GROWTH AND SKULL DEVELOPMENT IN THE SOUTH AMERICAN FUR SEAL, *ARCTOCEPHALUS AUSTRALIS* (ZIMMERMANN, 1783) (CARNIVORA: OTARIIDAE), FROM RIO GRANDE DO SUL COAST, BRAZIL

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Abstract – Skulls of 157 *Arctocephalus australis* (94 males and 63 females) from animals stranded dead on the Rio Grande do Sul coast from Torres to Barra do Arroio Chuí between July 1977 and September 1997 were examined. These were analyzed to explore aspects of the cranial development. The growth layers groups (GLGs) in the dentine and cementum from upper canine teeth were counted. The oldest male and female were 14 and 18 years of age, respectively. Parameters of the von Bertalanffy equation suggest that males and females attain physical maturity at about the eight and six years of age, respectively. Hotelling T² test and discriminant functions using metric characters showed sexual dimorphism in physically mature and immatures skulls. The developmental classes were also examined using non-metric characters, but no sexual dimorphism was observed using these variables. The principal component analysis (PCA) showed a clear separation between physically mature skulls of males and females. The first factor explained 80.2 % of the total variation and the second factor explained 4.6% of the observed variability.

Resumen – Fueron examinados 157 cráneos de *Arctocephalus australis* (94 machos y 63 hembras) provenientes de animales muertos en la costa de Río Grande do Sul, desde Torres hasta la Barra do Arroio Chuí entre Julio 1977 a Septiembre 1997. Estos cráneos fueron analizados para explorar el desarrollo craniano. En dientes caninos superiores fueron contados los grupos de capas de crecimiento (GLGs) en la dentina y cemento. El macho y hembra de mayor edad fue de 14 años y 18 años, respectivamente. Parámetros de la ecuación de von Bertalanffy sugieren que los machos y hembras alcanzarían la madurez física aproximadamente a los ocho y seis años de edad, respectivamente. Análisis de test Hotelling T² y funciones discriminantes utilizando los caracteres métricos mostraron dimorfismo sexual en cráneos físicamente maduros y físicamente inmaduros. Las clases de desarrollo también fueron examinadas usando caracteres no-métricos, pero el dimorfismo sexual no fue observado usando estas variables. El análisis de componentes principales (PCA) mostró una clara separación entre cráneos de machos y hembras físicamente maduros. El primer factor explico 80.2% de la variación total y el segundo factor explico 4.6% de la variabilidad observada.

Keywords: age estimation, *Arctocephalus australis*, growth, physical maturity, sexual dimorphism, southern Brazil.

Introduction

The South American fur seal, *Arctocephalus australis*, is widely distributed from Rio de Janeiro (23°18'S, 44°30'W), Brazil to Peninsula of Paracas (13°53'S, 76°22'W), Peru (Bonner, 1981; Majluf and Trillmich, 1981; Vaz-Ferreira, 1982; Pinedo *et al.*, 1992; Jefferson *et al.*, 1993). In Uruguay the species breeds on the Isla del Marco, in the Castillos group (34°21'S, 53°5'W); on the Islote Encantada and Isla Rasa, in the Torres group (34°24'S), mainly on the Isla de Lobos (35°01'S), and also on the Islote (Vaz-Ferreira, 1982). The population was estimated at 300000 individuals in 1996 (Páez, 1999).

A. australis is one of the most common pinniped species in the coast of Rio Grande do Sul, occurring mainly during fall and winter. Most of the strandings in Rio Grande do Sul coast probably originate from Uruguay. Given that most of them are found dead or debilitated, physical exhaustion or diseases are suspected (Pinedo, 1990).

Morphometric studies on the South American fur seal are limited. Repenning *et al.* (1971) described the characteristics of the skull of nine adult males of the Falklands Islands. Sexual dimorphism in size and shape was observed on adult skulls (24 males and 24 females) of *A. australis* from Uruguay (Ximénez *et al.*, 1984). Páez (1989) analyzed the cranial development of 286 individuals from Uruguay (Isla de Lobos and Cabo Polonio), based on morphometric variables, and the ages were estimated from upper canines teeth bisectioned longitudinally and decalcified in a solution of 5% formic acid. Batallés *et al.* (1990) studied the external development in 500 females and 500 males of the Isla de Lobos. Oliveira (1999), Brunner (2000), Oliveira and Danilewicz (2000), Oliveira *et al.*, (2001) and Sanfelice (2004) also studied skull shape and size in the South American fur seal using traditional and geometric morphometrics techniques.

In taxonomical and stock identification studies it is recommended that comparisons among different geographic populations be preceded by identification of the individual variation in adults that occur within populations (Perrin, 1984; Schnell *et al.,* 1985). However, before identifying variation at the individual and population levels, studies of the ontogenetic variation and age estimation are required to select the physically mature individuals to avoid selecting traits related with development, *i.e.*, those expressed by physically immature individuals (Calzada, *et al.*, 1997; Brunner, 2000).

In this study the metric and non-metric characters were used as a function of age to explore the growth pattern of

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A. australis and detect individual variation in males and females occurring in Rio Grande do Sul coast, Brazil.

Material and Methods

Study area

Skulls of 157 *A. australis* (94 males and 63 females) of animals found dead on the coast of Rio Grande do Sul (612km of beach) from Torres (29°20'S, 49°44'W) to Barra do Arroio Chuí (33°45'S 53°22'W) between July 1977 and September 1997 were examined (Figure 1). This coast has been surveyed as part of a long-term beach monitoring program conducted by the Laboratory of Marine Mammals and Marine Turtles (LMM) of the Oceanography Department of the Fundação Universidade Federal do Rio Grande (FURG), Brazil. The analyzed skulls are deposited at LMM.

Analysis of metric characters and age estimation

Nineteen cranial measurements were utilized (Table 1, Figure 2). Seventeen measurements were previously used by Repenning *et al.* (1971), Ximénez *et al.* (1984) and Páez (1989). Rostral width and greatest width of internal nasal opening were introduced for the first time (Figure 2).

