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SYSTEMATICS OF STELLER SEA LIONS (*EUMETOPIAS JUBATUS*): SUBSPECIES RECOGNITION BASED ON CONCORDANCE OF GENETICS AND MORPHOMETRICS

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ABSTRACT

Previous studies have revealed discontinuities in the distribution of genetic markers that led to the recognition of eastern, western, and Asian stocks of Steller sea lions (*Eumetopias jubatus*). The most profound break separates the eastern and western stocks and is based upon both nuclear and mitochondrial genetic markers. Here, a morphometric analysis of skulls was used to re-evaluate geographic variation in light of the genetics data and to possibly identify characters to distinguish between the eastern and western stocks. For males, three variables were used in stock assignment to correctly identify 88.13% and 86.59% of individuals from the eastern and western stocks, respectively. Through the same method the correct identification in stock assignment using five selected variables for female eastern and western stock individuals was 86.27% and 88.1%, respectively. Furthermore, plots from canonical discriminant analyses clearly separate individuals into stocks with very minimal overlap. Based on the observed morphological differences between these genetically differentiated stocks, we recognize two subspecies of *E. jubatus*; one includes the Asian and western stocks, and the other the eastern stock. The vernacular name Loughlin's northern sea lion is used to signalize the eastern subspecies.

Key words: genetics, morphometrics, Steller sea lions, subspecies, taxonomy

INTRODUCTION

The Steller sea lion, *Eumetopias jubatus*, ranges from central California, along the North Pacific Rim to the Sea of Okhotsk in Russia (Fig. 1; Loughlin et al. 1987). The observation that the population size of this species began to seriously decline over the latter half of the last century (Merrick et al. 1987) led to the 1990 listing of *E. jubatus* as protected under the U.S. Endangered Species Act (ESA). Efforts to diagnose the cause of the decline have produced several possible explanations, however none unequivocally has been identified as the chief mediator of the population reduction and, in reality the decline was likely the result of a combined effect of multiple influences. Irrespective of the reasons for the decline, accurate description of geographic variation is essential not only to our understanding the biology of *E. jubatus*, but also to provide a reasonable basis for management decisions. Bickham et al. (1996) were the first to provide evidence of a discrete genetic discontinuity at 144°W (based on mitochondrial DNA (mtDNA) control region sequences

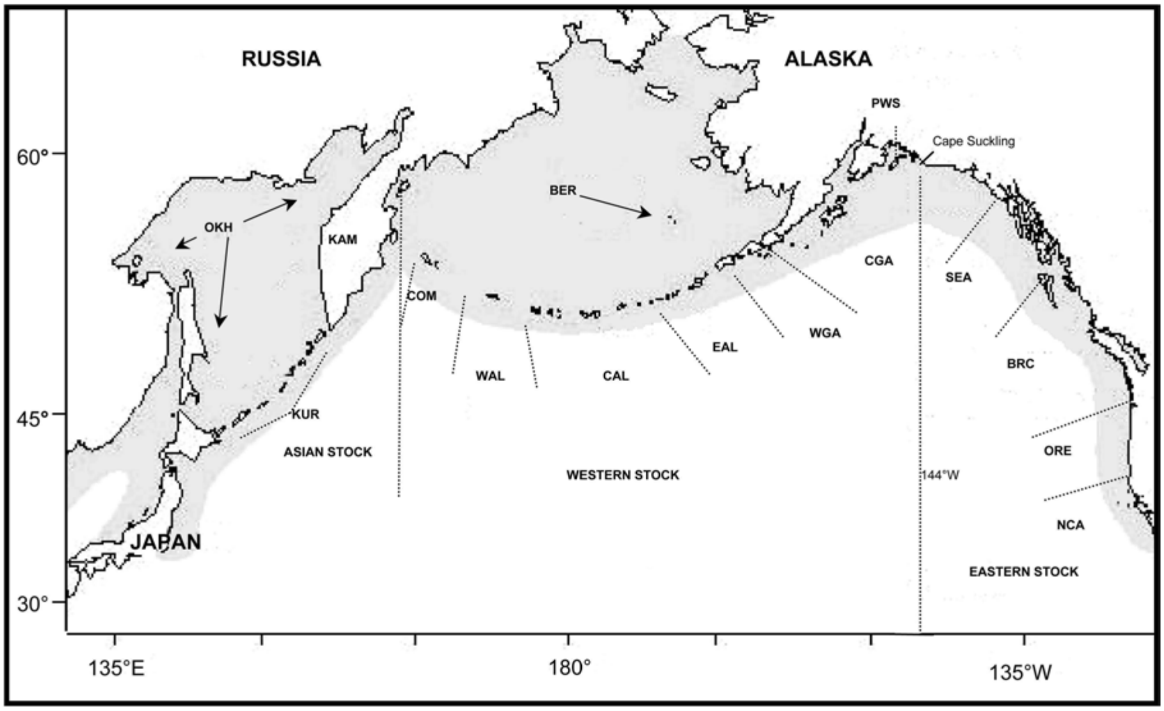

Figure 1. Map of the distribution of *E. jubatus*. Region designations are as follows: OKH = Sea of Okhotsk, KUR = Kuril Islands, KAM = Kamchatka Peninsula, COM = Commander Islands, WAL = Western Aleutian Islands, CAL = Central Aleutian Islands, EAL = Eastern Aleutian Islands, WGA = Western Gulf of Alaska, BER = Bering Sea, CGA = Central Gulf of Alaska, PWS = Prince William Sound, SEA = Southeastern Alaska, BRC = British Columbia, ORE = Oregon, NCA = Northern California.

