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FULL PAPER

Growth variation in skull morphology of Kuril harbor seals (*Phoca vitulina stejnegeri*) and spotted seals (*Phoca largha*) in Hokkaido, Japan

Emiko Nakagawa[1, 2], Mari Kobayashi[3, *], Masatsugu Suzuki[4] and Toshio Tsubota[1]

[1] Laboratory of Wildlife Biology, Department of Environmental Veterinary Sciences, Graduate School of Veterinary Medicine, Hokkaido University, Sapporo 060–0818, Japan

[2] Hokkaido University Research Center for Zoonosis Control, Sapporo 001–0020, Japan

[3] Laboratory of Aquatic Management, Department of Aqua-Bioscience and Industry, Faculty of Bioindustry, Tokyo University of Agriculture, Abashiri 099–2422, Japan

[4] Laboratory of Zoo and Wildlife Medicine, Faculty of Applied Biological Sciences, Gifu University, Gifu 501–1193, Japan

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Abstract

We examined morphological growth variations in skull features between the Kuril harbor seal and the spotted seal in Hokkaido, Japan. Skulls from 80 Kuril harbor seals and 41 spotted seals were collected, and we measured 29 metric and 6 non-metric cranial characteristics. Three growth classes were defined according to the postnatal developmental stage: pups (0 year), subadults (1–4 years old) and adults (more than 5 years old). We detected sexual dimorphism in Kuril harbor seal pups, subadults, and adults. Although interspecies differences were detected in each growth class, Kuril harbor seals were larger and more massive than spotted seals; this feature was already detectable in pups. We did not detect certain cranial characteristics with which to identify the two species, but it was possible to identify any unknown specimens to their species, sex, and growth class using the cranial data generated in this study. Using 6 non-metric cranial characteristics, we identified significant interspecies differences with regard to the shape of the temporozygomatic suture and the extent of the nasal-incisive suture; the shape of the temporozygomatic suture and the shape of the nares were indicators of growth class in Kuril harbor seals. Although non-metric cranial characteristics have a lower discriminating power than metric characteristics, they are easy to use in the field even by inexperienced researchers.

Key words: Kuril harbor seal, Skull morphology, Spotted seal

*Corresponding author: Mari Kobayashi, Laboratory of Aquatic Management, Department of Aqua-Bioscience and Industry, Faculty of Bioindustry, Tokyo University of Agriculture, Abashiri 099–2422, Japan
Phone & Fax: +81–152–48–3907. E-mail: m3kobaya@bioindustry.nodai.ac.jp

Introduction

The harbor seal (*Phoca vitulina*) and the spotted seal (*Phoca largha*) are widely distributed in the North Pacific Ocean. Five subspecies of harbor seal are recognized on the basis of their geographic distribution[2,10]; one of these subspecies, the Kuril harbor seal (*P. v. stejnegeri*), is distributed in the northwestern Pacific Ocean. The spotted seal is distributed from the Bering Sea to the northern Yellow Sea, due to their pagophilic (ice-breeding) nature[3,10]; they also migrate to the Sea of Japan and the Okhotsk coasts of Hokkaido[14]. In recent years, the numbers of both seals have increased in Hokkaido. The Kuril harbor seal is distributed on the coastal Pacific side[14] and numbered approximately 350 in 1984[9], subsequently increasing to over 900 in 2004[8]. Although there is no detailed information on the past numbers of spotted seals, the increase in the number migrating to the Sea of Japan has been especially remarkable over the last few years[8]. In addition, some spotted seals have been observed on the Pacific side. Both of these species are sympatric throughout the year at Erimo and Akkeshi.

The harbor seal and the spotted seal are sibling species, but some studies had revealed morphological, ecological, and genetic differences between them[1,4,14,18]. Some morphological studies on the skulls of harbor and spotted seals have been performed. In general, the harbor seal's skull is more massive, the premolar teeth of adults are mostly obliquely set, the caudal margin of the jugal bone is mostly angular, and the hyoid bones are incomplete[4,14,18]. In adult spotted seals, the line of the premolar teeth is straight, the caudal margin of the jugal bone is rounded, and the hyoid bones are complete[4,14,18]. However, some morphological features of each species in Hokkaido are in the process of changing. The cranial measurements of the Kuril harbor seal in Nosappu have downsized in comparison to specimens from 20 years ago[7]. Spotted seals had no sexual dimorphism in the 1980s[19]; however, it was apparent in specimens from 1997–98[11]. Although intraspecies variations in the cranial features of each species have been described, the recent interspecific variations between Kuril harbor and spotted seals have not been adequately characterized. In general, adult skull specimens are used in morphological studies because of their physiological maturity. Both harbor and spotted seal pups have a high mortality rate during the nursing period[3]; in Hokkaido, the majority of seals that are washed ashore or that die as bycatch are pups[8]. In the wild, the dead bodies of seals are often putrid or skeletonized, making it problematic to identify these sympatric species by the pelage. Therefore, it is extremely useful to identify these sibling species by their skull characteristics. However, there is a paucity of information regarding the morphological characteristics of the skulls of seal pups and their associated developmental morphological changes.

The aim of this study was to provide detailed information on cranial development in the Kuril harbor seal and the spotted seal in Hokkaido. We examined metric and non-metric characteristics to reveal growth variations and to assess the application of skull characteristics for the identification of the two sibling species in the field.

Materials and Methods

Samples: We collected the skulls from 80 Kuril harbor seals and 41 spotted seals. Kuril harbor seals were taken from Nosappu (41 males [M] and 39 females [F]) in 2005. Spotted seals were taken from Nosappu (6M, 2F), Erimo (1M, 1F), Hamamasu (3M, 4F), Yagishiri Island (5M, 2F), and Rausu (9M, 8F) in 2005 and 2006. The locations of the sampling sites are shown in Fig. 1. We previously demonstrated that Kuril harbor seals in Hokkaido can be divided into two populations, the Erimo and the eastern Hokkaido populations (Akkeshi and Nosappu), on the basis

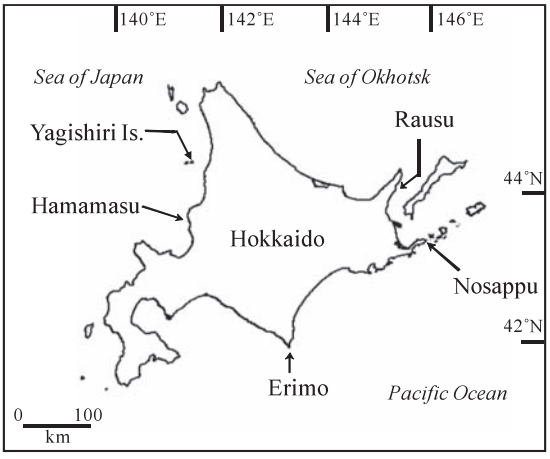

Fig. 1. Geographical locations of the sampling sites in Hokkaido, Japan

of mitochondrial DNA (mtDNA) cytochrome *b* region sequences[15]. To reduce the biases of genetic populations, we only used specimens of Kuril harbor seals from Nosappu. There are no local populations of spotted seals in Hokkaido[12], so we collected individuals from the five sampling sites described above. The seals from Nosappu, Erimo, and Hamamasu were bycatch from fishery nets. The seals from Rausu were killed for fishery damage control and those from Yagishiri Is. were dead seals washed ashore. Seal capture was conducted under a license from the Japanese Ministry of the Environment. Skulls were boiled for 15–20 min and skeletonized, then placed in water containing 10% proteinase (Tasinase N-11-100: Kyowahakkokogyo, Tokyo, Japan) at 50°C for 7–8 hr and cleaned. The skulls were then bleached white by soaking them in 4% hydrogen peroxide for a few days and dried under natural conditions for two or more days[6].

