FULL PAPER *Anatomy*

Cranial Features of the Spotted Seal, *Phoca largha*, in the Nemuro Strait, Considering Age Effects

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ABSTRACT. Cranial features (development, individual variation, and sexual dimorphism) were examined from the 23 metrical characters and 2 nonmetrical characters (the degree of closure of the 9 cranial sutures and the presence of sagittal crest) in the two spotted seal specimen groups at the Nemuro Strait, Hokkaido. One specimen group was incidentally taken in the salmon trap nets between 1982 and 1983 (n=70), and the other was randomly sampled by damage control kill between 1997 and 1998 (n=82). The development of morphometrical characters of skulls ceased at 5.6, 10.7, 7.9, and 11.9 yr. old, for 1982–83 male, 1982–83 female, 1997–98 male and 1997–98 female, respectively. The sutures were half ankylosed till approximately 10 yr. old in both sexes. The sagittal crest began from about 5 yr. old in male. Individual variation of skull was large in the feeding, breathing, and facial-expression apparatus. On the other hand, the variation of braincase, and skull concerning to the movement of head/neck tended to be small. Only 1997–98 specimens exhibited a sexual dimorphism in skull characters except for the braincase, whereas the dimorphism was not found in 1982–83 specimens. We could not detect the significant difference between two specimen groups, although there were a few differences in characters related to the rostrum and mandible.

KEY WORDS: growth, individual variation, principal component analysis, sexual dimorphism, skull morphology.

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The spotted seal, *Phoca largha*, which is widely distributed in the Sea of Okhotsk, the Japan Sea, and the Bering Sea [20], exhibits regional variations in morphology. In the Bering Sea, the three geographical populations was found using non-metrical characters of skulls [5]. In the Sea of Okhotsk, it was confirmed of the cranial differentiation based on metrical and non-metrical characters between the northern area (Shelekhova Bay) and the southern area (Terpeniya Bay in Sakhalin) [6]. In the Japan Sea, cranial features in the Mamiya Strait concentration have been reported; almost characters did not show a sexual dimorphism except for the rostrum and nasal bone, and the skulls of female were larger than those in the Peter the Great Bay [12]. However, these studies used the sexual mature specimens, without consideration of the age-based cranial development. There are a few studies to describe the cranial developments. One study reported the development of condylobasal lengths with age [15]. Another study reported the developments of 17 cranial morphometric characters, and denied the sexual dimorphism of sexual mature seal [22], as well as the review study [2].

Clarification of the development of morphometric characters provides the basic data for the analysis of geographical variations among neighboring populations. Estimation of the age when development ceases will make it possible to use all the measurements from animals exceeding this age for a morphological comparison [23]. No such studies have, however, previously been conducted for spotted seals.

Offshore of Hokkaido, including the Nemuro Strait, spotted seals appeared mostly in fall for following salmon, and also in the sea ice season for reproduction [15]. Since most morphological studies in this area focus on the inter-species differences between spotted seals and the sympatric species of harbour seals, *Phoca vitulina stejnegeri* [10, 14, 15, 22], intra-specific variations in the cranial features of spotted seals were not described enough.

The purpose of this study is to describe the cranial features of spotted seals in the Nemuro Strait. We report here growth with age, individual variation, and sexual dimorphism of the skulls, considering age structure, capture methods, and seasons which contribute to the specimen features.

MATERIALS AND METHODS

Sampling and skull specimen: Spotted seals were collected in coastal waters of eastern Hokkaido from the Shiretoko Peninsula to the Nemuro Peninsula (Fig. 1) between 1982 and 1983 (n=70; 37 males and 33 females) and again between 1997 and 1998 (n=82; 52 males and 30 females). The former specimens were primarily collected by incidental take in salmon trap nets between September and November, and the latter specimens were collected by damage control kills during February and March (around the breeding season). The sex of each seal was referred from the register for 1982–83 specimens, and from the morphological features of the external genitalia for 1997–98 specimens. Skulls were boiled and skeletonized, then put in 50°C water with proteinase (TasinaseN–11–100: Kyowahakkokogyo, Tokyo, Japan) [7]. All of skulls are stored in the Graduate School of Veterinary Medicine, Hokkaido University.

