FULL PAPER *Anatomy*

Age-Related Change and Allometry of Skull and Canine of Sea Otters, *Enhydra lutris*

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ABSTRACT. Skulls and canines of 460 sea otters from Lopatka Cape, Kamchatka, were examined to assess development patterns, individual variation and sexual differences. An allometric formula was applied to morphometrical data, and the relative growth of each character to total length of skull was analyzed. In both sexes, most morphometrical characters ceased growth at about 2 years of age. Canine root length increased rapidly during the first year of life, while crown length decreased due to remarkable wear. There was large individual variation in the feeding and breathing/sniffing apparatus, while there was little variation in braincase size. There were sexual differences in most characteristics, although males and females showed similar growth patterns. The coronoid process of the mandible showed positive allometry in both sexes, and we attributed this finding to feeding habits. The fact that only male mastoids showed positive allometry may be due to the need for male otters to maintain a passing territory.
KEY WORDS: allometry, *Enhydra lutris*, growth, morphology, skull.

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The sea otter, *Enhydra lutris*, is a member of the Mustelidae, order Carnivora. It is highly adapted to the marine environment in a number of ways, including senses, feeding and behavior. Three subspecies of sea otters are commonly recognized: Asian (*E. l. lutris*), Alaskan (*E. l. kenyoni*) and southern sea otters (*E. l. nereis*) [2].

Morphological studies of skulls of this species revealed geographic variation, and supported the above subspecies designations [3, 18, 29, 36]. In most of these analyses, only adult specimens were used; the animals were considered adults if the basioccipital-basisphenoid suture was closed on the lower surface of the braincase [30]. Green [13] and Morejohn *et al.* [23] proposed criteria for relative age based on skull characters, tooth eruption and tooth wear. They used non-metric characters that indicate cessation of growth but not the age at which cessation occurred. The age of attainment of physical maturity is an important datum, because its variation can indicate changes in the nutritional condition of the population [25]. However, no detailed descriptions of age-related patterns of change have been available in sea otter skulls.

Bodkin *et al.* [4] evaluated the accuracy and precision of using cementum layers of canine teeth to estimate sea otter age. They concluded that this method was sufficiently accurate for estimating age class distributions of relatively large samples.

In this study, we used skull specimens to examine development of cranial structure in sea otters (*E. l. lutris*) in Lopatka Cape. We described growth over time, sexual differences and individual variation in the skulls and canines. Allometry was used to study relative growth of the different cranial components. We interpreted allometry coefficients as growth rates, although, in truth, they represented size rates. Discussion of our findings was based on functional grounds.

MATERIALS AND METHODS

We analyzed 460 skull specimens. All skulls were collected from beach-cast carcasses at Lopatka Cape, at the southern tip of Kamchatka, Russia, from 1983 to 1989 (n= 418) and in 1997 (n= 42), and were kept at the Kamchatka Institute of Ecology and Nature Management. Lopatka Cape was inhabited predominantly by males [19]. The sex of 286 specimens was known prior to the beginning of the study (male, 268; female, 18). Sex of the 174 sex-unknown specimens was determined by DNA analysis (male, 149; female, 25)[14]. Six skulls from captive-born otter carcasses (*i. e.*, known age) were used as age standards.

For age determination, upper canine teeth were removed from each skull. Some teeth were identified as less than 1 year of age based on the presence of a root hole [31] (Fig. 1), and were categorized as 0 or 0.5 years based on eruption and replacement of dentition, compared with captive-born. Age of other specimens was estimated from cementum annuli count in stained sections of canines [12, 31].

We measured 26 morphometric characters (Figs. 1, 2 and Table 1) with calipers to the nearest 0.1 mm, according to the methods of Inoue and Mukuta [15], Isono [16] and Wilson *et al.* [36]. Closure of the basioccipital-basisphenoid suture (Fig. 2) was visually assessed, and specimens with the closed suture were classified as adult [30]. Due to damage to the skulls and limited availability of material, sample sizes for each measurement varied. Two groups of specimens (1983–1989 and 1997) were pooled for growth analysis.