from pups sampled at their natal rookeries) in an otherwise nearly continuous distribution. Those authors recognized eastern and western stocks to either side of this line. Subsequent studies confirmed this genetic subdivision and recognized a third population, the Asian stock, also using the maternally inherited mtDNA genome (Fig. 2; Bickham et al. 1998; Baker et al. 2005; Harlin-Cognato et al. 2005). Loughlin (1997) further legitimized the separation of eastern and western stocks through phylogeographic methods. A recent study also validated the genetic subdivision between the eastern and western stocks utilizing bi-parentally-inherited nuclear microsatellite markers but the Asian stock was not well resolved (Hoffman et al. 2006). Based upon a branding study carried out over 24 years, there is little indication of exchange between the eastern and western stocks (Raum-Suryan and Pitcher 2002). In contrast, Brunner (2002) investigated the geographic structuring across the distribution of *E. jubatus* using cranial morphometrics. She found patterns of geographical partitioning of morphological differences, however apparently not concordant with previously identified genetic clines. Rather, she reported specimens from California to be morphometrically distinct from Alaskan eastern and western stock samples. Unfortunately, adequate specimens do not exist in collections to perform a meaningful study of geographic variation and she only sampled two individuals from southeastern Alaska. It is clear from the genetics data that Californian Steller sea lions are not distinct from other eastern stock populations including southeastern Alaska.

Currently, the eastern and western stocks are being managed independently largely due to the observed significant differences in population trends separating them. For example, the western stock numbers were previously observed to decline at a rate of about 5% per year (Sease and Gugmundson 2002), but now show potential signs of stabilization and growth (Fritz and Stinchcomb 2005). In contrast, eastern stock numbers have been documented as being close to their highest recorded size (Calkins et al. 1997). Recognizing the

