

Craniological Analysis of Harbor and Spotted Seals of the North Pacific Region

JOHN J. BURNS,¹ FRANCIS H. FAY,² and GENNADII A. FEDOSEEV³

ABSTRACT

We reexamined the taxonomic status of the *geronimensis*, *richardsi*, and *stejnegeri* forms of harbor seals, *Phoca vitulina*, in the North Pacific Ocean by comparing the cranial differentiation among them with the differentiation of *P. vitulina* from its sibling species *P. largha*, the spotted seal. This assessment was based primarily on the results of three discriminant analyses and a Q-mode cluster analysis, for which we used both measurements and nonmetrical characters of skulls. The results showed that the differentiation of *vitulina* from *largha* is greater than that among the three Pacific forms of *vitulina*. Within *vitulina*, the *geronimensis* form in southern California and Mexico is not clearly differentiated from *richardsi*. The *stejnegeri* form, conversely, has become differentiated sufficiently for subspecific status. The "boundary" between *stejnegeri* and *richardsi* is not in Near Strait as proposed earlier; instead, it seems to be in the vicinity of the eastern Aleutian Islands and Alaska Peninsula. A firm conclusion on that point cannot be reached, however, without study of additional specimens from that region.

РЕЗЮМЕ

Нами проведён таксономический статус разновидностей обыкновенного тюленя [*Ph. vitulina*] *geronimensis*, *richardsi* и *stejnegeri* в северной части Тихого океана путем сравнения краниологических различий среди них и с их видом двойником пятнистым тюленем [*Ph. largha*]. Эти исследования основаны главным образом на результатах дискриминантного и кластерного «Q-mode» анализов с использованием метрических и неметрических признаков черепов. Результаты показали, что дифференциация между *vitulina* и *largha* больше, чем среди трёх тихоокеанских разновидностей обыкновенного тюленя [*vitulina*].

Разновидности обыкновенного тюленя *geronimensis* южной Калифорнии и Мексики плохо дифференцированы от *richardsi*. Форма *stejnegeri* напротив дифференцировалась и отвечает статусу подвида.

Самый большой разрыв в градиенте морфологических различий кажется в соседних районах восточной части Алеутских островов и полуострова Аляска.

В заключение отметим, что изложенная точка зрения не может быть окончательной без дополнительных исследований этих подвигов в указанных районах.

INTRODUCTION

A series of recent works on the taxonomy of seals of the genus *Phoca* (in the strict sense) of the North Pacific region by Chapkii (1955, 1960, 1967, 1969), Belkin (1964), Mohr (1965), McLaren (1966), Bigg (1969, 1981), Naito and Nishiwaki (1972, 1975), and Shaughnessy and Fay (1977), has led to worldwide recognition of the sibling species, *P. largha* Pallas, the spotted or larga seal of the seasonal pack ice, and *P. vitulina* Linnaeus, the harbor or common seal of the coasts and islands. The taxonomic status of two other forms, described earlier by Allen (1902) and Doutt (1942) as *P. stejnegeri* of the Commander Islands and eastern Asia and *P. v. geronimensis* of southern California and Mexico, still remains unsettled. The *stejnegeri* form was redescribed by Inukai (1942) as *P. okhotensis kurilensis* and later by Belkin (1964) as *P. insularis*. At present it is regarded as rare and endangered in both Japan and the Soviet Union; for that reason alone, its taxonomic status needs to be resolved.

Shaughnessy and Fay (1977) reviewed the information on harbor and spotted seals of the North Pacific region and concluded (as had Mohr 1965; Chapkii 1969; Bychkov 1971; Burns and Fay 1974;⁴ and Kosygin et al. 1975⁵) that the coastal harbor seals of the North Pacific region, from northern Hokkaido in the west to Baja California in the east, appeared to comprise only one polytypic taxon, *P. vitulina richardsi* (Gray), rather than two or three. The concept of a single subspecies of *P. vitulina* in the North Pacific, however, has not been popular. To test that taxonomic theory with somewhat greater rigor than before, we statistically examined both the differences and the similarities among a large series of crania of those seals, collected throughout the North Pacific region. This work, begun in 1970, has been continued since 1973 in the context of the US-USSR Marine Mammal Project.

METHODS

We examined skulls of 435 Pacific harbor and spotted seals, the

¹Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA.

²Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, USA.

³Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MOTINRO), Nagaevskaya 51, Magadan 685013, USSR.

⁴Burns, J. J., and F. H. Fay. 1974. New data on taxonomic relationships among North Pacific harbor seals, genus *Phoca* (sensu stricto). [Abstr.] Trans. First Int. Theriol. Congr. 1:99. Nauka, Moscow.

⁵Kosygin, G. M., A. E. Kuzin, and E. I. Sobolevskii. 1975. Systematic position, morphology, and ecology of the Kuril seal. In Marine mammals. Materials 6th all-union conf. 1:151-153. [Abstr.] Naukova Dumka, Kiev.

majority of which were adult animals. These were drawn from 21 of the major osteological collections in the Northern Hemisphere (Appendix I).

For each specimen, insofar as possible, we recorded 37 cranial characters, including 29 measurements and 8 nonmetrical attributes (Figs. 1, 2), in addition to date and location of collection, sex, and relative age. Those characters were selected in part on the basis of universal mammalogical methods and in part on the basis of our mutual experience and our interpretations of Chapskii's (1967, 1969) contributions. Relative age of each specimen was determined from the degree of closure of eight cranial sutures (after Doutt 1942): Occipito-parietal, squamoso-parietal, interparietal, fronto-parietal, interfrontal, basioccipital-basisphenoidal, basisphenoidal-

presphenoidal, and intermaxillary. The degree of closure of each suture was assessed visually and assigned a numerical score from 1 to 4. The minimal value of 1 was given for sutures which were open wide; the maximum of 4 was given for those fully ankylosed. Females with total scores of 28 to 32 and males with total scores of 30 to 32 were regarded as adults, usable in the analysis. Skulls with lower scores were not included in the analyses because most of the cranial measurements tend to increase with age during the juvenile and subadult stages of growth.

Each variable was measured to the nearest 0.1 mm; each nonmetrical character was ranked and assigned a numerical score, based on our judgement of its conformity to one of the diagrams in Figure 2. The rank-order of those nonmetric characters is debatable in some