Measurements for metric and non-metric cranial characteristics: Metric and non-metric cranial characteristics are shown in Table 1 and Figs. 2 and 3. Twenty-nine metric characteristics were measured for each specimen using calipers to the nearest 0.1 mm, following previous studies[4,11]. Six non-metric characteristics were ranked and assigned a numerical score, based on our judgment of its conformity to one of the diagrams in Fig. 3. Low scores for these characteristics were features of spotted seals; while, high scores were features of harbor seals[4,14]. Characteristic I described the shape of the temporozygomatic suture, score 1 indicated a rounder shape, and score 3 indicated more right-angled shape. Characteristic II described the angle of the upper second premolar, score 1 was indicated a straight angle along the line of teeth, and score 4 indicated a more slanted shape. Characteristic III described the extent of the nasal-incisive suture, score 1 was indicated wide contact, and score 4 indicated no contact. Characteristic IV described the shape of the pterygoid hamulus, score 1 indicated an inward shape, and score 4 indicated an outward shape. Characteristic V described the shape of the bulla, score 1 indicated a less ungular shape, and score 3 indicated a more ungular shape. Characteristic VI described the shape of the nares, score indicated an upper distended shape, and score 3 indicated a lower distended shape. All specimens were measured by one person (E. Nakagawa) to avoid interobserver errors.

Growth class determination: Specimens were grouped by species, sex, and growth class. Three growth classes were defined according to the postnatal developmental stage as described by Uno (1986): pups (0 year), subadults (1–4 years old), and adults (more than 5 years old). These classes were assigned depending on the condylobasal length (CBL) as described in previous studies[7,11,19]. For male Kuril harbor seals, the CBL of pups were less than 187 mm, those of subadults ranged from 187 to 212 mm, and those of adults were more than 212 mm; for female Kuril harbor seals, the CBL of pups were less than 182 mm, those of subadults ranged from 182 to 205 mm, and those of adults were more than 205 mm. For male spotted seals, the CBL of pups were less than 182 mm, those of subadults ranged from 182 to 210 mm, and those of adults were more than 210 mm; for female spotted seals, the CBL of pups were less than 181 mm, those of subadults ranged from 181 to 200 mm, and those

Table 1. Cranial characteristics of Kuril harbor seals and spotted seals used in this study (as shown in Fig. 2 and 3).

No.	Characteristics
Metric characteristics	
1	Condylobasal length
2	Palatal length
3	Upper tooth row length
4	Mastoid width
5	Greatest width of cranium
6	Zygomatic width
7	Cranium height
8	Mandible length
9	Height of mandible at coronoid process
10	Lower tooth row length
11	Height of mandible behind the molar
12	Overall length of nasals
13	Length of maxillo-frontal suture to caudal end of nasals
14	Width of nasals at maxillo-frontal suture
15	Maximal width of external nares
16	Width of snout at canine
17	Least interorbital width
18	Greatest mesial-distal length of second upper premolar
19	Width of palate behind first molars
20	Least width of palate at pterygoid hamulus
21	Width of bulla from notch rostral to auditory process to middle of carotid foramen
22	Length of bulla
23	Width at condyles
24	Foremen magnum width
25	Foremen magnum height
26	Length of snout from rostral edge of nasals
27	Jugal length
28	Width of bulla from tip of auditory process to rostral edge of carotid foramen
29	Width of corocoid process at rostral margin
Non-metric characteristics[a)]	
I	Shape of temporozygomatic suture (1-3)
II	Angle of second upper premolar (1-4)
III	Extent of nasal-incisive suture (1-4)
IV	Shape of pterygoid hamulus (1-4)
V	Shape of bulla (1-3)
VI	Shape of nares (1-3)

[a)]The numeral scores of the non-metric characteristics are shown in parentheses.

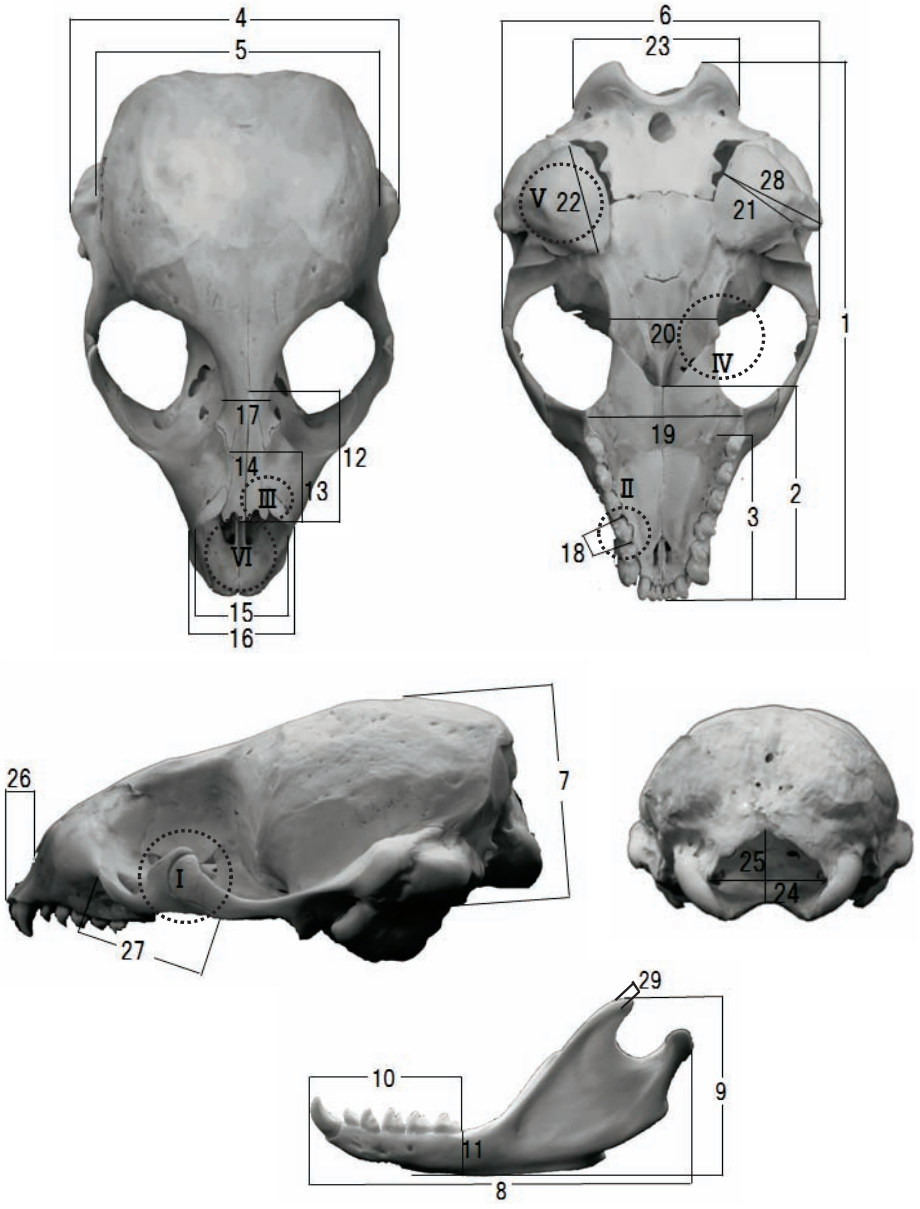

Fig. 2. Cranial characteristics used in this study (photographs are from the spotted seal). Numbers refer to the characteristics listed in Table 1 and circles show the point of non-metric characteristics in Fig. 3.

of adults were more than 200 mm.