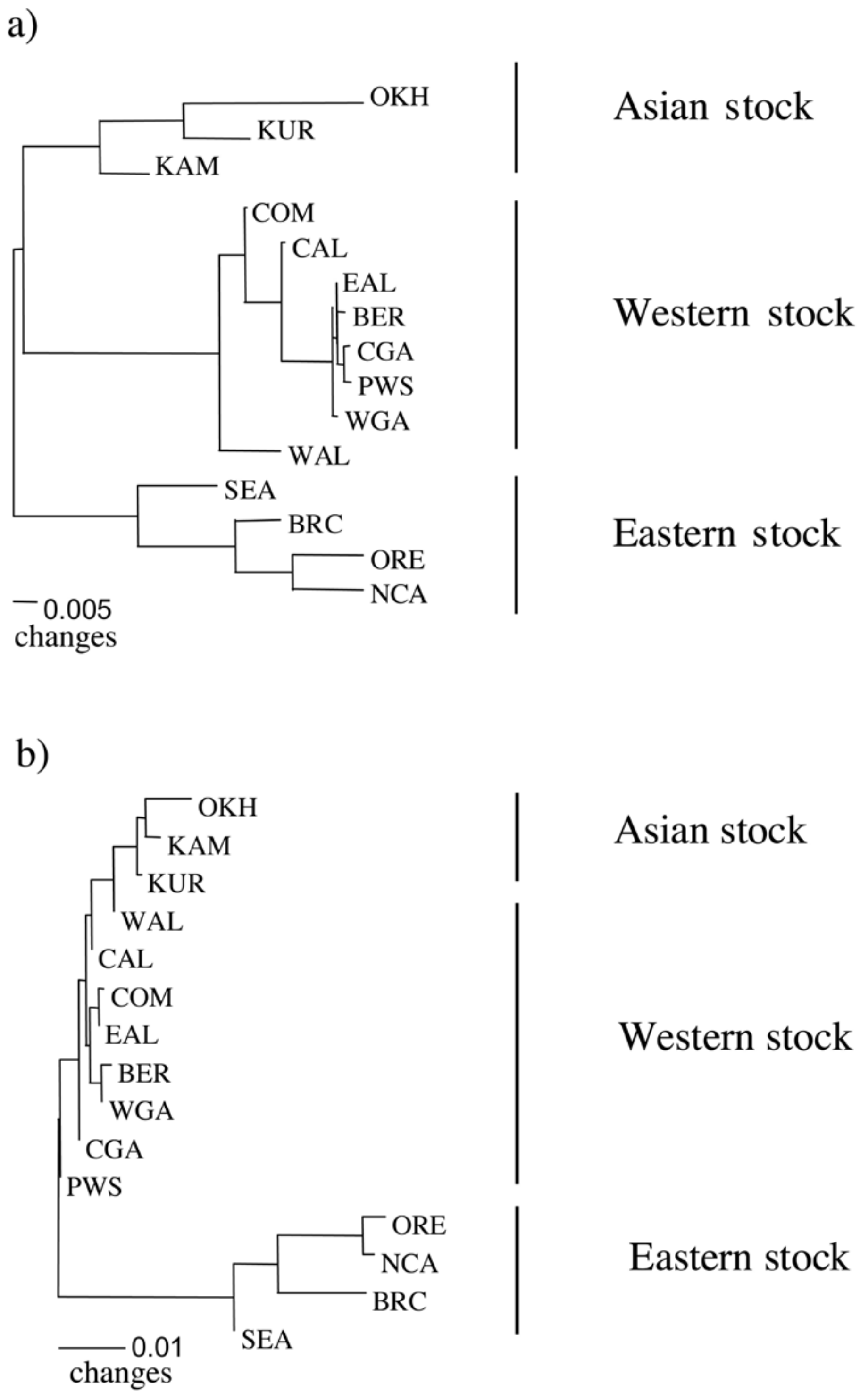

Figure 2. Neighbour-joining trees constructed from Slatkin's linearized Fst for a) the mitochondrial control region (Baker et al. 2005; *n* = 1,568) and b) 13 microsatellite loci (Hoffman et al. 2006; *n* = 668). Region designations are as described in Figure 1.

observed dissimilarities in population trends and the genetic differentiation of these two populations (Bickham et al. 1996; Loughlin 1997), the western stock is now considered endangered while the eastern stock is listed as threatened under the ESA (Loughlin 1998; Calkins et al. 1999).

Because numerous genetic studies and contrasting patterns of population growth have demonstrated the validity of the population subdivision of *E. jubatus*, the purpose of the current study was to further investigate if the eastern and western stocks differ in skull morphology, and if so, to reassess the taxonomy of the species to reflect this major feature of geographic variation. Gray (1859) described *Arctocephalus monteriensis* based on a skull of a Steller sea lion and a skin of a fur seal and this name could apply to any recognized taxon related to the Steller sea lion. Typically the skull is considered to be most diagnostic in mammalian systematics and it should represent the type specimen for the taxon. While there has traditionally been debate over the application of subspecies designations, it should be apparent that this rank contains substantial information regarding geographic variation. Its use is particularly pertinent when it describes the major patterns of geographic variability found within a species and when there is concordance of genetic and morphological patterns (Avise and Ball 1990).

Materials and Methods

Skulls of 61 male and 66 female *E. jubatus* were examined from various collections (Appendix). Forty skull measurements (Fig. 3, Table 1) were taken using Mitutoyo digital calipers. The measurements are almost identical to those used by Brunner (2002). Differences between our measurements and Brunner's (2002) pertain to a discrepency in the observed dental formula of *E. jubatus*. Apparently, the measurement description listing and skull illustration is that of the California sea lion, *Zalophus californicus*, and this is the basis of our decision to include a new listing and illustration of measurements in this manuscript rather than referencing the reader to Brunner (2002). Additionally, data collected by Brunner (2002) was not compiled with data gathered in this study because of spurious patterns that would likely arise due to comparing measurements taken by different individuals.

Data pertaining to sex and locality was also recorded for each individual. Only individuals that

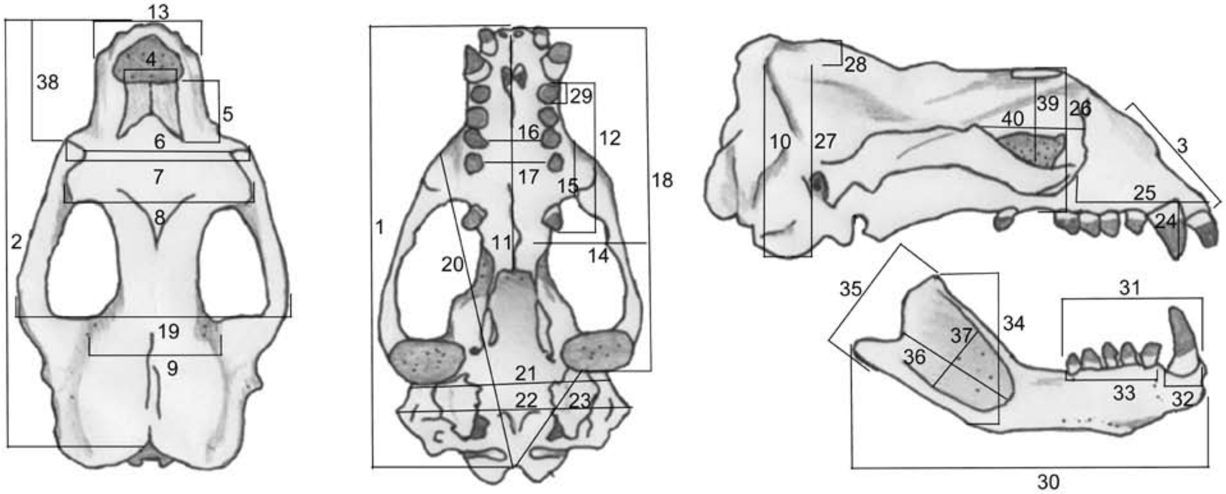

Figure 3. Sketch illustrating 40 measurements taken for each skull at dorsal, ventral, and lateral perspectives. See Table 1 for descriptions of characters.