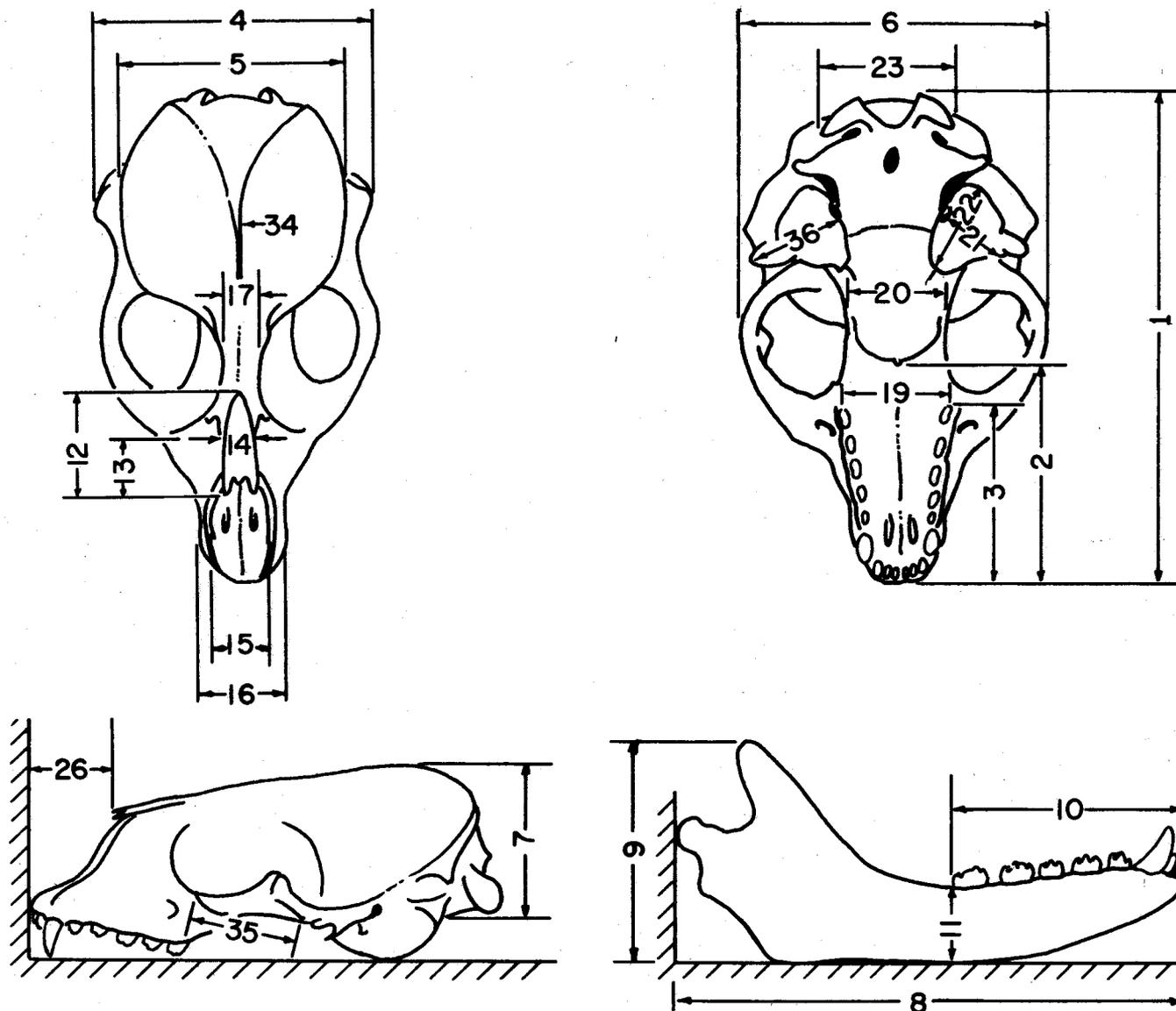


Figure 1.—Dorsal and ventral views of the skull (upper) and lateral views of the skull and mandible (lower) of seals of the *Phoca vitulina-P. largha* type, showing 26 of the measurements used in this study: 1) condylobasal length, 2) palatal length, 3) length of upper tooth row, 4) greatest width at mastoids, 5) greatest width of cranium, 6) greatest zygomatic width, 7) height of cranium, 8) length of mandible, 9) height of mandible at coronoid process, 10) length of lower tooth row, 11) height of mandible behind the molar, 12) overall length of nasals, 13) length of maxillo-frontal suture to anterior end of nasals, 14) width of nasals at maxillo-frontal suture, 15) maximal width of external nares, 16) width of snout at canines, 17) least interorbital width, 19) width of palate behind first molars, 20) least width of palate at pterygoid hamuli, 21) width of bulla from notch anterior to auditory process to middle of carotid foramen, 22) greatest length of bulla, 23) greatest width at condyles, 26) length of snout from anterior edge of nasals, 34) presence of sagittal crest, 35) greatest length of jugal, 36) width of bulla from tip of auditory process to anterior edge of carotid foramen.

instances and obviously not continuous in any. We recognized the weaknesses of combining such discontinuous data with the continuous data from the measured variables, but we did so initially because the emphasis in earlier taxonomy of these seals had been heavily on those categorical attributes. Ultimately, they mostly were not found to be powerful as discriminators.

The skulls of *largha* were from specimens taken in the pack ice of the Okhotsk, Bering, and Chukchi Seas. Those of *vitulina* were from coastal areas in the North Pacific Ocean and southern Bering Sea. Each of those coastal areas was given a numerical code, as shown in Figure 3. Skulls of the three forms of *vitulina* were from specimens taken in the following geographical areas, approxi-

mately conforming to the limits originally described by Allen (1902): Areas 100-150 = *stejnegeri*, areas 160-280 = *richardsi*, and areas 300-310 = *geronimensis*.

Males and females were treated separately because of differences in size and proportions, as shown by Fisher (1952), Bishop (1967), Chapskii (1967), Bigg (1969), Naito and Nishiwaki (1972), Burns and Fay (footnote 4), Pitcher and Calkins (1979),⁶ and Burns and

⁶Pitcher, K. W., and D. G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Final report, R.U. 229, 72 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

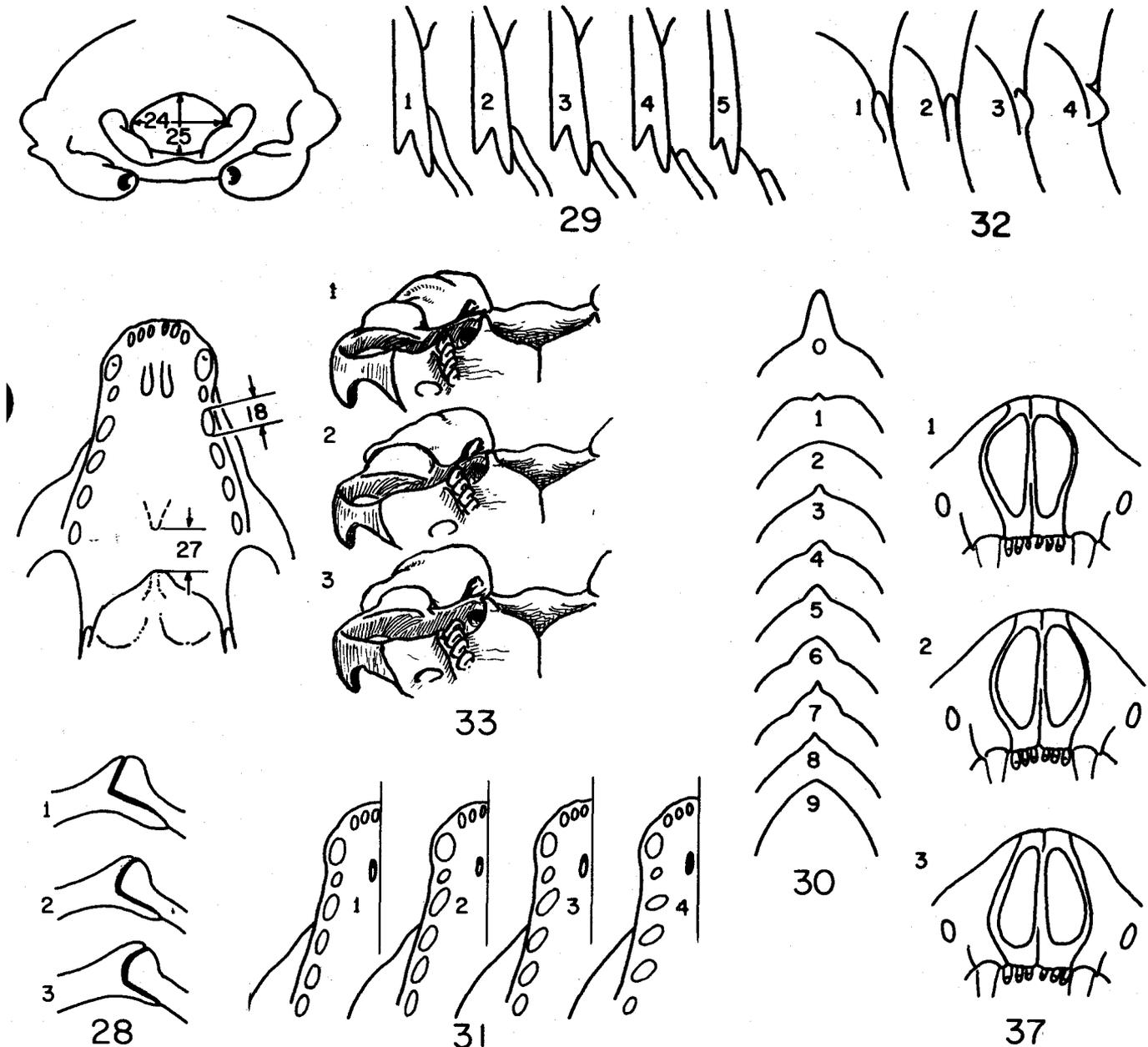


Figure 2.—Cranial measurements and nonmetrical characters in skulls of seals of the *Phoca vitulina-P. largha* type used in this study: 18) greatest anterior-posterior length of second upper premolar, 24) greatest width of foramen magnum, 25) greatest height of foramen magnum, 27) distance from posterior end of vomerine septum to medial edge of palate, 28) shape of jugo-squamosal suture, 29) extent of naso-premaxillary contact, 30) shape of palatal margin, 31) angle of second upper premolar relative to tooth row, 32) shape of pterygoid hamuli, 33) shape of bulla and auditory process in anterior view (skull inverted), 37) shape of anterior nares.

Gol'tsev (1984). Because many of the skulls were partly broken, the full suite of 37 characters was not available from all. For that reason, sample sizes varied among analyses, depending on which of the characters were being compared and the type of statistical treatment employed.

The data were analyzed in four ways. In the first, a set of 11 ratios of cranial dimensions which had been pointed out by Chapskii (1967) as being useful for discrimination between *largha* and *vitulina* were used in a discriminant analysis (Nie et al. 1975). Those ratios were of measurements 2, 3, 4, 12, 13, 22, and 35 relative to condylobasal length, of measurements 6, 16, and 17 relative to greatest width at mastoids, and of measurements 25/24 (see Figs. 1, 2). For that analysis, a sample of 39 specimens of *largha* (21 males (M), 18 females (F)) was compared with 229 specimens of Pacific *vitulina* (87M, 142F).

In the second procedure, we also employed discriminant analysis, but instead of ratios, we used all 37 of the metrical and nonmetrical characters. Our objective was to compare the discrimination between *largha* and *vitulina* with that among the three Pacific forms of *vitulina*. All samples were smaller than in the previous analysis (*largha* 14M, 12F; *stejnegeri* 8M, 12F; *richardsi* 38M, 74F; *geronimensis* 3M, 1F), because of the requirement that each specimen have the full suite of 37 characters.