Due to missing or broken bones in some skulls, sample sizes varied for each collected measurement. In cases of characters presenting symmetry, the left side was measured. The number of teeth and/or presence of alveoli in each mandibular and maxillary branch were counted.

The von Bertalanffy equation (1957) was used to describe cranial development for each variable according to sex and to determine which variables were correlated with age. The von Bertalanffy equation is expressed by $L_t = L_¥ (1 - e^{-k(t-t0)})$, where: L_t is the value of the measure at age t (*e.g.,* metric characters); *t* is a unit of time in years (estimated from growth layer groups present in each tooth); t_0 is the hypothetical age at which *A. australis* has length equals zero, assuming individual always growth in the manner described by the equation; $L_¥$ is the asymptotic length (*e.g.,* the average length the species reaches if it grows indefinitely); *k* is the growth-rate constant and *e* is the natural logarithm base. These parameters were obtained using the interaction quasi-Newton method (non-linear module) of the Statistics 6.0 for Windows. Growth curves were calculated for males and females.

Ages were estimated from counts in the upper canine teeth. The growth layer groups (GLGs) in the dentine and cementum of the teeth were counted. Two techniques were used for age estimation. The first technique used was decalcified and stained thin sections. Teeth were decalcified with RDO® (a rapid commercial bone decalcifier), and cut longitudinally using a CO_2 freezing microtome. On-center sections 25 to 30mm thick were stained in Harris' hematoxylin and examined under transmitted light according to Molina and Oporto (1993), Molina-Schiller (2000) and Molina-Schiller and Pinedo (2004). The second technique was half-tooth etched in 5% formic acid and rubbed with graphite powder according Schiavini *et al.* (1992) and Crespo *et al.* (1994). We interpreted each GLG as equivalent to one year's growth (Perrin and Myrick, 1980; Schiavini *et al.*, 1992; Crespo *et al.*, 1994).

The age of attainment of physical maturity (*t*) in the skull was obtained by visual analysis of each variable in relation to the stabilization of the growth curve. Only variables with a high correlation (r≥0.90) in the von Bertalanffy curve were selected for growth analysis.
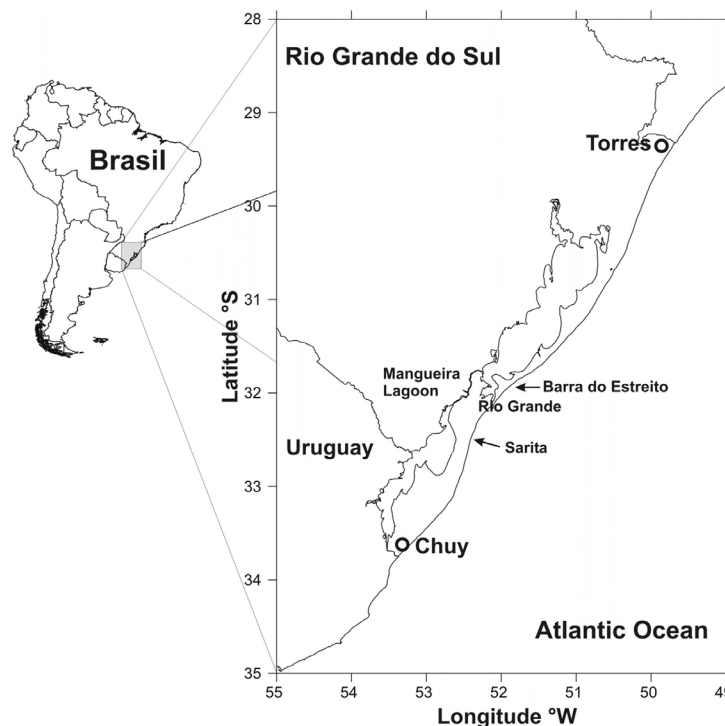

Figure 1. Areas of collection of *Arctocephalus australis* on the coast of Rio Grande do Sul, Brazil.

Table 1. Parameters of the von Bertalanffy equation for males and females of Arctocephalus australis, from Rio Grande do Sul coast, Brazil.

MEASUREMENTS	♂							♀						
	n	L_∞ (cm)	t_0	k	r	ASYMPTOTIC VALUE (cm)	t	n	L_∞ (cm)	t_0	k	r	ASYMPTOTIC VALUE (cm)	t
1. Condylobasal length	84	24.097	-4.174	0.259	0.96	22.76	7	49	19.960	-4.304	0.346	0.95	19.40	6
2. Basilar length of Hensel	84	21.670	-4.169	0.257	0.96	20.44	7	49	17.900	-4.571	0.322	0.94	17.30	6
3. Upper post canine length	92	5.880	-4.819	0.238	0.92	5.53	7	62	5.246	-8.317	0.172	0.87		-
4. Zygomatic width	89	14.786	-5.121	0.173	0.96	13.26	8	52	11.296	-5.994	0.239	0.92	10.65	6
5. Rostral width	70	5.483	-3.615	0.195	0.93	4.79	7	52	3.488	-4.236	0.322	0.90	3.36	6
6. Mastoid width	91	16.693	-3.561	0.238	0.96	15.63	8	54	9.919	-6.536	0.217	0.81		-
7. Skull height [a]	92	8.160	-7.325	0.185	0.90	7.68	8	58	6.630	-7.144	0.339	0.73		-
8. Palate length	80	10.298	-3.969	0.219	0.95	9.55	8	43	8.181	-4.889	0.267	0.94	7.73	6
9. Palate width in molar 1	76	2.821	-3.015	0.202	0.91	2.52	8	52	1.913	-3.161	0.336	0.83		-
10. Palate width in molar 3	73	3.072	-4.224	0.203	0.86		-	50	2.187	-4.491	0.332	0.73		-
11. Palate width in molar 5	71	3.562	-5.355	0.171	0.88		-	48	2.671	-4.183	0.325	0.81		-
12. Greatest width of condylo-occipital	92	5.263	-7.474	0.224	0.81		-	60	4.467	-4.547	0.574	0.49		-
13. Greatest length of nasal	36	3.982	-4.111	0.216	0.83		-	17	3.297	-5.657	0.205	0.88		-
14. Constriction interorbital width	92	4.009	-5.784	0.121	0.90		-	60	2.329	-4.162	0.387	0.71		-
15. Supraorbital process width	91	6.650	-8.958	0.081	0.86		-	59	3.901	-4.222	0.130	0.52		-
16. Greatest width of internal nasal opening	78	2.954	-4.519	0.204	0.89		-	46	2.313	-0.478	0.131	0.73		-
17. Mandible length	91	16.693	-3.561	0.238	0.96	15.63	8	61	13.287	-3.790	0.325	0.95	12.74	6
18. Mandible width	90	2.578	-3.357	0.201	0.93	2.32	8	61	1.591	-5.247	0.268	0.61		-
19. Mandible height [b]	91	6.128	-2.757	0.199	0.95	5.54	9	61	3.969	-3.758	0.289	0.89		-