Table 1. Description of cranial measurements (modified from Brunner 2002).

Variable #	Variable description
1	Condylobasal length, from gnathion to posterior of basin
2	Gnathion-middle of occipital crest
3	Gnathion-posterior margin of nasals
4	Width of anterior nares, from interior of nares at widest point
5	Greatest length of nasals, from anterior margin of nasal to posterior margin
6	Breadth of preorbital processes
7	Interorbital constriction
8	Breadth at supraorbital processes, measured at widest point
9	Breadth of braincase, measured dorsally at coronal suture
10	Occipital crest-mastoid, from mid-occipital crest to ventral margin of mastoid
11	Palatal notch-incisors, from anterior point of palatal notch to posterior edge of central incisor alveoli; where a palatal cleft was present, measurement was taken from palatal notch at margin of, but excluding, cleft
12	Distance behind border of canines, from posterior margin of canine alveolus to posterior margin of postcanine 5 alveolis
13	Rostral width, at widest margin of rostrum
14	Gnathion-posterior end of maxilla (palatal)
15	Breadth of zygomatic root of maxilla, maximal breadth anteroposterior from ventral perspective
16	Breadth of palate between postcanine 3, at medial edge of alveoli
17	Breadth of palate between postcanine 4, at medial edge of alveoli
18	Gnathion-caudal border of postglenoid process
19	Zygomatic breadth, at widest point of zygomatic arch, from posterior of squamosals
20	Basion-zygomatic root of maxilla, ventral perspective, from anterior of basion to anterior of zygomatic roots
21	Auditory breadth, greatest distance at auditory bullae
22	Mastoid breadth
23	Basion-bend of pterygoid, from anterior of basion to anterior of pterygoid
24	Height of canine above alveolus, a straight line from the anterior margin of alveolus to the tip of the canine
25	Gnathion-maxillary squamosal suture, from gnathion to ventral margin of suture
26	Height of skull at supraorbital process, from the base of skull at the middle of diastima to the top of the skull at supraorbital
27	Height of skull at bottom of mastoid, dorsoventrally from skull at base at sagital crest to ventral margin of mastoid
28	Height of sagital crest, at greatest height
29	Mesiodistal diameter of alveolus of postcanine 2
30	Length of mandible, from posterior margin of condyle to anterior margin of dentary
31	Length of mandibular teeth row (inclusive of canines), from anterior margin of canine alveolus to posterior margin of postcanine 6 alveolus
32	Mesiodistal diameter of canines, across base of canine at alveolus
33	Length of lower postconine row, from anterior margin of postcanine 1 alveolus to posterior margin of postcanine 6 alveolus
34	Height of mandible at meatus, from dorsal margin of angularis at meatus to dorsal margin of coronoid process
35	Angularis-coronoideus, from ventral margin of angularis to dorsal margin of coronoid process
36	Length of masseteric fossa, from anterior margin of fossa to posterior margin of coronoid process
37	Breadth of masseteric fossa, dorsoventrally through centre of fossa
38	Gnathion-hind border of preorbital process, from gnathion to posterior margin of preorbital process
39	Length of orbit-from ventral margin of supraorbital process to dorsal margin of the vase of orbit
40	Breadth of orbit-mesiodistal from inside margin of orbit

could be identified unequivocally as adults, based primarily on suture indexing following the methods of Sivertsen (1954), and when possible from age data obtained from tooth annulations, were measured to remove potential error associated with allometric growth and size variation of non-adult *E. jubatus*. Data on the exact geographic origin of skulls was not available; therefore specimens were assigned to the eastern or western stocks based on their collection locality rather than by affiliation with a specific rookery. For purposes of analysis, 144°W was used to define the geographic division between eastern and western stocks.

All analyses were performed using SAS 9.1 software (SAS Institute Inc.). Due to the fragmented nature of a portion of the skulls available for examination, 6.05% of the measurements were not taken for some individuals. A multiple imputation procedure was performed to predict the missing values (Rubin 1976; Schafer and Graham 2002). Measurements were standardized prior to analysis. Two-tailed t-tests were implemented to detect a statistically significant difference between males and females and were the basis for their separation in subsequent analyses. Two-tailed t-tests were also used to identify sex-specific variables significantly associated with stock assignment. Because the variance of the means of variables between stocks were found to be unequal for males, the Satterthwaite method (Satterthwaite 1946) of conducting t-tests was employed for these samples. This method provides a t statistic that asymptotically approaches a t distribution, thus allowing for a t-test to be calculated when variances are unequal. Pearson correlation matrices were generated to examine correlations of variables and variables with stock. Alpha values for t-tests calculated within each sex and for correlations were set at 0.1. This value was selected over the traditionally used 0.05 to avoid the exclusion of biologically significant findings due to overly strenuous statistical rigor. Because of the binary nature of the class variable (stock), a logistic regression with stepwise model selection was used to determine the optimal combinations of variables that predict correct stock assignment for each sex. Assessing the predictive power of the selected variables was done by randomly drawing two-thirds of the population to build a logistic regression model that was then applied to the remaining one-third of the population for which the failure rate of stock assignment by the model was retained. This process was iterated 1,000 times and the average failure rate was used as a means of assessing the predictive power of the selected variables. Finally, canonical discriminant analysis (CDA) was implemented as a multivariate variable reduction method to produce linear combinations of quantitative variables that summarize between-stock variation. The resulting orthogonal variables were plotted against each other to visualize patterns of stock differentiation.

