

GEOGRAPHIC VARIATION IN SKULL MORPHOLOGY OF ADULT STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

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ABSTRACT

Data from cranial specimens of adult *E. jubatus* were analyzed to compare intraspecific morphology of skulls. Males and females were grouped separately to avoid bias from sexual dimorphism. Geographic variation was observed in adult male *E. jubatus*, indicating the potential presence of three morphologically disparate groups: those from Alaska, those from California, and those from Japan and Russia. Although sample sizes were small, results from cluster and discriminant function analyses indicated that specimens from eastern and western Alaska were morphologically similar, and that the most divergent specimens for the species appeared to be those from Japan. Skulls from Alaska possessed a typically longer, less robust skull, whereas those from Japan appeared smaller, yet most robust. Skulls from California were intermediate.

Key words: skull, *Eumetopias jubatus*, Steller sea lion, geographic variation, cranial morphometrics.

The Steller sea lion, *Eumetopias jubatus*, is widely distributed on both sides of the Pacific Ocean, ranging from Hokkaido, along the coast of eastern Russia, the Aleutian Islands, the Gulf of Alaska, to the southern waters of California. The numbers of *E. jubatus* in the western portion of their range in Alaska have declined by approximately 80%–90% over the past three decades (Calkins *et al.* 1998, Trites and Larkin 1996). The decline originated in the eastern Aleutian Islands, spreading throughout the Aleutians, the Bering Sea, and the Gulf of Alaska. *Eumetopias jubatus* from the western portion of its range in Alaska was subsequently reclassified from Threatened to Endangered under the U.S. Endangered Species Act (Calkins *et al.* 1998). Bickham *et al.* (1996, 1998) confirmed a high level of haplotypic diversity in mtDNA in the western and central Gulf of Alaska that has been maintained, with little evidence of

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loss of diversity over the previous two decades. Nevertheless, populations of *E. jubatus* in the Gulf of Alaska have declined considerably, more so than other populations for the species. Decreased availability or reduced abundance of major prey species, such as juvenile walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*), appear to contribute to these declines (Merrick *et al.* 1987, Hobson *et al.* 1997). Juvenile *T. chalcogramma* are an important food resource for *E. jubatus* even though the sea lions consume greater amounts of "large-sized" *T. chalcogramma* than they do juveniles of this fish species (Hobson *et al.* 1997). If historical population trends continue for the next 30 yr, rookeries may begin to disappear in the western part of their range in the United States, and extinction probabilities will increase rapidly (York *et al.* 1996).

To date, no taxonomic studies based on cranial morphometrics at the level of species have been published for *E. jubatus*. Taxonomy is centrally important to our knowledge and appreciation of biological diversity, and should include morphometric, molecular, and ecological approaches. Controversy surrounding the assertion that the sperm whale, an odontocete, is more closely related to mysticete whales than to other odontocetes (Milinkovitch *et al.* 1993) has underlined the importance of anatomical observation and morphometric analysis to systematics. Rice (1998, p. 4) stated that the initial faith in the near-infallibility of molecular studies ". . . has now been tempered by a more sober appraisal of their strengths and weaknesses." Unlike morphological data, those from nuclear sequences generate only gene-phylogenies, not species-phylogenies: "In any given clade, gene-phylogenies are not necessarily congruent with the species-phylogeny or with each other, so that cladograms derived from different kinds of molecular data are frequently contradictory" Rice (1998, p. 4).

To gain a comprehensive understanding of the biological diversity of *E. jubatus*, it is necessary to observe interpopulation differences within the species. Rice (1998) stated that the number of specimens of marine mammals in collections is far too few to provide even a vague picture of their geographic variation; nevertheless, studies on geographic variation of otariids have been undertaken. These include genetic investigations for populations of *Zalophus californianus* (Maldonado *et al.* 1995) and *E. jubatus* (Bickham *et al.* 1996, 1998), blood transferrin types in *Arctocephalus pusillus pusillus* and *A. p. doriferus* (Shaughnessy 1982), cranial morphology of *Arctocephalus forsteri* and *A. pusillus* (Brunner 1998*b*), mean adult skull size (Kerley *et al.* 2000), and body size (Bester and Van Jaarsveld 1994) in populations of *Arctocephalus tropicalis*, and a recent taxonomic review of the Otariidae (Brunner 2000). This paper investigates cranial variables measured from skulls of *E. jubatus* as a preliminary study to describe intraspecific variation of skull morphology for the species.

METHODS

Data Collection and Preparation

Skull characteristics were measured on 104 specimens of adult male and female *E. jubatus*, held at various natural history museums and institutions.

Specimens were also photographed as a reference, showing dorsal, ventral, and lateral perspectives. Summary details of each specimen are listed in the Appendix.

Only skulls from adult *E. jubatus* were used for this study to avoid age-related bias. Specimens were grouped into categories of collection locality and sex. Sexual dimorphism was tested using univariate statistics, Student's *t*-test, and two-group discriminant function analysis, and was found to be significant; thus sexes were analyzed separately (Brunner 2000). To identify adult specimens, relative age was estimated by applying a suture ageing index (Doutt 1942, Sivertsen 1954); adult specimens were those with a suture index (SI) of 24 and 19 for males and females, respectively (Brunner 2000). Geographic groups consisted primarily of those described by Bickham *et al.* (1996): representatives from California, eastern and western Alaska, Russia, and Japan.

