SUBSPECIES OF THE SEA OTTER, *ENHYDRA LUTRIS*[1]

By ARYAN I. ROEST[2]

ABSTRACT: Two subspecies of *Enhydra lutris* are recognized: *E. l. lutris,* found from the Commander Islands through the Aleutians to Prince William Sound, and with a disjunct population along the California coast; *E. l. gracilis,* occurring in the Kurile Islands and extreme southern Kamchatka. Although the California population has some distinctive features, it represents the southern extreme of a cline which originally involved a continuous distribution of otters along the entire Pacific coast of North America.

The sea otter *(Enhydra lutris)* originally ranged along 6000 miles of the Asian and North American coastline, from northern Hokkaido to Baja California. Intensive hunting, for the fur trade, brought the species to the verge of extinction by the middle of the 19th century. In spite of its economic importance during this period, few specimens were obtained for scientific collections. Only recently have sufficient specimens become available to permit detailed taxonomic studies.

Three subspecies of *Enhydra lutris* have been described, all based on relatively small samples. The sea otters of central Kamchatka, the Commander Islands, and the Aleutians are considered the nominate race, *E. l. lutris* (Linnaeus) by Barabash-Nikiforov (1947), Miller and Kellogg (1955), and Hall and Kelson, (1959). Barabash-Nikiforov (1947) re-established *E. l. gracilis* (Bechstein), on the basis of five specimens from Cape Lopatka, Kamchatka. Merriam (1904) based his description of *E. l. nereis* on a single skull from the coast of California. Scheffer and Wilke (1950) questioned the validity of *E. l. nereis* after examining eight skulls from Washington, Oregon, and California; their conclusions were ignored by several later authors. Both of the two preceding references mention a size difference between Alaskan and Californian skulls, but present little data. The size of Aleutian otters was also discussed by Scheffer (1951), Lensink (1962), and Kenyon (1969). Miller and Kellogg (1955) recognized both *E. l. lutris* ('Kamchatka to western Aleutian Islands, Alaska') and *E. l. nereis* ('Washington, Oregon, and California coasts'). Hall and Kelson (1959) also recognized both subspecies, but indicated that *E. l. lutris* occurred along the Alaskan coast as far south as British Columbia, as well as in the Aleutians. Roest (1971) considered *E. l. nereis* to be a valid form during the earlier stages of the present study.

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Full protection has allowed sea otter populations to increase during the past 50 years, and adequate series of specimens from Alaska and California are now available for study. The present work re-examines the status of subspecies in the sea otter after a study of 267 Alaskan and Californian skulls, all adults. Data from most of these specimens was subjected to modern statistical analyses.

Alaskan specimens came from Amchitka and Adak Islands, in the Aleutians, and from the Alaska Peninsula, southern Alaska, and Prince William Sound (the latter regions are collectively termed southwestern Alaska below).

METHODS

A skull was considered adult if the basioccipital-basisphenoid suture was closed, since this suture closes at an age of about three years (Lensink, 1962). Twenty-four measurements were taken on each skull, in millimeters. Total length of many specimens was available, in centimeters, and was also used in preliminary analyses. Weight, in pounds, was known for a number of Alaskan specimens, largely from animals weighed shortly after being collected. Only a few weights were available for California animals, mostly from animals found dead on the beach for various undetermined periods of time. Since weight is a characteristic which depends greatly on the condition of the animal prior to death (Kenyon, 1969), it was not used in the analyses. However, available weight data are presented in Table 1.

TABLE 1.
Weights of sea otters from four localities, in pounds

	Males			Females		
Locality	*N*	*Mean*	*Range*	*N*	*Mean*	*Range*
Adak	17	72.4	59-89	43	47.0	35-74
Amchitka	2	69.0	65-73	23	47.0	38-55
S. W. Alaska	12	76.9	47-96	1	49.0	—
California	5	56.0	38-74	9	44.4	27-63

Stepwise Discriminant Analysis was used to analyze the data, the specific program being BMDO7M, revised July 24, 1969 (Dixon, 1970). Preliminary analyses indicated that the variables which discriminated (were statistically significant) between different groups of specimens included frontal notch, projecting coronoid, nasal length, and condylobasal length. These four measurements were selected for further analysis because they provided large F values (Table 2) and were of potential taxonomic value. Due to the distinct differences in size between males and females, reflected particularly in condylobasal length, sexes were analyzed separately. Total lengths were also considered separately, but were excluded from the final analyses when it was

TABLE 2

Statistical significance of the four variables submitted together for Stepwise Discriminant Analysis (BMDO7M); sexes were analyzed separately

Variable	*N*	*Degrees of Freedom*		*F value at step 1*
MALES:				
Notch	106	3	102	52.5813
Nasal length	106	3	102	35.9030
Coronoid process	106	3	102	34.8241
Condylobasal length	106	3	102	21.1130
FEMALES:				
Coronoid process	142	3	138	30.2828
Nasal length	142	3	138	18.7986
Notch	142	3	138	17.3719
Condylobasal length	142	3	138	5.7635

learned that there were some differences in the manner in which they were taken. Each of these variables is discussed below.

Frontal notch.—A distinct constriction in the frontal bones just anterior to the braincase was noted in most Alaskan skulls (Fig. 1). Skulls were classified as to whether a notch was present (which was assigned a value of 3 for statistical analysis), only a suggestion of a notch was present (assigned a value of 2), or complete absence of a notch (value of 1). Table 3 indicates the occurrence of a frontal notch in four populations of sea otters.