Statistical analysis: Statistical analyses were carried out using R for Windows version 2.9.1[17]. Standard statistical values obtained using metric data included the mean, standard deviation (SD), coefficient of variation (CV), and the range of each growth class. The *t*-test was performed to compare sexual differences, and analysis of variance (ANOVA) was used to compare the interspecies differences for each growth class. Principle component analysis (PCA) and canonical discriminant analysis were used in order to investigate interspecies variation for each growth class. Canonical discriminant analysis was performed, with the exception of the CBL because of its artificial bias, and the values of the original variables determined by both analyses were standardized so that each variable had an equal weight. Pearson's chi-square test revealed no

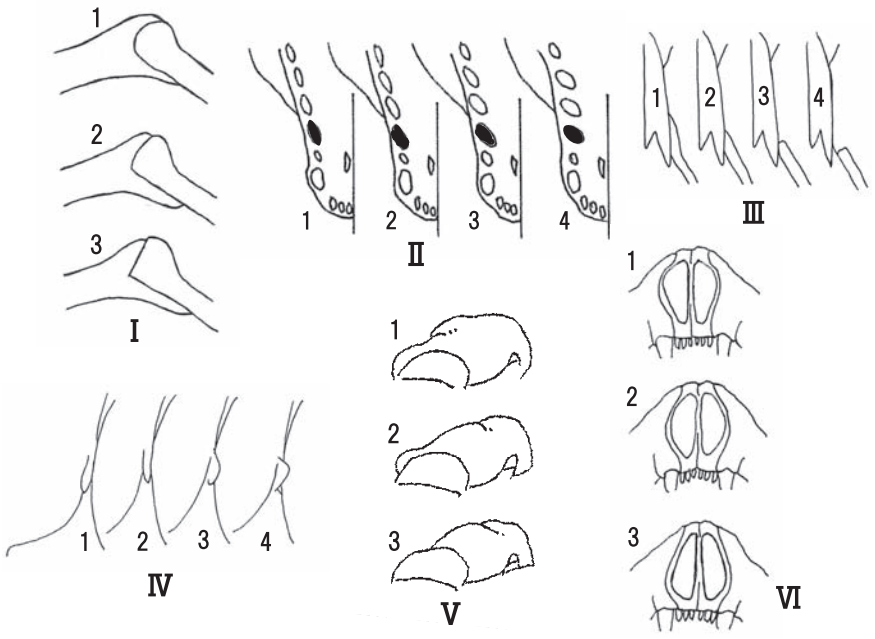

Fig. 3. Non-metric characteristics of seal skulls used in this study. Roman numerals refer to the characteristics listed in Table 1. Illustrations were reformed from a previous study[3].

sexual differences with regard to the non-metric data; therefore, we combined the male and female data. The frequency of each score was calculated and interspecies differences were investigated using Pearson's chi-square test. As many of the skulls were partly broken, the full suite of 35 characteristics could not be determined for all specimens. For that reason, sample sizes varied among analyses, depending on which of the characteristics were being compared and the type of statistical treatment employed. The sample sizes are stated in the Tables and Figures.

Results

Kuril harbor seals

Twenty-one metric cranial characteristics of Kuril harbor seal pups, 11 characteristics of subadults, and 15 characteristics of adults showed significant sexual differences by the *t*-test (Table 2). Characteristics nos. 2, 3, 4, 5, 6, 16, and 20 demonstrated sexual differences in all growth classes, and, among these, nos. 4, 5, 16, and 20 were also accepted as interspecies differences in all growth classes by ANOVA (Table 2). In addition, 20 metric cranial characteristics of pups, 25 characteristics of subadults, and 8 characteristics of adults demonstrated interspecies differences (Table 2).

PCA for the combined sample from both species was performed because of no prior grouping of material. The first principle component accounted for 91.0% of the total variation, and the second principle component accounted for 2.1%. The scatter plot of the first and second principle components revealed a clear separation among the growth classes between the two species (Fig. 4). The first principle component was mainly influenced by metric cranial characteristics nos. 1, 4, 5, 7, 10, 15, 20, 21, 22, 23, 24, and 28 (Table 3).

Canonical discriminant analysis was performed using the same samples as the PCA. This analysis correctly classified all Kuril harbor seals, but three female Kuril harbor seal subadults were incorrectly classified as one male pup and two male subadults (Table 4). The percentage contribution of the first canonical variate accounted for 69.6% and the second

canonical variate accounted for 14.3%. The standardized discriminant coefficients revealed that the variables that contributed to the discrimination between species, were nos. 4, 5, 7, 10, 15, 20, 21, 22, 23, 24, and 28 (Table 5). These were the same as the influential characteristics determined by PCA, with the exception of the CBL (no. 1).

Pearson's chi-square test on six non-metric cranial characteristics revealed significant interspecies differences for characteristics I and III ($P < 0.05$). For characteristics I and III, many of the Kuril harbor seals were ascribed to score 3 (Fig. 5). In addition, characteristics I and VI showed the variation in the proportion of growth class associated with the scores (Fig. 5). For characteristic IV, Kuril harbor seals were equally represented in each score category (Fig. 5).

Spotted seals

The spotted seal samples were particularly biased towards pups, and the *t*-test was not used to compare the sexual differences among adult spotted seals because of the small sample size (Table 2). Four characteristics of spotted seal pups and 10 characteristics of subadults showed significant sexual differences by the *t*-test ($P < 0.05$; Table 2).

Canonical discriminant analysis correctly classified each growth class of all spotted seals (Table 4). However, one male spotted seal pup was incorrectly classified as female (Table 4).

For the non-metric cranial characteristics, I, II, III, and VI, many spotted seals were scored as 1 (Fig. 5). On the contrary, the majority of spotted seals scored 4 for characteristic IV (Fig. 5).

Discussion

Kuril harbor seals

Sexual differences in the metric cranial characteristics identified by the *t*-test were more likely to be detected in each growth class of Kuril harbor seals than of spotted seals. This feature has been observed by other studies[4,14,18,19] and is probably a result of this species' polygamy by competing for females at limited haul-out sites[5]. This sexual dimorphism of the Kuril harbor seal was observed not only in adults but also in pups and subadults. The numbers of Kuril harbor seals have increased, but their haul-out sites have decreased over the last two decades[8]; therefore, their density at haul-out sites has grown. This density effect may be related to sexual dimorphism. The cerebral cranium and supramaxilla sizes of male Kuril harbor seals were larger than those of females; additionally, they were also larger in Kuril harbor seals than in spotted seals as determined with ANOVA. The body length of the Kuril harbor seal is larger than the spotted seal[13], and the skull sizes of the two seals are reflected by their body sizes.

PCA was performed using pooled data from both species, and the first principle component accounted for a very high proportion (91.0%). The measurements, which could be used to determine the whole size of the skull (characteristic nos. 1, 4, 5, 7, 20, 23, and 24), the rostrum (no. 15), mandible (no. 10), and auditory bulla (nos. 21, 22, and 28) influenced the growth classes of both seals. The growth of certain metric data was associated with that of the other data, and we could not identify the best characteristic with which to effectively identify either species.

In canonical discriminant analysis, only two specimens were discriminated incorrectly with regard to the sex and growth class; furthermore, the species of all specimens were discriminated correctly. Consequently, it is possible to almost exactly place any unknown specimen in their species, sex, and growth class with the cranial data set generated in this study.

When the shape of the temporozygomatic suture (characteristic I) and the extent of the nasal-incisive suture (Characteristic III) were significantly different between Kuril harbor and spotted seals in Pearson's chi-square test, the shape of the temporozygomatic suture and the shape of nares (characteristic VI) were indicators

Table 2. Standard statistics for the skull characteristics of Kuril harbor seals and spotted seals.