Forty-one measurements were recorded for each skull, using Mitotoyo digital calipers, and were mostly those from Sivertsen (1954) and Brunner (1998*b*, 2000) (Table 1, Fig. 1).

Analyses

All statistics were computed using SYSTAT 8.0. Principal Components Analyses (PCA) were applied to investigate morphological variation within *E. jubatus* by extracting independent facets of variation from a matrix measuring dispersion. Components were ordered in terms of magnitude of their variances (*i*th principal component having the *i*th largest variance). The values for the original variables were standardized initially to z-scores, so that each variable had equal weighting. This procedure removes bias of larger measurements dominating the smaller. Both PCA and cluster analyses using an unweighted pair-group method with arithmetic averages (UPGMA), were applied to identify relationships between specimens.

Multigroup discriminant function analyses (DFA) were computed to examine relationships between groups identified by PCA and UPGMA cluster analyses. Methods comprised MANOVA followed by multigroup DFA. MANOVA was used to test for statistically significant differences between group centroids, whereas multigroup DFA was applied as a tool for observing relationships between groups but not for classification purposes. When more than two groups are involved, the canonical functions have different properties to those of two-group analyses, becoming so different that "... their application to classification is unsatisfactory ..." (Pimentel 1979). The model for multigroup DFA is

$$y_{ij} = X_{jk}{}'_l \bar{X}_i - 1/2 \bar{X}_{i'li} + P_i \quad (1)$$

where *i* = 1, 2, ..., *g* groups of classification; *j* = 1, 2, ..., *g* groups of actual membership; *k* = 1, 2, ..., *N_g* individuals; *X* is an individual's data vector; *l* is a group discrimination vector; \bar{X} is a group centroid; *P* is the probability of group membership; *y* is a discrimination score for an individual; $X_{jk}{}'_l \bar{X}_i$ is equivalent to the discrimination function; and $1/2 \bar{X}_{i'li}$ is the dis-

criminant function constant (or constant) (Pimentel 1979). Specimens that possessed only the full suite of measurements were used in multivariate analyses to avoid bias in the results.

RESULTS

Low-level geographic variation was observed in skulls of adult male *E. jubatus* from Alaska (eastern and western stocks, $n = 13$), California ($n = 6$), Japan ($n = 31$), and Russia ($n = 2$). Results from the UPGMA cluster analyses showed a close relationship between eastern and western Alaskan specimens, whereas those from Japan were the farthest removed. Specimens from California were morphologically closer to Alaskan specimens than they were to those from Russia or Japan (Fig. 2).

Principal components analysis for adult male *E. jubatus* was based on standardized data for 11 variables. Component 1 was influenced by size, with most variables relating to length of skull; these included CBL (*variable number 1*), gnathion–middle of occipital crest (2), basion–zygomatic root of maxilla (anterior) (21), palatal notch–incisors (11) and gnathion–caudal border of post-glenoid process (19). The first Component accounted for 66.3% of the total variance, whereas the second accounted for a further 10.6% and was described by shape. Component 2 was affected primarily by variables related to breadth of skull (mastoid breadth (23), zygomatic breadth (20) and occipital crest–mastoid (10)), that possessed negative coefficients. The third Component explained another 8.1% of the total variance in which gnathion–posterior margin of nasals (3) and basion–zygomatic root of maxilla (palatal) were the most influential variables, with coefficients of -0.571 and 0.414 , respectively (Table 2). There was significant separation between specimens from western Alaska and Japan, whereas those from California appeared intermediate. Specimens from Russia and eastern Alaska were also intermediate but this may have been an artifact of small sample size (Fig. 3). Skulls from Alaska possessed a longer palate and maxillary region than those from California, Japan, and Russia (gnathion–posterior of maxilla (palatal) (14), palatal notch–incisors, gnathion–foramen infraorbitale (26)). Skulls from California appeared more robust than those from Alaska, reflected in greater breadth of nares (4), breadth of braincase (9), and height of skull at supraorbital processes (27) (Table 3).

For adult male *E. jubatus*, 16 variables that contributed to maximum separation of groups were used for the multigroup DFA, which was statistically significant (Wilks' lambda = 0.03, $P < 0.0001$). Figure 4a shows some overlap in specimens from Japan and California, whereas both Russian specimens grouped with skulls from Japan. Specimens from Alaska separated from Japanese, Russian, and Californian skulls, whereas no significant differences were observed between skulls from Japan and Russia. Specimens from Japan appeared to be the smallest, yet most robust, morphologically. Both eastern Alaskan specimens grouped together with those from western Alaska, indicating no significant morphological differences.

Sixteen variables were tested in the multigroup discriminant function anal-

Table 1. Measurements of skulls used in this study (from Brunner 2000).