For age-related growth patterns, we calculated means of measurements and coefficient of variation (CV %) in every age group, and calculated differences in means between the age groups x and x + 1. We compared means of male specimens among age groups by analysis of variance (ANOVA)

Fig. 1. Skull and upper canine of the sea otter. a) Skull of pup, dorsal view. b) Skull of adult, dorsal view. c) Upper canine, buccal view. *Upper*—Pup; root hole is still open. *Middle*—Young adult; root hole is closed. *Lower*—Aged adult; tip of crown is worn.

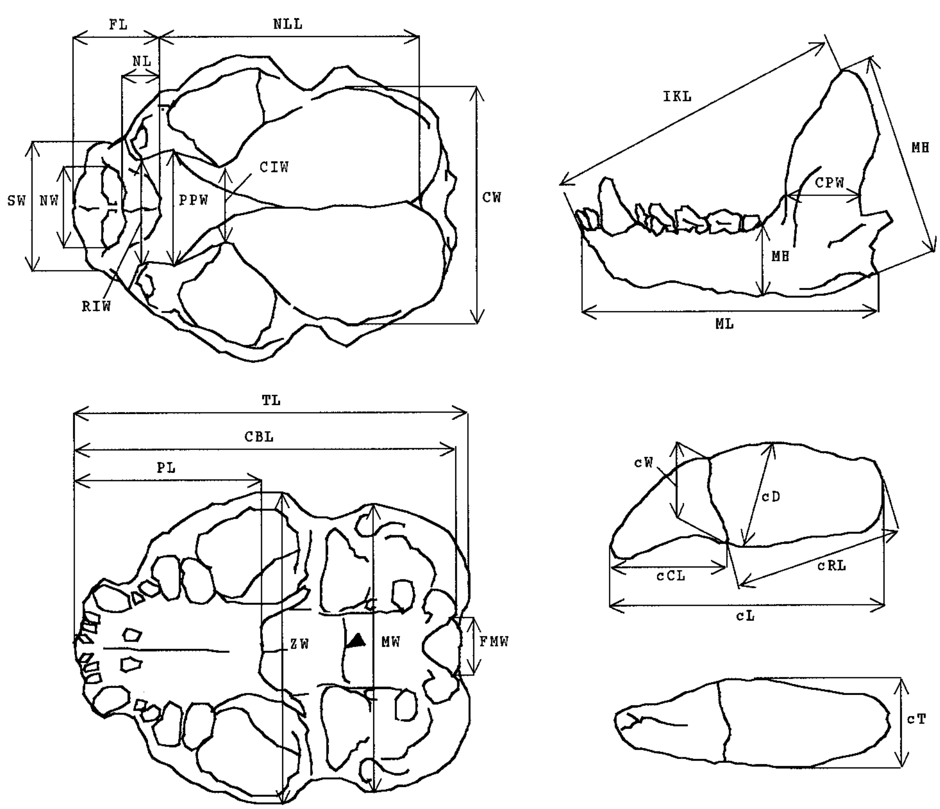

Fig. 2. Skull and upper canine measurements of the sea otter. Abbreviations refer to Table 1. The basioccipital-basisphenoid suture is shown (arrow head).

Table 1. List of the measurements and abbreviations (Abb.) of the sea otter

1. Skull	Abb.
Condylobasal length	CBL
Total length of skull	TL
Palatal length	PL
Zygomatic width	ZW
Mastoid width	MW
Facial length	FL
Nasal length	NL
Length from nasion to lambda	NLL
Greatest width of external nares	NW
Snout width at canines	SW
Rostral interorbital width	RIW
Width at postorbital processes	PPW
Caudal interorbital width	CIW
Cranial width	CW
Greatest width of foramen magnum	FMW
Mandibular length	ML
Height of mandibular ramus	MRH
Length from infradentale to koronion	IKL
Mandibular height	MH
Width of coronoid process	CPW
2. Upper canine	
Canine diameter	cD
Canine thickness	cT
Canine length	cL
Canine crown length	cCL
Canine root length	cRL
Canine crown width	cCW

and the Games-Howell test (α= 0.05)[35].