Characteristic[a] number	Species	Sex	Pup						Subadult						Adult					
			N	Mean ± S.D. (mm)	C.V. (%)	Range (mm)	*t*-test[b]	ANOVA[c]	N	Mean ± S.D. (mm)	C.V. (%)	Range (mm)	*t*-test[b]	ANOVA[c]	N	Mean ± S.D. (mm)	C.V. (%)	Range (mm)	*t*-test[b]	ANOVA[c]
1	Kuril harbor seal	M	8	181.18 ± 4.09	2.26	174.00 − 186.4			20	198.88 ± 5.97	3.00	187.9 − 209.8			13	219.03 ± 7.06	3.22	212.0 − 235.5		
		F	5	172.22 ± 4.26	2.47	165.50 − 178.4			19	195.23 ± 5.16	2.64	186.1 − 203.9			15	213.97 ± 7.22	3.37	206.0 − 229.3		
	Spotted seal	M	19	174.00 ± 5.34	3.07	156.00 − 181.1			4	191.65 ± 4.83	2.52	187.3 − 199.6			1	214.80	−			
		F	13	173.06 ± 4.54	2.62	165.80 − 180.5			2	184.95 ± 0.55	0.30	184.4 − 185.5			2	217.35 ± 2.25	1.04	215.1 − 219.6		
2	Kuril harbor seal	M	8	75.60 ± 1.44	1.90	73.50 − 77.8	*	††	20	85.25 ± 3.02	3.54	79.4 − 90.3	*	††	13	99.03 ± 9.60	9.69	90.0 − 130.0	*	
		F	5	72.44 ± 2.38	3.28	68.80 − 76.0			19	83.05 ± 3.40	4.09	76.0 − 89.0			15	92.79 ± 4.64	5.00	87.6 − 103.1		
	Spotted seal	M	19	71.86 ± 3.17	4.41	66.30 − 80.0			4	81.28 ± 1.35	1.66	79.7 − 83.3			1	92.40	−			
		F	13	70.44 ± 2.69	3.82	63.10 − 75.2			2	75.65 ± 2.25	2.97	73.4 − 77.9			2	94.55 ± 1.05	1.11	93.5 − 95.6		
3	Kuril harbor seal	M	8	61.61 ± 1.33	2.16	59.8 − 63.1	*	†††	20	67.23 ± 2.52	3.74	63.2 − 72.3	*	†††	13	74.93 ± 2.86	3.81	71.9 − 80.6	**	
		F	5	58.78 ± 1.99	3.38	55.8 − 60.9			19	65.72 ± 2.25	3.43	61.4 − 70.7			15	71.53 ± 2.34	3.27	68.2 − 75.8		
	Spotted seal	M	19	55.85 ± 4.54	8.13	51.8 − 73.5			4	60.58 ± 1.08	1.78	59.3 − 62.0	*		1	70.00	−			
		F	13	54.36 ± 2.47	4.54	49.7 − 59.7			2	58.30 ± 0.30	0.51	58.0 − 58.6			2	72.30 ± 0.50	0.69	71.8 − 72.8		
4	Kuril harbor seal	M	8	116.80 ± 2.43	2.08	112.3 − 120.3	**	†††	20	124.24 ± 3.60	2.90	117.4 − 132.3	**	†††	13	133.84 ± 3.48	2.60	127.6 − 140.4	**	††
		F	5	110.90 ± 1.91	1.72	108.6 − 113.9			19	121.56 ± 3.06	2.52	114.9 − 127.4			15	129.55 ± 4.01	3.10	124.5 − 137.1		
	Spotted seal	M	19	108.29 ± 3.40	3.14	98.3 − 115.3			4	116.00 ± 1.83	1.58	113.2 − 118.2	*		1	120.50	−			
		F	13	106.98 ± 2.62	2.44	103.7 − 111.6			2	109.60 ± 1.70	1.55	107.9 − 111.3			2	122.90 ± 0.50	0.41	122.4 − 123.4		
5	Kuril harbor seal	M	8	94.78 ± 1.58	1.67	92.2 − 97.4	**	†††	20	98.05 ± 2.13	2.18	95.1 − 102.4	*	†††	13	100.45 ± 2.15	2.14	97.3 − 104.3	**	†††
		F	5	92.28 ± 1.10	1.19	90.9 − 93.5			19	96.85 ± 1.57	1.62	92.9 − 99.5			15	97.61 ± 2.35	2.41	94.3 − 103.8		
	Spotted seal	M	18	89.16 ± 2.58	2.89	83.5 − 94.5			4	91.10 ± 1.49	1.64	89.9 − 93.6			1	94.00	−			
		F	13	88.61 ± 1.76	1.99	85.5 − 90.9			2	88.45 ± 1.25	1.41	87.2 − 89.7			2	92.00 ± 1.60	1.74	90.4 − 93.6		
6	Kuril harbor seal	M	8	110.79 ± 1.81	1.64	107.4 − 113.3	***	†††	20	120.60 ± 4.52	3.75	111.9 − 132.3	*	†††	13	134.47 ± 3.39	2.52	128.2 − 142.4	*	
		F	5	104.20 ± 1.81	1.73	102.8 − 107.7			19	117.51 ± 3.50	2.98	108.4 − 124.1			15	128.73 ± 7.93	6.16	119.2 − 149.8		
	Spotted seal	M	19	101.36 ± 3.16	3.12	91.0 − 105.0			4	111.28 ± 2.96	2.66	108.4 − 115.9	*		1	126.40	−			
		F	13	100.62 ± 2.46	2.45	95.8 − 106.3			2	104.10 ± 0.10	0.10	104.0 − 104.2			2	134.25 ± 2.55	1.90	131.7 − 136.8		
7	Kuril harbor seal	M	8	68.24 ± 2.25	3.30	64.9 − 72.0	*	†††	20	68.83 ± 2.85	4.14	64.2 − 74.7		†††	13	71.71 ± 2.02	2.82	68.5 − 75.6	*	
		F	5	64.66 ± 2.64	4.08	59.5 − 66.7			19	67.57 ± 2.44	3.61	64.4 − 73.7			15	69.95 ± 2.74	3.91	64.2 − 74.0		
	Spotted seal	M	19	63.63 ± 2.69	4.23	59.1 − 68.0			4	63.45 ± 1.50	2.37	61.4 − 65.6			1	70.80	−			
		F	13	62.18 ± 2.84	4.57	54.7 − 66.3			2	62.05 ± 0.85	1.37	61.2 − 62.9			2	69.90 ± 3.10	4.43	66.8 − 73.0		
8	Kuril harbor seal	M	8	117.43 ± 2.07	1.77	113.3 − 119.5	***	†††	20	129.81 ± 4.82	3.71	119.3 − 137.8		††	11	146.50 ± 5.01	3.42	140.6 − 158.7	*	
		F	5	110.96 ± 2.02	1.82	108.8 − 114.4			19	128.23 ± 4.32	3.37	116.7 − 134.0			14	142.46 ± 5.59	3.92	135.8 − 155.4		
	Spotted seal	M	19	110.41 ± 3.30	2.99	100.7 − 115.7			4	122.08 ± 2.78	2.28	118.0 − 125.8	*		1	141.70	−			
		F	13	108.96 ± 3.19	2.92	102.7 − 114.0			2	118.20 ± 0.20	0.17	118.0 − 118.4			2	143.60 ± 2.00	1.39	141.6 − 145.6		