For our third treatment, we excluded the *largha* phenotype and performed a factor analysis (Nie et al. 1975) of all 37 characters for all of the *vitulina* seals. Resultant factors with an eigenvalue >1.0 were considered. Ten factors for males accounted for 77% of the variance; eight factors for females accounted for 80%. From a varimax rotation, we selected characters with high loadings in the

individual factors. For each sex, we chose 14 nonredundant and, as far as possible, nonlinked characters.

After selecting the 14 characters for each sex, we performed a discriminant analysis with the entire series of *vitulina* samples, subdividing them into five geographical groups, as follows: 100-150 (Hokkaido to Commander Islands), 170-190 (Aleutian and Pribilof Islands), 200-220 (Bristol Bay and Alaska Peninsula to Kodiak Island and Cook Inlet), 230-280 (Prince William Sound to Washington), and 300-310 (California to Mexico). In the discriminant analysis, the objective is to optimize the statistical descriptors of difference among groups; the similarity among groups is not emphasized analytically.

In the final treatment, we performed a Q-mode cluster analysis (Parks 1970), with a simple distance function as a measure of similarity among specimens of the *vitulina* sample. Variables were the 14 selected by factor analysis for males and females. In the Q-mode cluster analysis, distance coefficients were weighted according to percent of total variance accounted for by each principal component. This procedure re-sorts the individual specimens into clusters on the basis of their similarities, rather than differences.

RESULTS

Discriminant Analysis with Measurement Ratios: *vitulina* vs. *largha*

The 11 ratios of cranial dimensions identified by Chapskii (1967) as being useful for discriminating *largha* from *vitulina* were not adequate in themselves to classify correctly all of the specimens.

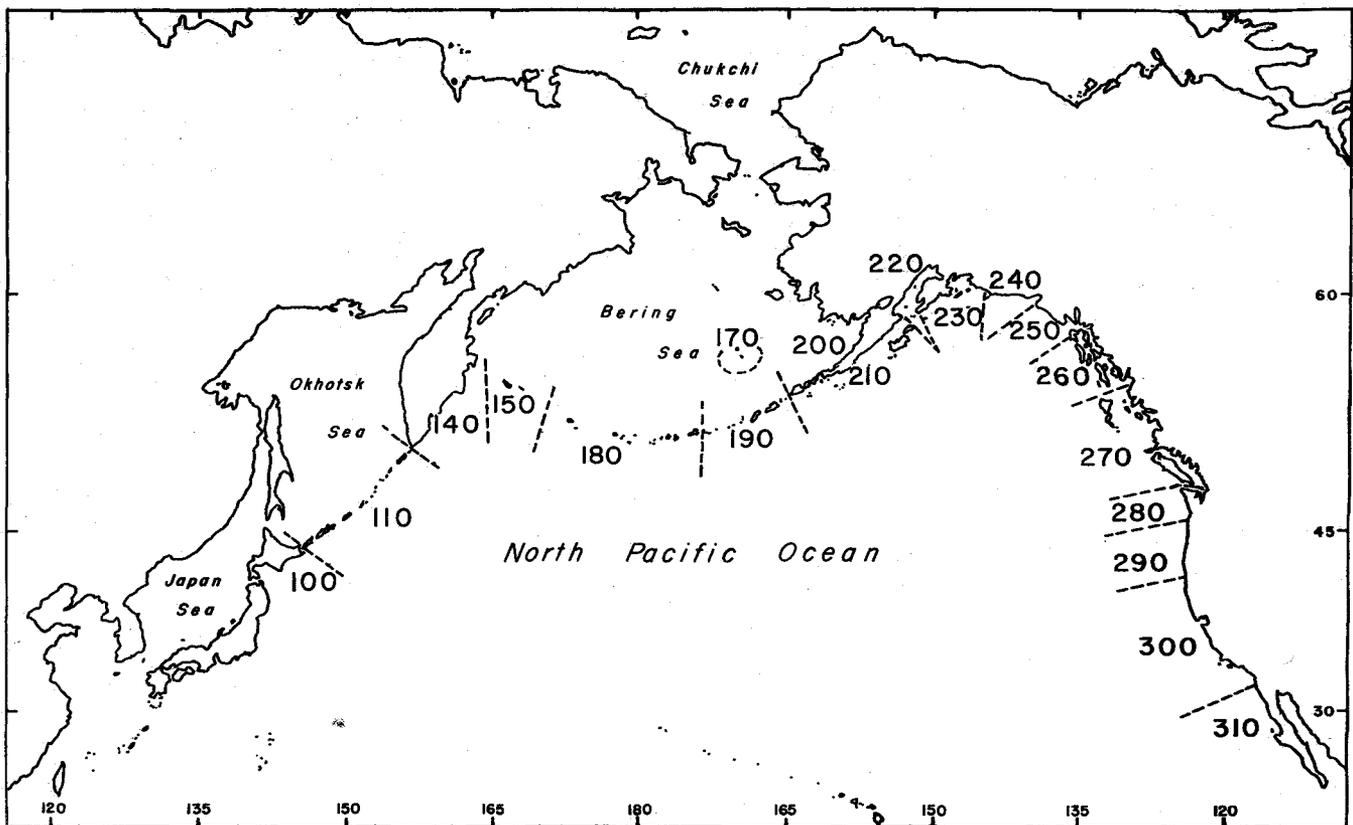


Figure 3.—Numerical codes and boundaries (dashed lines) of geographical sampling areas for harbor seals in the North Pacific region. Not shown is code 160, which was assigned to a single specimen from an unspecified locality in "southeastern Bering Sea."

The results of the discriminant analysis were that only 205 (76%) of the 268 skulls were correctly classified on the basis of those 11 ratios; the rest of the specimens were misclassified. Thus, the ratios alone are not as powerful in discrimination as Chapskii had implied, though they clearly have some value.

The discrimination of harbor seals collected in areas bordering the Okhotsk and Bering Seas showed a very strong tendency for greater success (84.5% correct) than did discrimination of harbor seals collected in western North America, from the Gulf of Alaska to Mexico (73.0% correct) (87/103 vs. 92/126, $\chi^2=3.708$; $0.05 < P < 0.06$). Spotted seals of the Okhotsk Sea also tended to be classified correctly more often than were those of the Bering Sea (Table 1), but the samples were small and the difference between them was not significant ($\chi^2=1.22$, $P > 0.25$).

Table 1.—Percent of Pacific harbor, *Phoca vitulina* and spotted, *P. largha*, seal skulls correctly and incorrectly identified by discriminant analysis, based on 11 ratios of cranial measurements.¹

Predicted taxon	Actual taxon			
	<i>largha</i>		<i>vitulina</i>	
	Okhotsk (N=12)	Bering (N=27)	Eastern (N=103)	Western (N=126)
<i>largha</i>	83	59	16	27
<i>vitulina</i>	17	41	84	73

¹Ratios identified by Chapskii (1967) as diagnostic of the *largha* phenotype.

Table 2.—Group means and standard deviations of ratios of skull measurements for male and female spotted and harbor seals.¹

Ratio of cranial measurement	<i>P. largha</i>		<i>P. vitulina</i>	
	Male (N=21) mean±SD	Female (N=18) mean±SD	Male (N=87) mean±SD	Female (N=142) mean±SD
2/1:Palatal length/CBL ²	36.4±18.1	41.2±10.4	38.6±16.3	39.2±14.1
3/1:Length upper tooth row/CBL	27.1±13.5	32.8± 0.8	29.2±12.4	30.7±10.2
4/1:Mastoid width/CBL	45.0±22.4	54.7±13.8	47.5±22.7	51.1±20.2
12/1:Nasal length/CBL	19.1±11.1	23.7± 1.9	20.6± 9.9	21.5± 8.8
13/1:Nasal width from maxillo-frontal suture/CBL	11.1± 5.7	12.8± 1.4	11.0± 5.4	11.2± 4.7
22/1:Length bulla/CBL	15.1± 7.5	19.0± 0.6	15.7± 7.0	16.6± 6.2
35/1:Length jugal/CBL	21.9±10.9	25.6± 6.5	24.5±10.4	25.0± 9.0
25/24:Height/width foramen magnum	65.1±28.0	72.2±18.6	63.5±31.8	67.8±29.0
6/4:Zygomatic width/mastoid width	91.0±38.4	97.6±24.8	89.4±41.2	90.3±35.9
16/4:Snout width/mastoid width	28.8±12.3	28.8± 7.5	29.8±13.4	28.7±11.1
17/4:Interorbital width/mastoid width	8.8± 5.2	10.7± 2.9	10.0± 4.7	9.6± 3.6

¹All ratios are (A × 100)/B.

²CBL = Condylbasal length.