Projecting coronoid.—Merriam (1904) considered a backward sloping coronoid process a characteristic of *E. l. nereis.* Scheffer and Wilke (1950) felt this distinction was of little value, since they found both sloping and upright processes in their California sample. In the present study it was observed that in mandibles which had a strongly sloping coronoid process, the tip of the process projected posteriorly past the base of the condyloid process, and the posterior edge of the coronoid process was concave in outline. Some mandibles had a coronoid process which extended posteriorly only as far as the base of the condyloid process; in these the posterior edge of the coronoid process was relatively straight. A third group had upright coronoid processes which did not project posteriorly at all, and in which the posterior edge of the process was convex (Fig. 2). Values were assigned to these variations as follows: projecting coronoid—3; coronoid equal to condyloid process—2; upright coronoid—1. The numbers and percentages of specimens which possessed, or lacked, projecting coronoid processes are presented in Table 4.

Nasal length.—Length of the internasal suture line. Even in mature specimens the internasal suture line can usually be discerned. Table 5 presents data on the nasal lengths found in four different sea otter populations.

Condylobasal length.—Distance from the anterior edge of the premaxilla to a line connecting the most posterior projection of the occipital condyles. Condylobasal lengths from five populations are presented in Table 6.

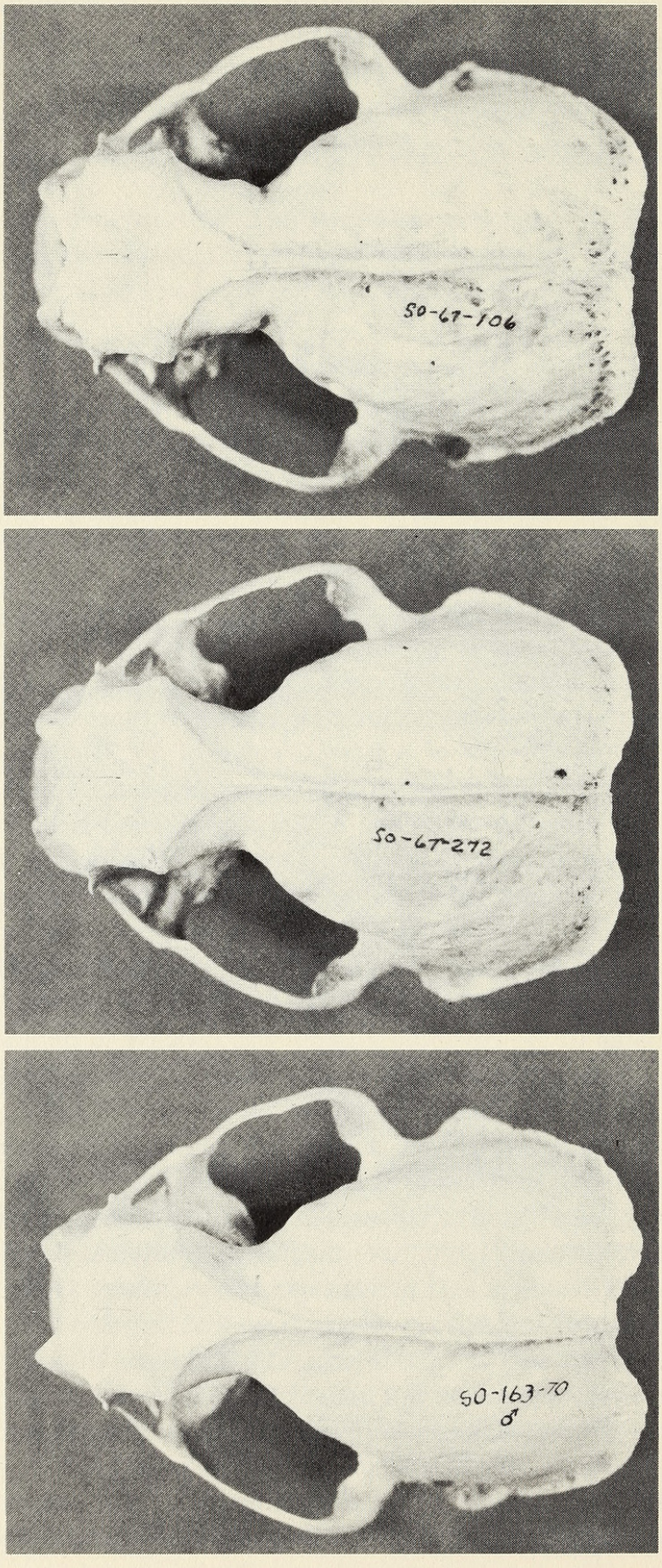
50-67-106
50-67-272
50-163-70
♂

TABLE 3

Occurrence of a frontal notch in sea otters from four localities. M/F indicates males/females

		Present		*Small*		*Absent*	
Locality	*N*	*Number (M/F)*	*%*	*Number (M/F)*	*%*	*Number (M/F)*	*%*
Adak	60	44 (12/32)	73.5	12 (5/7)	20.0	4 (0/4)	6.7
Amchitka	111	88 (33/55)	79.3	16 (2/14)	14.4	7 (3/4)	6.3
S.W. Alaska	41	5 (3/2)	12.2	25 (17/8)	61.0	11 (8/3)	26.8
California	43	3 (1/2)	7.0	7 (2/5)	16.2	33 (23/10)	77.0
Total:	255						

TABLE 4

Projection of coronoid processes in sea otters from four localities. M/F indicates males/females

		Projects		*Equal*		*No Projection*	
Locality	*N*	*Number (M/F)*	*%*	*Number (M/F)*	*%*	*Number (M/F)*	*%*
Adak	60	11 (5/6)	18.3	6 (1/5)	10.0	43 (11/32)	71.6
Amchika	111	6 (2/4)	5.4	14 (9/5)	12.6	91 (27/64)	82.0
S.W. Alaska	37	11 (7/4)	29.7	25 (18/7)	67.5	1 (0/1)	2.7
California	43	34 (22/12)	79.0	7 (3/4)	16.2	2 (1/1)	4.7
Total:	251						

Total length.—Length from the tip of the nose to the tip of the tail. The total lengths of specimens from four different regions are presented in Table 7.