9	Kuril harbor seal	M	8	48.38 ± 2.26	4.66	45.2 — 52.2		†††	20	54.38 ± 3.55	6.52	48.4 — 65.2		††	13	64.35 ± 3.86	6.00	58.6 — 70.8				
		F	5	46.38 ± 1.89	4.08	44.8 — 49.6			19	52.81 ± 2.38	4.52	49.6 — 57.4			15	62.00 ± 6.02	9.71	55.2 — 72.2				
	Spotted seal	M	19	44.78 ± 2.01	4.48	39.0 — 47.7			3	50.37 ± 0.26	0.52	50.0 — 50.6			1	65.00	—					
		F	13	44.10 ± 1.85	4.20	41.6 — 47.4			2	46.90 ± 2.20	4.69	44.7 — 49.1			2	65.60 ± 1.90	2.90	63.7 — 67.5				
10	Kuril harbor seal	M	8	56.38 ± 0.77	1.36	55.5 — 57.7	***	†††	19	59.40 ± 1.81	3.05	56.3 — 63.5		†††	11	64.75 ± 1.65	2.55	62.7 — 68.0				
		F	5	52.92 ± 1.18	2.24	51.3 — 54.9			17	58.09 ± 3.24	5.58	50.5 — 66.9			14	61.29 ± 1.60	2.62	59.8 — 64.7				
	Spotted seal	M	19	51.23 ± 1.50	2.93	48.0 — 54.5	*		4	54.00 ± 0.57	1.06	53.1 — 54.7			1	60.80	—					
		F	13	50.05 ± 1.93	3.86	47.4 — 54.1			2	52.65 ± 0.55	1.04	52.1 — 53.2			1	61.10	—					
11	Kuril harbor seal	M	8	18.04 ± 1.14	6.31	16.2 — 19.8	*	†††	20	19.97 ± 1.18	5.89	18.0 — 22.5	**	†††	13	23.62 ± 1.23	5.20	21.3 — 26.2				
		F	5	16.40 ± 1.16	7.05	15.2 — 18.5			18	18.82 ± 1.15	6.12	17.1 — 20.6			15	21.22 ± 1.57	7.42	19.3 — 25.3				
	Spotted seal	M	19	15.06 ± 1.09	7.22	13.6 — 17.7	*		4	16.50 ± 0.87	5.30	15.5 — 17.9			1	19.90	—					
		F	13	14.17 ± 0.92	6.52	13.1 — 16.7			2	16.25 ± 0.05	0.31	16.2 — 16.3			2	20.65 ± 0.45	2.18	20.2 — 21.1				
12	Kuril harbor seal	M	8	42.63 ± 1.68	3.95	40.3 — 45.2	***		20	46.36 ± 2.96	6.39	40.7 — 51.0		†	13	53.38 ± 2.88	5.40	48.1 — 59.8				
		F	5	38.12 ± 1.16	3.04	36.5 — 39.7			19	45.87 ± 3.30	7.20	39.8 — 51.0			15	51.53 ± 5.07	9.83	47.0 — 66.6				
	Spotted seal	M	19	40.17 ± 2.02	5.04	36.1 — 43.5			4	43.10 ± 2.77	6.44	39.8 — 47.1			1	48.60	—					
		F	13	39.69 ± 3.22	8.10	30.7 — 43.1			2	39.95 ± 1.85	4.63	38.1 — 41.8			2	48.75 ± 3.65	7.49	45.1 — 52.4				
13	Kuril harbor seal	M	8	22.10 ± 1.21	5.49	20.3 — 24.0	**		20	23.09 ± 1.52	6.60	19.8 — 25.3			13	27.25 ± 1.55	5.70	25.4 — 31.1				
		F	5	19.96 ± 0.94	4.68	18.5 — 21.2			19	23.03 ± 2.16	9.39	19.0 — 28.0			15	26.01 ± 3.28	12.63	21.9 — 34.5				
	Spotted seal	M	19	21.97 ± 1.14	5.21	19.6 — 24.2			4	24.68 ± 2.52	10.21	21.2 — 27.9			1	30.20	—					
		F	13	21.35 ± 1.98	9.29	16.0 — 24.3			2	21.05 ± 2.15	10.21	18.9 — 23.2			2	25.45 ± 2.45	9.63	23.0 — 27.9				
14	Kuril harbor seal	M	8	10.45 ± 1.09	10.42	8.9 — 12.1			20	12.17 ± 1.06	8.75	10.2 — 14.2	*		13	14.33 ± 1.05	7.33	11.8 — 15.8				
		F	5	9.88 ± 0.84	8.55	9.0 — 11.4			19	11.36 ± 1.10	9.67	9.4 — 13.7			15	13.49 ± 2.32	17.22	8.1 — 19.0				
	Spotted seal	M	19	10.41 ± 0.78	7.47	9.3 — 12.0			4	11.25 ± 1.06	9.46	10.0 — 12.7			1	14.60	—					
		F	13	10.34 ± 1.00	9.68	8.8 — 12.5			2	10.60 ± 0.80	7.55	9.8 — 11.4			2	13.85 ± 0.75	5.42	13.1 — 14.6				
15	Kuril harbor seal	M	8	25.04 ± 1.09	4.36	23.5 — 26.7			20	27.18 ± 1.58	5.81	24.6 — 30.2		†	13	30.56 ± 0.98	3.22	28.1 — 32.3	*			
		F	5	24.22 ± 0.28	1.15	23.9 — 24.7			19	27.00 ± 1.24	4.60	24.6 — 29.0			15	29.69 ± 1.51	5.09	26.3 — 31.7				
	Spotted seal	M	19	24.17 ± 1.15	4.75	22.0 — 26.0			4	26.73 ± 1.20	4.49	24.8 — 28.1	**		1	29.70	—					
		F	13	24.56 ± 1.48	6.01	21.4 — 26.1			2	23.95 ± 0.25	1.04	23.7 — 24.2			2	28.10 ± 0.10	0.36	28.0 — 28.2				
16	Kuril harbor seal	M	8	37.09 ± 1.40	3.78	35.4 — 40.0	**	†††	20	40.53 ± 1.92	4.73	35.5 — 45.0	**	†††	13	45.52 ± 2.12	4.66	41.8 — 48.9	**			
		F	5	34.36 ± 1.03	2.99	32.8 — 35.6			19	38.90 ± 1.40	3.59	37.0 — 42.2			15	42.37 ± 2.97	7.02	39.4 — 49.8				
	Spotted seal	M	19	30.56 ± 0.99	3.22	29.0 — 32.2			4	32.05 ± 0.39	1.22	31.5 — 32.6	*		1	39.80	—					
		F	13	30.00 ± 3.05	10.16	22.0 — 36.6			2	29.65 ± 0.45	1.52	29.2 — 30.1			2	38.50 ± 2.70	7.01	35.8 — 41.2				

[a)]Characteristic numbers are referred to Table 1.
[b)]Significant differences between the sexes by the t-test (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$).
[c)]Significant differences between the species by ANOVA (†††, $P < 0.001$; ††, $P < 0.01$; †, $P < 0.05$).

Table 2. continued.