In this analysis, a single discriminant function accounted for all of the discriminating power of the factor matrix for each sex. For males, the eigenvalue of that function was 0.22802; for females, it was 0.13453. Three of the ratios contributed significantly to that function for both sexes (jugal length/ condylbasal length; nasal length from maxillo-frontal suture/condylbasal length; interorbital width/ mastoid width); two contributed nothing (mastoid width/ condylbasal length; length upper tooth row/condylbasal length); each of the other ratios contributed in one sex but not in both. The means and standard deviations of all ratios are shown in Table 2.

Discriminant Analysis—37 Characters: *largha* vs. *vitulina*

With the full suite of 37 metrical and nonmetrical characters, the discriminant analysis correctly distinguished all of the harbor seals from the spotted seals. Within sexes, it also distinguished 98% of the three forms of harbor seals from each other (Table 3). The distinction of the three forms was less effective among sexes; significant overlap developed between *richardsi* and *geronimensis*, though not with *stejnegeri* (Fig. 4). Among the three harbor seal forms, *richardsi* was most similar to *largha*.

For males, two discriminant functions accounted for 90.8% of the relative power to discriminate among the four forms. Within the first function (70.5% relative; eigenvalue 12.35458), the seven variables with the largest standardized coefficients were 10 (length lower tooth row), 27 (length vomerine septum), 16 (width of snout),

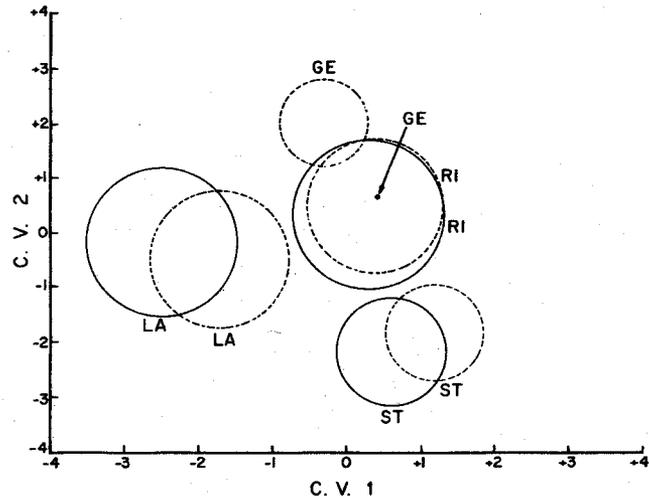


Figure 4.—Distribution of samples of male (dashed circles) and female (solid circles) seals of the *largha* (LA), *geronimensis* (GE), *richardsi* (RI), and *stejnegeri* (ST) forms on the first two canonical variates (CV1 and CV2). Circles enclose 95% of the plotted values for each taxon.

Table 3.—Percent of seal skulls correctly and incorrectly identified to taxon by discriminant analyses, based on 37 cranial characters.

Predicted taxon	Actual taxon							
	<i>largha</i>		<i>richardsi</i>		<i>stejnegeri</i>		<i>geronimensis</i>	
	Male (N=14)	Female (N=12)	Male (N=38)	Female (N=74)	Male (N=8)	Female (N=12)	Male (N=3)	Female (N=1)
<i>largha</i>	100	100	0	0	0	0	0	0
<i>richardsi</i>	0	0	100	96	0	0	0	0
<i>stejnegeri</i>	0	0	0	4	100	100	0	0
<i>geronimensis</i>	0	0	0	0	0	0	100	100

7 (height of cranium), 8 (length of mandible), 19 (width of palate), and 22 (length of bulla). In the second function (20.3% relative; eigenvalue 3.55208), the three variables with the largest coefficients were 16, 22, and 15 (width of nares).

For females, also, the first two discriminant functions accounted for more than 90% of the relative discriminating power. Within the first function (71.4% relative; eigenvalue 6.45098), the seven most significant characters were 3 (length upper tooth row), 28 (jugo-squamosal suture), 21 (width of bulla), 9 (height at coronoid), 22, 36 (width bulla at auditory process), and 32 (pterygoid hamuli). In the second function (23.0% relative; eigenvalue 2.07899), the three most significant characters were 1 (condylobasal length), 2 (palatal length), and 16.

Factor Analysis: *vitulina* Polytype

In this test, from which *largha* was excluded, the 14 most significant cranial characters were selected for each sex in *vitulina* (Table 4). For the males, these were chosen from six of the first eight discriminant factors, which accounted for 79.5% of the sample variation. For the females, the 14 most significant variables were selected from 9 of the first 10 discriminant factors, which accounted for 77.4% of the sample variation. For both sexes, selection of characters was based on their having the largest coefficients in the varimax rotated factor matrix. Ten of the variables were the same for both sexes; four were specific to each sex.

Table 4.—Principal diagnostic characters selected by factor analysis from the set of 37 metric and nonmetric characters of skulls of Pacific harbor seals.

Sex	Factor	Percent of variation	Principal diagnostic characters ¹	
Male	1	45.7	1,2,6,8,9,10,11,16,35 (condylobasal, palatal, mandibular, lower tooth row, and jugal length; zygomatic and snout width; height of mandible at coronoid and behind the molar)	
	3	6.0	24 (width of foramen magnum)	
	4	4.7	31 (angle of second upper premolar)	
	6	4.9	37 (shape of anterior nares)	
	7	3.6	29 (extent of premaxillary-nasal contact)	
	8	3.1	32 (shape of pterygoid hamuli)	
	Female	1	40.4	1,2,6,8,9,16 (condylobasal, palatal, and mandibular length; zygomatic and snout width; coronoid height)
		2	8.0	24 (width of foramen magnum)
3		4.8	14 (width of nasals)	
4		4.4	25 (depth of foramen magnum)	
5		4.1	31 (angle of second upper premolar)	
7		3.3	28 (shape of jugo-squamosal suture)	
8		3.1	32 (shape of pterygoid hamuli)	
9		2.9	22 (length of bulla at auditory process)	
10		2.8	37 (shape of anterior nares)	

¹Refer to Figures 1 and 2.

Discriminant Analysis: *vitulina*— 5 Geographical Groups

Using the 14 variables selected by the factor analysis for each sex, we compared five geographical groups of the *vitulina* samples by discriminant analysis. The geographical boundaries between groups were drawn arbitrarily, mainly with the objective of comparing the variation among regional samples of *richardsi* with that between *richardsi* and the *stejnegeri* and *geronimensis* samples. In effect, group 1 was *stejnegeri* as defined by Allen (1902), groups 2,

3, and 4 were regional samples of *richardsi* from Alaska to Washington, and group 5 included some *richardsi* from California and all (5) of the available *geronimensis*. The sexes were analyzed separately; the results are combined in Table 5. The classification function coefficients for each group are given in Table 6.

The discrimination among the five groups was moderate to high. About two-thirds to four-fifths of the specimens were correctly placed in their respective geographic groups. The highest proportions of correct placements were at each end of the series: 82% in group 1, 75% in group 5. Of the specimens in group 5, only three (60%) of the *geronimensis* from southern California and Mexico were correctly placed, compared with nine (82%) of the *richardsi* from central and northern California. This difference, however, was not significant ($\chi^2=0.097$, $P>0.25$).

The clinal nature of the morphological variation among geographical groups was shown clearly by this analysis, but a discontinuity in the cline also was indicated. Whereas in most instances

Table 5.—Percent of harbor seal skulls classified to the correct geographical region by discriminant analysis, based on the 14 most diagnostic characters for each sex. Vertical lines connect regional groups with closest affinities.

Predicted region	Actual region of origin ¹				
	100-150 (N=38)	170-190 (N=28)	200-220 ² (N=50)	230-280 (N=47)	300-310 (N=16)
100-150	82	14	0	0	6
170-190	8	71	6	2	0
200-220	3	4	64	17	6
230-280	3	7	22	68	13
300-310	5	4	8	13	75

¹Refer to Figure 3.

²Includes one specimen from "southeastern Bering Sea," for which location was not specified.

Table 6.—Classification function coefficients (Fisher's linear discriminant functions) resulting from discriminant analyses of skulls of male and female *vitulina*, grouped by geographical areas.

Sex	Variable ¹	Geographical group ²				
		100-150 (N=16)	170-190 (N=13)	200-220 ³ (N=11)	230-280 (N=20)	300-310 (N=9)
Males	1	0.616	0.608	0.556	0.574	0.596
	2	-0.242	-0.240	-0.171	-0.189	-0.235
	9	-0.293	-0.299	-0.282	-0.295	-0.250
	16	-0.288	-0.267	-0.314	-0.302	-0.323
	24	0.861	0.838	0.844	0.785	0.774
	29	-0.152	-0.025	-0.207	-0.132	-0.090
	31	0.214	0.101	0.188	0.141	0.334
	35	0.409	0.395	0.412	0.376	0.381
	Constant	-700.551	-676.579	-628.634	-604.483	-637.337
	Females	2	0.146	0.164	0.184	0.187
14		0.479	0.384	0.365	0.396	0.405
16		0.240	0.189	0.135	0.126	0.177
22		1.022	1.045	0.970	0.936	0.875
24		0.765	0.741	0.691	0.675	0.717
25		0.593	0.546	0.572	0.556	0.571
28		0.932	1.014	1.074	0.960	1.034
31		0.802	0.689	0.664	0.666	0.815
32		1.092	1.176	1.026	1.012	0.997
37		-8.823	-7.571	-6.449	-6.576	-7.482
Constant	-601.158	-575.862	-528.916	-507.420	-531.924	

¹Refer to Figures 1 and 2.