Total lengths of Alaskan and Californian otters in Table 7 are not directly comparable, since most of those from Alaskan specimens are curvilinear, while those from Californian animals are standard lengths. The difference in the two methods of measuring is probably not large, but there is little evidence to indicate its magnitude. One Alaskan specimen (AFG SO 72-13) was measured both ways; it had a curvilinear length of 76 cm and a standard length of 70 cm. Since male Californian otters have standard lengths which are about 20 cm shorter than the curvilinear lengths of male Alaskans, and the standard lengths of female Californians are 11 cm shorter than the curvilinear lengths of female

FIGURE 1. Frontal notch. *Upper*—typical Aleutian skull with a distinct notch clearly visible in the narrowest part of the frontal region. *Middle*—Aleutian skull with a suggestion of a notch. *Lower*—typical Californian skull without a frontal notch; the frontal bones flare smoothly into the cranial region. All three skulls are from adult males. Note also the longer internasal suture of the California specimen (lower).

FIGURE 2. Coronoid process. *Upper*—typical Aleutian mandible with highest point of coronoid process anterior to the base of the condyloid process; posterior edge of coronoid process slightly convex. *Middle*—Aleutian mandible with suggestion of posterior projection of the coronoid process; posterior edge of coronoid process is essentially straight. *Lower*—typical Californian mandible with coronoid process projecting backward; posterior edge of coronoid process concave.

Alaskans, a size difference between otters from the two regions probably exists. It is not as great, however, as the data in Table 7 suggests.

During the early part of this study, very few specimens were available from southwestern Alaska. Comparisons of otters from the Aleutian Islands with those from California led to the conclusion that California otters could be readily distinguished from the Aleutian form, and hence deserved subspe-

TABLE 5

Nasal length in sea otters from four localities, in millimeters

	Males			*Females*		
Locality	*N*	*Mean ± S.D.*	*Range*	*N*	*Mean ± S.D.*	*Range*
Adak	17	17.5 ± 1.16	15.0-19.6	43	16.9 ± 1.64	13.2-20.8
Amchitka	38	16.1 ± 1.90	11.2-19.7	73	16.2 ± 1.65	11.6-20.4
S.W. Alaska	24	19.6 ± 1.35	16.6-22.0	10	18.3 ± 1.21	16.4-20.0
California	27	19.1 ± 1.04	16.7-21.1	16	19.0 ± 0.98	17.2-20.8
Totals:	106			142		

TABLE 6

Condylobasal length in sea otters from five localities, in millimeters. Commander Island data from Stroganov (1962)

	MALES			*Females*		
Locality	*N*	*Mean ± S.D.*	*Range*	*N*	*Mean ± S.D.*	*Range*
Commander Ids.	17	136.5	130-140	7	125.4	120-128
Amchitka	38	135.5 ± 3.29	128-144	73	128.5 ± 3.69	115-136
Adak	17	137.8 ± 3.71	129-144	43	128.2 ± 3.83	121-136
S.W. Alaska	24	136.2 ± 2.75	130-142	10	125.6 ± 2.32	122-134
California	27	130.4 ± 3.90	124-136	16	125.0 ± 2.61	119-130

TABLE 7

Total length of sea otters from four localities, in centimeters. Measurements of Alaskan otters are curvilinear lengths; those of Californian otters are standard lengths. Curvilinear lengths may be 5 to 15 cm longer than standard lengths

	MALES			FEMALES		
Locality	*N*	*Mean ± S.D.*	*Range*	*N*	*Mean ± S.D.*	*Range*
Adak	17	146.5 ± 6.85	135-153	43	131.8 ± 6.08	118-145
Amchitka	2	146.0 ± 2.83	144-148	23	131.2 ± 4.99	121-140
S.W. Alaska	12	145.6 ± 7.08	131-161	3	121.3 ± 6.13	117-130
California	11	127.1 ± 6.19	117-137	11	118.7 ± 6.03	106-127
Totals:	42			80		

cific recognition (Roest, 1971). Subsequently additional material from southwestern Alaska became available in November, 1972 and has been included in the final analyses presented here.

Barabash-Nikiforov (1947), in discussing subspecies in the sea otter, presented some data in terms of percentages of the total length of the skull. Among the measurements he used were condylobasal length, zygomatic width

(width across zygomatic arches), mastoid width (width between mastoid processes), infraorbital width (width between infraorbital foramina), and postorbital width (width between postorbital, or supraorbital, processes). These measurements were also taken on specimens examined in this study. To permit comparisons, all measurements were recalculated as percentages of condylobasal length. Condylobasal length was used instead of total skull length in order to eliminate variation due to the size of the lambdoidal crest in older specimens. The results of these calculations are presented in Table 8.