Characteristic[a] number	Species	Sex	Pup						Subadult						Adult					
			N	Mean ± S.D. (mm)	C.V. (%)	Range (mm)	*t*-test[b]	ANOVA[c]	N	Mean ± S.D. (mm)	C.V. (%)	Range (mm)	*t*-test[b]	ANOVA[c]	N	Mean ± S.D. (mm)	C.V. (%)	Range (mm)	*t*-test[b]	ANOVA[c]
17	Kuril harbor seal	M	8	14.53 ± 1.22	8.43	11.6 — 15.7	*	†	20	15.14 ± 1.00	6.62	13.1 — 16.8		†††	13	17.16 ± 0.91	5.33	15.2 — 18.7	**	
		F	5	12.90 ± 0.94	7.26	11.6 — 14.3			19	13.57 ± 0.90	6.66	11.8 — 16.0			15	15.39 ± 1.94	12.61	13.1 — 20.0		
	Spotted seal	M	19	13.15 ± 0.97	7.35	10.9 — 14.8			4	12.63 ± 1.85	14.65	10.0 — 15.0			1	16.90	—			
		F	13	12.92 ± 1.35	10.46	10.8 — 15.1			2	11.10 ± 0.60	5.41	10.5 — 11.7			2	15.30 ± 0.20	1.31	15.1 — 15.5		
18	Kuril harbor seal	M	8	9.68 ± 0.24	2.52	9.3 — 10.0	**	†††	20	10.06 ± 0.64	6.32	9.0 — 11.5	**	†††	13	10.17 ± 0.41	4.03	9.4 — 10.8		
		F	5	8.94 ± 0.31	3.51	8.4 — 9.3			19	9.45 ± 0.85	9.00	6.6 — 10.6			15	9.82 ± 0.72	7.29	8.8 — 11.8		
	Spotted seal	M	19	8.37 ± 0.59	7.06	7.5 — 9.6	**		4	8.43 ± 0.45	5.33	7.8 — 8.9	**		1	9.20	—			
		F	13	7.60 ± 0.75	9.89	6.0 — 8.9			2	6.90 ± 0.10	1.45	6.8 — 7.0			2	10.15 ± 0.45	4.43	9.7 — 10.6		
19	Kuril harbor seal	M	8	51.74 ± 1.65	3.18	48.6 — 53.8	**	†††	20	55.75 ± 1.84	3.30	51.5 — 58.0		†††	13	61.52 ± 1.52	2.46	59.0 — 64.0	**	†
		F	5	48.76 ± 1.52	3.12	47.2 — 50.7			19	55.47 ± 1.73	3.12	51.9 — 58.6			15	58.65 ± 3.73	6.36	53.4 — 66.5		
	Spotted seal	M	19	45.23 ± 2.51	5.55	39.5 — 50.2			4	49.68 ± 2.23	4.50	47.2 — 52.5	*		1	51.40	—			
		F	13	44.86 ± 2.37	5.28	42.0 — 51.4			2	45.70 ± 0.60	1.31	45.1 — 46.3			2	56.20 ± 0.20	0.36	56.0 — 56.4		
20	Kuril harbor seal	M	8	36.70 ± 1.57	4.27	34.1 — 38.7	**	†††	20	38.67 ± 1.48	3.84	34.9 — 41.5	*	†††	13	41.56 ± 1.54	3.71	38.1 — 43.8	**	††
		F	5	34.20 ± 1.29	3.77	32.0 — 35.9			19	37.77 ± 1.31	3.47	35.0 — 41.5			15	38.99 ± 2.65	6.79	32.0 — 42.5		
	Spotted seal	M	19	33.07 ± 1.16	3.51	30.0 — 35.5			4	34.10 ± 1.02	3.00	33.2 — 35.8			1	35.00	—			
		F	13	32.38 ± 1.66	5.11	29.9 — 36.5			2	33.25 ± 0.25	0.75	33.0 — 33.5			2	35.00 ± 1.00	2.86	34.0 — 36.0		
21	Kuril harbor seal	M	8	29.26 ± 3.39	11.57	24.0 — 33.8			20	31.20 ± 1.19	3.81	29.6 — 34.0	*	†††	13	32.05 ± 1.51	4.72	29.6 — 34.8	*	††
		F	5	29.34 ± 0.91	3.11	28.2 — 30.3			19	30.92 ± 1.11	3.60	28.8 — 33.4			15	30.77 ± 1.72	5.60	27.7 — 34.6		
	Spotted seal	M	19	28.27 ± 1.40	4.96	25.6 — 30.4			4	28.58 ± 1.79	6.25	26.7 — 31.1			1	25.00	—			
		F	13	27.87 ± 1.44	5.16	25.4 — 30.0			2	27.65 ± 0.15	0.54	27.5 — 27.8			2	29.50 ± 0.10	0.34	29.4 — 29.6		
22	Kuril harbor seal	M	8	39.65 ± 0.81	2.04	38.1 — 40.8	*		20	41.14 ± 1.40	3.40	38.1 — 43.5		†	13	42.77 ± 1.24	2.90	40.8 — 44.5	*	
		F	5	37.24 ± 1.61	4.33	35.0 — 39.8			19	40.11 ± 1.46	3.65	36.2 — 42.2			15	41.48 ± 1.60	3.86	38.6 — 44.6		
	Spotted seal	M	19	37.97 ± 1.68	4.44	35.7 — 42.1			4	39.55 ± 0.93	2.35	38.1 — 40.5			1	41.00	—			
		F	13	37.77 ± 1.31	3.48	35.7 — 39.9			2	37.60 ± 1.10	2.93	36.5 — 38.7			2	40.55 ± 1.25	3.08	39.3 — 41.8		
23	Kuril harbor seal	M	8	59.60 ± 2.92	4.90	53.3 — 63.4		††	20	59.60 ± 1.65	2.76	56.9 — 63.2			13	61.03 ± 1.99	3.26	58.0 — 64.9		
		F	5	57.24 ± 1.72	3.00	55.1 — 59.6			19	57.86 ± 5.04	8.72	40.0 — 64.2			15	60.29 ± 2.34	3.89	56.3 — 64.0		
	Spotted seal	M	19	56.69 ± 2.03	3.58	52.3 — 60.5			4	58.18 ± 1.18	2.04	57.2 — 60.2	*		1	61.00	—			
		F	13	55.85 ± 2.19	3.92	53.1 — 61.4			2	55.65 ± 0.65	1.17	55.0 — 56.3			2	60.85 ± 0.55	0.90	60.3 — 61.4		
24	Kuril harbor seal	M	8	35.33 ± 1.34	3.79	32.6 — 36.9	*	†††	20	33.79 ± 1.67	4.95	31.7 — 37.6		†††	13	33.38 ± 2.20	6.58	30.7 — 38.4		
		F	5	34.22 ± 0.62	1.81	33.2 — 35.0			19	34.07 ± 1.69	4.96	31.3 — 36.8			15	32.93 ± 1.46	4.43	29.6 — 34.9		
	Spotted seal	M	19	31.49 ± 1.70	5.40	28.6 — 35.0	*		4	30.70 ± 1.19	3.87	29.0 — 32.2			1	33.10	—			
		F	13	29.82 ± 2.34	7.84	24.9 — 34.4			2	31.50 ± 0.90	2.86	30.6 — 32.4			2	30.05 ± 1.55	5.16	28.5 — 31.6		