Variable No.	Parameter
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 at 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 6 alveolus
13	Rostral width, at widest point 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 postcanines 3 and 4, between postcanines 3 and 4 alveoli
17	Breadth of palate between postcanines 4 and 5, between postcanines 4 and 5 alveoli
18	Breadth of palate at postcanine 5, from proximal margin of postcanine 5 alveoli
19	Gnathion–caudal border of postglenoid process
20	Zygomatic breadth, at widest point of zygomatic arch, from posterior of squamosals
21	Basion–zygomatic root of maxilla, ventral perspective, from anterior of basion to anterior of zygomatic roots.
22	Auditory breadth, greatest distance at auditory bullae
23	Mastoid breadth
24	Basion–bend of pterygoid, from anterior of basion to anterior of pterygoid
25	Height of canine above alveolus, a straight line from the posterior margin of alveolus to the tip of the canine
26	Gnathion–foramen infraorbitale, from gnathion to anterior of foramen infraorbitale
27	Height of skull at supraorbital processes, from base of skull at postcanine 6 alveolus to top of skull at supraorbital processes
28	Height of skull at bottom of mastoid, dorsoventrally, from skull at base at sagittal crest to ventral margin of mastoid
29	Height of sagittal crest, dorsoventrally, from highest point of crest to skull at base of crest
30	Mesiodistal diameter of postcanines, at root of postcanine above alveolus
31	Length of mandible, from posterior margin of condyle to anterior margin of dentary

Table 1. Continued.

Variable No.	Parameter
32	Length of mandibular teeth row (inclusive of canines), from anterior margin of canine alveolus to posterior margin of postcanine 6 alveolus
33	Mesiodistal diameter of canines, across base of canine at alveolus
34	Length of lower postcanine row, from anterior margin of postcanine 1 alveolus to posterior margin of postcanine 6 alveolus
35	Height of mandible at meatus, from dorsal margin of angularis at meatus to dorsal margin of coronoid process
36	Angularis–coronoideus, from ventral margin of angularis to dorsal margin of coronoid process
37	Length of masseteric fossa, from anterior margin of fossa to posterior margin of coronoid process
38	Breadth of masseteric fossa, dorsoventrally through centre of fossa
39	Gnathion–hind border of preorbital process, from gnathion to posterior margin of preorbital process
40	Length of orbit—from ventral margin of postglenoid process to dorsal margin of the base of orbit
41	Breadth of orbit—mesiodistal from inside margin of orbit

ysis for female *E. jubatus* (Table 4). Separation of females into geographic groups (Alaska, $n = 6$; California, $n = 7$; Japan, $n = 23$; and Russia, $n = 4$) was not statistically significant (Wilks' lambda = 0.12, $P = 0.110$) (Fig. 4b), although this result may be a reflection of small sample size.

DISCUSSION

Skulls of adult male *E. jubatus* from Alaska appeared morphologically divergent from those of other groups measured; they possessed a longer, less robust skull, whereas those from Japan appeared the smallest, yet most robust. The most substantial divergence appeared to be between specimens from western Alaska and Japan. Bickham *et al.* (1996) showed that there is a distinct break in the distribution of mtDNA haplotypes between *E. jubatus* from eastern Alaska, California, and Oregon (eastern population) and those from western Alaska and Russia (western population). Although the sample size was small, results for adult male *E. jubatus* appeared not to support a grouping of Russian specimens with those from western Alaska; rather, the two Russian specimens grouped with those from Japan in DFA and separately in UPGMA cluster analyses. In the multigroup DFA, two adult male specimens from Japan overlapped with skulls from California, but these may have been collected during the non-breeding season at which time movement of male *E. jubatus* from breeding grounds increases significantly. From UPGMA cluster analyses and DFA, skulls from eastern Alaska did not appear to separate from western Alaskan specimens, as described by Bickham *et al.* (1996), potentially indicating that the current east-west stock structure may require re-examination.

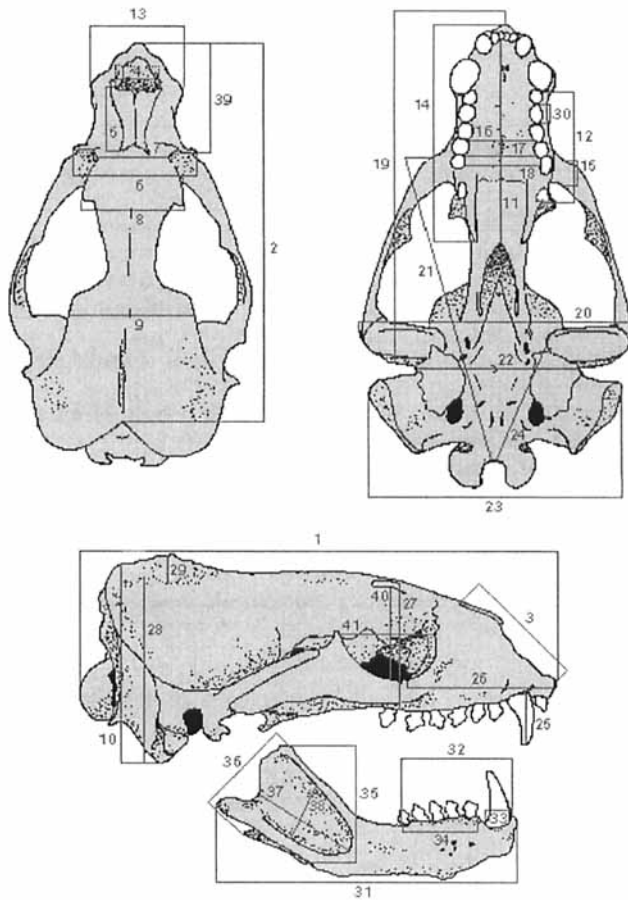


Figure 1. Typical adult male otariid skull, showing measurements used in this study. Dorsal (a), ventral (b), and right lateral (c) perspectives are illustrated (modified from Brunner 1998a).