RESULTS

For males, ten variables yielded significant values in t-tests and showed significant correlation (P = 0.1) with stock (Table 2). Of these variables, three (15, 16, 22; Fig. 1, Table 1) were chosen through the stepwise selection procedure of the logistic regression as the best combination for correctly assigning males to eastern or western stocks. Through 1,000 iterations of model building and testing, these variables correctly assigned male skulls to their stock of origin 88.13% and 86.59% for the eastern and western stocks, respectively.

Analyses conducted for female sea lions showed that six variables were significant in t-tests and showed significant correlations with stock (Table 3). Of these six variables, five (4, 11, 14, 15, 29, 40; Fig. 1, Table 1) were also selected in the stepwise selection procedure of the logistic regression to be the optimal combination of discriminating variables. Through 1,000 iterations of model building and testing, these variables correctly assigned female skulls to their stock of origin 86.27% and 88.1% for the eastern and western stocks, respectively.

For both sexes, plots of the first two canonical variables from the CDA produced two major clusters of data points with minor overlap representative of the eastern and western stocks (Fig. 4)

Table 2. Summary statistics for male E. jubatus *grouped by stock including means, standard deviations, parameter estimates for the t-test, Pearson correlation coefficient, and corresponding parameter estimate. Variables listed were significant for t-tests and those demarked with an asterisk (*) were selected through the stepwise procedure of the logistic regression.*

Variable	Eastern stock	Western stock	P	Correlation with stock	P
13	95.04 ± 6.27	88.81 ± 10.31	0.009	0.355	0.005
14	184.33 ± 8.45	179.5 ± 12.74	0.097	0.225	0.080
15*	50.925 ± 3.12	46.494 ± 4.65	0.000	0.501	0.000
16*	57.68 ± 4.75	52.46 ± 7.31	0.003	0.402	0.001
17	61.54 ± 5.13	56.40 ± 7.39	0.004	0.385	0.002
20	261.03 ± 12.26	252.05 ± 18.84	0.038	0.281	0.029
22*	205.30 ± 14.18	196.18 ± 24.88	0.090	0.229	0.076
26	101.06 ± 5.10	95.69 ± 9.28	0.010	0.351	0.006
28	24.939 ± 6.91	17.59 ± 8.84	0.001	0.429	0.000
40	74.84 ± 3.18	72.80 ± 4.52	0.053	0.230	0.043

Table 3. Summary statistics for female E. jubatus *grouped by stock including means, standard deviations, parameter estimates for the t-test, Pearson correlation coefficients, and corresponding parameter estimates. Variables listed were significant for t-tests and those demarked with an asterisk (*) were selected through the stepwise procedure of the logistic regression.*

Variable	Eastern stock	Western stock	P	Correlation with stock	P
4*	32.44 ± 2.54	31.37 ± 2.01	0.07	0.23	0.07
11*	141.20 ± 6.38	144.54 ± 6.44	0.05	-0.24	0.05
14	145.57 ± 6.9	149.78 ± 8.08	0.04	-0.25	0.04
15*	37.77 ± 4.64	36.21 ± 2.28	0.03	0.27	0.03
29*	12.73 ± 0.97	13.39 ± 1.04	0.02	-0.30	0.02
40*	65.77 ± 2.87	64.42 ± 2.60	0.06	0.23	0.06

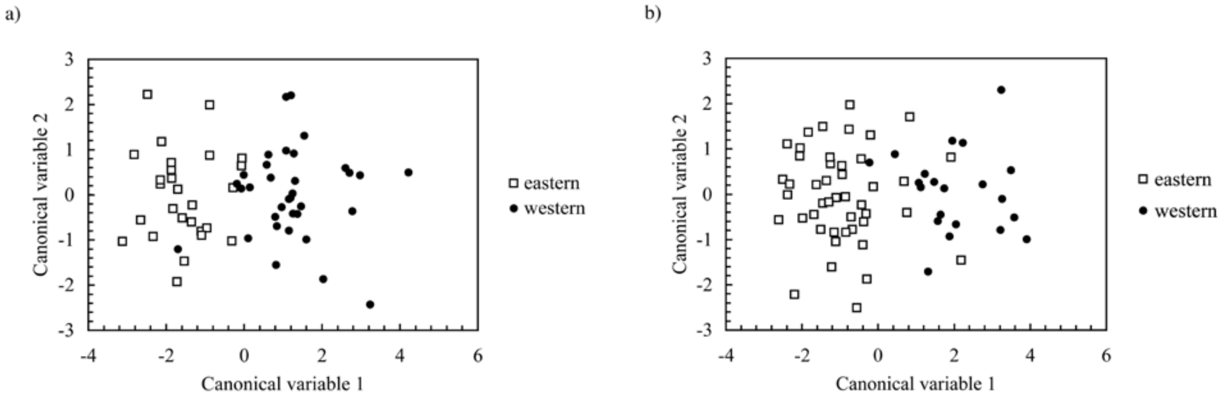

Figure 4. Plots of canonical vaiables 1 and 2 from the canonical discriminant analysis for a) males and b) females.