²Refer to Figure 3.

³Includes one specimen from "southeastern Bering Sea," for which location was not specified further.

affinity between adjacent groups was indicated by about 10 to 20% of incorrect placements, this did not occur between groups 2 and 3. That is, the seals from Hokkaido to the eastern Aleutian Islands appeared to be a craniologically interrelated unit, divergent from the other interrelated unit in the Gulf of Alaska to Mexico. This appeared to confirm Chapskii's (1967, 1969) predictions that the delimitation of *stejnegeri* from *richardsi* would be found at or near the eastern end of the Aleutian Islands.

Cluster Analysis: *vitulina* Polytype

Using the 14 variables identified by the factor analysis for each sex, we submitted *vitulina* to a cluster analysis, which grouped the individual specimens by similarity. For each sex, the specimens tended to be clumped into two primary clusters (I and II), each of which was made up of two secondary clusters (A-B and C-D), as shown in Figures 5 and 6. The compositions of the clusters, in terms of specimens drawn from each of the geographical areas, were similar between sexes but not identical (Table 7).

For the sexes combined, the larger (I) of the primary clusters included 58 (92%) of the specimens from eastern Asia and the Aleutian and Pribilof Islands (areas 100-190), but they also included 17 (71%) of the specimens from the southern coast of the Alaska Peninsula to Kodiak Island (area 210) and 13 (93%) of those from California (area 300). Specimens from the rest of the western coast

of North America, between southern Alaska and Washington State, were poorly represented in primary cluster I, but they made up most of primary cluster II for both sexes. Included in cluster II were 38 (79%) of the specimens from localities between Cook Inlet and the coast of Washington (areas 220-280) and both of the specimens from Mexico (area 310); Asian and Aleutian specimens were very poorly represented. The specimens from the Pribilof Islands and Bristol Bay (areas 170, 200) had questionable affiliations. All of the females from the Pribilofs and the males from Bristol Bay were placed in primary cluster I with the Asian-Aleutian group, whereas the one Pribilof male and most of the Bristol Bay females we placed in primary cluster II with the North American group.

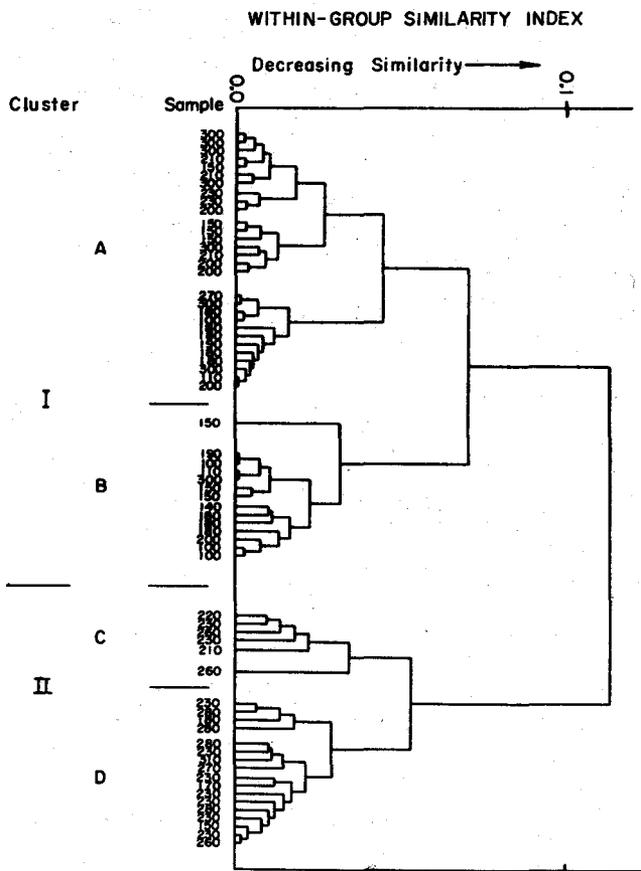


Figure 5.—Dendrogram of results of Q-mode cluster analysis of 66 male seals of the *Phoca vitulina* group in the North Pacific region. The individual specimens making up the primary clusters (I and II) and secondary clusters (A to D) are listed along the vertical axis by the numerical code for the area where they were collected (see Fig. 3).

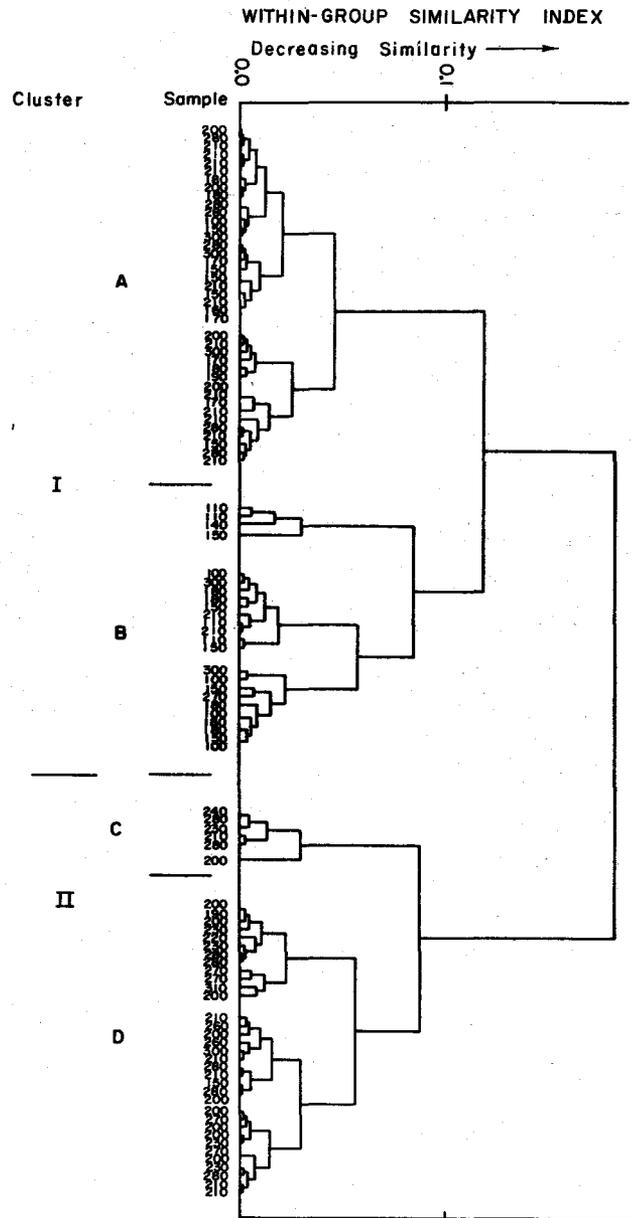


Figure 6.—Dendrogram of results of Q-mode cluster analysis of 104 female seals of the *Phoca vitulina* group in the North Pacific region. The individual specimens making up the primary clusters (I and II) and secondary clusters (A to D) are listed along the vertical axis by the numerical code for the area where they were collected (see Fig. 3).

Table 7.—Numbers of specimens per sex/area making up the two primary clusters of Pacific harbor seals, as indicated by the cluster analysis.

Area ¹	Primary cluster I		Primary cluster II	
	Male	Female	Male	Female
100	4	5	0	0
110	2	4	0	0
140	1	1	0	0
150	7	10	1	1
160	0	1	0	0
170	0	4	1	0
180	8	8	1	0
190	2	1	0	1
200	5	4	0	10
210	3	14	1	6
220	0	0	1	1
230	2	0	9	5
240	0	0	0	1
260	0	0	3	2
270	1	1	1	4
280	0	6	4	7
300	8	5	0	1
310	0	0	1	1

¹Refer to Figure 3.

In the secondary clusters, the specimens from the coast of Asia (areas 100-140) were placed mainly in cluster B, whereas those from the Commander and Aleutian Islands (areas 150, 180, 190) were about equally distributed in A and B (Table 8). The majority from the Pribilof Islands (area 170), Bristol Bay (area 200), and the Alaska Peninsula-Kodiak area (210) were split about 60/40 between clusters A and D, respectively. The majority of specimens from Cook Inlet to Washington (areas 220-280) were placed in cluster D. A minority of the Alaskan specimens (220-260) was placed in cluster C, and of British Columbia-Washington specimens (270, 280), in cluster A. Accordingly, most of the specimens from California and Mexico (areas 300, 310) were placed in clusters D and A.