Nevertheless, results support patterns of east-west geographic variation, albeit different from that depicted by Bickham *et al.* (1996): specimens of *E. jubatus* from Japan and Russia separated from Californian specimens, and those from Alaska diverged from Japanese and Californian skulls.

Bickham *et al.* (1998) stated that the recognition of two genetically differentiated populations of *E. jubatus* seems inconsistent with the high level of estimated effective migration of *E. jubatus*, and that recognition of two distinct stocks was not warranted because there was no evidence for monophyly of the mtDNA haplotypes that characterized the two populations. The greatest morphological differences found here indicate not only an east-west divergence (between specimens from California and Japan/Russia), but also a possible north-south differentiation between skulls from Alaska and those from California. The primary morphometric findings from this study indicate there may be three

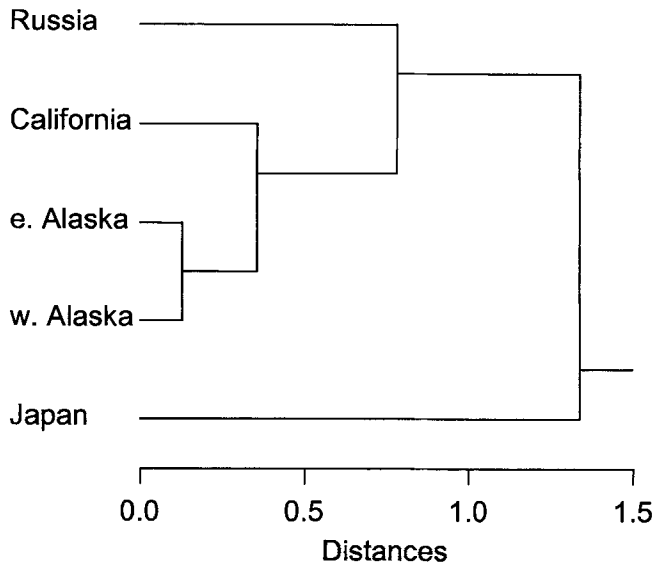


Figure 2. UPGMA cluster analysis for adult male *Eumetopias jubatus* from eastern and western Alaska, California, Russia, and Japan.

stocks present: those from Alaska (largest specimens), those from California, and those from Japan and, potentially, Russia (most robust specimens).

Adult female *E. jubatus* showed no statistically significant differences in populations, although some grouping was observed (only one skull from Alaska overlapped with specimens from California). Adult female *E. jubatus* showed less morphological variation in skulls than did males, a trait found in skulls of most otariid species (Brunner 2000) and one which may contribute to the lower resolution of statistical results. Bickham *et al.* (1996), mentioned that

Table 2. Component loadings from principal components analysis for adult male *Eumetopias jubatus* ($n = 52$).

Variable	Component I	Component II	Component III
Gnathion–upper end of nasals	0.722	0.256	-0.571
Basion–zygomatic root of maxilla (anterior)	0.790	-0.207	0.414
Gnathion–posterior margin of preorbital processes	0.806	0.384	-0.291
Mastoid breadth	0.722	-0.536	-0.268
Palatal notch–incisors	0.836	0.215	0.262
Zygomatic breadth	0.744	-0.493	-0.243
Condylobasal length	0.948	0.034	0.214
Gnathion–posterior of maxilla (palatal)	0.810	0.345	0.162
Gnathion–caudal border of postglenoid process	0.927	0.101	0.142
Occipital crest–mastoid	0.768	-0.412	0.097
Gnathion–middle of occipital crest	0.846	0.181	-0.077
Percent of total variance explained	66.3	10.6	8.1

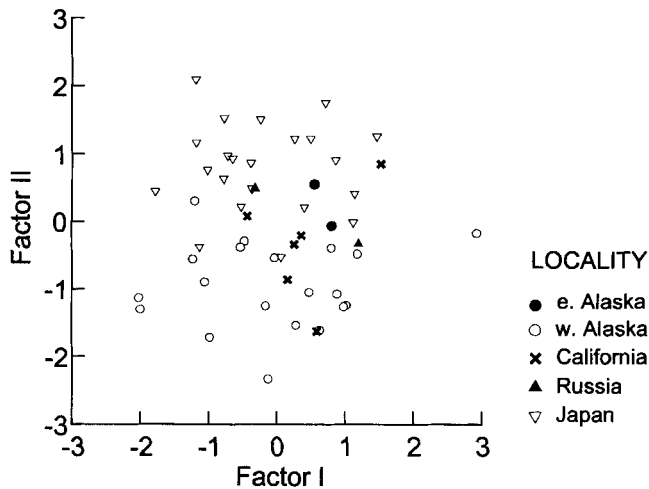


Figure 3. Factor scores with 0.95 confidence ellipses for adult amle *Eumetopias jubatus* from eastern and western Alaska, California, Russia, and Japan.