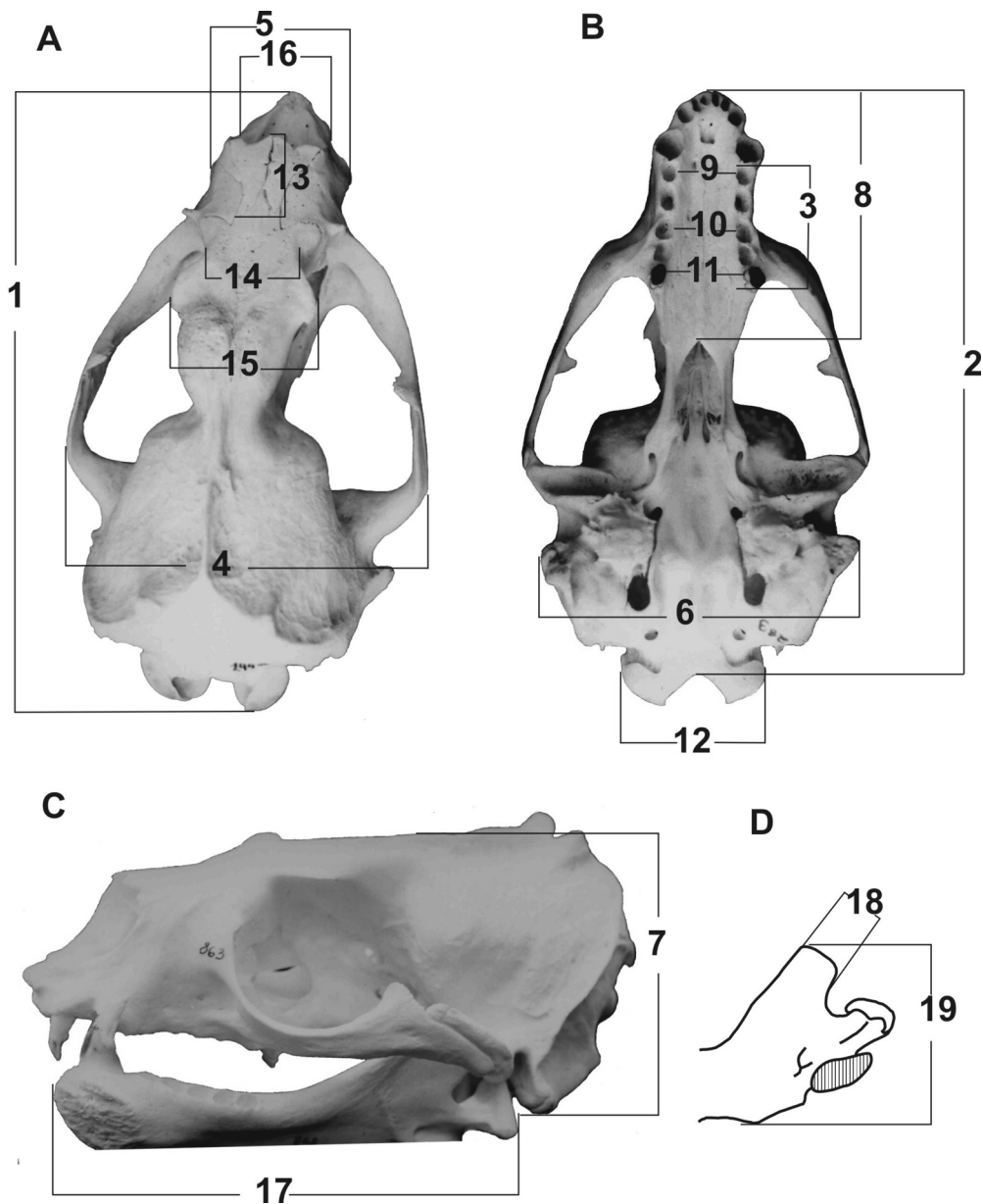[a] at insertion basisphenoidal-interparietal-occipital suture, [b] at coronoid process.

Figure 2. Skull metric characters of *Arctocephalus australis*. 1. Condylobasal length, 2. Basilar length of Hensel, 3. Upper post canine length, 4. Zygomatic width, 5. Rostral width, 6. Mastoid width, 7. Skull height (at insertion basisphenoidal-interparietal-occipital suture), 8. Palate length, 9. Palate width in molar 1, 10. Palate width in molar 3, 11. Palate width in molar 5, 12. Greatest width of condylo-occipital, 13. Greatest length of nasal, 14. Constriction interorbital width, 15. Supraorbital process width, 16. Greatest width of internal nasal opening, 17. Mandible length, 18. Mandible width, 19. Mandible height (at coronoid process).