To estimate the age of completion of development for a particular character, we assumed that growth virtually ceased at the age at which length reached 95% of its asymptotic length ($t_{.95}$), following the previous studies [20, 37]. We calculated $t_{.95}$ from the estimates of growth parameters using the monomolecular model [20, 24]. This model has already been successfully used to describe growth of spotted seals, *Phoca largha* [20], and brown bears, *Ursus arctos* [24]. The monomolecular equation is as follows: $L_t=L_\infty$-exp [-K (t-I)], where L_t=the length at age t, L_∞=the asymptotic length, K=a growth-rate constant, and I=the age at the inflection point. To fit the model, the estimated age, x was substituted with x + 0.5, and the skull from a captive newborn (age, 0) was used.

Sexual differences in skulls were examined by *t*-test, using specimens whose growth was considered to have ceased.

Allometrical techniques were applied to 19 skull measurements and 1 canine measurement. The relation between each variable and total length of skull (TL) was examined using the following allometry equation: Log Y = α log X + b [38]. Significance of allometry coefficients was evaluated using 1-tailed *t*-tests [1]. Subsequently, we used 1-tailed *t*-tests with the null coefficient set at 1.0 to assess significant deviations from isometry [1, 7].

RESULTS

Figure 3 shows the age structure of specimens. Most specimens were males (90.7%). Overall age distribution of the specimens, based on the method of Bodkin *et al.* [5], was as follows: juvenile (0–3 years), 56.7%; adult (4–10 years), 39.8%; aged (>10 years), 3.5%. Estimated maximum age was 13 years for males and 20 years for females.

Growth: skull

For males, the size of most cranial features increased with age, except for nasal length (NL) (which showed no age-related change, P=0.367), and caudal interorbital width (CIW) (which decreased, P<0.05) (Fig. 4). Under 1 year of age, condylobasal length (CBL) showed the largest CV% and difference in means between age groups (Fig. 4). Over 2 years of age, there were no differences in mean CBL between x and x + 1 (P>0.05). However, mean CBL was slightly greater at 5 years than at 2 years (P=0.007). This finding indicates that CBL increased rapidly during the first 1 year, and nearly reached adult size at 2 years, with slight growth afterward. The other 20 skull measurements showed a similar trend. Females and males showed similar age-related changes in means.

Figure 5 shows the growth curve and scatter plot of CBL with age. Model fit was fairly good for both males and females (corrected R^2=0.74 and 0.87, respectively). The basioccipital-basisphenoid suture began to close at about 1 year in males and 3 years in females (Fig. 5). Although 1 aged specimen (11-year-old male) had an open suture, the sutures in all other specimens closed by approximately 3 years, as found in previous studies [23, 29].

In the growth model, CBL grew rapidly until 1 year of age. CBL growth then slowed, and nearly stopped at 2 years of age. Most features showed similar curves of age-related increase. Most $t_{.95}$ values were between 1 and 2 years for both males and females.

Both male and female specimens 2 or more years of age showed nearly complete development, based on results of both ANOVA and the growth model.

Growth: canine

Canine root length (cRL) reached adult size at 1 year of age. Canine crown length (cCL) reached adult size before eruption of the canine (2.7 to 4 months of age [31]; Fig. 6). The cCL began to decrease at about 6 years, and then showed great CV%. Canine thickness (cT) increased slowly through all of life, although canine diameter (cD) nearly stopped increasing at 2 years (Fig. 6).

Individual variation

Table 2 shows means, standard deviation and individual variations (CV%) in the morphometric characters of skulls 2 or more years of age. There tended to be variation in the apparatus for feeding (mandibular height [MH], width of coronoid process [CPW], height of mandibular ramus [MRH]) and breathing/sniffing (NL, greatest width of external nares [NW] and width at postorbital processes [PPW]). The braincase apparatus (cranial width [CW]) showed some of the least variability. There was great variation in all