25	Kuril harbor seal	M	8	28.94 ± 1.63	5.64	26.9	—	31.7		†††	20	27.96 ± 2.35	8.40	24.5	—	32.3		†††	13	27.70 ± 2.07	7.48	23.4	—	31.9		††
		F	5	27.22 ± 1.56	5.74	25.0	—	29.4			19	27.72 ± 1.84	6.64	24.8	—	31.3			15	26.49 ± 1.36	5.15	23.4	—	29.0		
	Spotted seal	M	19	24.03 ± 2.01	8.37	20.3	—	27.9			4	22.95 ± 1.49	6.48	21.5	—	25.4			1	25.70	—					
		F	13	24.57 ± 3.40	13.85	20.3	—	34.5			2	22.25 ± 1.15	5.17	21.1	—	23.4			2	22.35 ± 0.05	0.22	22.3	—	22.4		
26	Kuril harbor seal	M	8	25.63 ± 1.12	4.35	23.7	—	27.3			20	30.10 ± 1.34	4.46	28.0	—	32.8		†	13	34.85 ± 2.58	7.40	31.9	—	40.2		
		F	5	24.66 ± 1.10	4.48	22.5	—	25.6			19	29.82 ± 1.64	5.50	27.0	—	33.5			15	33.72 ± 1.56	4.63	31.6	—	37.6		
	Spotted seal	M	19	25.09 ± 1.83	7.30	21.3	—	27.3			4	28.83 ± 0.71	2.46	27.8	—	29.8			1	36.00	—					
		F	13	24.54 ± 1.79	7.30	21.6	—	27.5			2	26.80 ± 1.30	4.85	25.5	—	28.1			2	37.25 ± 0.05	0.13	37.2	—	37.3		
27	Kuril harbor seal	M	8	48.05 ± 1.34	2.78	46.0	—	50.2	*	†††	20	53.36 ± 2.61	4.89	46.8	—	58.5		†††	13	60.91 ± 2.48	4.07	58.2	—	66.7		
		F	5	46.74 ± 0.84	1.80	45.8	—	47.9			19	52.61 ± 2.58	4.90	46.4	—	56.8			15	59.07 ± 3.83	6.49	53.8	—	68.4		
	Spotted seal	M	19	44.53 ± 2.11	4.74	40.3	—	48.1			4	48.68 ± 0.49	1.01	48.1	—	49.3			1	57.30	—					
		F	13	42.99 ± 2.73	6.35	38.0	—	48.7			2	45.95 ± 1.85	4.03	44.1	—	47.8			2	60.90 ± 0.00	0.00	60.9	—	60.9		
28	Kuril harbor seal	M	8	39.83 ± 1.89	4.75	35.6	—	42.6	**		20	42.20 ± 1.06	2.52	39.8	—	44.1		†	13	46.05 ± 1.55	3.36	43.9	—	49.6	**	†††
		F	5	37.28 ± 0.75	2.02	36.2	—	38.4			19	42.69 ± 4.24	9.92	39.6	—	59.7			15	44.08 ± 1.81	4.11	41.3	—	48.6		
	Spotted seal	M	19	38.35 ± 1.30	3.38	35.0	—	40.1			4	39.73 ± 1.37	3.45	38.2	—	41.5			1	38.50	—					
		F	13	37.75 ± 1.79	4.74	32.2	—	39.8			2	38.95 ± 1.05	2.70	37.9	—	40.0			2	41.15 ± 0.15	0.36	41.0	—	41.3		
29	Kuril harbor seal	M	8	3.26 ± 0.47	14.29	2.5	—	3.9	*	†	20	3.97 ± 0.73	18.49	2.7	—	6.3		†††	13	5.90 ± 1.05	17.83	4.4	—	8.1		
		F	5	2.68 ± 0.50	18.79	2.2	—	3.5			19	4.06 ± 0.75	18.35	2.5	—	5.6			15	5.59 ± 1.19	21.23	3.8	—	8.2		
	Spotted seal	M	19	2.55 ± 0.45	17.48	1.7	—	3.2			3	2.90 ± 0.16	5.63	2.7	—	3.1	*		1	5.90	—					
		F	13	2.68 ± 0.61	22.81	2.3	—	4.7			2	2.15 ± 0.15	6.98	2.0	—	2.3			2	4.65 ± 0.45	9.68	4.2	—	5.1		

[a)]Characteristic numbers are referred to Table 1.
[b)]Significant differences between the sexes by the t-test (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$).
[c)]Significant differences between the species by ANOVA (†††, $P < 0.001$; ††, $P < 0.01$; †, $P < 0.05$).

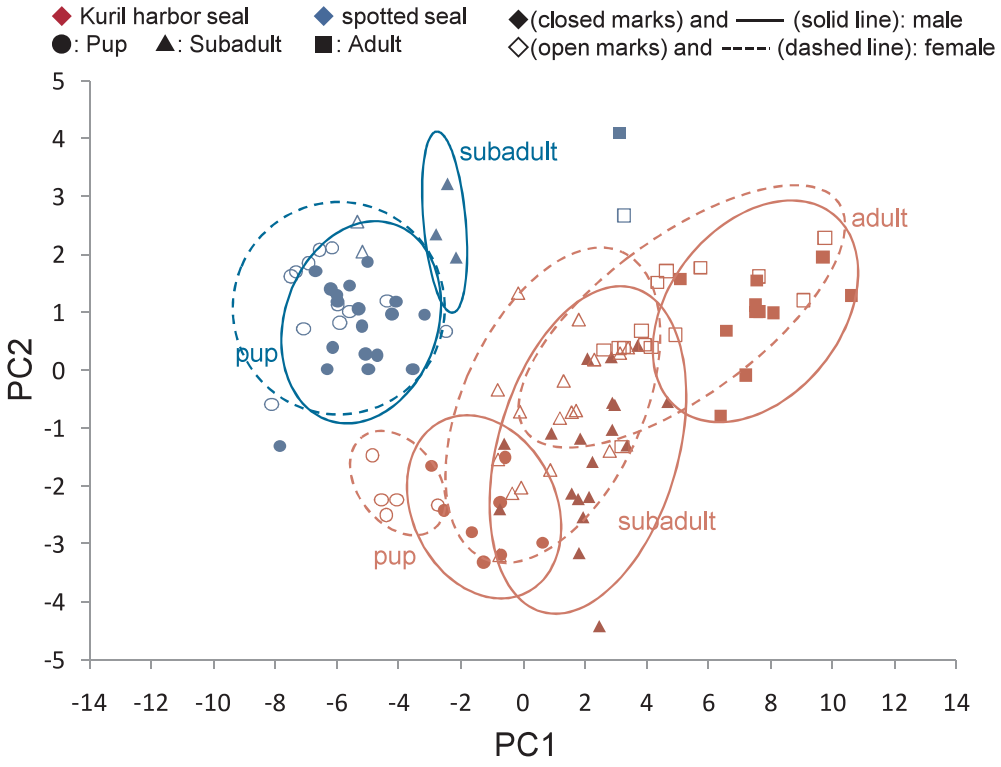

Fig. 4. Scatter plots of the first principle component (PC1) and the second principle component (PC2). Circles show the probability ellipsoid 95% of plotted values for each species, sex, and growth class.

Table 3. Factor matrix from the 29 value principle component analyses of both the Kuril harbor seal and the spotted seal specimens.

Characteristic[a)] number	First Principle component	Standardized first principle component	Characteristic[a)] number	First principle component	Standardized first principle component
1	0.212	11.060	**16**	0.209	6.518
2	0.206	7.868	**17**	0.164	7.754
3	0.209	8.671	**18**	0.163	8.252
4	0.215	12.299	**19**	0.210	8.383
5	0.190	20.317	**20**	0.198	10.998
6	0.214	9.273	**21**	0.137	13.887
7	0.175	16.486	**22**	0.181	18.226
8	0.213	9.106	**23**	0.116	17.788
9	0.209	6.863	**24**	0.075	13.975
10	0.209	11.211	**25**	0.091	9.205
11	0.209	5.727	**26**	0.197	6.887
12	0.197	8.341	**27**	0.208	7.775
13	0.153	8.614	**28**	0.172	11.572
14	0.165	6.172	**29**	0.185	2.592
15	0.197	10.352			

[a)]Characteristic numbers are referred to Table 1.

Table 4. Numbers of specimens that predicted the species, sex and growth class[a)] by discriminant analysis.

Original			Predicted											
			Kuril harbor seal						Spotted seal					
Species	Sex	Growth	Male			Female			Male			Female		
			P	S	A	P	S	A	P	S	A	P	S	A
Kuril harbor seal	Male	P	8	0	0	0	0	0	0	0	0	0	0	0
		S	0	19	0	0	0	0	0	0	0	0	0	0
		A	0	0	11	0	0	0	0	0	0	0	0	0
	Female	P	0	0	0	5	0	0	0	0	0	0	0	0
		S	1	2	0	0	14	0	0	0	0	0	0	0
		A	0	0	0	0	0	14	0	0	0	0	0	0
Spotted seal	Male	P	0	0	0	0	0	0	17	0	0	1	0	0
		S	0	0	0	0	0	0	0	3	0	0	0	0
		A	0	0	0	0	0	0	0	0	1	0	0	0
	Female	P	0	0	0	0	0	0	0	0	0	12	0	0
		S	0	0	0	0	0	0	0	0	0	0	2	0
		A	0	0	0	0	0	0	0	0	0	0	0	1

[a)]Growth class: Pup (P),:Subadult (S) and Adult (A)

Table 5. Discriminant coefficients and standardized discriminant coefficients from discriminat analysis.