DISCUSSION

Results of the statistical analysis for both males and females show a notable difference in skull morphology of the eastern and western stocks of *E. jubatus*. Selected combinations of variables for males and females proved to correctly assign individuals to their respective putative stocks more than 85% of the time.

The observation that all 10 statistically significant variables for males were on average larger for eastern specimens suggests that a major distinguishing morphological characteristic separating the eastern and western stocks of male *E. jubatus* is overall size of skull, with the eastern stock being larger. In addition, it was observed that each of the statistically significant variables for males showed higher levels of within-stock variation in the western stock relative to the eastern stock (Table 2). These findings indicate that while male western stock *E. jubatus* on average have smaller skulls than eastern stock individuals, there is an elevated level of skull size variation in the western stock relative to the eastern.

Summary statistics for the females indicate differences between stocks to have a shape basis, rather than one of size, as four significant variables show greater mean values in the western stock and two significant variables have greater mean values in the eastern stock.

In the previous study of skull morphology of *E. jubatus*, Brunner (2002) observed clustering patterns for males that grouped Alaskan eastern stock and western stock specimens together separate from Californian (eastern stock) specimens and was interpreted as being discordant with previous genetic findings; however this conclusion was based on a sample size of two from eastern Alaska. Clearly this is insufficient to refute the highly corroborated genetics findings (including both maternally inherited mtDNA and biparentally inherited nuclear microsatellites) which are also consistent with the unique population trends of the two stocks. Brunner's (2002) study also included specimens from the Asian stock and found them to be morphologically distinct, showing the largest amount of differentiation between the western stock and the Asian stock. In the current study we do not address the relationship of the Asian stock to the western and eastern stocks as the degree of genetic differentiation between them is not as strong as between the eastern and western stocks.

Subspecies are the least inclusive category recognized with formal taxonomic rank and consist of geographically defined populations within a species that differ taxonomically from other populations within the same species (O'Brien and Mayr 1991). Avise and Ball (1990) suggested subspecies be recognized using multiple, independent, genetically based traits. We follow the Turtle Taxonomy Working Group (2007) who propose that "subspecies classification, if used, should describe the major patterns of variation found within a species." O'Brien and Mayr (1991) also provide some guidance when diagnosing subspecies by stating that subspecies should share a "unique geographic range or habitat, a group of phylogenetically concordant characters, and a unique natural history relative to other subdivisions of the species." Multiple studies (Bickham et al. 1996; Bickham et al. 1998; Baker et al. 2005; Hoffman et al. 2006) as well as the current study have established the first and second criteria, and the third criterion is apparent due to the different population trajectories of the eastern and western stocks.

From an evolutionary perspective, Harlin-Cognato et al. (2006) discovered through nested-clade analysis that the most ancient subdivision within *E. jubatus* is that separating the eastern and western stocks and that this separation was repeated through multiple glacial cycles. Furthermore, those authors showed that the break between the eastern and western stocks is geographically concordant with phylogeographic breaks of several other species of marine mammals. While the evolutionary fate of any subspecies is unknown (subdivision, extinction, intergradation, or speciation), the utilization of subspecific taxonomic designations provides information about geographic variation in and of itself (Zusi 1982). Although some taxonomists believe the subspecies category should be discarded, we feel that because of the importance of Steller sea lions as an indicator of the environmental health of the North Pacific Ocean, the endangered status of the western stock of Steller sea lions, and the historical importance of subspecies in systematic mammalogy, it is appropriate to elevate these populations to subspecies rank.

The western and Asian stocks will receive the taxonomic designation of *Eumetopias jubatus jubatus* because the type locality for the species is the Commander Islands. The potential that the Asian stock is a unique subspecies itself should be investigated by additional research, but currently will be classified with the western stock based on the their relationship interpreted through genetic data. The name *Arctocephalus monteriensis* (Gray 1859) is available with the type locality being Monterey, California, USA. Clearly, the samples used in this study and by Brunner (2002) correspond to the taxon described by Gray. The appropriate trinomen for the eastern stock becomes *Eumetopias jubatus monteriensis*. We propose the vernacular name "Loughlin's northern sea lion" to honor Dr. Thomas R. Loughlin in recognition of his many years of research on all aspects of the biology of Steller sea lions. We interpret the distribution of *E. j. monteriensis* to correspond to that of the eastern stock because of the strong genetic signal and thus all rookeries east of 144°W are included in this taxon.