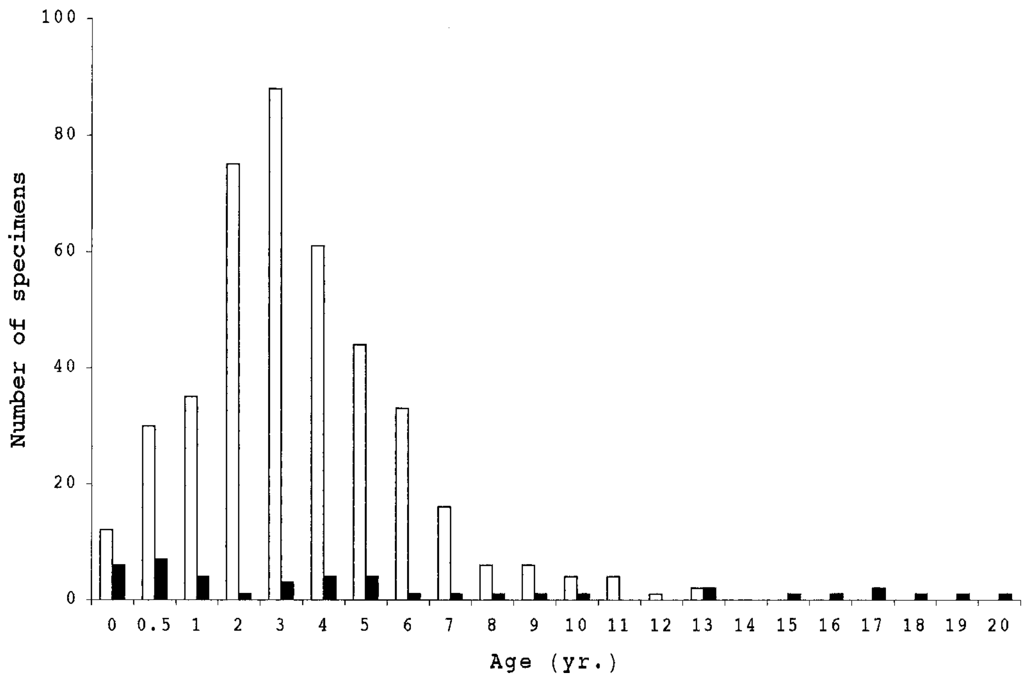

Fig. 3. Age structures of the sea otter specimens sampled. Open and closed squares represent males and females, respectively.

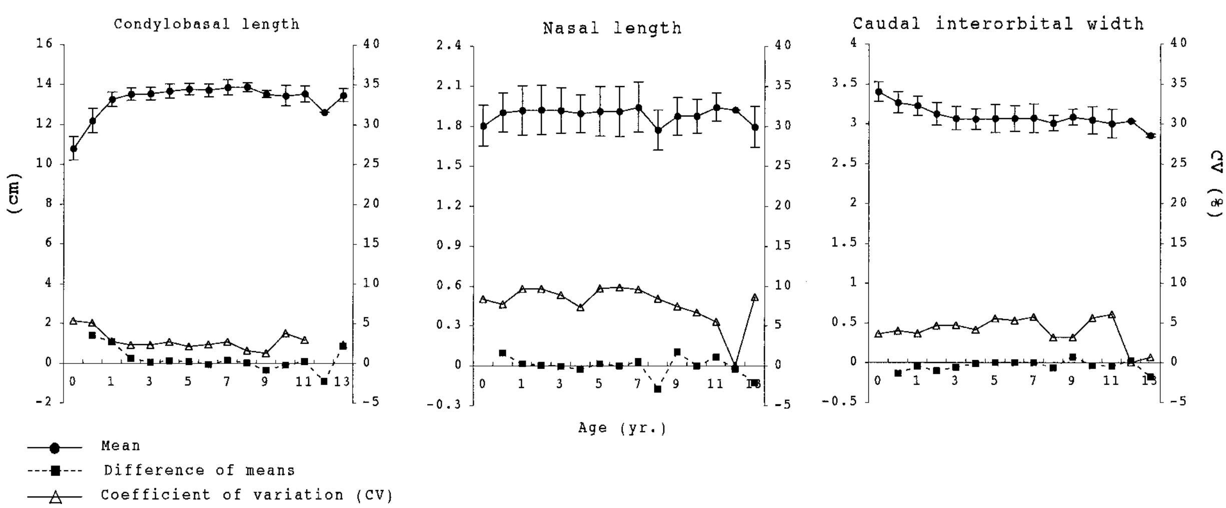

Fig. 4. Age-related change of condylobasal length, nasal length and caudal interorbital width of the male sea otter.

canine characters, especially those of the crown.