Age determination: For age determination, lower canine teeth were taken from each animal, sectioned 20 μm and stained by Delafield's hematoxylin, following the fundamental methods on the textbook [7]. When lower canine

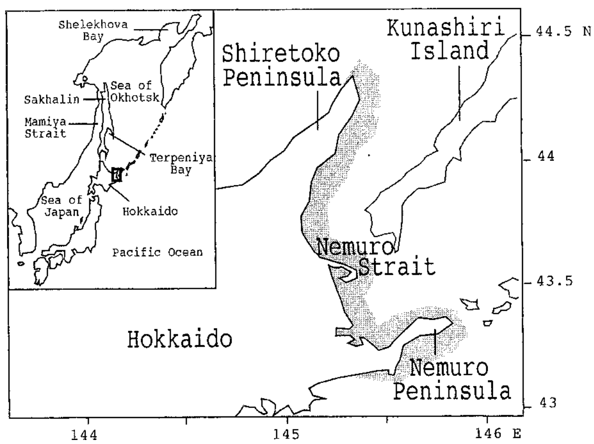

Fig. 1. Location of sampling area (represented as shadow area) and distribution area of spotted seals around Japan.

teeth were lost, upper canine teeth were used. Ages were estimated from count of cementum annuli [13]. The assumed mean birth date was set at the 25th March [14]. Ages were calculated to the nearest 0.01 year old to accommodate differences in the timing of collections.

Measurements for metrical and non-metrical cranial features: Twenty-three morphometric characters (Table 1, Fig. 2) were measured following the previous studies [3, 22]. Functional components were identified referring to textbooks of the anatomy [4, 11]. Each character was measured with calipers to the nearest 0.05 mm. Some skulls were partly damaged by shot so that those measurements were removed from the analysis. The degree of closure of nine cranial sutures (occipito-parietal, squamoso-parietal, interparietal, fronto-parietal, interfrontal, basioccipital-basisphenoidal, basisphenoidal-presphenoidal, intermaxillary, and incisivomaxillary) were assessed visually and assigned a numerical score from 1 to 4, following the previous studies [3, 9]. Score 1 was that the suture was open wide, and score 4 was that the suture was fully ankylosed. We also observed the presence of sagittal crest.

Apply for the growth models: To examine the growth of skull, we used the monomolecular model within four growth models (the von Bertalanffy, Gompertz, logistic, and monomolecular models), because the monomolecular model showed the best fit to the growth of condylobasal length in all groups (both males and females in each period). This model has already been used successfully for the growth of brown bears, *Ursus arctus* [16]. We then used the monomolecular model for the other characters. The monomolecular equation is: $L_t = L_\infty$ -exp (-K (t-I)), where L_t is the length at age t, L_∞ is the asymptotic length, K is a growth-rate constant, and I is the age at the inflection point. Parameters in these models were estimated by the nonlinear least squares method with the SPSS [21].

Estimate the age to cease the cranial development: To estimate the age of completion of development on a particular character, we assumed the growth of skull virtually ceased at the age at which length attains 95% of its asymptotic length ($t_{.95}$) [23]. $T_{.95}$ was calculated from the estimates of growth parameters in each measurement. In order to verify the completion of development, the zero growth rate (L_t = constant, $t \geq t_{.95}$) was tested by linear regression analysis, using the specimens that the ages were more than the median value of $t_{.95}$ among all 23 characters. We regarded the specimens over the age when the zero growth rate was

Table 1. Skull measurements of the spotted seal

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	Width of palate behind first molars
18	Greatest length of bulla
19	Greatest width at condyles
20	Length of snout from anterior edge of nasals
21	Greatest length of jugal
22	Width of bulla from tip of auditory process to anterior edge of carotid foramen
23	Width of coronoid process at anterior margin

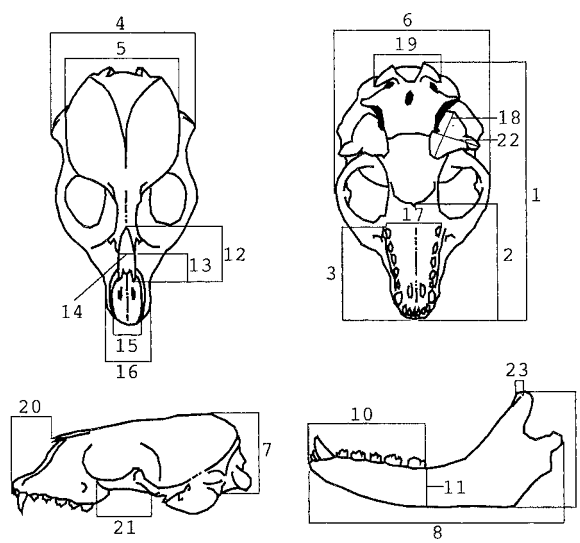

Fig. 2. Skull measurements of the spotted seal. Numbers refer to characters described in Table 1.

accepted in all characters, as the completion of the development, and used them for the comparisons between groups.