the estimate of the number of effective female migrants per generation was high but concluded that sufficient genetic differentiation has occurred between eastern and western populations to allow recognition of two distinct stocks. Results from this study indicate a minor difference between skulls of adult female *E. jubatus* from Alaska and those from California. A more significant result might be attained with a larger sample size.

Geographic variation in skull morphology of *E. jubatus* may be attributed to a number of factors including genetic divergence, resource availability, and environmental perturbations. Other biological factors have also indicated a north-south differentiation of *E. jubatus*. Hobson *et al.* (1997) observed a north-south cline in ^{13}C values in otariids, both in skeletal muscle and in hair. Muscle tissues least enriched in ^{13}C were those of northern fur seals (*Callorhinus ursinus*) from the Bering Sea; those most enriched were from harbor seals (*Phoca vitulina*) from the Washington coast near the Columbia River. *Eumetopias jubatus* and *P. vitulina* from the Gulf of Alaska were intermediate in ^{13}C , with *P. vitulina* being more enriched in ^{13}C relative to *E. jubatus* (Hobson *et al.* 1997). Dunton *et al.* (1989) described a latitudinal and longitudinal gradient in $^{13}\text{C}/^{12}\text{C}$ ratios in northern Alaska; enrichment of ^{13}C increased from the eastern Beaufort and East Siberian seas to the western Beaufort and Chukchi seas to the Bering Sea.

Brunner (2000) found latitudinal variation in skull size for many species of otariids, including *E. jubatus*, that changed with latitude and primary productivity. The change in skull size with latitude for most otariids follows Bergmann's rule, which states that "races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates" (Mayr 1973). This may be occurring within populations of *E. jubatus*, where specimens with the largest skulls are found at the highest

Table 3. Group means and standard deviations of variables used in discriminant function analysis for adult male *Eumetopias jubatus* from eastern Alaska ($n = 2$), western Alaska ($n = 11$), California ($n = 6$), Japan ($n = 22$) and Russia ($n = 2$).

Variable	Alaska (mm)	California (mm)	Japan (mm)	Russia (mm)
Gnathion-upper end of nasals	145.80 ± 6.26	147.62 ± 5.51	144.78 ± 6.78	145.67 ± 2.35
Breadth of nares	56.97 ± 4.00	61.59 ± 2.68	57.24 ± 2.59	57.18 ± 6.01
Length of nasals	60.39 ± 4.12	64.04 ± 3.47	59.60 ± 5.20	64.45 ± 7.43
Breadth of skull at preorbital processes	139.94 ± 9.72	136.50 ± 4.76	133.23 ± 5.29	139.33 ± 4.64
Breadth of braincase	91.91 ± 3.75	94.50 ± 3.45	93.73 ± 3.39	95.19 ± 2.11
Palatal notch-incisors	199.62 ± 8.86	194.72 ± 3.67	194.13 ± 6.75	190.31 ± 7.15
Gnathion-posterior of maxilla (palatal)	192.60 ± 8.47	191.71 ± 7.46	191.92 ± 6.77	191.00 ± 5.02
Zygomatic breadth	240.58 ± 8.72	240.64 ± 5.88	236.40 ± 11.00	244.98 ± 5.44
Auditory breadth	188.66 ± 7.60	190.09 ± 3.54	188.55 ± 11.72	194.13 ± 6.70
Basion-bend of pterygoid	11.33 ± 6.67	111.94 ± 4.24	107.12 ± 3.94	113.56 ± 3.12
Gnathion-foramen infraorbitale	136.03 ± 8.25	133.29 ± 11.46	134.92 ± 4.38	138.37 ± 0.99
Gnathion-caudal border of periorbital process	139.54 ± 6.07	138.48 ± 4.25	137.21 ± 4.39	139.65 ± 2.21
Height of skull at supraorbital processes	118.46 ± 6.02	125.86 ± 3.92	117.36 ± 7.31	115.08 ± 0.25
Height of sagittal crest	28.82 ± 7.13	34.78 ± 4.33	27.28 ± 4.11	29.50 ± 8.98
Breadth of palate at postcanines 4-5	63.33 ± 5.44	63.87 ± 5.80	61.57 ± 3.72	60.88 ± 7.23
Breadth of palate at postcanine 5	55.92 ± 4.45	55.60 ± 5.41	55.95 ± 3.90	56.45 ± 5.85