The following synonymy modified from Loughlin et al. (1987) details the taxonomic changes proposed in this paper:

Eumetopias jubatus (Schreber 1776)
Steller sea lion or northern sea lion

Synonyms:

Leo marinus Steller 1751:360. No type specimen; based on description from Commander Islands; unavailable name (pre Linnaean).

Phoca jubata Schreber 1776:300, pl. 83b. Type locality "northern part of the Pacific Ocean," Russian Commander Islands, Bering Island. Description based on Steller's notes (Scheffer 1958).

Otaria stellerii Lesson 1828:420. A renaming of *Phoca jubata* Schreber.

Arctocephalus monteriensis Gray 1859:358, 360, pl. 72. Type locality, Monterey, California. (Based on a skull of *Eumetopias* and skin of *Callorhinus*; we establish the *Eumetopias* skull to be the type specimen.)

Eumetopias jubatus jubatus (Schreber); western Steller sea lion, distributed from 144°W west to Sea of Okhotsk. (NMML 316 skull is here designated to be the type specimen.)

Eumetopias jubatus monteriensis (Gray) new combination; Loughlin's northern sea lion, distributed from central California to southeastern Alaska.

While the long-term survival of the Steller sea lion is uncertain, there is indication that the species has maintained a relatively high level of genetic diversity in spite of the recent decline in population numbers (Bickham et al. 1998). In light of this, the management of *E. j. jubatus* and *E. j. monteriensis* as distinct taxa will help to promote the species' continued existence and the stability of the Northern Pacific ecosystem.

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APPENDIX

General information for specimens of *E. jubatus* used in the analysis. Acronym prefixes included in specimen accession numbers refer to the museum from which they were obtained. CAS = California Acadamy of Sciences; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; NMML = National Marine Mammal Laboratory, Washington; RB = Ray Bandar's home collections.

Specimen accession no.	Sex	Date collected	Collection locality
CAS1120	f	28 June 1915	San Mateo Co., CA
CAS13818	f	24 February 1966	San Mateo Co., CA
CAS13819	f	31 July 1966	Pacifica Co., CA
CAS21393	f	17 August 1973	Pacifica Co., CA
CAS21394	f	7 August 1973	Sonoma Co., CA
CAS21395	f	22 June 1975	Marin Co., CA
CAS21397	f	16 September 1972	Marin Co., CA
CAS21398	f	2 August 1973	Marin Co., CA
CAS21755	f	26 May 1977	Marin Co., CA
CAS23005	f	29 December 1987	Marmot Island, AK
CAS23013	f	3 August 1988	Mendocino Co., CA
CAS23167	f	27 September 1989	San Francisco Co., CA
CAS23964	f	8 July 1996	San Mateo Co., CA
MVZ118620	f	23 July 1956	Monterey Co., CA
MVZ172086	f	26 February 1982	Sonoma Co., CA
MVZ186326	f	16 September 1999	San Mateo Co., CA
MVZ191004	f	4 March 1902	Marin Co., CA
MVZ4114	f	29 September 1908	Monterey Co., CA
MVZ4770	f	1 April 1906	Seward, AK
MVZ4967	f	1 April 1906	Seward, AK
MVZ88876	f	15 August 1939	Clatsof Co., OR
NMML1296	f	2 February 1977	Port Fidalgo, AK
NMML1297	f	28 April 1977	Kodiak Island, AK
NMML1300	f	8 October 1982	Akutan Island, AK
NMML1313	f	21 March 1984	Shelikof Strait,AK
NMML1523	f	28 April 1977	Cape Ugak, AK
NMML1535	f	11 October 1976	Sea Otter Island, AK
NMML1536	f	12 October 1976	Marmot Island, AK
NMML1542	f	14 October 1976	Marmot Island, AK
NMML1545	f	11 February 1977	Goose Island, AK
NMML1546	f	12 February 1977	Port Fidalgo, AK
NMML1549	f	12 February 1977	Port Fidalgo, AK
NMML1550	f	16 February 1977	Pleiades Islands, AK
NMML1554	f	22 March 1977	Outer Island, AK

APPENDIX (CONT.)