Sexual difference

Significant sexual difference was detected by *t*-test in 19 characters (P<0.05). In all 19 of these characters, dimensions were greater for males than for females (Table 2). Only cT was greater in females than in males, and this difference was not significant (P=0.90).

Relative growth

Most variables other than NL for male were significantly related to TL (most R^2 values > 0.60; Table 3). For males, mastoid width (MW) and NW showed positive allometry, whereas, for females, there were no significant departures from isometry for NW or MW. For males and females, NLL, CW and greatest width of foramen magnum (FMW) showed negative allometry, and MRH, CPW and cRL showed positive allometry.

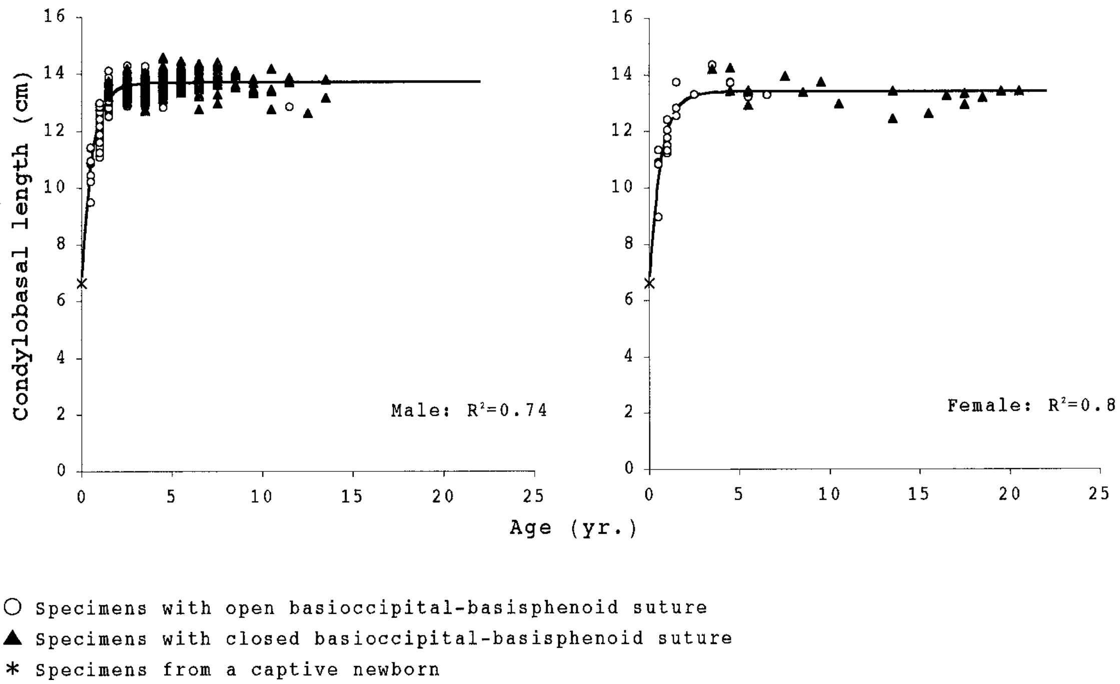

Fig. 5. Growth curve of condylobasal length of the male and female sea otter.