TABLE 8

Skull ratios of sea otters from various localities, expressed as percentages of condylobasal length. ZW = zygomatic width; MW = mastoid width; IO = infraorbital foramen width; PO = postorbital width; CBL = condylobasal length. Russian localities and "Aleutians" are data recalculated from Barabash-Nikiforov, 1947

Locality	*N*	*Range* ZW/CBL	*N*	*Range* MW/CBL	*N*	*Range* IO/CBL	*N*	*Range* PO/CBL
S. Kamchatka (C. Lopatka)	3	85.9-86.5	4	80.5-83.5	4	37.6-38.8	4	39.9-41.7
Mednyi Island	4	74.7-77.6	4	71.8-74.7	5	32.2-34.8	5	30.2-36.3
Bering Island	1	75.2	1	75.2	1	35.3	1	36.1
Commander Id.	2	71.5-72.0	1	72.0	2	32.8-34.6	2	32.4-33.6
"Aleutians"	5	74.7-80.6	5	73.1-78.0	5	32.2-34.6	5	29.4-35.2
Adak	10	74.3-83.2	10	68.5-76.5	10	32.4-35.3	10	31.6-35.1
S.W. Alaska	18	74.3-80.4	18	72.8-78.8	18	31.2-35.2	18	30.9-37.3
California	18	73.3-80.0	18	67.5-77.5	18	31.2-34.8	18	29.1-34.9

RESULTS AND DISCUSSION

In all analyses, specimens from Amchitka and Adak Islands, in the Aleutians, are not significantly different. This is shown well on the canonical graphs produced by the discriminant analysis program, and reproduced as Figures 3 and 4 (males and females, respectively). Also shown is the fact that California specimens differ from Aleutian animals, but specimens from southwestern Alaska are clearly intermediate. Further indication of the relationship between these sea otter populations is presented in Table 9, which duplicates the discriminant function assignment of individual specimens to specific populations.

Otters from southwestern Alaska are similar to those from the Aleutians in condylobasal length, total length, and weight (Tables 6, 7, 1). They are similar to Californian otters in nasal length (Table 5), and are intermediate between the other two populations in their display of frontal notches and coronoid processes. Examination of the particular combination of characters in skulls from specific localities in southwestern Alaska indicates there may be a slight gradient from more Aleutian features near Umnak Island and along the north shore of the Alaska Peninsula (3 specimens show primarily

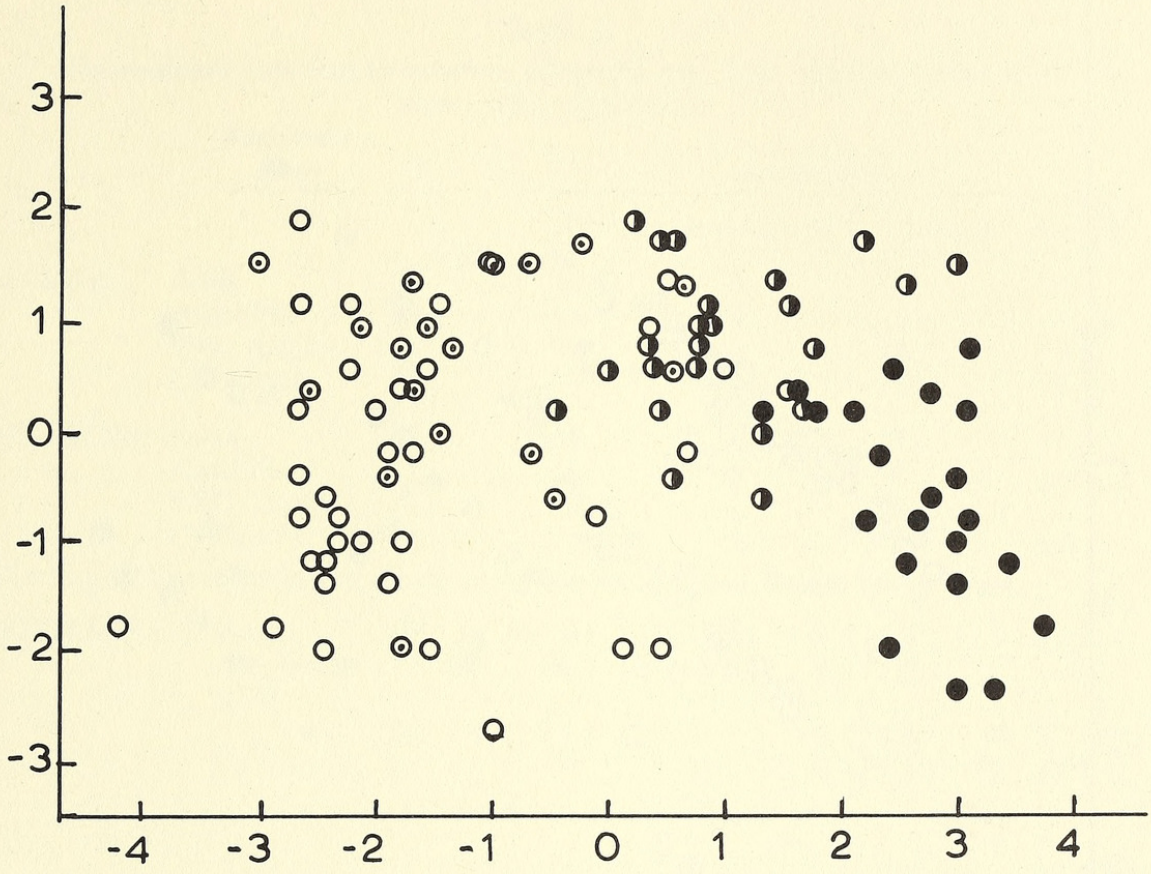

FIGURE 3. Canonical graph produced by BMDO7M Program for male sea otters. Open circle = specimen from Amchitka, dotted circle = Adak, half black circle = southwestern Alaska, solid back circle = California. Abscissa is first canonical axis, ordinate is second.

Alaskan features, 6 are intermediate, and 1 could be considered Californian) toward more Californian features in Prince William Sound (2 Alaskan, 2 intermediate, 12 Californian).