Statistical comparison about the cranial features: Differences between sampling periods or sexual dimorphism in skull were examined by three statistical methods {*t*-test, principal component analysis (PCA), and analysis of covariance (ANCOVA)}. The *t*-test was used for comparing the difference between means, using specimens that the growth was considered to have ceased. PCA was used to elucidate the size and shape variation among groups, also using specimens which the development complete. The data of 17 characters of 24 specimens (*i. e.* 6, 5, 7, and 6 specimens for 1982–83 males, 1997–98 males, 1982–83 females, and 1997–98 females, respectively) except specimens with unmeasured portions were applied for PCA, because 6 characters (nos. 12, 13, 18, 19, 20, and 22) could not be measured in some specimens. In order to overcome the small sample size, ANCOVA was carried out using data obtained from all age individuals, following the previous study [23]. We first assumed an allometric relationship between measurements of two characters: $y=bx^a$, where x is the condylobasal length, and y is a measurement of another character. Parameters a and b were estimated by regression analysis after the equation was linearized by a log transformation. Period differences and sexual dimorphism in these parameters were examined by ANCOVA using the GLM procedure of SPSS [21].

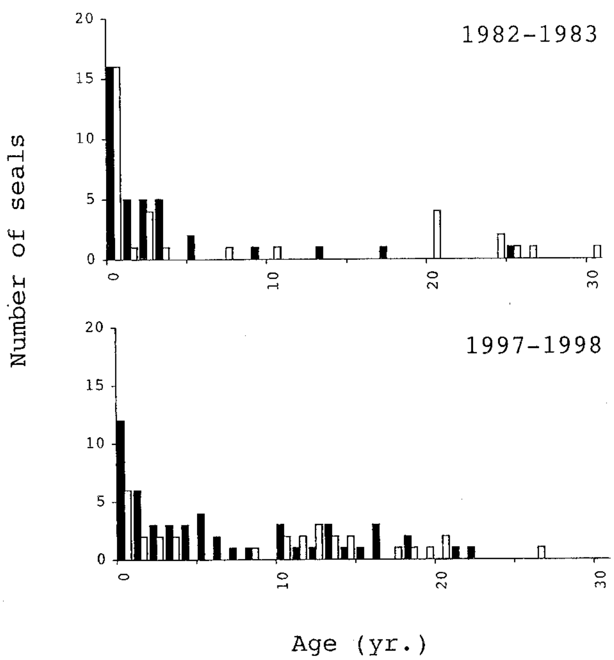

Fig. 3. Age structures of spotted seals collected in 1982–83 and 1997–98. Closed and open squares represent males and females, respectively.

RESULTS

Growth: Figure 3 shows the age structures of the specimen groups. The sutures were half ankylosed till approximately 10 yr. old in both sexes (Fig. 4). The sagittal crest began from about 5 yr. old in male, whereas the presence in

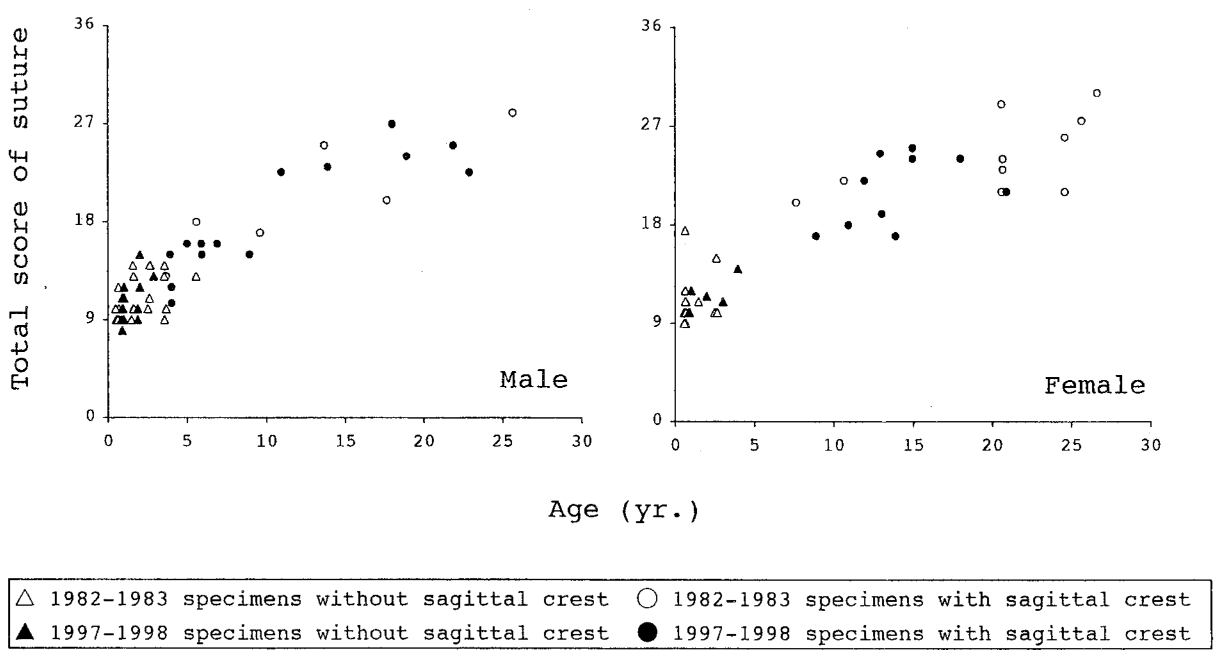

Fig. 4. Relationship between age and total score of suture, and the presence of sagittal crest in male and female spotted seals.