DISCUSSION

Age-related change: Most cranial features showed rapid growth during the early postnatal period, and most reached adult size at about 2 years. There were no sexual differences in the growth pattern of the skull or canine. The relationship between the age at which cranial development ceases and the age of sexual maturity was studied in species including spotted seals [20] and brown bears [24]. Sea otters reach sexual maturity later (males, 5–6 years; females, 2–5 years) [9, 21] than they reach cranial maturity. Kenyon [18] suggested that young sea otters are more precocial than the young of either *Lutra* species or the giant river otter (*Pteronura brasiliensis*). As with many other marine mammals, the period of maternal care in sea otters is relatively long, and milk fat content is high [28]. Such intensive maternal investment helps prepare the young for survival in a harsh environment after weaning [28], and may also promote early morphological development.

In the present study, canine crown size decreased with age, and the individual variation became remarkable from about 6 years, apparently due to wear (Fig. 1). Canine teeth are probably used for breaking shells [10], prying shells from submarine gardens, and, especially in males, for fighting [33]. Fisher [11] suggested that differences in food habits might explain differences in number and size of cavities in the teeth of skulls from different populations. Although degree of tooth wears is not a very reliable indication of age, the age at which marked wear of canines is observed may indicate differences in food habits among populations.

The cD used for sex determination [30, 32] nearly stopped increasing at 2 years in the present study. In contrast, cT showed continuous slow growth with no significant sexual difference. Thus, cT may be useful for approximate age classification, because it was apparently not affected by tooth wear.

Individual variation: Individual variations in feeding and breathing/sniffing apparatus were greater than other features. Although little is known about olfaction in sea otters, the presence of extensive nasal turbinate suggests acute olfaction [28]. In a study of Commander Islands' sea otters, rostral interorbital width (RIW) and PPW were found to be highly variable [3]. In the present study, values of RIW and PPW were relatively high. These findings support the commonly recognized subspecies designations [29, 36].

Sexual difference: Most characteristics showed sexual difference, but these differences were not as great as those found in other studies [3, 36]. Scheffer [34] reported that sex differences in sea otter skulls are not pronounced, although female skulls tend to be smaller. Roest [30] found that both large females and small males accounted for many medium-sized skulls, and proposed a method for determining sex of sea otter skulls using 5 measurements. In the present study, this method was not suitable for determining the sex of our sex-unknown specimens seemingly due to our extremely small sample size of female skulls (compared to males) and/or a bias toward large size among our female skulls. More precise analysis will require a greater number of female specimens.