The ratios of skull widths to condylobasal lengths in Alaskan and Californian otters are essentially the same as those of otters from the Commander Islands (Table 8). Condylobasal lengths of Commander Island otters are similar to those from Alaskan animals (Table 6). Barabash-Nikiforov (1947) did not mention frontal notches or coronoid projections, but illustrated skulls from the Commander Islands (Figs. 5, 16, 18) which show a notch in three skulls and a possible notch in a fourth. Projecting coronoids are illustrated by Ognev (1931: Figs. 134, 135), and an 'equal' projection by Barabash-Nikiforov (1947: Fig. 20). Novikov (1956: Fig. 149) and Stroganov (1962: Fig. 72) both illustrate skulls with a frontal notch and mandibles which lack projecting coronoids. The available data indicates that otters from the Commander Islands are essentially similar to those from Alaska, as previously suggested by Barabash-Nikiforov (1947).

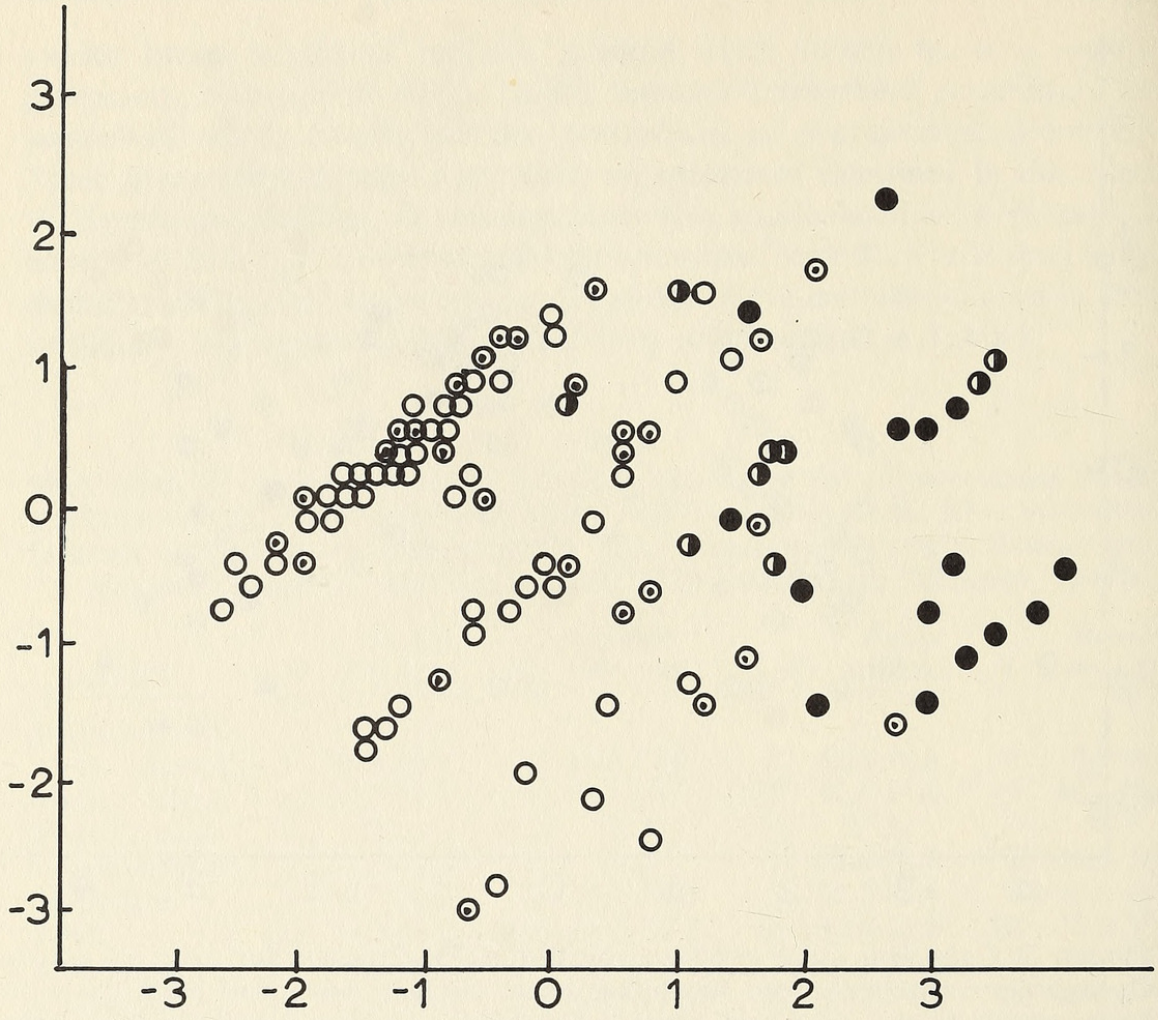

FIGURE 4. Canonical graph produced by BMDO7M Program for female sea otters. Open circle = specimen from Amchitka, dotted circle = Adak, half black circle = southwestern Alaska, solid black circle = California. Abscissa is first canonical axis, ordinate is second.

In addition to skull differences, total length is also greater in Alaskan sea otters. Table 7 indicates that these northern animals are probably about 10 cm longer than those from California, even allowing for the differences generated by taking curvilinear instead of standard length measurements. They are also larger than those from the Commander Islands; Barabash-Nikiforov (1947) indicates a maximum length of only about 144 cm, with the average of adult specimens ranging between 101 and 130 cm, the oldest animals being the largest. However, he does not differentiate between males and females, which undoubtedly resulted in a lower average figure. Among Alaskan and Californian specimens, the size difference is essentially parallel in both sexes, and is reflected also in the weight data (Table 1) and the condylobasal lengths (Table 6).

Barabash-Nikiforov (1947) indicates that the fur of *E. l. lutris* is most commonly dark brown, ranging to nearly black, although occasionally nearly

TABLE 9

Discriminant function assignment of specimens: four skull variables and four otter populations.