Table 2. Estimates of parameters for growth of morphometric characters in spotted seal. Character number refers to Table 1 and Fig. 2.

Character	Male in 1982–83					Male in 1997–98					Female in 1982–83					Female in 1997–98				
no.	n[a)]	L_∞ (mm)	K (mm/yr)	I (yr)	$t_{.95}$ (yr)	n[a)]	L_∞ (mm)	K (mm/yr)	I (yr)	$t_{.95}$ (yr)	n[a)]	L_∞ (mm)	K (mm/yr)	I (yr)	$t_{.95}$ (yr)	n[a)]	L_∞ (mm)	K (mm/yr)	I (yr)	$t_{.95}$ (yr)
1	40	215.0	7.33	2.69	2.59	33	224.7	4.38	4.77	4.50	34	214.5	6.25	3.13	3.02	21	211.4	5.04	3.89	3.78
2	41	95.2	5.90	2.28	3.54	49	100.5	3.74	3.92	5.76	37	95.3	4.97	2.69	4.18	27	93.5	4.68	2.89	4.51
3	41	73.1	4.07	2.25	4.72	57	76.1	2.56	3.92	7.69	37	72.6	3.41	2.55	5.52	34	71.5	2.29	3.72	8.21
4	41	123.1	9.10	1.18	1.71	38	123.5	7.33	1.49	2.14	37	119.9	9.92	0.98	1.50	24	117.5	13.26	0.69	1.09
5	40	94.1	13.05	0.25	0.82	39	95.0	12.94	0.31	0.89	36	94.7	12.75	0.31	0.89	24	93.0	33.96	0.10	0.32
6	40	131.4	3.61	3.98	5.14	44	135.8	2.66	5.82	7.28	37	129.3	4.37	3.24	4.24	25	124.8	3.42	3.89	5.27
7	41	67.9	12.14	0.27	1.16	31	68.8	7.77	0.45	1.82	35	67.7	9.51	0.31	1.45	22	66.8	9.74	0.24	1.36
8	41	142.4	5.31	3.09	3.73	57	148.1	3.44	5.02	5.90	37	140.3	5.33	3.01	3.68	34	139.1	4.00	4.08	4.99
9	41	67.3	3.69	3.14	6.09	58	68.9	3.21	3.83	7.15	37	65.4	4.79	2.36	4.69	35	63.5	3.01	3.54	7.36
10	41	61.7	4.18	1.16	3.97	58	63.5	2.48	2.29	6.92	37	60.6	3.05	1.26	5.17	34	59.6	2.69	1.48	5.97
11	41	21.2	2.09	–1.32	9.40	58	21.8	1.57	–1.09	13.03	37	20.5	2.14	–1.67	8.96	36	24.4	0.44	1.78	49.38
12	40	54.4	3.54	1.79	5.47	48	57.7	2.16	3.65	9.39	36	54.9	2.21	2.77	8.63	28	53.0	2.45	2.27	7.68
13	40	31.5	2.84	0.62	7.13	50	31.4	1.95	0.63	10.16	36	30.7	1.78	0.28	10.82	30	29.2	2.96	–0.20	6.30
14	41	14.2	3.49	–1.75	5.83	52	14.1	3.15	–1.87	6.55	37	13.3	5.97	–1.18	3.37	32	13.3	2.60	–2.65	7.77
15	40	33.2	2.80	0.21	6.62	54	32.7	2.93	0.15	6.33	36	30.6	2.70	–0.85	6.11	32	29.4	4.24	–0.58	3.94
16	41	46.1	1.61	3.62	12.72	56	46.2	1.76	3.56	11.88	35	41.5	2.25	1.47	8.46	33	39.4	1.88	1.09	9.75
17	41	60.8	2.63	2.00	6.53	54	60.9	2.21	2.44	7.82	37	58.5	3.02	1.28	5.34	33	56.9	2.49	1.05	6.11
18	41	41.0	14.45	–0.14	0.96	43	42.3	6.24	–0.20	2.29	37	39.3	13.95	–0.31	0.85	25	39.8	7.34	–0.52	1.67
19	39	59.7	12.76	–0.05	0.89	31	59.8	13.84	–0.05	0.82	33	59.0	11.23	–0.13	0.95	20	58.7	12.26	–0.15	0.85
20	40	33.4	10.09	0.49	2.26	49	37.3	4.60	1.42	5.08	36	36.1	6.83	0.90	3.40	30	33.7	5.10	0.99	4.48
21	39	57.4	5.37	1.39	3.72	47	61.2	2.94	2.95	6.98	36	57.9	5.64	1.39	3.59	30	57.6	4.65	1.71	4.39
22	41	42.8	10.56	0.01	1.47	46	43.3	7.47	0.08	2.13	37	42.2	6.28	–0.10	2.38	27	41.5	9.84	–0.10	1.50
23	41	5.2	3.49	–3.64	6.84	58	5.5	2.10	–5.29	11.76	37	4.8	4.33	–3.21	5.41	35	4.3	1.58	–10.17	14.12

a) Six age known specimens were used for fitting growth curves.