Relative growth: The negative allometry of NLL, CW and

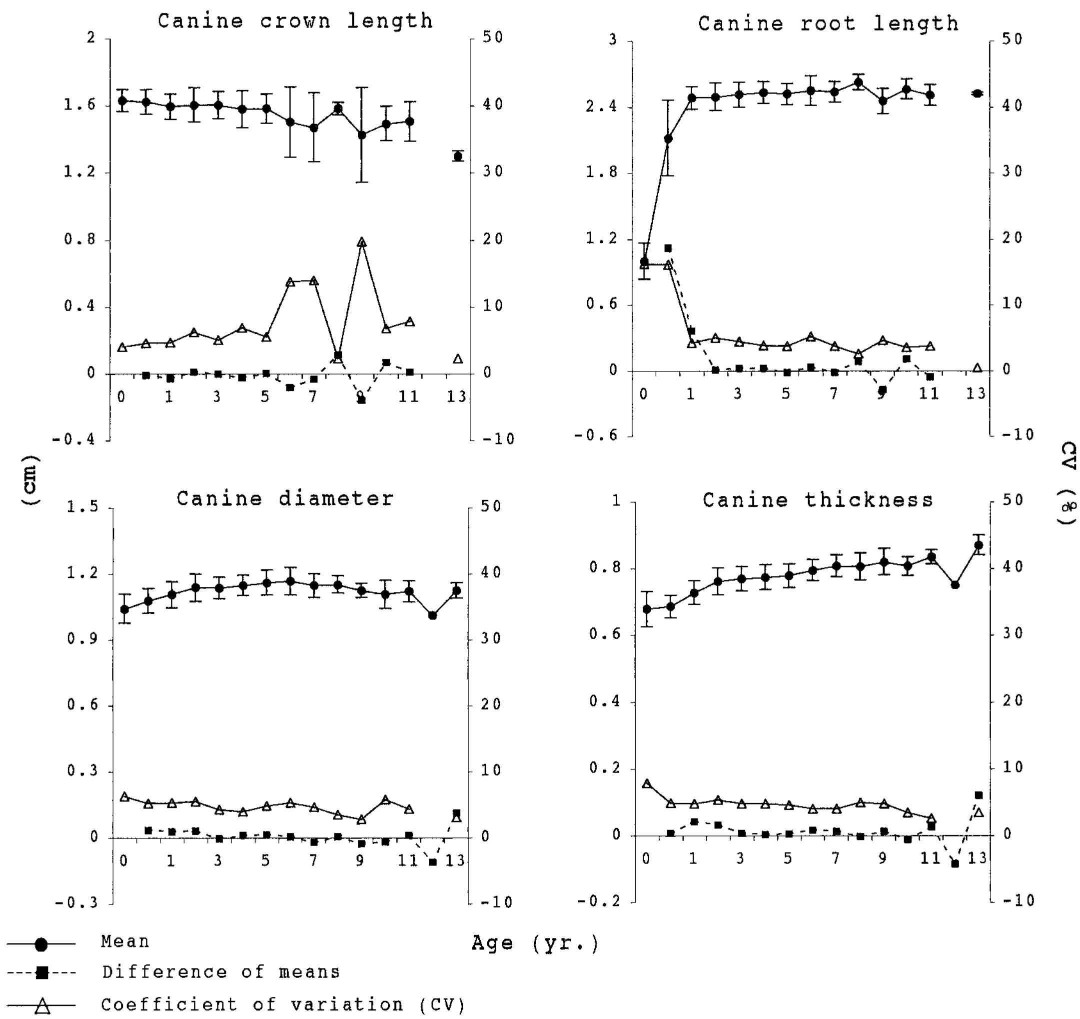

Fig. 6. Age-related change of canine crown length, canine root length, canine diameter and canine thickness of the male sea otter.

FMW was considered to relate to growth of the braincase apparatus, and the positive allometry of MRH, CPW and cRL was considered to relate to growth of the feeding apparatus.

The positive allometry of the coronoid process is apparently associated with enlargement and improvement of surfaces for origin or insertion of jaw musculature, specifically, the masseter muscle and the temporalis muscle. These muscles are extremely well developed in carnivores, whose mandibular joint primarily moves up and down like scissors [6]. Radinsky [26, 27] suggested that mustelids might have the most powerful bite of all carnivores, based on their relatively large temporalis muscle and strong jaws. The diet of sea otters predominantly consists of fish and benthic invertebrates (*e. g.*, mollusks, crabs and sea urchins); the latter have hard shells [18].

The mastoid process showed positive allometry in males, and showed isometry in females. Parts of the cleidomastoid muscle and the sternomastoid muscle attach to the mastoid process [17]. The function of these muscles is to raise the head and neck and pivot them right and left. The male head and neck are heavier and more muscular than those of females [8, 18]. Isono [16] reported similar development of muscle around the neck in male Steller sea lions, *Eumetopias jubatus.* He suggested that this feature of males was associated with territoriality. Sea otter males also maintain a passing territory [28], and this may be related to the positive allometry of MW in males.

In other studies, neurocranial components show negative allometry and most non-neurocranial components scale isometrically or with slight positive allometry, usually [1, 26]. This was also the case in the present study. The nervous system and its adnexa grow rapidly during prenatal and early postnatal life [22].

In the present study, we described skull and canine development of sea otters in Lopatka Cape. In some species, such as Steller sea lions [16] and brown bears [24], it has been suggested that there is geographical and historical variation

Table 2. Mean, standard deviation (SD), and individual variation (CV%) of measurements of the sea otter specimens whose growth completed