These results, like those from the discriminant analyses, further describe the clinal nature of craniological variation within the *vitulina* polytype. They indicate that the Commander-Aleutian seals are most uniform, and that the boundary between the *stejnegeri* and *richardsi* phenotypes definitely is not in Near Strait, as supposed by Allen (1902); neither does it appear to be in the vicinity of Kamchatka Strait. The representation of geographical samples in the

Table 8.—Relation of the three forms of Pacific harbor seals (as originally defined) to the composition of the secondary clusters, as indicated by the percent of specimens from the regional samples in each cluster.

Phenotype ¹	Area code ²	N	Percent in secondary clusters			
			A	B	C	D
<i>stejnegeri</i>	100,140	17	18	82	0	0
	150	19	47	42	0	10
<i>richardsi</i>	180,190	21	48	43	0	9
	³ 170,200,210	49	57	6	6	31
	220-260	* 24	8	0	29	63
	270,280	24	29	4	8	58
<i>geronimensis</i>	300	11	82	18	0	0
	300,310	5	20	20	0	60

¹As defined by Allen (1902) and Doult (1942).

²Refer to Figure 3.

³Includes one specimen from "southeastern Bering Sea," for which the exact locality was not specified.

clusters suggests that a steepening of the cline between the comparatively stable Aleutian-Asian series and the highly variable North American series takes place between the eastern Aleutian Island and the Alaska Peninsula. A significant discontinuity in relationships is shown in that area also by the pair-matrix of specimens in the clusters (Fig. 7). Specimens from Asia and the Commander and Aleutian Islands (ACA) were paired in the clusters very significantly more often with specimens from that same region than with those from farther east, on the Pribilof Islands and the North American continent (PNA) (ACA=39/57, PNA=17/113; $\chi^2=46.48$, $df=1$, $P<0.001$).

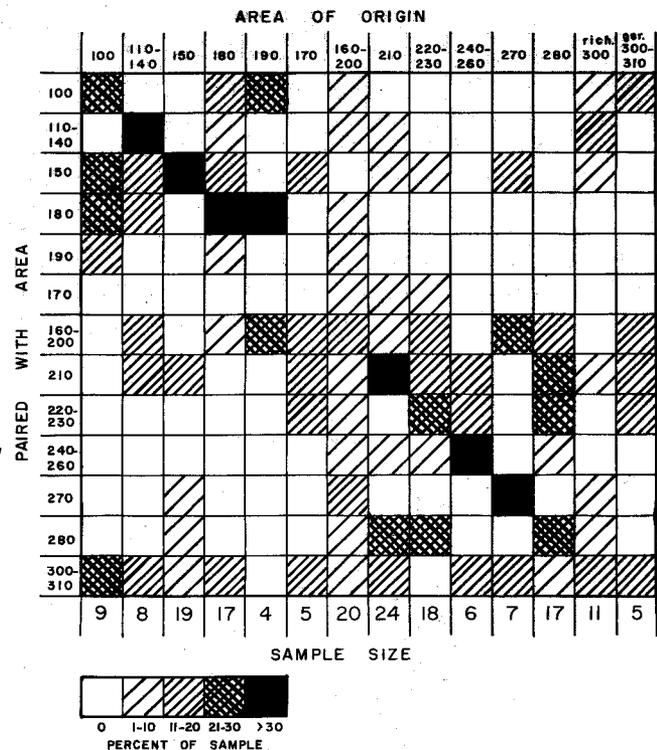


Figure 7.—Pairing frequency matrix from cluster analysis (both sexes) of North Pacific *Phoca vitulina*. Shading indicates comparative percentages of specimens from each geographic sample that were paired (as most similar) with specimens from their own or other localities.

Discriminant Analysis of Secondary Clusters

We performed a discriminant analysis on the four secondary clusters for each sex to identify the characters that contributed the most to their grouping. The most powerful variables in the first function for females were (in descending order of importance) numbers 16 (snout width), 22 (bulla length), 2 (palatal length), and 8 (mandible length); for males, they were 16, 8, 9 (coronoid height), and 35 (jugal length).

The clusters tended to be ordered by size (Table 9). For both the males and the females, the largest skulls were those from the Asian-Commander-western Aleutian seals (cluster B); the smallest (cluster C) were mostly from seals taken in Prince William Sound to southeastern Alaska. A comparable geographical trend in size was shown by Burns and Gol'tsev (1984) for body length.

Table 9.—Means and standard deviations (mm) of the four principal diagnostic variables in the first discriminant function for each sex among the secondary clusters A to D, shown in Figures 5 and 6.

Sex	Principal character ¹	Secondary clusters			
		A (N=29M,40F) mean±SD	B (N=14M,24F) mean±SD	C (N=6M,6F) mean±SD	D (N=17M,34F) mean±SD
Male	16	471.5±30.7	531.0±25.8	390.3±14.8	427.8±19.6
	8	1,534.5±51.4	1,624.7±36.1	1,373.5±29.1	1,447.6±44.7
	9	737.4±47.4	793.5±37.4	618.3±19.1	655.0±28.1
	35	658.3±30.7	705.5±23.9	584.5±42.9	610.9±22.4
Female	16	409.8±17.4	446.5±22.4	356.2±15.6	375.5±17.9
	22	399.5±20.6	415.3±21.5	367.0± 9.7	381.2±13.0
	2	935.2±34.3	969.4±33.0	843.3±28.4	883.3±44.3
	8	1,392.2±39.8	1,463.0±44.9	1,271.0±53.5	1,325.9±44.2

¹Refer to Figures 1 and 2. 16=snout width, 8=length of mandible, 22=length of bulla, 9=coronoid height, 2=palatal length.

DISCUSSION

The harbor or common seals of the North Pacific Ocean were divided by Scheffer (1958) into two taxa, *Phoca vitulina richardsi* of western North America and *P. v. largha* of eastern Asia, essentially following the conclusions of Doult (1942). Those two taxa were believed to adhere to the coasts and be isolated to some degree from each other in the North Pacific and Bering Sea by the broad expanses of open water in Near and Bering Straits, respectively, where the political boundaries lie between the Soviet Union and Alaska. The anatomical, physiological, and ecological differences between the two forms were not well understood at that time, and the fact that each taxon crossed one of those boundaries and "intruded" into the geographical range of the other was not yet appreciated.

Understanding of the differentiation and geographical distribution of Pacific harbor and spotted seals has been advanced greatly in recent years. We now know that 1) the center of abundance of the spotted seal is in the Okhotsk Sea, whereas that of the Pacific harbor seal is in the Gulf of Alaska, 2) these two taxa are widely sympatric in the southern parts of both the Bering and Okhotsk Seas, even more than was shown by Bigg (1981, fig. 1), and 3) each form maintains its identity clearly in those areas of sympatry. Although both forms haul out at the same time in several of the same locations, even during their respective breeding seasons, they ordinarily do not mix but tend to stay in discrete groups. That they do not interbreed freely is indicated by the scarcity of specimens identifiable as intergrades. Where the two forms coexist in the eastern Bering Sea, parasitological findings also indicate that they are socially and nutritionally divergent (Fay and Furman 1982; Delyamure et al. 1984).

Our analyses of the 11 ratios of cranial measurements selected by Chapskii (1967) for discrimination of harbor from spotted seals showed that *vitulina* tends to be most divergent cranially from *largha* in areas where the two species coexist; it is least divergent where *vitulina* occurs alone. That is, cranial differentiation of Pacific harbor seals from the spotted seals appears to have been enhanced by sympatry. As Shaughnessy and Fay (1977) observed, the same enhancement has taken place in the color of the pelage and in the timing of reproduction and molt.

Thus *P. vitulina* and *P. largha* are now recognizable as sibling species. Superficially, they are very similar and obviously closely related; nevertheless, upon closer inspection they are found to be morphologically, ecologically, socially, and reproductively distinct.

Because of their sibling status, their slight craniological differentiation is ideally suited as the standard for comparison with that among the three North Pacific forms of *vitulina* (i.e., *richardsi*, *stejnegeri*, and *geronimensis*).

Our goal from the outset of this study was to reach a firm, final decision about the taxonomic rank of those three forms. Doult (1942), Scheffer (1958), Chapskii (1960, 1967, 1969), and Mohr (1965) were unable to weigh enough of the evidence needed to reach such a decision because none of them had access to all of the world's collections. Shaughnessy and Fay's (1977) approach was mainly through review of the literature, but they also had already surveyed most of the world's collections, as well as viewed the living seals in many of the different habitats around the North Pacific. Because of insufficient information, however, they were obliged to take the conservative view in concluding that *geronimensis* was just the southern end of a north-south gradient of increasing frequency of dark pelage in *P. v. richardsi*. Likewise, they conservatively concluded that *stejnegeri* might qualify for subspecific status under *P. vitulina*, but it did not appear to meet the requirements for full specific rank because of extensive primary intergradation with *richardsi*. Our conclusions here are similar.

Our analyses indicated that the cranial differentiation among the three forms of Pacific harbor seals was less than that between *vitulina* and *largha*, and that *richardsi* showed the poorest differentiation from *largha*. The specimens from California and Mexico, which included *geronimensis*, were discriminated well by the 37-character analysis, but the samples were too small (3M, 1F) to give reliable results. Slightly larger samples (9M, 7F) from that region were 75% correctly discriminated in the 14-character analysis of geographic groups, but only five of those specimens (2M, 3F) were from the range described by Allen (1902) for *geronimensis* in southern California and Mexico; the rest were from central and northern California, which is within the described range of *richardsi*.