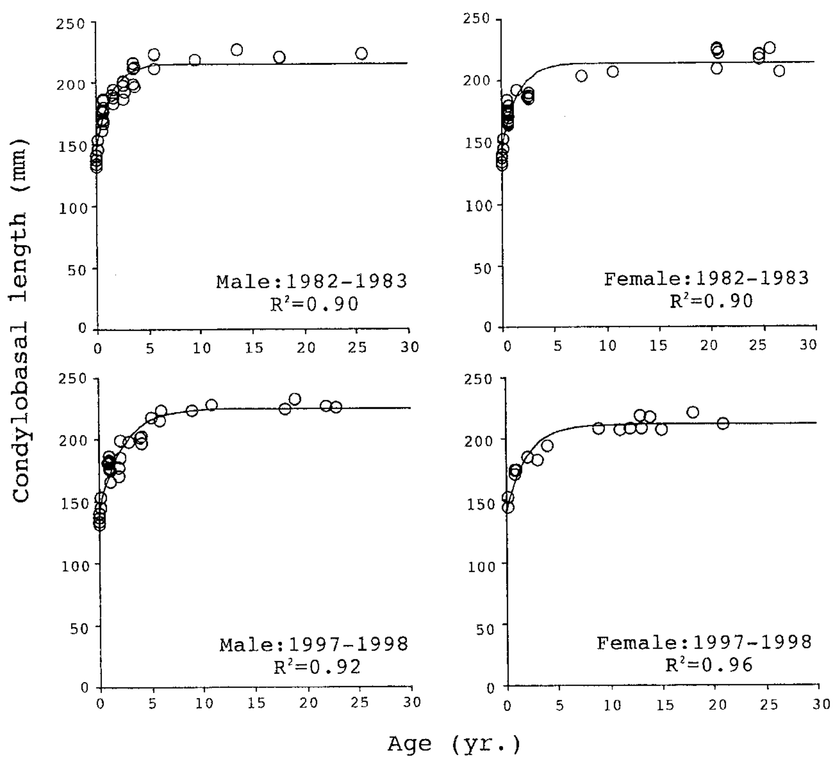

Fig. 5. Relationship between age and condylobasal length in male and female spotted seals in 1982–83 and 1997–98. Growth parameters are given in Table 2.

Table 3. Mean, standard deviation (SD), and individual variation (CV%) of measurements of spotted seals which the skull growth completed. Character number refers to Table 1 and Fig. 2.