	Specimen from	*N*	*Assigned to:*			
			Adak	*Amchitka*	*S.W. Alaska*	*California*
MALES:	Adak	17	10	5	2	—
	Amchitka	38	8	27	3	—
	S.W. Alaska	24	2	—	20	2
	California	27	—	—	5	22
FEMALES:	Adak	43	19	16	7	1
	Amchitka	73	18	49	6	—
	S.W. Alaska	10	2	—	6	2
	California	16	—	—	3	13

Combining the sexes in the above assignments, and calculating percentages:

BOTH SEXES:	Adak	60	29 (48%)	21 (35%)	9 (15%)	1 (2%)
	Amchitka	111	26 (23%)	76 (69%)	9 (8%)	—
	S.W. Alaska	34	4 (12%)	—	26 (76%)	4 (12%)
	California	43	—	—	8 (19%)	35 (81%)

orange individuals are taken. Alaskan otters are also dark, but those from California are most commonly medium brown in color. The fur is grayish at the base, as can be easily determined by parting the hairs to examine the underfur. Kenyon (1969) quotes observations by Victor Scheffer that the pelage is "light smoky gray near the skin, darkening gradually to smoky brown" at the tips. Over 40 fresh pelts of California otters were examined during the present investigation, as well as several tanned skins, and in all cases the underfur was essentially grayish, with a suggestion of brownish or even silvery color, becoming darker at the tips.

In summary, sea otters from the Commander Islands, the Aleutians, southwestern Alaska, and California are all part of a single population which varies from large, dark, short-nasaled forms in the north to smaller, lighter, longer-nasaled forms in the south. This suggests an example of Bergmann's Rule (larger forms of a species in the northern parts of its range). Specimens from near the two ends of this cline (Aleutian Islands and California) can be distinguished from each other on the basis of differences in size, nasal length, shape of coronoid process, and presence or absence of a frontal notch. Merriam (1904) compared specimens from the ends of this cline, and described *E. l. nereis* as a distinct, southern form. Roest (1971) followed suit on the basis of many more specimens from California and the Aleutians. As has happened in the course of studying geographic variation in other species, the subsequent examination of specimens from intervening regions established the existence of intergrade populations. In this case, the intermediate speci-

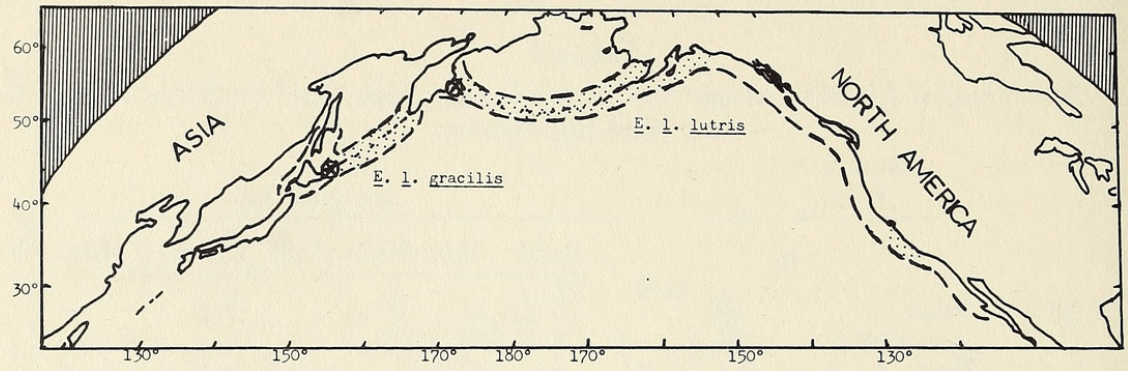

FIGURE 5. Distribution of the sea otter, *Enhydra lutris*. Original distribution includes all areas within the dashed lines. Present distribution indicated by stippling; note small, disjunct population of *E. l. lutris* along the California coast. *E. l. gracilis* is currently restricted to the Kurile Islands and extreme southern Kamchatka. The circled x's indicate the type localities of the two forms.

mens are from southwestern Alaska, which still leaves a distributional gap of 2000 miles southward to California. Examination of otter remains from Indian shell mounds (middens) or similar deposits, from localities between Prince William Sound and Monterey Bay, may provide additional data to support the concept of a cline. For example, Grinnell, Dixon, and Linsdale (1937: Fig. 109) illustrate a skull from a shell mound in Oakland, California, which shows a notch (Aleutian feature) and has nasals over 18 mm long (Californian feature).

Sea otters from southern Kamchatka (Cape Lopatka) have wider skulls than do those from other localities in the North Pacific (Table 8). Since no specimens of this population were personally examined, and none have been illustrated in the Russian literature, it is not known whether they possess any of the cranial features noted in Alaskan and Californian otters. Barabash-Nikiforov (1947) indicated that they are smaller in size than typical *E. l. lutris*, darker in color, and had a distinct reddish tint to the underfur: "the corresponding hair in the Kamchatkan sea otter is a cinnamon hue throughout the entire length, approximating orange or pinkish-cinnamon in tone." He considered these animals to be a distinct subspecies, *E. l. gracilis*, occurring not only in southern Kamchatka but also in the Kurile Islands. Since most authors have considered the range of the sea otter to be continuous from the Kuriles to Baja California, it would be desirable to study the variation of Kurile sea otters to determine whether their broad heads, small size, and reddish underfur are involved in a cline along the western side of the Pacific. Figure 5 indicates geographical ranges.