Specimen accession no.	Sex	Date collected	Collection locality
NMML1561	f	23 May 1977	Latex Rocks, AK
NMML1562	f	26 May 1977	Marmot Island, AK
NMML1563	f	26 May 1977	Marmot Island, AK
NMML1565	f	13 November 1977	Glacier Island, AK
NMML1566	f	14 November 1977	Chernabura Island, AK
NMML1572	f	21 March 1977	Cape St. Elias, AK
NMML1573	f	25 March 1977	Cape St. Elias, AK
NMML1574	f	19 April 1978	Wide Bay, AK
NMML1576	f	27 June 1978	Wide Bay, AK
NMML1630	f	21 October 1985	Marmot Island, AK
NMML1631	f	25 October 1985	Izhut Bay, AK
NMML1633	f	27 October 1985	Sea Otter Island, AK
NMML322	f	14 July 1958	Chernabura Island, AK
NMML323	f	20 June 1958	Chernabura Island, AK
NMML324	f	20 June 1958	Chernabura Island, AK
NMML331	f	11 July 1958	Chernabura Island, AK
NMML332	f	9 July 1958	Chernabura Island, AK
NMML333	f	11 July 1958	Chernabura Island, AK
NMML339	f	1 June 1958	Chernabura Island, AK
NMML343	f	27 June 1958	Chernabura Island, AK
NMML344	f	18 July 1958	Chernabura Island, AK
NMML347	f	22 July 1958	Chernabura Island, AK
NMML353	f	1 July 1958	Chernabura Island, AK
NMML355	f	27 July 1958	Chernabura Island, AK
NMML356	f	24 July 1958	Chernabura Island, AK
NMML357	f	19 July 1958	Chernabura Island, AK
NMML362	f	20 June 1958	Chernabura Island, AK
NMML363	f	9 July 1958	Chernabura Island, AK
NMML367	f	3 March 1958	Pigeon Point, AK
NMML372	f	5 June 1960	Little Kondiaji Island, AK
NNML1538	f	12 October 1976	Ecola State Park, OR
CAS1118	m	26 June 1915	San Mateo Co., CA
CAS21399	m	6 September 1973	San Mateo Co., CA
CAS23213	m	3 August 1988	Marin Co., CA
CAS23735	m	17 July 1992	Marin Co., CA
CAS23862	m	16 September 1994	Mendocino Co., CA
CAS24451	m	3 July 1999	San Mateo Co., CA
CAS3683	m	4 April 1909	St Paul Island, AK

APPENDIX (CONT.)

Specimen accession no.	Sex	Date collected	Collection locality
CAS3684	m	4 April 1909	St. Paul Island, AK
CAS6	m	30 June 1919	San Mateo Co., CA
CAS7659	m	19 July 1933	San Mateo Co., CA
CAS8	m	4 April 1909	Santa Cruz Co., CA
MVZ101430	m	5 September 1948	San Mateo Co., CA
MVZ119669	m	25 April 1959	Marin Co., CA
MVZ138679	m	9 June 1972	Monterey, Co., CA
MVZ138680	m	25 July 1925	San Mateo Co., CA
MVZ186325	m	26 August 1996	San Mateo Co., CA
MVZ4112	m	2 July 1907	San Mateo Co., CA
MVZ4117	m	2 July 1907	Monterey Co., CA
MVZ8821	m	30 June 1907	Santa Cruz Co., CA
MVZ91069	m	19 June 1940	Alameda Co., CA
NMML1321	m	28 March 1984	Shelikof Strait,AK
NMML1553	m	22 March 1977	Outer Island, AK
NMML1559	m	23 May 1977	Sugarloaf Island, AK
NMML1614	m	14 March 1982	Marmot Island, AK
NMML1640	m	26 April 1989	Camando Island, AK
NMML1641	m	17 December 1991	Shi Shi Beach, AK
NMML1660	m	5 August 1993	Seaview Beach, AK
NMML316	m	22 June 1950	St Paul Island, AK
NMML325	m	7 July 1958	Cherndabura Island, AK
NMML326	m	1 July 1958	Cherndabura Island, AK
NMML327	m	1 June 1958	Cherndabura Island, AK
NMML329	m	27 June 1958	Cherndabura Island, AK
NMML335	m	19 July 1958	Cherndabura Island, AK
NMML336	m	8 July 1958	Cherndabura Island, AK
NMML338	m	28 June 1958	Cherndabura Island, AK
NMML33O	m	13 June 1958	Clubbing Rocks, AK
NMML341	m	1 July 1958	Cherndabura Island, AK
NMML342	m	7 July 1958	Cherndabura Island, AK
NMML346	m	1 July 1958	Cherndabura Island, AK
NMML351	m	22 July 1958	Cherndabura Island, AK
NMML352	m	3 July 1958	Clubbing Rocks, AK
NMML354	m	5 July 1958	Cherndabura Island, AK
NMML359	m	24 July 1958	Clubbing Rocks, AK
NMML360	m	1 July 1958	Cherndabura Island, AK
NMML361	m	19 July 1958	Cherndabura Island, AK

APPENDIX (CONT.)

Specimen accession no.	Sex	Date collected	Collection locality
NNML1298	m	13 November 1977	Glacier Island, AK
NNML350	m	2 July 1958	Cherndabura Island, AK
RB1029	m	1 July 1967	Cape Blanco Lighthouse, OR
RB2386	m	1 June 1976	San Mateo Co., CA
RB26609	m	18 July 1964	Marin Co., CA
RB2721	m	1 June 1979	Humboldt Co.,CA
RB2853	m	1 July 1980	Del Norte Co., CA
RB2854	m	1 July 1980	Humboldt Co., CA
RB3337	m	1 July 1986	Marin Co., CA
RB3451	m	1 July 1988	San Mateo Co., CA
RB3630	m	1 June 1991	San Mateo Co., CA
RB3805	m	1 October 1983	Marin Co., CA.
RB5152	m	1 July 1903	Marin Co., CA
RB5651	m	1 July 1905	Sonoma Co., CA
RB5654	m	1 June 1905	Marin Co., CA
RB5739	m	1 July 1906	Sonoma Co., CA

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