Character	Male in 1982–83				Male in 1997–98				Female in 1982–83				Female in 1997–98			
no.	n	Mean (mm)	SD (mm)	CV (%)	n	Mean (mm)	SD (mm)	CV (%)	n	Mean (%)	SD (%)	CV (%)	n	Mean (mm)	SD (mm)	CV (%)
1	6	220.4[b]	5.17	2.35	6	227.0[Ab]	3.15	1.39	9	217.9	8.03	3.69	7	213.4[A]	5.62	2.63
2	6	97.5[b]	3.26	3.35	15	101.6[Ab]	3.29	3.24	9	97.0[c]	2.83	2.92	11	93.8[Ac]	2.95	3.14
3	6	72.9	2.13	2.92	18	75.6[A]	3.13	4.14	9	73.1	2.85	3.90	13	70.1[A]	3.57	5.09
4	6	124.0	5.34	4.31	10	123.3[A]	3.07	2.49	9	121.7	2.73	2.25	10	119.4[A]	2.38	1.99
5	6	95.3	1.98	2.08	10	95.5	2.49	2.61	9	96.0	2.36	2.46	10	94.4	3.43	3.63
6	6	129.3[b]	6.63	5.13	14	135.2[Ab]	3.90	2.89	9	130.1[c]	3.42	2.63	10	125.0[AC]	4.01	3.21
7	6	68.6	1.22	1.78	5	69.5	1.96	2.82	9	68.3	2.60	3.81	8	67.8	2.00	2.95
8	6	144.0	5.48	3.81	18	148.3[A]	4.69	3.16	9	142.4	4.36	3.06	14	139.2[A]	3.67	2.63
9	6	67.2	4.10	6.10	19	68.8[A]	2.92	4.24	9	65.8	5.95	9.03	14	63.0[A]	3.18	5.05
10	6	61.4	1.93	3.15	19	62.9[A]	3.46	5.50	9	60.9	1.26	2.07	14	59.3[A]	2.45	4.14
11	6	20.2	1.12	5.55	19	20.9[A]	1.24	5.93	9	20.4[c]	0.83	4.05	14	19.0[AC]	0.97	5.09
12	6	53.8[b]	2.46	4.58	14	56.7[ab]	2.72	4.80	8	55.0	1.53	2.77	11	53.2[a]	4.01	7.54
13	6	31.1	2.21	7.11	15	30.6	2.56	8.38	8	30.5	1.90	6.23	13	29.0	2.94	10.13
14	6	14.2	1.74	12.28	16	14.2[a]	1.56	10.95	9	13.5	1.84	13.65	14	13.1[a]	1.40	10.70
15	6	32.3	2.25	6.97	18	32.6[A]	1.78	5.46	9	30.6	1.84	6.00	13	29.2[A]	1.77	6.05
16	6	42.6	4.24	9.95	18	44.7[A]	2.25	5.04	7	41.3[c]	1.37	3.31	13	38.5[AC]	1.41	3.67
17	6	58.6	4.06	6.92	18	60.2[A]	2.83	4.70	9	58.6[c]	1.88	3.22	13	55.8[AC]	1.83	3.28
18	6	41.4	2.07	5.00	11	42.7[A]	2.01	4.70	9	39.9	1.65	4.13	10	40.3[A]	1.42	3.51
19	5	59.7	3.27	5.48	5	60.4	1.37	2.26	9	59.5	1.71	2.88	6	58.9	1.14	1.94
20	6	35.7	2.68	7.52	12	38.1[A]	3.10	8.12	8	37.0[c]	1.37	3.71	13	33.9[AC]	2.41	7.11
21	6	58.1	3.17	5.45	14	61.2[a]	3.39	5.53	9	58.7	2.91	4.96	14	58.4[a]	2.52	4.32
22	6	43.3	1.73	4.00	13	43.9[A]	1.18	2.68	9	42.7	2.06	4.83	12	41.9[A]	0.87	2.08
23	6	5.2	0.71	13.61	19	5.3[A]	1.04	19.44	9	4.8[c]	0.78	16.20	14	4.1[Ac]	0.74	18.35

Significantly different pairs of means are indicated with same superscript letters. Lowercase letters indicate $p<0.05$, capital letters $p<0.01$.

female was not certified because of few female specimens between 5 and 10 yr. old (Fig. 4). Table 2 includes parameter estimates for the growth of all 23 morphometric characters.

Figure 5 shows the growth of condylobasal length for males and females. The median ages of $t_{.95}$ from all 23 measurements were 4.0, 4.2, 6.6, and 5.0 yr. for 1982–83 male, 1982–83 female, 1997–98 male and 1997–98 female, respectively. We tested the zero growth of the cranial characters over the median ages in each group. Only 1982–83 male group was accepted the zero growth for all characters ($P>0.01$), when the minimal specimen age was 5.6 yr. old. Whereas, in other groups, some characters were disproving the zero growth; nos. 12, 16, and 17 in 1982–83 females; no. 10 in 1997–98 males; and nos. 8 and 9 in 1997–98 females ($P<0.01$). The latter three groups were accepted the zero growth for all characters, when the minimal age among the specimens were 10.7, 7.9, and 11.9 yr. or older, for 1982–83 female, 1997–98 male and 1997–98 female, respectively ($P>0.01$). We considered these specimens to complete the development, and used for the comparison of means by the *t*-test, and for the principal component analysis (PCA).

Individual variation: Table 3 gives individual variations (CV %) in the morphometric characters of the skull. Variation of feeding (nos. 9, 16, 17, and 23) and breathing/facial-expression apparatus (nos. 12, 13, 14, 15, and 20) were seemed to be large in all groups, especially nos. 14 and 23. Variation of braincase (nos. 5 and 7) and head/neck movement apparatus (nos. 4 and 19) are seemed to be small.

Sexual dimorphism: Sexual dimorphism was detected by *t*-test in 19 of 23 characters of 1997–98 specimens ($P<0.05$), whereas it was not detected in all characters of 1982-83 specimens ($P>0.05$) (Table 3). On the other hand, sexual dimorphism in $\log_{10}$ b by ANCOVA was detected in nos. 6, 9, 18, 22 ($P<0.01$), and no. 3 ($p<0.05$) of 1982-83, and nos. 1, 13, and 18 ($p<0.05$) of 1997–98 (Table 4).