Differences between physically mature and immature males and females were examined by Hotelling T^2 multivariate test and a stepwise discriminant analysis using Statistic 6.0 for Windows. A discriminant score function was performed to ascertain sex.

Analysis of non-metric characters

The analyses of non-metric characters of the skull were based on the work of Sivertsen (1954). For the analyses of ontogenetic variation, physical maturity and of individual variation, we choose as characters the closure level of four cranial sutures, the opening level of the pulp cavity and the degree of wear at the apex of the crown of the upper canine teeth. The cranial sutures used in this study were: occipito-parietal, interparietal, premaxillary-maxillary, and interfrontal. The criteria used for the analyses of the cranial sutures were: 0=open, 1=closed-visible, 2=closed-invisible (Figure 3). In the upper canine teeth the characters analyzed were the degree of opening of the pulp cavity and the criteria used were 0=open, 1=open (smaller or equal to 2 mm) and 2=closed. The degree of wear the apex of the crown the criteria were: 0=absence and 1=presence. The analysis of Kolmogorov-Smirnov (K-S) for two independent samples was applied to determine if these characters were dimorphic in adult individuals.
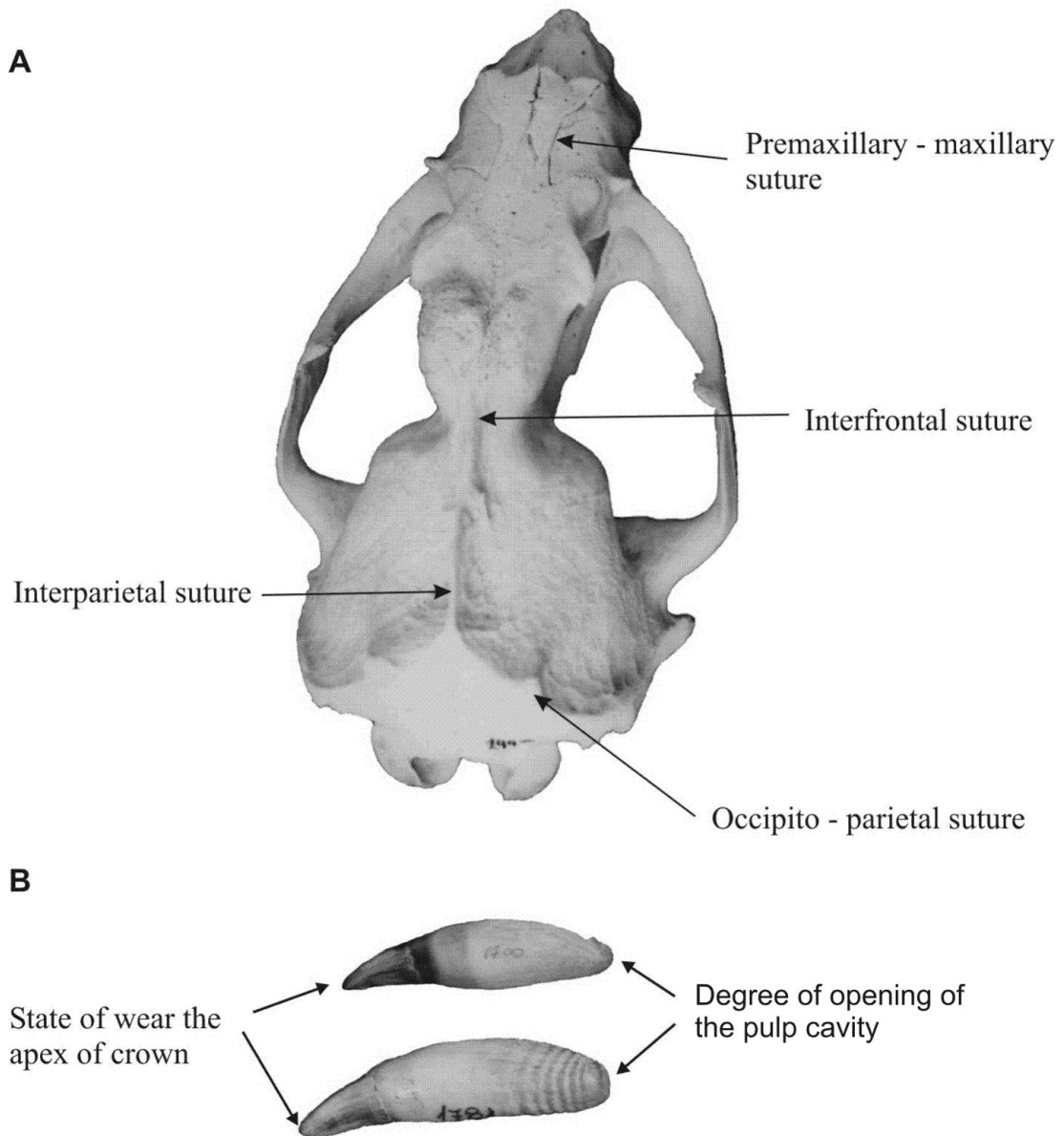
A

Premaxillary - maxillary suture

Interfrontal suture

Interparietal suture

Occipito - parietal suture

B

State of wear the apex of crown

Degree of opening of the pulp cavity

Figure 3. Non-metric characters of the skull of *Arctocephalus australis.* a) sutures and b) state of wear at the apex of the crown in the upper canine tooth and degree of opening of the pulp cavity.

Individual variation

Parametric and non-parametric methods of univariate and multivariate analyses (Zar, 1984) were utilized to identify the metric and non-metric characters which correlated with age, and selected those that best expressed the individual variation. The analysis of the individual variation through coefficients of variation (CV%) was applied only to physically mature skulls, assuming these specimens represented a single panmictic population, and that the study population originated from the colonies in Uruguay (Pinedo, 1990). To detect the more suitable variables expressing the variation in the population, the criterion of Simpson *et al.* (1960 *apud* Pinedo, 1991) was used as guideline. However, a principal components analysis (PCA)

with MD deletion case wise was applied to investigate the variation of all variables within each group. The method was applied with Statistic 6.0 for Windows.