Characteristic[a)] number	Discriminant coefficient	Standardized discriminant coefficient	Characteristic[a)] number	Discriminant coefficient	Standardized discriminant coefficient
2	0.056	7.882	**16**	− 0.128	6.577
3	− 0.138	8.718	**17**	0.032	7.827
4	− 0.097	12.331	**18**	0.039	8.365
5	− 0.035	20.365	**19**	0.098	8.400
6	− 0.074	9.297	**20**	− 0.051	11.073
7	− 0.026	16.536	**21**	− 0.020	13.960
8	− 0.209	9.137	**22**	0.284	18.179
9	0.174	6.868	**23**	0.077	17.800
10	− 0.107	11.273	**24**	− 0.334	14.149
11	− 0.451	5.934	**25**	− 0.031	9.248
12	0.000	8.378	**26**	0.050	6.922
13	0.220	8.589	**27**	− 0.003	7.807
14	0.100	6.207	**28**	0.020	11.615
15	0.305	10.310	**29**	− 0.061	2.767

[a)]Characteristic numbers are referred to Table 1.

of the growth class of Kuril harbor seals. The differences in non-metric characteristics between the two seals became clear with the growth variation of the Kuril harbor seal.

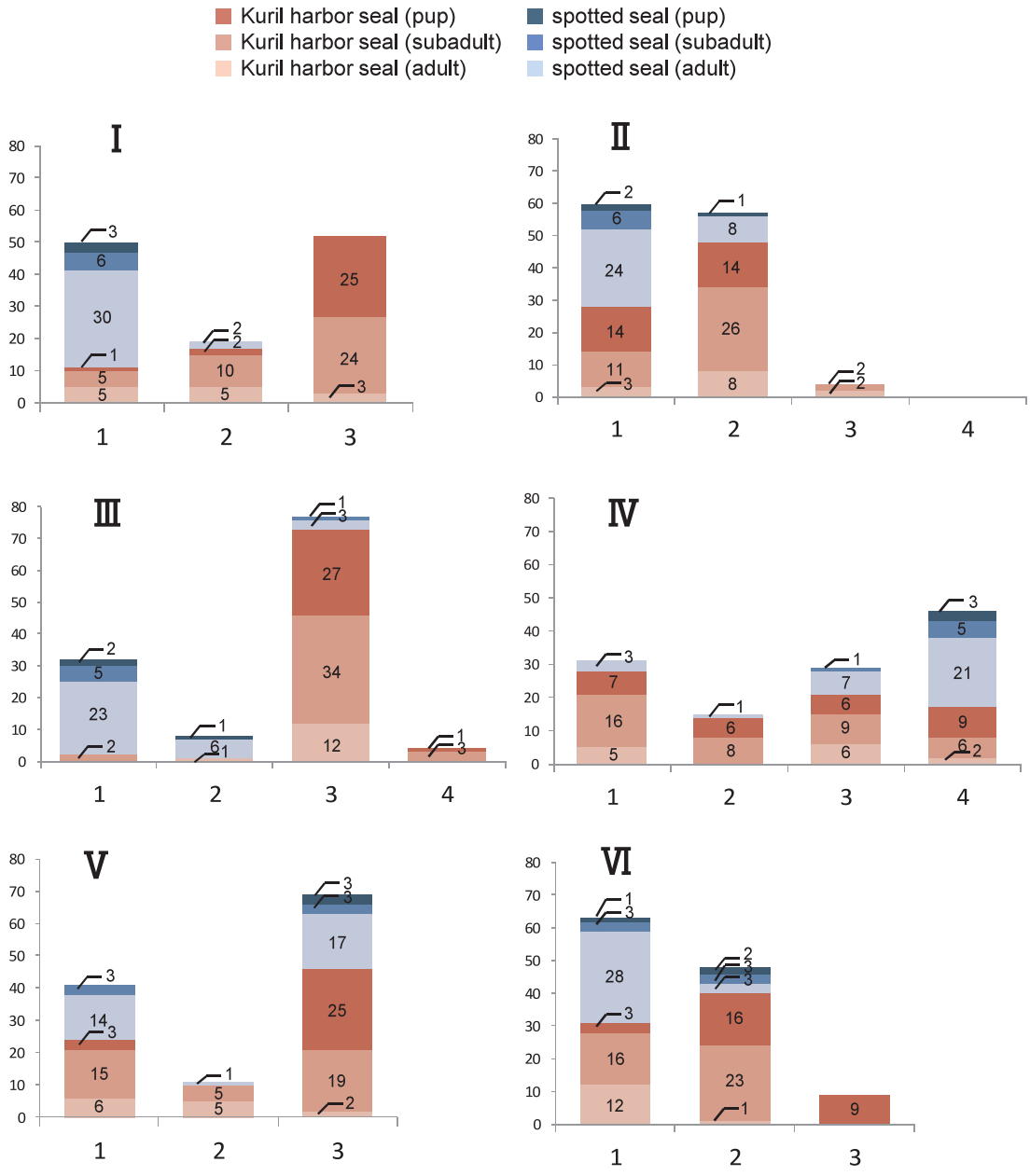

Fig. 5. Frequencies of each numeric score for non-metric characteristics. The numbers of specimens show on each bar.

Spotted seals

Although ANOVA revealed interspecies differences between the two seals for many metric characteristics of pups and subadults, we observed fewer differences for adults. Adult spotted seals were remarkably large in this study; besides, the number of subadult and adult spotted seals was biased and inadequate for a definitive conclusion about the growth variation in their skull morphology.

Although the spotted seal had few sexual differences in skull morphology[4,19], differences were recognized for some metric characteristics by the *t*-test. The measurements, which could determine the width of the skull (characteristics nos. 4 and 6), foremen magnum (nos. 23 and 24), the size of the supramaxilla (nos. 3, 15, and 16), mandible (nos. 8, 10, 11, and 29), and second

upper premolar (no. 18) showed sexual differences among spotted seal pups and subadults.

The non-metric characteristics of the spotted seal did not have as much growth variation as was observed in the Kuril harbor seal. Alternatively, we obtained different results for the shapes of the pterygoid hamulus (characteristic IV) of both seals as compared to those obtained in a previous study[4], in particular, this was a confirmed characteristic (score 4) in the majority of spotted seals. The pterygoid hamulus is related to the motion of the mandible. The sexual differentiation of masticatory function was also observed in the metric cranial characteristics. The increase in the number of spotted seals migrating to the Sea of Japan[8] could be responsible for this morphological variation in masticatory function, which differed from that observed in previous studies[4,19], and may be related to the variation of prey species. To clarify the variation in masticatory function and the growth variation in their skull morphology, we need to collect a larger number of specimens from a range of sites.

Although non-metric cranial characteristics have a lower discriminating power than metric characteristics[4,16], they are easy to use in the field and can be used by inexperienced researchers. It is possible to identify the Kuril harbor seal or the spotted seal with considerable accuracy on the basis of the two non-metric characteristics (characteristics I and III). These findings will be very useful to identify the species and growth class of unknown seal skulls in the field, where the two species are sympatric.

The characteristics of Kuril harbor seals were confirmed with those of other harbor seal subspecies, and the morphological differences between the Kuril harbor seal and the spotted seal corresponded with those observed in a previous study[4,19]. Future studies with a larger number of samples would clarify the degree of morphological variation both within and between the two species.

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