	Male				Female				
1. Skull	n	Mean (cm)	SD (cm)	CV (%)	n	Mean (cm)	SD (cm)	CV (%)	
CBL	323	13.63	0.35	2.56	25	13.41	0.46	3.46	*a)
TL	326	14.64	0.38	2.58	25	14.38	0.53	3.71	*
PL	335	6.41	0.19	2.95	26	6.28	0.22	3.50	
ZW	331	10.50	0.33	3.11	26	10.45	0.31	2.96	
MW	331	10.47	0.32	3.03	25	10.33	0.40	3.88	*
FL	336	5.85	0.18	3.10	26	5.67	0.28	4.91	*
NL	413	1.91	0.17	9.10	44	1.78	0.20	11.30	*
NLL	325	10.33	0.34	3.32	26	10.24	0.42	4.10	
NW	335	2.74	0.13	4.80	26	2.73	0.11	4.16	
SW	335	4.34	0.15	3.41	26	4.20	0.20	4.85	*
RIW	334	4.35	0.18	4.09	26	4.20	0.21	4.93	*
PPW	335	4.65	0.26	5.68	26	4.62	0.23	5.05	
CIW	417	3.11	0.17	5.39	45	3.11	0.23	7.40	*
CW	331	8.61	0.23	2.71	25	8.47	0.23	2.76	*
FMW	321	2.64	0.10	3.84	25	2.58	0.11	4.25	*
ML	322	8.37	0.21	2.50	24	8.18	0.30	3.63	*
MRH	319	4.59	0.20	4.26	24	4.45	0.22	4.99	*
IKL	319	9.11	0.33	3.59	24	8.85	0.45	5.05	*
MH	322	2.35	0.12	5.26	24	2.30	0.12	5.03	*
CPW	320	2.34	0.14	5.89	24	2.28	0.16	7.16	*
2. Upper canine									
cD	339	1.14	0.06	4.90	26	1.08	0.08	7.57	*
cT	339	0.78	0.04	5.22	26	0.80	0.07	8.56	
cL	329	4.06	0.22	5.48	24	3.96	0.17	4.23	*
cCL	398	1.58	0.13	7.94	38	1.51	0.11	7.52	*
cRL	328	2.52	0.11	4.52	25	2.50	0.11	4.28	
cCW	401	0.93	0.05	5.02	38	0.84	0.07	8.54	*

a) Significantly different characters of means are indicated by * ($P<0.05$).

in growth patterns, due to nutritional condition. We hypothesize that the rapid growth of sea otter skulls observed in the present study reflects the quality of their habitat in early life.

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Table 3. Summary of regressions on the total length of skull. Abbreviations: n=sample size, R^2=adjusted coefficient of determination, α = allometry coefficient (least squares)

	Male				Female			
1. Skull	n	R^2	α		n	R^2	α	
CBL	395	0.91	1.03	ns[a)]	40	0.96	1.02	ns
PL	400	0.85	0.98	ns	43	0.95	1.07	ns
ZW	396	0.83	1.05	ns	43	0.94	1.10	ns
MW	400	0.85	1.14	+[b)]	43	0.98	1.08	ns
FL	401	0.78	0.95	ns	43	0.93	1.02	ns
NL	398	0.02	0.25	*[c)]	42	0.25	0.52	ns
NLL	400	0.75	0.83	–[d)]	43	0.93	0.87	–
NW	398	0.66	1.25	+	43	0.88	1.19	ns
SW	399	0.67	0.86	–	42	0.94	0.96	ns
RIW	400	0.67	1.04	ns	43	0.89	0.87	ns
PPW	401	0.34	0.79	–	43	0.70	0.69	–
CIW	400	0.09	-0.33	–	42	0.23	–0.31	–
CW	401	0.47	0.48	–	43	0.89	0.56	–
FMW	389	0.09	0.24	–	40	0.26	0.25	–
ML	380	0.83	0.95	ns	38	0.94	1.02	ns
MRH	378	0.69	1.32	+	38	0.82	1.37	+
IKL	377	0.70	0.97	ns	38	0.93	1.09	ns
MH	380	0.47	0.94	ns	38	0.85	0.99	ns
CPW	379	0.59	1.30	+	38	0.89	1.36	+
2. Upper canine								
cRL	381	0.56	2.49	+	36	0.65	2.99	+

a) ns: Nonsignificant deviations from isometry.
b) +: Positive allometry.
c) *: Nonsignificant relation to TL.
d) –: Negative allometry.

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