Some of the differences among various sea otter populations around the rim of the northern Pacific may be due to the fact that all existing otter populations are descendants of small relict groups of survivors from the early fur-trading days. Kenyon (1969) indicates that nine such groups survived into the twentieth century. Each of these groups was reduced to very small num-

bers by the turn of the century, and each may have possessed, by chance, a unique combination of characteristics which had previously occurred in a more general way throughout the entire range of the species. If such a local combination of characters did occur in a restricted group of animals, then their descendants would be likely to retain those features–the 'Founder Effect.' This possibility, combined with the complete geographic and genetic isolation of the California population, may have been instrumental in bringing about the smaller size, lighter color, and longer nasals so prevalent in modern specimens from California.

At the present time there appear to be only two forms of sea otter that merit subspecific recognition. These are discussed below.

SUBSPECIES ACCOUNTS

1. *Enhydra lutris lutris* (Linnaeus)

1758. *Mustela lutris* Linnaeus, Systema naturae, ed. 10, 1:45. Type locality, Kamchatka, U.S.S.R.

1777. *Lutra marina* Erxleben, Systema regni animalis . . . p. 445. Type locality, unknown.

1816. *Pusa orientalis* Oken, Lehrbuch der Naturgeschichte. 3, abt. 2:986.

1827. *Lutra stelleri* Lesson, Manuel de mammalogie, ou histoire naturelle des Mammiferes, p. 156. Type locality, Kamchatka.

1843. *Enhydra lutris,* Gray. List of the . . . Mammalia in the . . . British Museum, p. 72.

1880. *Enhydris marina* Brandt, Beobacht. uber die verschied. Kleider Seeotter, "Melang, Biolog. Bullet. de l'Academ. Imp. de St. Petersb.," 9:15.

1884. *Enhydris lutris,* True, Proc. U.S. Nat. Mus., 7 (App., Circ. 29): 609.

1898. *Latax lutris* Stejneger, The Asiatic fur-seal islands and the fur seal industry, *in* The fur seals and fur seal islands of the North Pacific Ocean, by David Starr Jordan, U.S. Treasury Dept. Doc. 2017, p. 4:29.

1922. *Enhydra lutris kamschatica* Dybowski, Arch. Tow. Nauk. Lwow. 1:350.

1924. *Enhydra lutris lutris* Miller, List of North Amer. Recent Mamm. (1923), U.S. Nat. Mus. Bull. 128:131.

Type locality.–Kamchatka, U.S.S.R. Should probably be restricted to the east central coast of Kamchatka, opposite the Commander Islands.

Distribution.–Currently ranging from the Commander Islands eastward through the Aleutian Islands to the Alaska Peninsula; along the north coast of the Alaska Peninsula to at least Port Heiden; along the south shore of the Alaska Peninsula, Kodiak Island, the Kenai Peninsula, and throughout Prince William Sound to the vicinity of Kayak Island and Cape Suckling; along the

California coast from Monterey Bay south to Morro Bay. Formerly distributed as a continuous population from the central Kamchatka coast eastward through the Aleutians and along the southern coast of Alaska, British Columbia, Washington, Oregon, California, and Baja California to at least Morro Hermoso (27°32′ N. lat.) (Kenyon, 1969).

Descriptive remarks.—Zygomatic and mastoid widths less than 80% of the condylobasal length; infraorbital and postorbital widths less than 37% of the condylobasal length. Underfur grayish.

This form varies clinally from one end of its range to the other. Northern animals are large, while those from California are distinctly smaller (Tables 1, 6, 8). Individual adult males have reached a maximum weight of 46.25 kg (102 lbs.; Schneider, personal communication), although most are between 27 and 36 kg. Maximum length reported is 166 cm curvilinear length (Schneider, personal communication). Nasal lengths vary from about 11 mm in Aleutian specimens to over 21 mm in California animals.

The California population can be distinguished from the Aleutian population, but not from the population in southwestern Alaska. California specimens are smaller than Aleutian animals, have nasal lengths usually over 18 mm, lack a frontal notch, and have coronoid processes which project backwards at an angle.

When the fur of specimens of this form is parted, the underfur thus exposed is characteristically grayish. Typical pelts from northern animals are dark brown to nearly black, while California specimens are usually medium brown.

In the list of *specimens examined,* the following abbreviations have been used to identify collections: ADFG—Alaska Department of Fish and Game, Anchorage, Alaska; CAS—California Academy of Sciences, San Francisco, California; CFG—California Department of Fish and Game (specimens at California Polytechnic State University and at Moss Landing Marine Laboratories); CPSU—California Polytechnic State University, San Luis Obispo, California; HSU—Humboldt State University, Arcata, California; LLU—Loma Linda University, Loma Linda, California; MLML—Moss Landing Marine Laboratories, Moss Landing, California; MML—Marine Mammal Laboratories, Bureau of Sport Fisheries and Wildlife, Seattle, Washington; MVZ—Museum of Vertebrate Zoology, Berkeley, California; PGMNH—Pacific Grove Museum of Natural History, Pacific Grove, California; SBMNH—Santa Barbara Museum of Natural History, Santa Barbara, California; SDMNH—San Diego Museum of Natural History, San Diego, California; SSU—Sacramento State University, Sacramento, California.