Results

Analysis of metric characters

In this study the oldest male and female were 14 and 18 years of age, respectively. The parameters of fitted von Bertalanffy curves differed between males and females (Table 1, Figure 4). The correlation coefficient (*r*) obtained through the von Bertalanffy model revealed that 13 characters (68.4%) in males and six characters (32%) in females presented a larger correlation with the age ($r \geq 0.90$) (Table 1).

The variables expressing higher correlation with age in males (r=0.96) were condylobasal length, basilar length of Hensel, mastoid width, mandible length and zygomatic width. In females (r=0.95), those were condylobasal length and mandible length (Table 1).

The growth constant (k) was greater for females than for males (Table 1). In males, the condylobasal length and basilar length of Hensel presented the faster growth (k=0.26), followed by the upper post canine length and the mandible length (k=0.24). A slower growth was observed in the supraorbital process width (k=0.08) and the constriction interorbital width (k=0.12) (Table 1).

In females, the greatest width of condylo-occipital presented the faster growth (k=0.57), followed by the constriction interorbital width (k=0.39), condylobasal length (k=0.35), skull height and palate width in molar 1 (k=0.34). The supraorbital process width had a slower growth (k=0.12), followed by the greatest width of internal nasal opening (k=0.13) (Table 1).

Differences were observed in the stabilization of the asymptotic growth of the variables selected with $r \geq 0.90$. In males, the stabilization of the asymptotic growth of the condylobasal length, basilar length of Hensel, upper post canine length and rostral width started at seven years of age (Table 1, Figure 4a). The stabilization of the asymptotic growth started at eight years of age in six variables (zygomatic width, mastoid width, skull height, palate length, palate width in molar 1 and upper post canine length) (Table 1, Figure 4b). However, the stabilization of the mandible height started at nine years of age (Table 1, Figure 4c). Considering that the average age of all variables selected was eight years, we suggest that males attain physical maturity about the eight years of age in our study area.

In females, the stabilization of the asymptotic growth began at six years of age in six variables (condylobasal length, basilar length of Hensel, rostral width, zygomatic width, palate length and mandible length) (Table 1, Figures 4a,b). Therefore, we considered that females attain physical maturity at about six years of age.

The results of the Hotelling T² multivariate test showed than in male and female skulls all variables were dimorphic (T²=104,708 $F(19,23)$=3,0915, p<0.00557). In physically mature skulls all variables were dimorphic (T²=621,236 $F(19,5)$=7,1080, p<0,01951) (Table 2). In physically immature skulls the Hotelling T² test could not be computed. However, Student t-test showed than only one measurement (greatest width of internal nasal opening) was non-dimorphic (p=0.057), while the other variables were dimorphic (p<0.001) (Table 3).

The discriminant analysis classified four variables (palate length-LP, rostral width-RW, palate width in molar 1-PM1W and greatest width of condylo-occipital-COW) as dimorphic for male and female physically mature skulls (Wilks' Lambda=0.10674; $F(4,30)$=62.763; p<0.00001). The discriminant function showed 100% of success in the correct classification of sex. The functions by sex for physically mature skulls were:
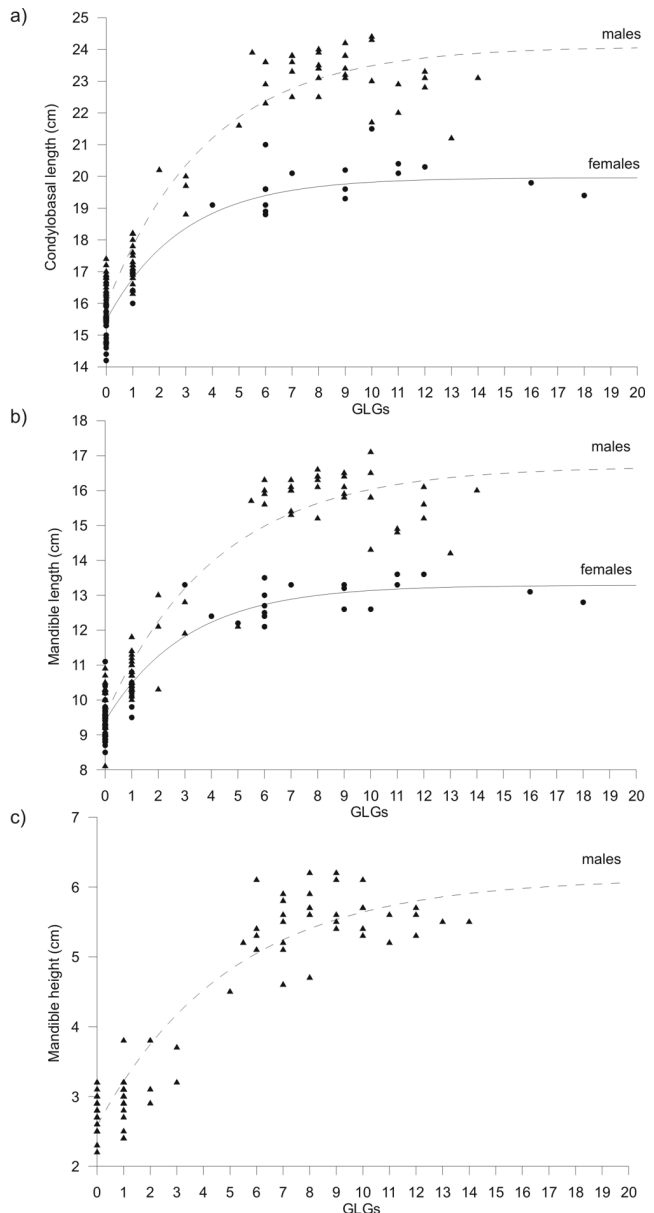

Figure 4. Von Bertalanffy growth curve for *Arctocephalus australis*. a) condylobasal length, b) mandible length and c) mandible height (growth curve only for males). (▲) males, (●) females.