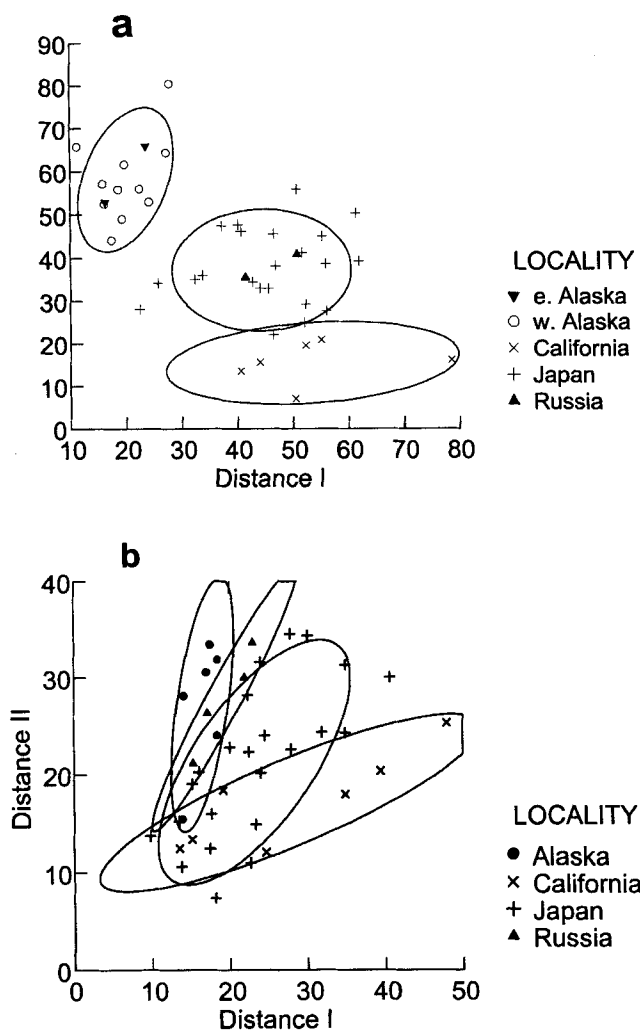


Figure 4. Mahalanobis distances with 0.95 confidence ellipses for adult male (a) and female (b) *Eumetopias jubatus* from Alaska, California, Russia, and Japan.

latitudes. Conversely, Brunner (2000) showed that skull size in *A. tropicalis* varied in size with latitude, albeit in reverse to Bergmann's rule; the largest specimens were found on Amsterdam Island ($37^{\circ}55'S$), intermediates on Gough Island ($40^{\circ}20'S$), and the smallest on Marion Island ($46^{\circ}55'S$). Although Kerley *et al.* (2000) found no significant differences in skull morphology of *A. tropicalis* from Gough and Marion Islands, Bester and Van Jaarsveld (1994) observed geographic variation in body size of *A. tropicalis* that was congruent with patterns of variation found in skull size by Brunner (2000). Ross and Cockroft (1990) showed the size and morphological features of bottlenose dolphins (*Tursiops* spp.) differed between coastal and offshore popula-

Table 4. Group means and standard deviations of variables used in discriminant function analysis, for adult female *Eumetopias jubatus* from Alaska ($n = 6$), California ($n = 7$), Japan ($n = 23$) and Russia ($n = 4$).

Variable	Alaska (mm)	California (mm)	Japan (mm)	Russia (mm)
Breadth of nares	40.50 ± 2.80	39.24 ± 3.38	41.36 ± 2.23	38.71 ± 2.44
Length of nasals	47.80 ± 4.06	49.26 ± 3.91	48.57 ± 4.59	45.24 ± 4.89
Breadth of skull at supraorbital processes	89.31 ± 6.15	82.61 ± 6.85	88.88 ± 7.03	86.00 ± 3.74
Breadth of braincase	87.25 ± 3.97	87.06 ± 2.32	89.20 ± 1.87	90.35 ± 2.78
Distance behind border of upper canines	94.47 ± 6.12	91.99 ± 3.61	93.63 ± 3.07	94.85 ± 2.45
Rostral width	62.29 ± 3.55	58.72 ± 4.13	63.34 ± 3.15	59.68 ± 2.65
Gnathion—posterior of maxilla (palatal)	155.11 ± 9.10	151.49 ± 5.91	155.57 ± 5.37	152.76 ± 3.75
Gnathion—caudal border postglenoid process	243.20 ± 9.02	239.30 ± 7.21	243.80 ± 6.81	238.23 ± 7.26
Masroid breadth	155.48 ± 8.82	149.56 ± 7.32	156.40 ± 6.98	155.38 ± 5.02
Basion—bend of pterygoid	90.55 ± 5.28	92.59 ± 9.87	89.42 ± 3.45	92.01 ± 3.56
Gnathion—foramen infraorbitale	108.27 ± 5.77	100.83 ± 6.72	105.89 ± 3.92	107.91 ± 3.81
Gnathion—caudal border of preorbital process	107.46 ± 3.71	105.80 ± 4.32	108.94 ± 4.07	104.18 ± 2.72
Height of skull at supraorbital process	77.75 ± 4.59	79.15 ± 5.46	83.05 ± 3.73	79.46 ± 2.30
Height of skull at ventral margin of mastoid	114.26 ± 7.79	109.77 ± 7.80	113.34 ± 4.97	115.29 ± 5.48
Breadth of palate at postcanines 3-4	47.78 ± 3.84	45.50 ± 4.23	47.77 ± 2.49	44.99 ± 2.33
Breadth of palate at postcanines 4-5	48.71 ± 3.99	47.65 ± 4.10	49.42 ± 3.04	46.70 ± 1.87

tions, in relation to average water temperature. Amano and Miyazaki (1992) found a clear pattern of geographic variation in overall size in skulls of Dall's porpoise, *Phocoenoides dalli*, which corresponded with the distribution of primary productivity.