Adult specimens examined.—(267) RUSSIA: *Medny Island:* MML—1 specimen, no number. ALASKA: *Amchitka Island:* ADFG-SO-67-305, 349, 351, 364, 365, 368, 380, 387, 390, 391, 394, 407, 411, 436, 443, 445, 446, 450, 455, 456, 461, 478, 485, 490, 492, 497, 498, 500; HSU—3 specimens, no numbers; MML—KWK 59-5, 59-6, 59-16, 59-21, 59-23, 59-34, 59-38, 59-39, 59-40, 59-43, 59-48, 59-49,

59-56, 59-57, 59-64, 59-67, 59-69, 59-71, 59-80, 59-84, 59-90, 59-91, 59-92, 59-94, 59-96, 59-98, 59-100, 59-118, 59-130, 59-134, 60-4, 62-7, 62-11, 62-21, 62-24, 62-47, 62-50, 62-72, 62-77, 62-78, 62-80, 62-89, 62-94, 62-105, 62-111, 62-118, 62-121, 62-124, 62-131, 62-135, 62-136, 62-138, 62-145, 62-147, 62-152, 62-156, 62-159, 62-175, 62-176, 62-184, 62-211, 62-226, 62-268, 62-272, 16-56, 17-56, 19-56, 39-56, 44-56, 46-56, 52-56, 59-56, 70-56, 71-56, 72-56, 73-56, AIWR 4-53, 6-53, 7-53, 9-53, 16-53, 32-53, 33-53, 48-53, 50-53, 54-53, 63-53, 75-53, J-53, K-53, L-53, X-53, 8-54, 42-54, 66-54, 71-54, 37-55, 27-56, JEB 63-80, 63-273, 130-1949, 133-1949; MVZ 113396; *Adak Island:* ADFG SO-67-5, 7, 9, 11, 17, 23, 26, 27, 28, 29, 34, 39, 44, 63, 70, 77, 79, 85, 86, 88, 98, 104, 106, 107, 108, 114, 116, 118, 131, 133, 135, 177, 242, 260, 261, 272, 278, 281, 293; MLML SO-67-22, 195; *St. Paul Island, Pribilof Islands:* ADFG SO-72-7; *Amak Island:* MML, 1 specimen, no number; *Port Moller:* ADFG SO-67-511; *Ilnik:* ADFG SO-71-3, 4, 5, 6; *Port Heiden:* ADFG SO-71-2, 10, 72-1; *Sanak Island:* MML KWK 60-15; *Sandman Reefs:* ADFG CJL 1-58; *Popof Island:* ADFG SO-69-4; *Nagai Island:* MML KWK 60-12, 60-13, 60-14; *Simeonof Island:* MML KWK 60-5, 60-6, 60-8, 60-10; *Tugidak Island:* ADFG SO-66-1, 68-22; *English Bay:* ADFG SO-68-6, 72-5; *Prince William Sound:* ADFG 1 specimen, no number, CJL 1-56, 2-56, No. 1, No. 2, No. 3, 2, 61, 80, 1500, 1501, SO-72-10, 72-12, 72-15, 72-16, 72-17, 72-19, 72-20. CALIFORNIA: *Monterey:* CFG 150-69, 155-69, 175-70, LLU 1 specimen, no number, SBMNH 225, SDMNH 18865; *Hopkins Marine Station:* CFG SO-134-70, 189-70; *Point Pinos:* CFG SO-181-70; *Asilomar:* CFG SO-249-72, PGMNH 2436A, 2439A; *Seventeen-mile Drive:* MLML 412; *Carmel:* CFG SO-98-68, 1 specimen, no number; *Point Lobos:* CFG SO-134-69, 190-69, MVZ 114550, 119829; *Bixby Creek:* MVZ 84812; *Point Sur:* CAS 637, MLML 1225; *Gorda:* MVZ 116213; *San Luis Obispo County:* MVZ 116611; *San Carpoforo Creek:* CFG SO-141-70; *Cambria:* CFG SO-160-69, 186-70; *Cayucos:* CFG SO-248-72; *Morro Bay:* CFG SO-117-69, 159-69, 163-70, CPSU M-263, M-983, MLML 0-3; *Montana de Oro State Park:* CFG SO-187-70; *No specific locality:* CAS 4428, MLML SO-5, 0-7, 494, 495, MVZ 123192, 123194, 123196, 123197, 123198, 123199, SSU 1202, SDMNH 16371.

2. *Enhydra lutris gracilis* Bechstein

1799. *Lutra gracilis* Bechstein, Thomas Pennant's allgemeine Uebersicht der vierfussigen Thiere . . ., v. 2, p. 248. Type locality "Staatenland" (= southernmost of the Kurile Islands: see Hollister, 1921).

1931. *Enhydra lutris,* Ognev, Mammals of eastern Europe and northern Asia, 2:402.

1947. *Enhydra lutris gracilis,* Barabash-Nikiforov, The sea otter, p. 20.

Type locality:—Kurile Islands; possibly Kunashir Island.

Distribution:—The northern Kurile Islands and the southern tip of Kamchatka. Formerly found along the coasts of southern Sakhalin and northern Honshu and Hokkaido, and the southern Kuriles (Barabash-Nikiforov, 1947).

Descriptive remarks:—Smaller than northern specimens of *E. l. lutris,* although about the same size as specimens from California. The largest measurement reported is a condylobasal length of 133.6 mm. This form is distinguished from *E. l. lutris* by its broad head (Table 8). The zygomatic and mastoid widths are greater than 80% of the condylobasal length, and the

infraorbital foramen and postorbital widths are over 37% of the condylobasal length. Another distinctive feature is the reddish tone of the underfur.

Specimens examined:—None. The above description and remarks are based entirely upon the discussion by Barabash-Nikiforov (1947).

KEY TO SUBSPECIES

Differences between the two subspecies of *Enhydra lutris* are summarized in the following key:

1A. Zygomatic width and mastoid width less than 80% of condylobasal length; infraorbital foramen width and postorbital width less than 37% of condylobasal length; underfur grayish: ..... *E. l. lutris*

1B. Zygomatic width and mastoid width more than 80% of condylobasal length; infraorbital foramen width and postorbital width more than 37% of condylobasal length; underfur reddish: ..... *E. l. gracilis*

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