♂ = - 545.35 + 84.06 (LP) − 11.19 (RW) − 43.18 (PW1W) + 84.73 (COW)

♀ = - 397.37 + 72.23 (LP) − 18.71 (RW) − 34.69 (PW1W) + 78.46 (COW)

Analysis of non-metric characters

The analysis of the degree of wear at the apex of the crown in the upper canine tooth of males started at 5 years old (n=48 males) and at six years (n=20) in females. The analysis of the degree of opening of the pulp cavity showed

Table 2. Descriptive statistics of the metric characters (cm) from physically immature skulls of males and females of *Arctocephalus australis*, from Rio Grande do Sul coast, Brazil.

MEASUREMENTS	♂					♀					
	n	MEAN	MIN.	MAX.	SD	n	MEAN	MIN.	MAX.	SD	*p*
1. Condylobasal length	61	18.38	14.80	23.90	2.77	33	15.76	14.80	23.90	0.93	***
2. Basilar length of Hensel	61	16.47	13.00	21.60	2.50	33	14.05	13.00	21.60	0.87	***
3. Upper post canine length	50	3.52	2.40	9.00	0.86	38	2.71	2.40	9.00	0.35	***
4. Zygomatic width	69	4.51	3.40	9.80	0.65	46	4.07	3.40	9.80	0.25	***
5. Rostral width	67	9.91	4.00	14.00	1.82	36	8.78	4.00	14.00	0.64	***
6. Mastoid width	68	8.78	3.00	13.10	1.84	38	7.68	3.00	13.10	0.83	***
7. Skull height [a]	69	6.56	5.70	8.30	0.69	43	6.18	5.70	8.30	0.50	***
8. Palate length	57	7.20	4.10	10.30	1.38	27	6.05	4.10	10.30	0.37	***
9. Palate width in molar 1	53	1.81	1.20	6.60	0.83	37	1.29	1.20	6.60	0.19	***
10. Palate width in molar 3	51	2.13	1.50	3.50	0.47	35	1.73	1.50	3.50	0.20	***
11. Palate width in molar 5	50	2.54	1.90	4.90	0.57	33	2.04	1.90	4.90	0.24	***
12. Greatest width of condylo-occipital	70	4.46	2.60	5.60	0.47	44	4.18	2.60	5.60	0.28	***
13. Greatest length of nasal	20	3.31	2.40	4.10	0.52	6	2.30	2.40	4.10	0.15	***
14. Constriction interorbital width	70	2.35	1.60	4.10	0.51	44	1.91	1.60	4.10	0.21	***
15. Supraorbital process width	69	3.80	2.10	5.80	0.69	44	3.32	2.10	5.80	0.33	***
16. Greatest width of internal nasal opening	57	2.34	1.40	14.40	1.68	30	1.75	1.40	14.40	0.19	0.057
17. Mandible length	70	11.05	1.80	16.30	2.72	45	9.76	1.80	16.30	0.96	***
18. Mandible width	70	1.75	1.10	10.20	1.16	46	1.24	1.10	10.20	0.22	***
19. Mandible height [b]	70	3.29	1.00	6.10	1.07	45	2.74	1.00	6.10	0.37	***

([a]) at insertion basisphenoidal-interparietal-occipital suture, ([b]) at coronoid process, (***) *p*< 0.001

that the upper canine tooth with opening of the pulp cavity smaller or equal to 2 mm started at six years of age in males (n=18) and females (n=3). The pulp cavity was closed at 10 years of age in males (n=4) and six in females (n=9).

The cranial sutures presented variations related to age. The occipito-parietal suture started to be closed-invisible at three years of age in males (n=41) and at four years in females (n=18). In males, the interparietal suture started to be close-invisible at five years of age (n=34) and at four years of age in females (n=16). The premaxillary-maxillary suture was also closed-visible in males at 14 years of age (n=85) and eight years in females (n=55). However, only one male presented the suture premaxillary-maxillary closed at eight years of age. The interfrontal suture also was closed-visible in males at 14 years of age (n=85) and at 18 years in females (n=55). In three males this suture started to be invisible at six to eight years of age.

The analysis of six non-metric characters using Kolmogorov-Smirnov test (K-S) showed differences between physically immature (n=116) and mature skulls (n=40) in all characters analyzed (*p*<0.001) (Tables 2 and 3). Only the greatest width of internal nasal opening in physically immature skulls was not dimorphic (*p*=0.057) (Table 2).

No sexual dimorphism was observed when the developmental classes (physically immature and physically mature) were analyzed separately.

Individual variation

In males (n=23), the palate width in molar 3 presented the highest coefficient of variation (CV=11.63%), while condylobasal length and basilar length of Hensel presented the smallest values (CV=3.5%) (Table 3). In females (n=17), the greatest length of nasal presented the highest coefficient of variation (CV=11.83%), while the skull height presented the smallest (CV= 4.36%) (Table 3).

All characters (Table 3) were included in the principal component analysis (PCA). The component I explained 80.2% of the total variation, with all negative coefficients and eigenvalue of correlation matrix of 15.24. The component II explained 4.6% of the observed variability and eigenvalue of correlation matrix of 0.87 (Figure 5). In the component I (x), all the characters presented factor loadings more than 0.700, but on the component II (y) the

higher factor loadings were palate width in molar 3 (0.4976) and palate width in molar 5 (0.4765).