Eumetopias jubatus appears to be declining most where primary productivity has been reduced significantly and where water temperatures have warmed dramatically. For example, since 1951 the biomass of macrozooplankton in waters off southern California has decreased by 80%, the surface layer has warmed by more than 1.5°C in some places, and the temperature difference across the thermocline has increased (Roemmich and McGowan 1995). The observed trends in the California Current may be related to basin-scale changes in wind forcing, which involved a strengthening of the North Pacific wintertime atmospheric circulation that began in the 1970s (Roemmich and McGowan 1995). The strengthening of this atmospheric circulation seems to coincide with the onset of severe population decline of *E. jubatus* in both California and Alaska, thus indicating a similar trend in oceanographic change in Alaskan waters. The annual average rate of productivity for north polar seas is low, approximately 25 g C/m²/yr, due to reduced daylight hours that drive photosynthesis (Falkowski 1980). In northern subpolar seas and around the Antarctic continent, upwelling of deep, nutrient-rich water supports very high summertime primary production and annual productivity rates of over 100 g C/m²/yr (Falkowski 1980).

As a species, *E. jubatus* is a relatively lean pinniped; estimates of blubber and total body lipids range from 5% to 17% of total body mass (Pitcher *et al.* 2000). It is the largest (possibly the most metabolically expensive) otariid, and is currently the species most affected by oceanographic change and depleted food resources (Sydeman and Allen 1999). The Alaskan population of *E. jubatus* which, from this study, includes some of the largest specimens for the species (CBL max. 413 mm), appears to be declining faster than those containing individuals at lower latitudes with skulls that are smaller and morphologically more robust.

The observed geographic variation in skulls of *E. jubatus* was not significant enough to warrant separation of the species into subspecies, although further analyses are required. A comparison of almost any two (or more) natural populations will reveal at least some statistically significant differences, but it would serve no purpose to name each slightly differentiated population as a subspecies (Rice 1998). Nevertheless, although sample sizes were small, the low-level geographic variation observed in adult *E. jubatus* indicates the potential presence of morphologically diverging groups, different from those currently described by Bickham *et al.* (1996) as eastern and western stocks.

A comprehensive morphological study of *E. jubatus* using large sample sizes would be beneficial in understanding the biodiversity of the species, and should provide more conclusive results on the classification of populations. A combined approach encompassing morphometric, genetic and ecological studies would contribute significantly towards a better perspective of population dynamics and, thus, conservation efforts for *E. jubatus*.

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Appendix. Summary details of specimens of *Eumetopias jubatus* used in this study. ASD = Asahi University, Gifu Prefecture (Japan); BMNH = British Museum of Natural History (London); DMNH = Denver Museum of Natural History, Denver (USA); HU = Hokkaido University, Hakodate (Japan); LACM = Los Angeles County Museum, Los Angeles (USA); NMNH = National Museum of Natural History, Washington DC (USA); UAM = University of Alaska Museum, Fairbanks (USA); and ZMB = Zoological Museum of Berlin (Germany).

Accession no.	Location collected	Sex	SI	Date collected	Museum
18552	Barren Is, AK	f	19	12/04/78	UAM
31904	Galena Bay	f	19	1995	UAM
lacm52313	Año Nuevo Is, CA	f	19	27/06/15	LACM
97012	Rausu, east Hokkaido	f	19	1997	HU

Appendix. Continued.