Differences between specimen groups: Difference between 1982–83 and 1997–98 males by *t*-test was detected in the cranial characters nos. 1, 2, 6, and 12 ($P<0.05$), and those of females was detected in nos. 6, 11, 16, 17, 20 ($P<0.01$), 2 and 23 ($P<0.05$) (Table 3). These characters were in rostrum, mandible and greatest zygomatic width. On the other hand, group differences in $\log_{10}$ b by ANCOVA were detected only in nos. 20 ($P<0.01$), 16 and 23 ($p<0.05$) of females (Table 5). These characters were in rostrum and mandible.

Principal component analysis: The principal component charts between the first and second transformed variables from 17 measurement items are given in Fig. 6. The two clusters of male and female in 1997–98 were obviously distinguished in this chart. On the other hand, two clusters of male and female in 1982–83 were not distinguished,

Table 4. A summary of analyses of covariance on sexual dimorphism in skull measurements of spotted seal. Character number refers to Table 1 and Fig. 2.

1982–83			1997–98		
Character no.	Adjusted mean (mm)		Character no.	Adjusted mean (mm)	
	Male	Female		Male	Female
Covariate: standard length (mm)			Covariate: standard length (mm)		
1	187.9	188.8	1[a)]	199.1	194.5
Covariate: codnylobasal length (mm)			Covariate: condylobasal length (mm)		
2	80.0	80.4	2	83.8	84.1
3[a)]	60.8	61.8	3	63.7	63.7
4	114.3	113.0	4	116.9	115.1
5	91.0	91.6	5	93.1	92.5
6[b)]	109.9	112.5	6	114.8	115.1
7	64.9	64.1	7	65.8	65.3
8	120.5	121.3	8	125.9	126.8
9[b)]	50.8	52.8	9	54.6	54.7
10	53.8	53.8	10	55.6	55.5
11	16.3	16.8	11	17.0	17.0
12	44.3	44.6	12	46.2	47.9
13	24.4	24.4	13[a)]	25.0	26.9
14	11.4	11.4	14	12.0	11.8
15	27.2	26.9	15	28.1	28.2
16	33.5	34.2	16	35.8	35.0
17	50.7	51.5	17	52.1	53.1
18[b)]	39.4	38.0	18[a)]	39.9	38.6
19	57.5	56.9	19	58.7	57.9
20	28.8	29.6	20	30.5	29.4
21	48.8	49.5	21	51.9	52.8
22[b)]	40.2	38.5	22	40.7	40.3
23	3.6	3.7	23	3.8	3.5

a) The difference was significant at the 5% level.
b) The difference was significant at the 1% level.

although the points of each sex tended to be plotted adjacent to the same sex clusters of 1997–98 (Fig. 6). The percentage of variation explained by the first principal component (PC1) is 51.1%, and that by the second principal component (PC2) is 11.8%. The items, which largely contribute to PC1, were almost characters in higher ranking except nos. 5 and 7 (braincase), and to PC2 were nos. 5, and 7 for positive, and nos. 11, 14, 15, 16, and 17 (rostrum) for negative. PC1 represented the total skull size except braincase, and showed the tendency of sexual dimorphism in 1997–98 and the little of the dimorphism in 1982–83. PC2 represented the proportion between braincase and rostrum, and denied both sex and period differences in this proportion because of the large variation in each group.

DISCUSSION

Growth: The morphometric characters from the median values of t_{95} indicate that skull growth ceased mostly around 5 yr. old. This is corresponded with the age of the sagittal crest appearances in male, and the age of sexual maturity in both sexes [14]. After 5 yr. old, there would be moderate development in some skull characters, because the completion ages for all character development in our specimens were about 8 and 12 yr. old in males and females, respectively. This moderate growth correspond with those of the sexual organs such as ovaries and testes after the sexual maturity at 5 yr. old [14]. The difference of the completion age of skull development between sexes would have caused from few female specimens aged between 5 and 10 yr. old. This age specimens in female are required for more precise analysis of skull development. Sutures did not complete to ankylose at 5 yr. old, and they tended to continue ankylosing after 10 yr. old. Although almost morphometrical developments ceased until 10 yr. old, it is not necessarily to complete the ankylosing after the completion of skull growth and even in older animals [4].

Individual variation: Individual variations of feeding and breathing apparatus were the greatest, and it is shown in finless porpoises (*Neophocaena phocaenoides*) [23] and spotted porpoises (*Stenella attenuata*) [17]. In addition, spotted seals have a great individual variation in the facial-expression apparatus with regard to movements of the nose and vibrissae, both of which play a unique role in the behaviors of pinnipeds. Seals frequently open and close their nose not only in relation to breathing, but also to smelling the water and diving [19]. The vibrotactile sensors are best developed in pinnipeds, which is useful not only for catching prey in

Table 5. A summary of analyses of covariance on period difference in skull measurements of spotted seal. Character number refers to Table 1 and Figure 2.