In the cluster analysis, the five specimens of *geronimensis* were paired with some from Hokkaido, Bristol Bay, Kodiak, Prince William Sound, and California. The specimens of *richardsi* from central and northern California were paired with a similarly broad geographical series. The relationships of both forms were so diverse and so similar that no discreteness was indicated. Hence, we feel that even with larger samples, *geronimensis* probably would not qualify as a subspecies; it appears to be simply the terminal ecomorph in a long, unbroken cline of *richardsi* in western North

America. Certainly, *geronimensis* is much less divergent from *richardsi* than is *stejnegeri*, and the latter's differentiation appears to be of no more than subspecific rank.

The skulls of *stejnegeri* (Commander Islands to Hokkaido) showed differentiation from *richardsi* nearly as great as that between *richardsi* and *largha*, mainly in size. Belkin (1964), McLaren (1966), and Naito and Nishiwaki (1972, 1973) argued for recognition of the large, black seals of the Kuril Islands as a full species, *Phoca insularis* or *P. kurilensis* (= *stejnegeri*), primarily on the basis of marked differentiation from *P. largha* of the Okhotsk Sea. Not necessarily in disagreement but with a broader biogeographical overview, Mohr (1965), Chapkii (1969), Burns and Fay (footnote 4), Kosygin et al. (footnote 5), and Shaughnessy and Fay (1977) responded that the Kuril seal appeared to be conspecific with *P. v. richardsi* and possibly was just the western end of a cline of morphological variation that extends from the Gulf of Alaska to Hokkaido.

The relationship of the Kuril seal to the Pacific harbor seal of western North America is no longer a point of contention, but the degree of that relationship is a question that has not yet been answered to the satisfaction of all parties concerned. In this study, every analysis that we conducted confirmed that the Kuril seal (*stejnegeri*) is well enough differentiated from the harbor seals of western North America (*richardsi*) to qualify for subspecific rank, but in our opinion the requirements for a full species were not met. Although typically large, dark *stejnegeri* of the Kuril Islands may be quite different in appearance from the typically small, pale *richardsi* of Prince William Sound, e.g., they live in similar habitats, behave in similar ways, and both are clearly identifiable as "harbor seals" from their anatomical conformity (in about equal degrees) with *Phoca vitulina* of the North Atlantic Ocean.

The typical *stejnegeri* and *richardsi* are allopatric, but they are not isolated. In the 6,000 km between them is a long series of freely interbreeding populations, in which the diagnostic characters of those two phenotypes vary clinally in degree and/or frequency of occurrence, from the one extreme to the other. Our discriminant analyses appeared to define some sort of "discontinuities" in the cline between the two phenotypes, on the one hand in Near Strait (as assumed by Allen 1902) and on the other in the vicinity of Unimak Pass (as predicted by Chapkii 1967). The discontinuity in Near Strait certainly was not a natural break in the gradient; it was the product of our choice of a potential boundary between *stejnegeri* and *richardsi*, based on Allen's (1902) diagnosis and Shaughnessy and Fay's (1977) assessment of geographic barriers. The other discontinuity, in the vicinity of Unimak Pass, was partly attributable to our grouping of samples, but it was more strongly expressed than any other in the discriminant analyses.

The best indicator of natural discontinuities in the east-west cline was the cluster analysis, because it was not biased by our geographical compartmentalization of the samples. For both sexes, the specimens sorted out into essentially four clusters, which bore some resemblance to the previous geographical groups. More than 90% of the Hokkaido-Kuril-Commander-Aleutian specimens were contained in the first primary cluster; the second primary cluster held about two-thirds of those from the North American coast. Least distinctive were the specimens from the intervening region, the southeastern Bering Sea and Alaska Peninsula, which were almost evenly distributed between the two primary clusters. This intermediacy suggested a point of demarcation between the eastern and western forms in the vicinity of the eastern Aleutians-Alaska Peninsula. A strong discontinuity in that region was indicated also by the makeup of the secondary clusters and was strongly confirmed

further by the matrix of paired specimens in the clusters. Because the cline in ratio of color phases also appears to be much steeper in the eastern Aleutians than elsewhere (Shaughnessy and Fay 1977, fig. 3), we suggest that this is the most probable location for a genetic "boundary" between *P. v. stejnegeri* (Allen 1902) and *P. v. richardsi* (Gray 1864), if such a boundary exists.

We are skeptical still about the existence of that boundary, because the present series of specimens is not uniformly representative of seal populations throughout the region. That is, we cannot rule out the possibility that the perceived discontinuity is simply the result of uneven sampling. In these analyses, the specimens from area 180 (western Aleutians) were mostly (16/17) from Amchitka and Adak Islands, some 800 to 1,100 km west of Unalaska Island, where most (3/4) of the specimens for area 190 (eastern Aleutians) were taken. For areas 200 and 210, the samples were principally from Port Heiden (12/19) and Tugidak Island (24/24), respectively, which are about 700 to 800 km east of Unalaska. Thus, the largest samples were from localities 1,500 to 1,900 km apart, and the genetic discontinuity indicated by them may, in actuality, be nonexistent. The whole range of morphologically intermediate forms could be present in that 1,500 to 1,900 km gap. In our opinion, study of many additional specimens from that region will be needed before a firm decision can be reached about the boundary between *richardsi* and *stejnegeri*.

ACKNOWLEDGMENTS

We thank especially the many colleagues and curatorial personnel of the museums and smaller collections who generously made available to us more than half of the specimens used in this study. Many of the rest were collected by us, by K. W. Pitcher of the Alaska Department of Fish and Game, and by other co-workers, with logistic support principally from the Alaska Department of Fish and Game, the United States Coast Guard, the U.S. National Science Foundation, and the Soviet Ministry of Fisheries. We are grateful for advice on statistical procedures received from I. V. Frohne, and from S. J. Harbo, Jr., D. B. Hawkins, A. A. Hoover, I. A. McLaren, and E. H. Miller, who also assisted us by critically reading an earlier draft of this paper. Computer programming services were provided by G. Hanson, L. R. Miller, and J. A. Venable. Our work was sponsored in part (Burns and Fay) by the Alaska Sea Grant Program, the U.S. Marine Mammal Commission, the Alaska Department of Fish and Game, and the University of Alaska, and in part (Fedoseev) by the Soviet Ministry of Fisheries, Pacific Research Institute of Fisheries and Oceanography, Magadan Section.

LITERATURE CITED

- ALLEN, J. A.
1902. The hair seals (family Phocidae) of the North Pacific Ocean and Bering Sea. Bull. Am. Mus. Nat. Hist. 16:459-499.
- BELKIN, A. N.
1964. A new species of seal from the Kuril Islands—*Phoca insularis* sp. n. Dokl. Akad. Nauk SSSR 158:1217-1220.
- BIGG, M. A.
1969. The harbour seal in British Columbia. Fish. Res. Board Can., Bull. 172, 33 p.
1981. Harbour seal *Phoca vitulina* Linnaeus, 1758 and *Phoca largha* Pallas, 1811. In S. H. Ridgway and R. J. Harrison (editors), Handbook of marine mammals, Vol. 2 Seals, p. 1-27. Acad. Press, Lond.
- BISHOP, R. H.
1967. Reproduction, age determination, and behavior of the harbor seal, *Phoca vitulina* L., in the Gulf of Alaska. M.S. Thesis, Univ. Alaska, Fairbanks, 121 p.