Accession no.	Location collected	Sex	SI	Date collected	Museum
95014	Rausu, east Hokkaido	f	19	1995	HU
1897.1.18.7	St George Is	f	20	—	BMNH
1950.7.21.5	Año Nuevo Is, CA	f	20	—	BMNH
99013	Rausu, east Hokkaido	f	20	1999	HU
94023	Rausu, east Hokkaido	f	20	1994	HU
47104	Bering Is	f	21	3/6/1892	NMNH
lacm620	Año Nuevo Is, CA	f	21	3/07/21	LACM
99008	Rausu, east Hokkaido	f	21	1999	HU
98011	Rausu, east Hokkaido	f	21	1998	HU
95015	Rausu, east Hokkaido	f	21	1995	HU
21302	Tuleni Is, Okhotsk Sea	f	22	1883	NMNH
21309	Tuleni Is, Okhotsk Sea	f	22	—	NMNH
95016	Rausu, east Hokkaido	f	22	1995	HU
98022	Rausu, east Hokkaido	f	23	1998	HU
95019	Rausu, east Hokkaido	f	23	1995	HU
31916	St Paul Is	f	24	23/05/94	UAM
8162	St George Is	f	25	—	NMNH
8163	Bering Str	f	25	1840	NMNH
94017	Rausu, east Hokkaido	f	25	1994	HU
1950.7.21.6	Año Nuevo Is, CA	f	26	—	BMNH
38220	Tuleni Is, Okhotsk Sea	f	26	1883	NMNH
188982	St Paul Is	f	26	8/1892	NMNH
lacm52311	Año Nuevo Is, CA	f	26	27/06/15	LACM
256492	Kodiak Is	f	27	1930	NMNH
94026	Rausu, east Hokkaido	f	27	1994	HU
5210	Bering Sea	f	28	—	UAM
97309	Hokkaido	f	28	1997	HU
97307	Hokkaido	f	28	1997	HU
95011	Rausu, east Hokkaido	f	28	1995	HU
2744	Año Nuevo Is, CA	f	29	6/24	DMNH
14	Hokkaido	f	29	—	HU
15861	Unalaska Is	f	30	1876	NMNH
38228	Tuleni Is, Okhotsk Sea	f	30	1883	NMNH
98NT1	Hokkaido	f	30	1998	HU
94020	Rausu, east Hokkaido	f	30	1994	HU
99204	Rebun Island	f	30	1999	HU
95018	Rausu, east Hokkaido	f	30	1995	HU
94022	Rausu, east Hokkaido	f	30	1994	HU
159964	Point Pinos, CA	f	31	22/06/09	NMNH
188980	Chehalis Co. Washington	f	31	10/1885	NMNH
276209	St Paul Is	f	31	12/07/48	NMNH
94014	Rausu, east Hokkaido	f	31	1994	HU
98201	Rebun Island	f	31	1998	HU
98009	Rausu, east Hokkaido	f	31	1998	HU
95021	Rausu, east Hokkaido	f	31	1995	HU
98301	Hokkaido	f	31	1998	HU
97203	Rebun Island	f	32	1997	HU
94021	Rausu, east Hokkaido	f	33	1994	HU
23457	Farallones Is, CA	f	24	—	NMNH
21523	Farallones Is, CA	f	31	9/1884	NMNH

Appendix. Continued.

Accession no.	Location collected	Sex	SI	Date collected	Museum
21537	Farallones Is, CA	f	33	9/1884	NMNH
32733	St George Is, Alaska	m	24	5/05/94	UAM
21303	Tuleni Is, Okhotsk Sea	m	25	1883	NMNH
22072	Bering Is	m	26	—	NMNH
22071	Bering Is	m	26	—	NMNH
83887	St Paul Is	m	26	1897	NMNH
114830	Pribilof Is	m	26	7/1902	NMNH
lacm616	Año Nuevo Is, CA	m	26	7/07/21	LACM
97302	Hokkaido	m	26	1997	HU
98105	Shakotan, Hokkaido	m	26	1998	HU
99104	Shakotan, Hokkaido	m	26	1999	HU
94	Hokkaido	m	26	1994	HU
929/29	Hokkaido	m	26	1992	HU
72815	St Paul Is	m	27	1872	ZMB
7140	St Paul Is	m	27	—	NMNH
11470	Otter Is, Bering Sea	m	27	10/07/74	UAM
870524	Hokkaido	m	27	1987	HU
13217	Farallone Is, CA	m	28	—	NMNH
261229	Aleutian Is	m	28	1936	NMNH
43370	St George Is	m	28	16/05/96	UAM
5216	Bristol Bay, Bering Sea	m	28	—	UAM
AF19493	St Paul Is	m	28	1997	UAM
98CH02	Hokkaido	m	28	1998	HU
188981	St Paul Is	m	29	4/8/1891	NMNH
5217	Bristol Bay, Bering Sea	m	29	—	UAM
43367	St Paul Is	m	29	25/02/96	UAM
43367	St Paul Is	m	29	25/02/96	UAM
97304	Hokkaido	m	29	1997	HU
99105	Shakotan, Hokkaido	m	29	1999	HU
1950.3.29.12	St Paul Is	m	30	—	BMNH
49730	St Paul Is	m	30	—	NMNH
276031	St Paul Is	m	30	7/07/46	NMNH
276354	St Paul Is	m	30	7/07/48	NMNH
99106	Shakotan, Hokkaido	m	30	1999	HU
98029	Rausu, east Hokkaido	m	30	1998	HU
98ST01	Hokkaido	m	30	1998	HU
1950.3.29.11	St George Is	m	31	—	BMNH
267526	Aleutian Is	m	31	1937	NMNH
246499	Lynn Canal, AK	m	31	6/02/25	NMNH
276032	Tahola, Washington	m	31	13/06/42	NMNH
4702	San Francisco Bay	m	32	7/1834	NMNH
285509	St Paul Is	m	32	22/06/49	NMNH
43365	St Paul Is	m	32	22/04/96	UAM
4701	Farallones Is, CA	m	33	2/1856	NMNH
15359	Unalaska Is	m	33	—	NMNH
8655	Dall Is, AK	m	33	1960	DMNH
6906	Monterey, CA	m	28	—	NMNH
21108	Massett, BC	m	31	7/1883	NMNH
3631	Monterey, CA	m	32	—	NMNH