Male			Female		
Character no.	Adjusted mean (mm) 1982–83	1997–98	Character no.[a)]	Adjusted mean (mm) 1982–83	1997–98
Covariate: condylobasal length (mm)			Covariate: condylobasal length (mm)		
2	81.5	81.8	2	81.3	81.7
3	62.1	62.2	3	62.7	61.8
4	115.6	115.6	5	91.8	91.8
5	91.6	92.5	6	113.5	112.5
6	111.7	112.7	7	64.6	64.7
7	65.3	65.3	8	123.0	123.0
8	123.0	123.0	9	54.0	52.6
9	52.2	52.8	10	54.3	54.3
10	54.7	54.6	11	17.1	16.4
11	16.7	16.6	12	45.2	45.9
12	45.4	45.2	13	24.8	25.6
13	25.1	24.4	14	11.6	11.5
14	11.6	11.6	15	27.1	27.6
15	27.7	27.5	16[b)]	34.7	33.7
16	34.4	34.8	17	52.1	51.8
17	51.5	51.2	18	38.1	38.3
18	39.7	39.6	19	57.0	57.5
19	57.9	58.3	20[c)]	30.1	28.2
20	29.5	29.7	21	50.1	51.1
21	49.8	50.7	22	38.8	39.5
22	40.6	40.4	23[b)]	3.8	3.3
23	3.7	3.6			

a) Character no. 4 in female was omitted because differences in parameter a were significant between periods (P<0.01).
b) The difference was significant at the 5% level.
c) The difference was significant at the 1% level.

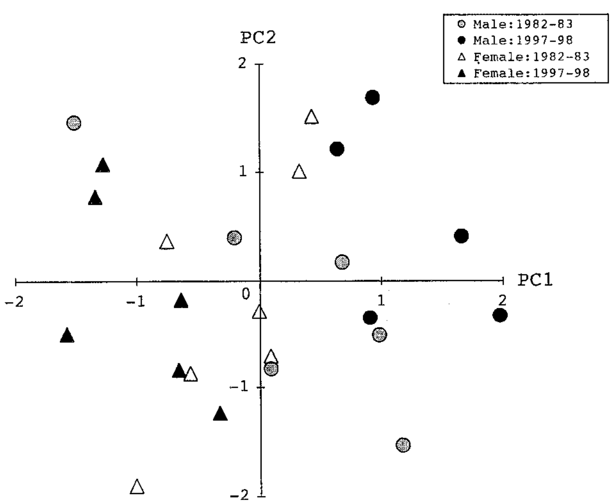

Fig. 6. The principal component chart of skulls between the first and second transformed variables from 17 measurement items. PC1, the first principal component. PC2, the second principal component. The percentage of variation explained by PC1 is 51.1 %, and that by PC2 is 11.8 %.

the water, but also possibly in relation to the nonuse of their reduced forelimbs as tactile agents [18].

Explanation for the different results among analysis: The results between ANCOVA and *t*-test/PCA seem to be inconsistent. ANCOVA detected less period differences and little sexual dimorphism in both specimen groups. On the other-hand, *t*-test and PCA detected more number of period differences in the skull morphometric features related to the rostrum and mandible, and indicated strong sexual dimorphism only in 1997–98 specimens, not in 1982–83 specimens, that was consistent with the result of previous study [22]. However, since ANCOVA can analyze including the growth effects [8] and can use larger sample size than *t*-test [23], it might be considered that ANCOVA and *t*-test/PCA detect the features of "the population" and those of "each specimen group", respectively. This statement would explain our results; some cranial differences between 1982–83 and 1997–98 specimen groups were detected by the results of *t*-test/PCA, but both groups would not be obviously separated as population by the results of ANCOVA.

Sexual dimorphism and population contaminants: The capture methods and seasonal effects should be considered for the cranial differences between sexes and between specimen groups. 1997–98 specimens were taken by the random sampling of damage control kill in the breeding season, and they would represent the "breeding population" in the Nemuro Strait. Many pinniped species have developed the sexual dimorphism by the large body size of breeding males, where the degrees of the dimorphism are related to the breeding system [1, 9]. Although spotted seals reported as monogamy [19], well-developed males could get females easily and therefore some sexual dimorphism might appear in the "breeding population", such as in 1997–98 specimen group. Concerning about 1982–83 specimens, it would represent the "incidentally taken seal group". One of reasons for little sexual dimorphism in this group might be a small number of mature male specimens. However, the information was not enough to confirm that the mature males are not taken easily in the trap nets, and that most of them are not inhabited in the autumn Nemuro Strait. The estimation of sampling bias for entanglement will partly explain these issues. Conclusive resolution of spotted seal population contaminates between two specimen groups requires further detailed analysis of large number of skulls, the genetic comparison, and seasonal movement patterns by the satellite-linked telemetry.

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