- BURNS, J. J., and V. N. GOL'TSEV.
1984. Comparative biology of harbor seals, *Phoca vitulina* Linnaeus, 1758, of the Commander, Aleutian, and Pribilof Islands. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:17-24.
- BYCHKOV, V. A.
1971. Review of the status of pinnipeds of the fauna of the USSR. In L. K. Shaposhnikov, V. A. Borisov, L. V. Zhirnov, and N. V. Shkarban (editors), Scientific elements of nature conservation, p. 59-74. Ministerstvo Sel'skogo Khozyaistvo, Moscow.
- CHAPSKII, K. K.
1955. An attempt at revision of the systematics and diagnostics of seals of the subfamily Phocinae. Tr. Zool. Inst. Akad. Nauk SSSR 17:160-199.
1960. Morphologie systematique, differenciation intra-specificque et phylogeneze du sous-genre *Phoca sensu stricto*. Mammalia 24:343-360.
1967. Morpho-taxonomic characteristics of the pagetoda form of the Bering Sea larga. In K. K. Chapskii and M. Y. Yakovenko (editors), Investigations of marine mammals, p. 147-176. Polyarnaya Pravda, Murmansk.
1969. Taxonomy of seals of the genus *Phoca sensu stricto* in the light of contemporary craniological data. In V. A. Arsen'ev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 294-304. Nauka, Moscow.
- DELYAMURE, S. L., M. V. YURAKHNO, V. N. POPOV, L. M. SHULTS, and F. H. FAY.
1984. Helminthological comparison of subpopulations of Bering Sea spotted seals, *Phoca largha* Pallas. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:61-65.
- DOUTT, J. K.
1942. A review of the genus *Phoca*. Ann. Carnegie Mus. 29:61-125.
- FAY, F. H., and D. P. FURMAN.
1982. Nasal mites (Acari:Halarachnidae) in the spotted seal, *Phoca largha* Pallas, and other pinnipeds of Alaskan waters. J. Wildl. Dis. 18:63-68.
- FISHER, H. D.
1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Fish. Res. Board Can., Bull. 93, 58 p.
- INUKAI, T.
1942. Hair seals from the northern waters of Japan. [In Jpn.] Shokubutsu Oyobi Dobutsu 10:927-932, 1025-1030. (Engl. transl., Marine Mammal Div., Northwest Alaska Fish. Cent., Seattle, Wash.)
- McLAREN, I. A.
1966. Taxonomy of harbor seals of the western North Pacific and evolution of certain other hair seals. J. Mammal. 47:466-473.
- MOHR, E.
1965. Über *Phoca vitulina largha* Pallas, 1811 und weissgeborene Seehunde. Z. Säugetierkd. 30:273-287.
- NAITO, Y., and M. NISHIWAKI.
1972. The growth of two species of the harbour seal in the adjacent waters of Hokkaido. Sci. Rep. Whales Res. Inst. Tokyo 24:127-144.
1973. Kurile harbour seal (*Phoca kurilensis*). In Seals: Proceedings of a working meeting of seal specialists on threatened and depleted seals of the world, held under the auspices of the Survival Service Commission of IUCN, p. 44-49. Int. Union Conserv. Nature Nat. Resour. Publ., n.s., Suppl. Pap. 39.
1975. Ecology and morphology of *Phoca vitulina largha* and *Phoca kurilensis* in the southern Sea of Okhotsk and northeast of Hokkaido. In K. Ronald and A. W. Mansfield (editors), Biology of the seal, p. 379-386. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, and D. H. BENT.
1975. Statistical package for the social sciences. 2d ed. McGraw-Hill Book Co., N.Y., 675 p.
- PARKS, J. M.
1970. Fortran IV program for Q-mode cluster analysis on distance function with printed dendrogram. Kansas Geol. Surv. Computer Contrib. 46, 32 p.
- SCHEFFER, V. B.
1958. Seals, sea lions, and walruses; a review of the Pinnipedia. Stanford Univ. Press, Stanford, Calif., 179 p.
- SHAUGHNESSY, P. D., and F. H. FAY.
1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool. (Lond.) 182:385-419.

APPENDIX I

Sources and Acquisition Numbers of Harbor and Spotted Seal Specimens Used in These Analyses

Harbor Seals

Alaska Department of Fish and Game (ADF&G), Anchorage and Fairbanks, Alaska, USA. (The transfer of specimens to the Geist Museum, University of Alaska, Fairbanks, is in progress.)

Males: 66-20, S-00, S-33, B-4, B-5, B-41, PWS-73-3, PWS-16-75, PWS-19-75, PWS-26-75, PWS-32-75, PWS-76-75, PWS-78-75, PWS-82-75, PWS-107-75, 12-6-65, AH-17-72, AH-10-73, AH-39-73, AH-52-73, AH-56-73, AH-9-74, AH-9a-74, JNO-2-72, JNO-12-72, JNO-13-72, JNO-18-72, JNO-19-72, HS-72-1, HS-72-3, HS-72-6, HS-72-15, N-7-68, CR-3-75, CR-23-75.

Females: 66-12, 66-21, 66-22, 66-23, 66-25, 66-29, 66-30, 66-31, 66-34, 66-39, A-7, A-26, A-27, A-34, A-36, B-1, B-12, B-15, B-16, B-17, B-18, B-27, B-28, B-29, B-30, B-32, B-35, B-37, B-39, PWS-73-13, PWS-73-15, PWS-14-75, PWS-85-75, AH-6-68, AH-21-72, AH-2-73, AH-11-73, AH-23-73, AH-28-73, AH-33-73, AH-35-73, AH-36-73, TU-1-71, TU-2-71, HS-72-4, HS-72-5, JNO-1-68, JNO-20-72, AMC-1-69, N-10-68, CR-2-75, NAN-4-73, KSK-27-73, ADF&G-1, 019, 020, 100, 101, 102, 103, 104, 105, 106.

All-Union Research Institute of Fisheries and Oceanography (VNIRO), Moscow, USSR.

Females: 3484, 29112.

Black Douglas Mammal Collection (BDM), National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Wash., USA.

Females: BDM-1272.

California Academy of Science (CAS), San Francisco, USA.

Males: 5, 411, 413.

Females: 527, 530, 15934.

Carnegie Museum (CMP), Pittsburgh, Pa., USA.

Female: 18738.

Fisheries Research Board of Canada (FRBC), Arctic Biological Station, Ste. Anne de Bellevue, Quebec, Canada.

Male: HS8.

Geist Museum, University of Alaska (GMUA), Fairbanks, USA.

Males: 3409, 7265, 7304.

Females: 3702, 7264.

Los Angeles County Museum (LACM), California, USA.

Females: 9539.

Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Mass., USA.

Male: 6157.

Female: 11455.

Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, USA.

Males: 101090, 114778, 140849, REJ-439.

Females: REJ-454, REJ-681.

National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA.

Males: 81515, 140401, 140402, 140403, 146430, 146432, 147700, 253045, 273532, 274152, 274155, 275176.

Females: 81517, 81518, 146433, 146434, 147680, 219868, 219873, 219874, 245915, 250712, 250713, 253042, 253043, 253046, 261781, 274146, 276362, 276365.

Ocean Research Institute (ORI), University of Tokyo, Japan.

Males: 69-6, 70-186, 70-208, 70-223, 70-228.

Females: 69-NE3, 70-13, 70-20, 70-35, 70-155, 70-168, 70-187, 70-222.

Pacific Research Institute of Fisheries and Oceanography (TINRO), Magadan, USSR.

Males: 57-1964, 80-1964, 26-1975, 33-1975, 34-1975, 35-1975, 39-1975, 47-1975.

Females: 225, 389, 1-1964, 27-1964, 43-1964, 83-1964, 86-1964, 3-1975, 10-1975, 11-1975, 13-1975, 14-1975, 18-1975, 20-1975, 24-1975, 27-1975, 28-1975, 29-1975, 40-1975, 45-1975, 46-1975.

Puget Sound Museum of Natural History, University of Puget Sound (UPSMNH), Tacoma, Wash., USA.

Males: 15182, 16040, 16043, 16103, 16430.

Females: 15211, 15274, 16039, 16041, 16044, 16054, 16096.

Dr. Robert L. Rausch (RLR), University of Washington, Seattle, USA.

Male: 39716.

Females: 39715, R11332.

Charles A. Repenning, United States Geological Survey, Menlo Park, Calif., USA.

Male: 6842.

Santa Barbara Museum of Natural History (SBMNH), California, USA.

Females: 251, 258, 1895.

University of Arizona (UAZ), Tucson, USA.

Males: 01, 22799.

Vertebrate Museum; University of British Columbia (VMUBC), Vancouver, Canada.

Males: 1470, 7339.

Females: 2159, 2167, 2168, 9530, 9539, 9540, 9541.

Zoological Institute, Academy of Sciences (ZIAS), Leningrad, USSR.

Males: 835, 2679, 26977.

Zoological Museum, University of Moscow (ZMUM), USSR.

Male: 45050.

Spotted Seals

ADF&G

Males: D-55-65, N-10-66, N-30-67, D-191-67, AH-63-73, AH-1-74, AH-2-74.

Females: N-12-66, N-17-66, N-51-67, G-9-69, N-26-72, AH-27-72, AH-28-72, NAN-3-73.

CMP

Male: DC-1586.

FRBC.

Female: PV-410.

GMUA.

Male: 1529.

ORI.

Males: 69-42, 69-49, 70-69, 70-107.

Females: 70-50, 70-56, 70-58.

TINRO.

Females: 7-1975, 41-1975.

USNM.

Males: 219885, 290655.

Females: 219865, 290653.

ZIAS.

Males: 3487, 3491, 29117.

ZMUM.

Males: 10095, 45024, 69371.

Females: 29925, 45025.

NOAA Technical Report NMFS 12



**Soviet-American Cooperative
Research on Marine Mammals.
Volume 1 - Pinnipeds**

*Under Project V.6. Marine Mammals,
of the US-USSR Agreement on Cooperation
in the Field of Environmental Protection*

Francis H. Fay and Gennadii A. Fedoseev (Editors)

September 1984

U.S. DEPARTMENT OF COMMERCE

Malcolm Baldrige, Secretary

National Oceanic and Atmospheric Administration

John V. Byrne, Administrator

National Marine Fisheries Service

William G. Gordon, Assistant Administrator for Fisheries