Dental formula

The number of incisive (i) and canine (c) teeth in each maxillary and mandibular branch were the same in 157 skulls (i=3/2; c=1/1). The number of upper post canine teeth in the right (pcr) and left (pcl) mandibular branch were also the same (pcr=6; pcl=5). The number of inferior post canine teeth was also always the same (pc=5). However, variations occurred (n=21) in the number of

upper post canine teeth right and left, respectively: 7 - 6 (n=1); 7 - 5 (n=1); 6 - 6 (n=1); 4 - 3 (n=1); 5 - 5 (n=11) and 5 - 6 (n=6). These variations were independent of sex. Therefore the dental formula (DF) was:

DF = (i 3/2 + c 1/1 + pcr 4-7/5 + pcl 3-6/5) = (31-37)

Discussion

Growth parameter values obtained by von Bertalanffy model fitted to metric variables-at-age of male and female *A. australis* showed a differentiated development between sexes. The

Table 3. Descriptive statistics of the metric characters (cm) in physically mature skulls of males and females of *Arctocephalus australis* from Rio Grande do Sul coast, Brazil.

MEASUREMENTS	♂						♀						
	n	MEAN	MIN.	MAX.	SD	CV	n	MEAN	MIN.	MAX.	SD	CV	p
2. Basilar length of Hensel	23	20.89	18.9	22.0	0.73	3.50	17	17.15	8.20	20.40	2.51	14.61	***
3. Upper post canine length	20	5.07	4.2	5.8	0.41	8.01	16	3.49	3.10	4.70	0.36	10.41	***
4. Zygomatic width	23	5.62	4.6	6.1	0.37	6.57	17	4.99	4.00	5.70	0.42	8.44	***
5. Rostral width	23	13.62	11.8	14.5	0.56	4.08	17	11.06	10.0	13.40	0.76	6.86	***
6. Mastoid width	23	12.53	10.9	13.7	0.73	5.84	17	9.69	8.40	12.70	0.92	9.53	***
7. Skull height [a]	23	7.75	7.0	8.4	0.35	4.55	17	6.63	6.30	7.30	0.29	4.36	***
8. Palate length	23	9.73	8.8	10.3	0.41	4.21	17	7.98	7.10	8.90	0.43	5.43	***
9. Palate width in molar 1	23	2.59	2.0	3.2	0.35	13.51	16	1.93	1.50	2.80	0.30	15.58	***
10. Palate width in molar 3	23	2.86	2.2	3.4	0.33	11.63	16	2.20	1.90	2.90	0.28	12.86	***
11. Palate width in molar 5	23	3.25	2.4	3.9	0.33	10.11	16	2.64	2.30	3.10	0.27	10.05	***
12. Greatest width of condylo-occipital	23	5.13	4.5	5.7	0.33	6.45	17	4.46	4.20	5.0	0.23	5.08	***
13. Greatest length of nasal	17	3.79	3.3	4.2	0.23	6.14	12	3.19	2.60	4.0	0.38	11.83	***
14. Constriction interorbital width	23	3.31	1.9	3.8	0.45	13.64	17	2.38	2.10	3.40	0.32	13.60	***
15. Supraorbital process width	23	5.13	4.2	6.2	0.50	9.77	17	3.84	3.10	5.30	0.53	13.83	***
16. Greatest width of internal nasal opening	23	2.77	2.2	3.3	0.27	9.61	17	2.14	1.90	2.50	0.18	8.59	***
17. Mandible length	23	15.82	14.2	17.1	0.74	4.71	17	13.13	12.10	15.60	0.78	5.91	***
18. Mandible width	23	2.36	1.9	2.7	0.20	8.57	17	1.64	1.30	2.50	0.38	23.08	***
19. Mandible height [b]	23	5.58	4.5	6.2	0.41	7.42	17	3.92	3.30	5.10	0.40	10.18	***

([a]) at insertion basisphenoidal-interparietal-occipital suture, (b) at coronoid process, (***) p< 0.001. Coefficient of variation (CV%)
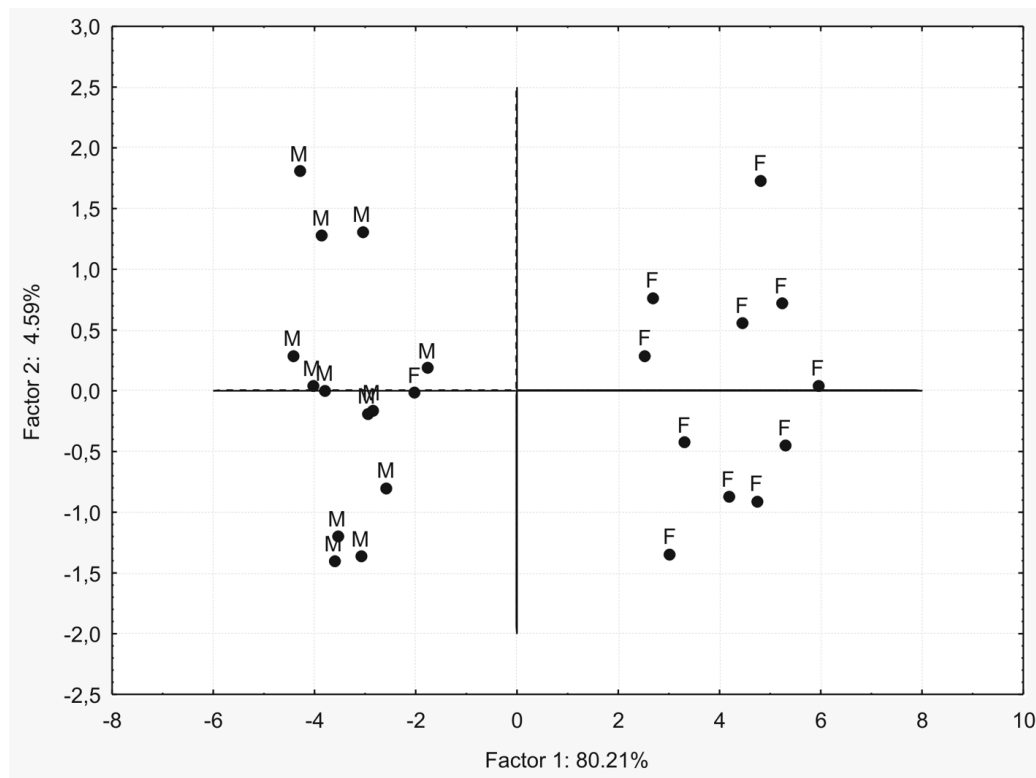
Figure 5. Results of principal component analysis (PCA) based on metric characters of physically mature skulls of *Arctocephalus australis*. (M) male, (F) female.

