	0.333	0.316	0.509	0.058	0.643
CHE	0.255	0.125	0.170	0.058	0.238	0.048	0.005	0.128	0.231	0.192	0.206
CHB	0.094	0.104	0.031	0.111	0.010	0.121	0.107	0.054	0.020	0.217	0.000
CHF	0.170	0.016	0.108	0.000	0.135	0.000	0.000	0.065	0.148	0.034	0.149
CHW	0.135	0.039	0.060	0.000	0.075	0.006	0.000	0.049	0.094	0.034	0.070
CHO	0.324	0.049	0.234	0.022	0.309	0.020	0.000	0.137	0.279	0.007	0 333
	0.145	0.001	0.081	0.000	0.077	0.000	0.000	0.043	0.110	0.020	0.077
EIG	0.143	0.001	0.061	0.000	0.077	0.000	0.000	0.045	0.006	0.020	0.077
FIS	0.123	0.000	0.063	0.007	0.069	0.002	0.000	0.040	0.096	0.034	0.085
FOR	0.000	0.033	0.000	0.046	0.025	0.051	0.000	0.000	0.051	0.117	0.035
GRA	0.103	0.000	0.043	0.000	0.037	0.000	0.000	0.012	0.064	0.000	0.062
HAZ	0.026	0.100	0.000	0.104	0.000	0.116	0.091	0.029	0.030	0.205	0.000
ION	0.162	0.189	0.076	0.156	0.019	0.189	0.202	0.146	0.013	0.276	0.016
KAS	0.286	0.000	0.203	0.021	0.229	0.016	0.000	0.122	0.252	0.000	0.296
CSS	0.121	0.000	0.070	0.012	0.077	0.000	0.000	0.029	0.111	0.044	0.089
LIE	0.167	0.000	0.107	0.036	0.096	0.033	0.000	0.077	0.138	0.022	0.153
KO7	0.114	0.000	0.043	0.030	0.000	0.033	0.000	0.077	0.030	0.130	0.026
LAT	0.114	0.004	0.045	0.070	0.000	0.102	0.011	0.077	0.050	0.157	0.020
	0.038	0.003	0.000	0.104	0.000	0.103	0.000	0.000	0.076	0.550	0.000
LOV	0.094	0.082	0.033	0.086	0.017	0.103	0.065	0.052	0.024	0.172	0.012
MAR	0.188	0.010	0.121	0.001	0.124	0.010	0.000	0.083	0.150	0.000	0.151
MED	0.110	0.000	0.057	0.021	0.050	0.021	0.000	0.039	0.087	0.034	0.081
NOR	0.044	0.170	0.019	0.178	0.146	0.190	0.176	0.065	0.154	0.291	0.172
OGC	0.111	0.040	0.055	0.013	0.085	0.033	0.000	0.032	0.080	0.080	0.086
PIN	0.140	0.009	0.080	0.000	0.095	0.000	0.000	0.044	0.116	0.016	0.099
RAY	0.091	0.076	0.031	0.076	0.014	0.090	0.044	0.042	0.026	0.164	0.000
ROG	0.000	0.101	0.006	0.106	0.044	0 1 1 4	0.075	0.037	0.057	0.187	0.055
SEA	0.129	0.000	0.075	0.000	0.086	0.000	0.000	0.040	0.111	0.017	0.095
SEA	0.122	0.000	0.075	0.000	0.060	0.000	0.000	0.040	0.006	0.017	0.005
SEG	0.122	0.000	0.064	0.000	0.008	0.000	0.000	0.058	0.096	0.012	0.093
SRE	0.103	0.117	0.036	0.110	0.011	0.130	0.114	0.071	0.000	0.219	0.000
SGR		0.119	0.017	0.138	0.089	0.144	0.109	0.024	0.109	0.246	0.098
SUG	0.340		0.068	0.004	0.082	0.000	0.000	0.025	0.124	0.016	0.115
TRI	0.000	0.368		0.082	0.015	0.086	0.029	0.000	0.041	0.176	0.027
UGA	0.355	0.011	0.398		0.096	0.000	0.000	0.048	0.112	0.023	0.103
ULA	0.090	0.070	0.076	0.080		0.113	0.088	0.058	0.019	0.194	0.000
WAL	0 348	0.000	0 374	0.000	0.086		0.000	0.042	0.132	0.035	0.126
WHA	0.303	0.000	0.320	0.000	0.000	0.000	0.000	0.000	0.100	0.000	0.128
WIIA	0.595	0.000	0.020	0.000	0.000	0.000	0.072	0.000	0.109	0.112	0.120
WHI	0.000	0.252	0.000	0.200	0.040	0.224	0.075	0.260	0.085	0.115	0.039
YAM	0.366	0.135	0.360	0.105	0.067	0.130	0.113	0.268		0.215	0.016
YUN	0.518	0.024	0.539	0.026	0.139	0.044	0.000	0.344	0.241		0.242
ZHE	0.272	0.075	0.257	0.039	0.025	0.060	0.116	0.134	0.006	0.172	

VITA

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PUBLICATIONS

Baker, A. R., T. R. Loughlin, C. W. Matson, J. C. Patton and J. W. Bickham. Submitted December 2003. Variation of mitochondrial control region sequences of Steller sea lions: the three-stock hypothesis. Journal of Mammalogy.