female skull presented an early maturation in relation to the male skull. These characters for males and females are related to the neural development (*e.g.*, braincase, visual and hearing apparatus) and somatic development (*e.g.*, feeding, breathing and vocalizing apparatus). In males, the upper post canine length, greatest width of internal nasal opening, greatest length of nasal and mastoid width showed a faster growth than females. These characters are related to somatic and neural development (hearing). The supraorbital process width, related to nervous system (visual apparatus), had a slower growth in both sexes.

The sexual dimorphism observed in skull of *A. australis* corroborates the differences observed in other studies (Vaz-Ferreira, 1982; Ximénez *et al.*, 1984; Páez, 1989; Dremer and Ferigolo, 1996; Sanfelice, 2004). Similar patterns of sexual dimorphism occur in many other polygynous species such as *Otaria flavescens* (Rosas *et al.*, 1993; Sanfelice, 2004), *Arctocephalus forsteri* and *Arctocephalus pusillus doriferus* (Brunner, 1998; 2000).

All the characters used in male and female skulls in this study were dimorphic, but in physically immature skulls greatest width of internal nasal opening was non-dimorphic. The lack of dimorphism in this character implies similar functions for males and females when they are physically immature.

Sexual growth differences should be greatest in highly polygynous species (Clutton-Brock *et al.*, 1982). Often times ontogenetic scaling is presented in the literature to explain

sexual dimorphism (Leutenegger and Larson, 1985). The Pinnipedia contain some of the most spectacular examples of sexual size dimorphism, which are frequently used to illustrate the theory of sexual selection (Lindernfors *et al.*, 2002). Shape differences between adult males and females result from the extension of relative growth (shape change) in the smaller females to larger overall size in males (Shea, 1986). In most pinnipeds, females reach the reproductive age much earlier than males, devoting a lot of energy to their offspring. Thus, ability for further somatic growth is limited. In contrast, males do not provide parental care and in most cases reach maturity later in life (Boness, 1991). Lindernfors *et al.* (2002) did not find a significant relationship between body size and sexual size dimorphism in pinnipeds, and postulated that sexual size dimorphism in pinnipeds was a result of selection working on males alone.

When comparing skull measurements from this study to those obtained for the same species in other localities, similarities and differences are observed. The maximum condylobasal length of physically mature males and females collected in the coast of Rio Grande do Sul was similar to the maximum reported for individuals from Uruguay (Vaz-Ferreira, 1982; Ximénez *et al.*, 1984) and the Falkland Islands (Sivertsen, 1954). Similar measurements for some skull characters and the same age classes observed for both sexes were also obtained by Páez (1989) in individuals from Uruguayan islands. Differences were

observed in the asymptotic length and age of physical maturity of the skull in the above studies. However, these differences could be related to different methodologies used for estimating age and accuracy for detecting GLGs. Batallés *et al.* (1990) determined the growth of body length using the von Bertalanffy model fitted for *A. australis* (500 males and 500 females) from Isla de Lobos taken from 1984 to 1987, with males being 22% larger than females. The 90% of asymptotic size was reached at 10.5-11.5 years of age in males and 7.5 years in females. These ages are close to the physical maturity of skull obtained in this study.

All analyzed non-metric characters showed differences between physically immature and physically mature skulls, but these characters were not useful to determine the sex in skull of *A. australis*. The cranial sutures showed variations related to age for males and females. The premaxillary-maxillary and interfrontal sutures showed a greater variation in relation to age when the condition closed-visible was analyzed. The occipito-parietal and the interparietal sutures started to be closed-invisible at earlier ages in males and females. The degree of wear at the apex of the crown in the upper canine tooth started at similar age for males and females. The pulp cavity closure was observed earlier in females than males, which is probably related to the smaller size of the canine tooth in females.

Differences were observed in the number of post canine teeth in this study and those cited for the species in Uruguay (Vaz-Ferreira, 1982) as well as for other species of *Arctocephalus*: *A. gazella*, *A. forsteri* and *A. galapagoensis* (King, 1983; Jefferson *et al.*, 1993); *A. towsendii*, *A. philippi*, *A. tropicalis* and *A. pusillus* (Jefferson *et al.,* 1993). This could be explained by differential counting method applied by these authors, *i.e.*, recording the minimum and maximum number of alveoli in both mandibular branches, indistinctly if at right or left position. Differences between physically immature and mature skulls of *A. australis* observed in this study were also observed by Sanfelice (2004), using traditional and geometric morphometrics techniques. Sexual dimorphism in canine teeth of *A. australis* was present in physically immature and mature individuals (Molina-Schiller and Pinedo, 2004).

The principal component analysis (PCA) of physically mature skulls showed a clear separation between males (n=23) and females (n=17). Despite the prolonged collection period (20 years), sample sizes of physically mature skulls of *A. australis* were relatively small in the present study, which reflects the lower occurrence of this age class in strandings along the coast of Rio Grande do Sul. The variation detected in the skulls characters of males and females showed that most of the variance between the sexes is expressed in the overall size of cranial characteristic, with shape expressing much less variation. They were considered to represent the individual variation of animals occurring along the coast of Rio Grande do Sul. Results of the present study will be potentially useful in future morphometrics studies for the species, including analyses of geographical variation among populations of Uruguay, Argentina, Falkland Islands, Chile and Peru.

Future genetic and morphometric studies (traditional and geometric morphometrics techniques) along the entire distribution of the species will provide insights into stock management and conservation.

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